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BULLETIN 86

**MIDDLE AND EARLY UPPER DEVONIAN
RHYNCHONELLOID BRACHIOPODS
FROM WESTERN CANADA**

D. J. McLaren

1962

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OF CANADA

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RHYNCHONELLOID BRACHIOPODS
FROM WESTERN CANADA

By
D. J. McLaren

DEPARTMENT OF
MINES AND TECHNICAL SURVEYS
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PREFACE

The emphasis in the geological mapping of sedimentary rocks in Canada is turning from reconnaissance surveys to detailed stratigraphic studies. It is therefore important to distinguish and correlate increasingly fine sedimentary units. To a great extent this is based on precise palæontological information, and the accuracy of such information is largely determined by the precision with which fossil species can be identified and the accuracy with which their time range is known.

The detailed study of the rhynchonelloid brachiopods reported in this bulletin supplies just such basic information. The fossils examined were collected from widely distributed exposures and from borings to establish the time range with all the accuracy possible. Modern techniques were used to ensure accurate identification of previously described species and precise definition of new genera and species.

J. M. HARRISON,
Director, Geological Survey of Canada

OTTAWA, May 15, 1961

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MIDDLE AND EARLY UPPER DEVONIAN RHYNCHONELLOID BRACHIOPODS FROM WESTERN CANADA

Abstract

Species of five genera of rhynchonelloid brachiopods are described. Their range in time is illustrated diagrammatically on a summary correlation chart, and the stratigraphy of the main areas of Devonian outcrop is discussed briefly. Three stages are represented: Eifelian, Givetian, and Frasnian. A rhynchonelloid zonal scheme has not yet been worked out for the Middle Devonian, but in the Frasnian Stage, four well-differentiated zones are recognized, with a fifth, typified by the spiriferoid genus *Theodossia*, at the top of the stage.

Genera have been differentiated by detailed consideration of internal structure as well as of external morphology. Interiors were investigated by serial sectioning and by preparing artificial internal moulds. Species and subspecies have been recognized largely by variation in external form. Special attention has been paid to growth and variation.

The genera include: *Calvinaria* Stainbrook, with two species and seven subspecies, of which three are new — *C. albertensis opima*, *C. albertensis feni*, and *C. variabilis jobensis*; *Cassidirostrum* McLaren, with one species; *Hadorrhynchia* McLaren, with one species; *Ladogioides* McLaren, with two species; *Leiorhynchus* Hall, with five species, three of which are new — *L. manetoe*, *L. awokanak*, and *L. russelli*.

Known occurrences of each species and subspecies are listed in an appendix.

Résumé

Le présent bulletin décrit les espèces de cinq genres de brachiopodes rhynchonellidés. Leur répartition dans le temps est représentée graphiquement à l'aide d'un tableau sommaire de corrélation. L'auteur y décrit brièvement la stratigraphie des principales régions où affleure le Dévonien. Trois étages sont présents: Eifélien, Givétien et Frasnien. Aucun schéma zonaire pour les rhynchonelles n'a encore été déterminé au Dévonien moyen, mais, à l'étage frasnien, l'auteur a reconnu quatre zones bien distinctes, de même qu'une cinquième, caractérisée par le genre spiriféridé *Theodossia*, au sommet de l'étage.

Les genres ont été différenciés grâce à une étude détaillée de la structure interne et de la morphologie externe. L'investigation interne s'est faite par coupe en série et moulage interne artificiel. Les espèces et les sous-espèces ont pu être identifiées grâce surtout à la variation de la forme externe. L'auteur a accordé une attention spéciale à la croissance et à la variation.

Les genres étudiés comprennent: *Calvinaria* Stainbrook, avec deux espèces et sept sous-espèces, dont trois nouvelles, à savoir *C. albertensis opima*, *C. albertensis feni* et *C. variabilis jobensis*; *Cassidirostrum* McLaren, avec une espèce; *Hadorrhynchia* McLaren, avec une espèce; *Ladogioides* McLaren, avec deux espèces; *Leiorhynchus* Hall, avec cinq espèces, dont trois nouvelles, à savoir *L. manetoe*, *L. awokanak* et *L. russelli*.

L'annexe du bulletin contient la liste des endroits où l'on a reconnu chacune des espèces et sous-espèces.

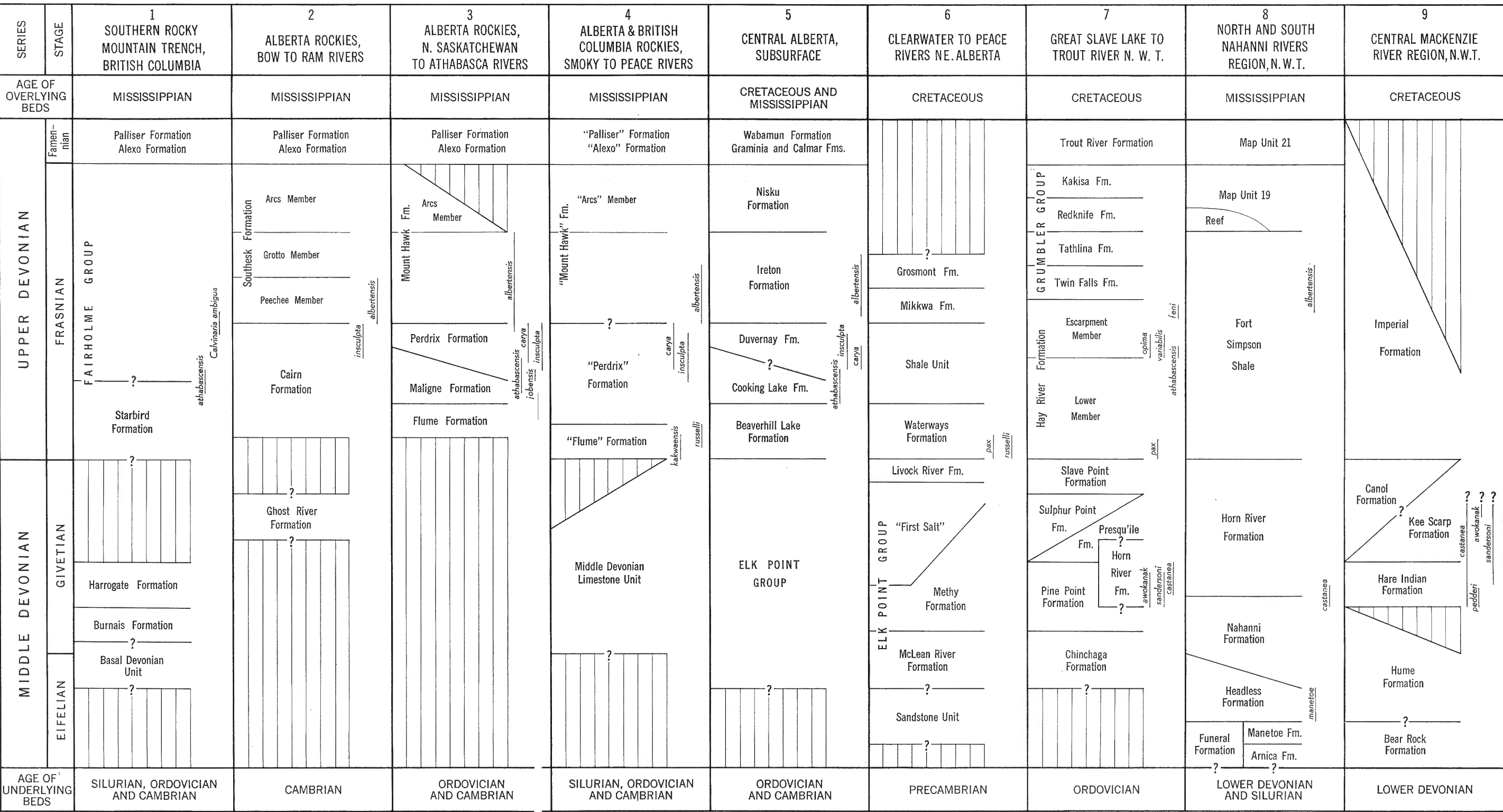


Figure 1. Correlation chart of Middle and Upper Devonian formations.

INTRODUCTION

Rhynchonelloids are among the most widespread of the many kinds of brachiopod that are found in the marine Middle and Upper Devonian formations of Western Canada. They occur in many kinds of rocks, ranging from black shales to pure limestones, and because of their variety and relative abundance, have proved of value in correlating the beds in which they are found. This study describes species and subspecies of five genera of rhynchonelloids from the Middle and early Upper Devonian which may be recognized and employed by workers in the field. In many cases the biozone (range-zone) of the species is well established, in others, much further collecting and stratigraphic work is required; monographic description is needed before the range and stratigraphic utility of these other species are known.

Growth and variation have been given special attention as the geographic extent and wide facies tolerance of many forms lead to considerable differences in mean size and in variation between populations from different localities. Species are thus kept as broad as is consistent with a stratigraphically useful classification. Subspecies are recognized when the consistency of differences between populations of the same species suggests either chronological or geographical distinction.

The stratigraphic range of the species and subspecies described is shown on a correlation chart (Fig. 1) and the chart is briefly discussed in the text. New zones are not proposed but existing schemes are considered and age assignment in terms of European Stages is attempted.

Much of the formational terminology in the Western Canadian Devonian is provisional. It has been necessary to use some names in preference to others on the correlation chart (Fig. 1), but it is recognized that some of these may need to be modified or replaced. Alternative names are given in the text in many instances. In the descriptions of localities, the stratigraphic horizon is cited, as far as possible, in the words of the collector from that locality. Where these are now known to be incorrect, this is pointed out under the discussion of "Occurrence" for the relevant species. The horizons of other localities remain uncertain but may be interpreted by workers familiar with the locality in question.

Information on every locality from which each species in the collections was collected, both stratigraphic and geographic, is listed in the Appendix. This is given in as great detail as possible in order that sections or localities that may have been miscorrelated may nevertheless ultimately be of value in establishing the full range of the species.

Some of the dimensions of the fossil specimens described are shown in parenthesis, thus "length (24) mm". This signifies that owing to damage it was not possible to obtain the particular dimension accurately, but that the figure shown is a reasonable estimate.

Type or figured specimens (hypotypes) are all deposited in the Geological Survey of Canada type collection unless otherwise indicated. The repository of types is shown as follows: U. of A., University of Alberta; USNM, United States National Museum; GSC, Geological Survey of Canada; in addition, some types are preserved in the collections of Imperial Oil Limited, Calgary and are so indicated.

This work is complementary to a similar study shortly to be published by Dr. Paul Sartenaer, of the Institut Royal des Sciences Naturelles de Belgique, and National Research Council Post-Doctorate Research Fellow with the Geological Survey of Canada, 1957-60, on the late Upper Devonian (Famennian) rhynchonelloids of Western Canada.

ACKNOWLEDGMENTS

I should like to record my gratitude to Dr. G. Arthur Cooper of the United States National Museum for the loan of Meek's Mackenzie River Devonian types, and the gift of species of *Calvinaria* from Iowa and New Mexico; to Dr. Arvo Rõõmusoks of Tartu, Estonia S.S.R. for the gift of specimens of *Ladogia meyendorfi*; to Dr. L. R. Laudon of the University of Wisconsin and Dr. J. L. Severson for the gift of specimens from Sunwapta Pass, Alberta; to the late Dr. M. A. Stainbrook for the gift of rhynchonelloids from Iowa; to Dr. C. H. Crickmay of Imperial Oil, and Professor P. S. Warren of the University of Alberta, for the loan of type specimens of rhynchonelloid species; to Dr. H. Gordon Bassett of Shell Oil Company for a copy of his manuscript (1961) in advance of publication; to Dr. Alfred C. Lenz of California Standard Company, Dr. J. C. Sproule and staff geologists of J. C. Sproule and Associates, Dr. Alan E. H. Pedder of Triad Oil Company, and to California Standard Company, Hudson's Bay Oil and Gas Company, Imperial Oil, Mobil Oil of Canada, and other western Canadian Oil Companies, for the gift of abundant and varied collections of rhynchonelloids from Western Canada. The work benefitted greatly at all stages from discussion and collaboration with Dr. Paul Sartenaer. Many officers of the Geological Survey of Canada assisted in material and in discussion; among these, A. W. Norris contributed important collections and much stratigraphic information, and Helen R. Belyea made extensive collections from the subsurface of Alberta and the Northwest Territories.

STRATIGRAPHIC PALÆONTOLOGY

Stratigraphic Distribution

The approximate stratigraphic distribution of the species of rhynchonelloids described in this report is shown on Figure 1. This represents an attempt at a correlation chart based on all available evidence to date in the areas mentioned. Brief critical comments on each column on the chart are offered below, but this is not intended to be a discussion on the stratigraphy of each area. Sufficient bibliographic references to recent work will enable the reader to find such a discussion where it exists.

(1) Southern Rocky Mountain Trench, B.C.

The stratigraphy of various map-areas in this region has been described by Walker (1926), Evans (1933), Henderson (1954), and Leech (1958). Faunal lists for the Harrogate formation (Kindle *in* Evans, 1933; Howell and Bassett *in* Henderson, 1954; and McLaren *in* Leech, 1958) show it to be of Middle Devonian age. The species of *Alveolites*, *Favosites*, *Atelophyllum*, *Productella*, and *Emanuella* suggest correlation with the Nahanni formation of southern Mackenzie Mountains and the Pine Point formation of Great Slave Lake.

Leech (1958) has summarized the evidence for assigning the Burnais Evaporite to the Middle Devonian. South of latitude 49°35', gypsum deposits appear to be of post-Harrogate age and the Harrogate may be absent.

Faunas of late Givetian age appear to be absent within this region. In the section on the Lussier syncline in Fernie map-area, west half (Leech, 1958, pp. 21-22), this interval may be represented by unfossiliferous limestones lying between the Harrogate faunas and a fauna of lower Waterways type.

The unfossiliferous lower beds of the Starbird formation may represent this interval in Windermere map-area (Walker, 1926, p. 35). The upper 30 feet of the Starbird contain a fauna whose age has been in question (Henderson, 1954, p. 27). The presence of *Eleutherokomma* and species of *Productella*, *Schizophoria*, and *Atrypa* strongly suggest an early Upper Devonian age, and these beds may be correlated with the fossiliferous beds above the limestones referred to above in the Lussier syncline (Leech, 1958, p. 22).

Northeast of Elko, there is no fossiliferous Middle Devonian and the Fairholme group rests on the basal Devonian unit which in turn rests on Cambrian and Precambrian beds (Leech, 1958, p. 23). In this section (pp. 23-26, *op. cit.*) the presence of *Calvinaria variabilis athabascensis* suggests beds equivalent to the Maligne formation; and *Calvinaria ambigua* may indicate upper Perdrix or lower Mount Hawk in the as yet undivided Fairholme group in this region. The next fossiliferous horizon above contains an Alexo fauna of early Famennian age.

(2) Alberta Rockies, Bow to Ram Rivers

The lower part of the Devonian sequence in this area lies almost entirely within the carbonate Fairholme group which has been subdivided into formations (McLaren, 1956) and members (Belyea and McLaren, 1956). These papers may be referred to for a summary of earlier work; also Fox (1951) and McLaren (1953). The nature of the rocks is such that fossils are scarce or poorly preserved, but correlation northwards is reasonably well established by stratigraphic means — intertonguing and marker beds. Fossiliferous shaly phases within the Fairholme succession allow checks on correlation at some horizons.

In the Front Ranges north of Bow River, the Fairholme rests on the Ghost River formation which overlies Cambrian rocks (Clark, 1949). This formation is unfossiliferous, but is generally considered Devonian and is assigned by some to the Middle Devonian (Clark, 1949; Webb, 1951; Gussow, 1957; and others).

(3) Alberta Rockies, North Saskatchewan to Athabasca Rivers

The Devonian stratigraphy of this region has been described in the papers referred to in the previous section. Belyea and McLaren (1957), and McLaren (1959) discuss further details. Mountjoy (1960) has elucidated several stratigraphic correlations by detailed mapping in the Miette map-area. Hargreaves (1959) has suggested alternative terminology and correlations. Many of these and earlier papers cite faunal lists and the broad sequence is established.

Warren and Stelck (1956) and McLaren (1958) have figured some of the abundant fossils found most commonly in shaly limestone phases of the various formations.

The Flume formation, a biostromal carbonate unit, is relatively poorly fossiliferous and is correlated outside the region only with difficulty. The basal beds at Medicine Lake contain a small silicified fauna which includes *Allanaria allani* (Warren) (figured McLaren, 1958, Pl. VIII), and a small *Athyris* sp. This suggests correlation with the upper part of the Waterways formation, and earliest Upper Devonian beds are presumed to be absent.

The lower part of the Perdrix formation is commonly unfossiliferous. The upper Flume (as previously used) thickens at the expense of the Perdrix when approaching a development of carbonate bank facies (McLaren, 1956, p. 18), and is normally fossiliferous. This unit was named the Maligne formation by Taylor (1957) and has been found useful in mapping (Mountjoy, 1960). The Flume formation is therefore restricted to the bedded biostromal carbonate previously defined as the lower Flume (deWit and McLaren, 1949).

The highest beds of the Mount Hawk formation are commonly massive carbonates and are assigned to the Arcs member. They contain a highly characteristic late Frasnian fauna which includes *Pachyphyllum cinctum* (Smith), *Thamnophyllum tructense* (McLaren), and many other corals, *Theodossia keenei* (Crickmay), and characteristic species of *Hypothyridina*, *Atrypa*, and *Cranaena*. This fauna is widespread in the upper Mackenzie River region between Hay and Liard

Rivers in the Kakisa formation. The assemblage everywhere overlies beds containing an abundant fauna, typified by *Calvinaria albertensis albertensis* and forms closely related to species found in the Sly Gap formation of New Mexico (Stainbrook, 1948).

In some sections, e.g. Deception Creek (McLaren, 1956, p. 26), the Arcs member or its equivalent is missing and *C. albertensis albertensis* is directly overlain by the Alexo formation which contains a fauna of Famennian age. There is evidence of erosion at this horizon in the upper Mackenzie region also.

(4) Alberta and British Columbia Rockies, Smoky to Peace Rivers

The Devonian stratigraphy of this region has not been described in any detail and formation names have been applied from other areas. Owing to facies changes along the strike of the mountains, many of the names are in danger of being misapplied and it is probable that a more local rock stratigraphic scheme is desirable. The names appearing on Figure 1 are used informally to indicate probable correlation but not necessarily lithologic equivalents.

Williams, in Williams and Bocock (1932, p. 201), lists a Devonian fauna from an island in Peace River above Clearwater River. The list contains both Middle and Upper Devonian elements. Mapping presently being carried out by the Geological Survey indicates that both series are present in the area (E. J. W. Irish and J. E. Muller, unpublished maps and fossil collections).

Fossils from a massive limestone in the Peace River area and to the south indicate a Middle Devonian age. Corals and brachiopods from shaly limestones in the same region and south to Pine Pass are of Mount Hawk age.

In the Cecilia, Kakwa, Jarvis Lakes area, beds loosely referred to the Flume formation have yielded a rich early Waterways fauna. In addition to species of *Ladogioides* and *Leiorhynchus*, species of *Schizophoria*, stropheodontids, *Atrypa*, and *Athyris*, and *Cyrtina billingsi* Meek allow positive correlation. This horizon is believed to be lower than that of the fauna found in the basal Flume at Medicine Lake (see previous section).

Overlying thick unfossiliferous shales assigned to the "Perdrix" formation, a limestone and shaly limestone sequence has yielded typical lower and upper Mount Hawk corals and brachiopods and is overlain by further limestones with Alexo and Palliser faunas.

At Winnifred Pass, just south of Smoky River, the earliest beds exposed, black calcareous shales and shaly limestones, have yielded a Perdrix fauna. Before the faunal sequence in the region was understood, facies differences between Winnifred Pass and Jasper led to a misinterpretation of this section (McLaren, 1954). The fauna listed (p. 174, op. cit.) as from the upper Alexo at Winnifred Pass, is, in fact, found in the highest (Arcs) member of the Mount Hawk in the Jasper region, and in the Kakisa formation on Trout River, Northwest Territories. There are in fact 860 feet of beds equivalent to the Mount Hawk formation farther south, and some 240 feet of beds equivalent to the Perdrix are exposed.

(5) Central Alberta Subsurface

A full bibliography of the Alberta subsurface Devonian has been given recently by Belyea (1960) and her previous work (notably 1955, 1957, 1958a and b) contains both a summary of earlier work and important additions to an understanding of the complex facies relations that obtain over the whole basin.

Correlations between a generalized off-reef subsurface section and outcrop regions suggested on Figure 1 are largely a result of fossils collected by Belyea from cores of drilled holes and have been discussed by McLaren *in* Belyea (1955, 1958b) and by Belyea and McLaren (1956, 1957a).

The upper part of the Beaverhill formation is now considered to be represented in the outcrop sections in the Jasper area by the Flume formation (restricted) and the Cooking Lake is equated with the Maligne. The Nisku formation is equated with the Arcs member of the Southesk and Mount Hawk formations.

(6) Northeastern Alberta, Clearwater to Peace Rivers

The Devonian stratigraphy of this region has been described in detail by A. W. Norris (*in press*) and column 6 on Figure 1 was prepared with his assistance. A full bibliography is given in his report together with faunal lists. Faunas have been figured from this region by Warren and Stelck (1956). In a recent work on the geology of the McMurray area, Carrigy (1959) rejected the use of the name Waterways as a formation, preferring the Central Alberta subsurface name, Beaverhill formation. Carrigy compiled considerable faunal data from certain of the formations in that area.

The fauna of the Methy formation is listed by Warren (*in* Greiner, 1956) and includes *Dendrostella*, *Stringocephalus*, and species of *Warrenella* and *Emanuella*. It is correlated with the Pine Point and higher beds on Great Slave Lake. The age of the Waterways has been considered late Middle (Givetian) or early Upper (Frasnian) Devonian at different times by various workers. The reasons for assigning it to the Upper Devonian are considered elsewhere (p. 13).

(7) Upper Mackenzie River, Great Slave Lake to Trout River

The Devonian stratigraphy of this area has been summarized recently by Douglas (1959), and Douglas and A. W. Norris (1960). These reports, which constitute notes to preliminary maps of the region, contain full bibliographies of earlier work. The stratigraphic column has been divided into map-units, some of which bear previously defined formation names. A. W. Norris (*in press*) has described the Middle Devonian rocks of the Great Slave Lake area in detail, and has formalized the complicated rock stratigraphic terminology in this area. Belyea and McLaren (1962) have summarized the surface and subsurface stratigraphy of the Upper Devonian between Hay and Liard Rivers and erected a formal rock stratigraphic terminology for these beds.

Column 7, Figure 1, for the Great Slave to Trout River region, is based on A. W. Norris' work (*in press*) for the Middle Devonian and on Belyea and McLaren (1962) for the Upper Devonian. Correlation with other areas depends largely on faunas collected by these and other Geological Survey workers from outcrops and well cores.

Views on the correlation of the Middle Devonian of this region have been influenced by belief in a "*Stringocephalus* Zone". Throughout the Mackenzie area, *Stringocephalus* spp. are abundant in beds considered of late Givetian age and have been correlated as such. The genus occurs, in fact, throughout a considerable thickness of rock, (*see* discussion in Crickmay, 1960b). In the Great Slave area *Stringocephalus* is common in the Presqu'île and Sulphur Point formations, but A. W. Norris has collected it also from low in the Pine Point. From the evidence of other fossils it appears that the genus ranges throughout beds believed equivalent to the Givetian Stage of the European succession.

The lowest beds of the Great Slave Lake Devonian are poorly fossiliferous and it is not possible to demonstrate an age earlier than Givetian for, e.g., the Chinchaga formation. The remainder of the succession below the Hay River formation is considered of Givetian age.

The earliest Upper Devonian rocks in the region outcrop on the north side of the lake in the vicinity of Sulphur Bay (GSC loc. 31082), where the presence of *Ladogioides pax* suggests correlation with early Waterways. Waterways fossils occur in the lower 150 feet of the Hay River shale in bore-holes on Hay River. Fossils in the upper part of the lower member of the Hay River shale (restricted) allow correlation with the Maligne formation of the Alberta Rockies.

The boundary between the Perdrix and Mount Hawk, or Cairn and Southesk formations of Alberta occurs within the Escarpment member on Hay River.

The highest beds on Hay River are the lowest 70 feet of the Tathlina formation of approximately middle Mount Hawk age. Beds equivalent to the Arcs member of the Mount Hawk first outcrop on Middle Kakisa River and westwards to Trout River, and are represented by the Kakisa and Redknife formations. On Trout River the earliest beds exposed are basal Redknife formation, so that there is no overlap between the succession on Hay and Trout Rivers.

(8) Upper Mackenzie River, North and South Nahanni Rivers Region

The stratigraphy of this region has been summarized in notes to preliminary maps by Douglas and D. K. Norris (1961). The formation names and map-unit numbers on column 8, Figure 1 are defined in their report. The fauna of the Headless formation is correlated with the "Hume" or lower Ramparts formation to the north (*see* subsequent discussion). *Leiorhynchus manetoe* which occurs at this horizon is known only in the western part of the region.

The Nahanni formation is correlated with at least part of the Pine Point formation of Great Slave Lake and is considered of early Givetian age, on the basis of characteristic corals, and species of *Emanuella*, *Elytha*, and *Mastigospira*.

It is succeeded by unfossiliferous black shales (Horn River formation) everywhere in the region, which are considered of late Middle Devonian age by analogy with the Central Mackenzie region (Bassett, 1961) and correlation with similar beds in Horn River map-area to the east (Douglas and A. W. Norris, 1960). The Middle-Upper Devonian boundary is drawn arbitrarily at a colour change from black to grey and greenish grey in an unfossiliferous shale and siltstone succession.

The shale succession is succeeded by variably sandy beds with coral-stromatoporoid bioherms developed at any horizon (unit 19). These beds contain faunas closely similar to those of the Redknife and Kakisa formations on the plains to the east. The shales below the reefy beds contain *Calvinaria albertensis albertensis* and may be correlated with the lower or middle Mount Hawk of the Alberta Rockies.

The Frasnian-Famennian faunal break occurs within beds of different lithological types and may not everywhere correspond to an obvious rock stratigraphic boundary (McLaren, 1959).

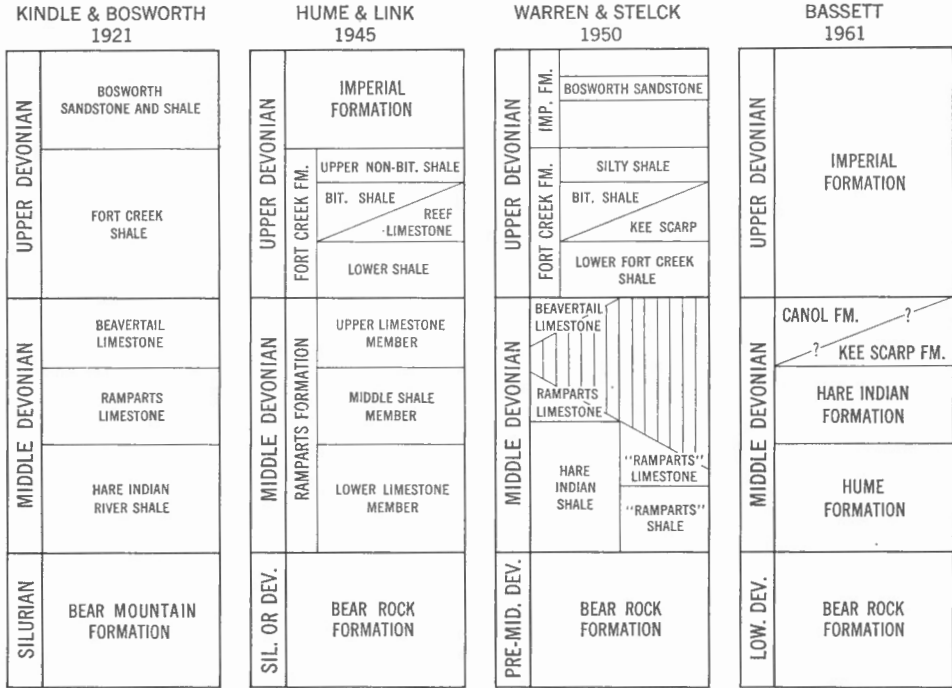
(9) Central Mackenzie River Region

Bassett (1961) has given a full discussion on the confused nomenclature of the rocks in this area and has proposed important changes in the terminology. His terminology is employed on column 9, Figure 1, as it avoids lengthy explanations of usage which are necessary if earlier terms are used. His terminology may, however, still be considered provisional in that his conclusions are largely untested by regional mapping. Figure 2 is copied from Bassett and will enable those familiar with the earlier terminology to envisage the proposed changes.

The earliest Middle Devonian fauna in the area occurs in the Hume formation, and is listed by Bassett (op. cit.). Many of the fossils figured by Warren and Stelck (1956) as from the Hare Indian River shale are in fact now to be considered as Hume. Bassett gives reasons for considering the Hume-Hare Indian contact to be equivalent to the top of the Nahanni formation to the south. The presence of *Leiorhynchus castanea* at this horizon lends support to this conclusion but, contrary to Bassett, the main fauna of the upper part of the Nahanni is believed to be of Givetian age and to correlate with the Pine Point, whereas the Hume fauna strongly suggests an earlier or Eifelian age, and correlation with, for example, the "*Spirifer pinyonensis*" zone of the lower Nevada formation in Nevada (Merriam, 1940). Either condensation of the section, or non-deposition, may account for the apparent absence of Nahanni forms. The *Leiorhynchus castanea*-bearing beds may alternatively be earlier than the upper Nahanni — or be more conveniently classified with the Hare Indian. The Hare Indian fauna is correlated with that of the upper Pine Point formation.¹

Crickmay (1960b, footnote p. 877) appears to propose a new formation, the Norman Wells, for the basal Devonian limestone at Norman Wells. This is pre-

¹Part of the Nahanni formation may correlate with the Hume, and the Eifelian-Givetian boundary may prove to be stratigraphically lower than the top of the Hume.



G S C

Figure 2. History of Devonian nomenclature in the central Mackenzie River region, after Bassett (1961). (Bassett stresses that this table is not a correlation chart.)

sumably equivalent to Bassett's Hume formation (1961), which it pre-dates. In the present report the author is not concerned with making an examination of the complicated history of formational terminology in the central Mackenzie area, and no conclusions are drawn regarding the validity or desirability of using certain names over others. As stated previously, Bassett's terminology forms a convenient framework, adequately described, within which to discuss the stratigraphy, and which has the advantage of being set in an historical matrix.

The Kee Scarp formation is shown to be the equivalent of the "Upper Ramparts" of earlier workers (Bassett, 1961; Crickmay, 1957, p. 11), and is correlated with the highest Middle Devonian units of Great Slave Lake. The genus *Stringocephalus* is commonest in the lower part of this formation (but see remarks on p. 7).

The main stumbling block to correlation in the region has been the failure to recognize the fact that the Upper Ramparts-Kee Scarp is absent in some areas and is replaced by black shale — now named the Canol formation (Bassett, op. cit.). Hence, the use of the term "Upper Ramparts" in previous reports is suspect, as in many instances the unit referred to is, in fact, the "Lower Ramparts" or Hume formation, e.g. on Hume River and on Carcajou River, south of Norman Wells. This is more fully discussed in Bassett (op. cit.).

On Carcajou Ridge, on the right bank of the Mackenzie River, beds believed equivalent to the Kee Scarp were assigned to the Beavertail formation by previous workers (*see* Hume, 1954, for full discussion). It is claimed that these beds have yielded the fauna illustrated by Warren and Stelck (1956, Pls. VIII and IX) as the "*Cyrtina panda* fauna". Carcajou Ridge consists of an asymmetrical east-west trending anticline with a steep, vertical to overturned south limb involving beds now described as Hume, Hare Indian, Kee Scarp, and Imperial formations. The structure, as mapped by Parker (1944, unpublished) is simple and there is little room for doubt that the correlation of the two limbs of the anticline and the stratigraphic order of the beds are correct. Nevertheless the *Cyrtina panda* fauna contains some surprising elements.

Using the names from Warren and Stelck (*op. cit.*), the following species recognized by them are unknown elsewhere in the Mackenzie region, nor have they been collected from Carcajou Ridge by earlier workers whose collections from that locality are stored in whole or in part in the Geological Survey of Canada, e.g. E. M. Kindle, J. W. Reede, G. S. Hume, J. M. Parker:

- Spirifer euryteines* Owen
- Pugnax* sp. nov.
- Atrypa* sp. (Pl. VIII, figs. 13-15)
- Atrypa andersonensis* Warren (var.)
- Athyris vittata* var. *buffaloensis* Stainbrook
- Spirifer* sp. (Pl. IX, figs. 28-30)

These species, or closely similar forms, are common in the lower part of the Waterways formation of northeastern Alberta which is considered to be of early Upper Devonian age and which overlies beds elsewhere correlated with the "upper Ramparts" or Kee Scarp formation.

The remaining species figured by Warren and Stelck (*op. cit.*) from the "*Cyrtina panda* fauna" are as follows:

- Pugnoides* [= *Hadorrhynchia*] *sandersoni* Warren
- Caryorhynchus castanea* (Meek) var. [here placed in synonymy with *Leiorhynchus castanea*]
- Martinia?* *occidentalis* Merriam
- Coenites* sp.
- Cyrtina panda* Meek
- Pugnoides solon* Thomas and Stainbrook

The three last-named forms are possibly non-diagnostic without detailed examination, but the first three are common Middle Devonian fossils. *Hadorrhynchia sandersoni* is widespread in the upper part of the Pine Point formation and elsewhere (*see* p. 63); *Leiorhynchus castanea* is common throughout the whole northern region (*see* p. 90); and the *Martinia?* *occidentalis*, renamed *Warrenella timetea* by Crickmay 1960a, is here considered merely a large form of *Warrenella franklini* (Meek), following examination of large collections involving all stages of growth from Carcajou Ridge. Elsewhere this assemblage would suggest a Pine Point-Hare Indian age for the beds in which it occurs.

This anomalous occurrence may have several possible explanations but cannot at present be resolved. It seems unlikely that some unobserved structural complexity can have caused a juxtaposition of beds of different ages (personal communication Dr. H. G. Bassett and Dr. W. G. E. Caldwell). The possibility must be borne in mind that an inadvertent mixing of a Waterways with a Middle Devonian fauna may have occurred at some time during the preliminary sorting and dividing of the Canol Project collections. It is of interest to note that an excellent series of plates prepared for Dr. T. A. Link, at that time of Imperial Oil Limited, of fossils deposited at the University of Chicago and selected by Dr. C. R. Stelck in 1943, figure a lower and upper Beavertail fauna (Pls. VI and VII). This fauna includes *W. franklini*, *L. castanea*, and *H. sandersoni* (as "*Pugnax pugnax*"), but not a single representative of the "Waterways species". The writer is indebted to Dr. A. E. Wilson for a copy of these plates which were given to her by Dr. Link.

It seems inescapable that *L. castanea* and its associates range higher on Carcajou Ridge than elsewhere in the Mackenzie basin (see p. 91), with some possible exceptions, e.g. near mouth of Ontaratue River (GSC loc. 41154, see appendix), and that they occur above the "*Stringocephalus* Zone" of the lower Kee Scarp (see preceding section).

Bassett uses the occurrence of *L. castanea* as a zone in correlating the Hume-Hare Indian contact (his *Nudirostra* zone on fig. 3, op. cit.), and this seems to constitute a widespread marker. It can only represent a "teilzone", however, as *L. castanea* ranges throughout the upper Pine Point, the Hare Indian, and, as discussed above, may extend at least as high as about middle Kee Scarp.

The Imperial is unfossiliferous in its lowest part and in some areas has been almost or entirely removed by erosion. Southwards from Norman Wells late Frasnian and Famennian faunas are encountered, e.g. on Redstone River (approximately latitude 63°50', longitude 125°35').

Stages

Eifelian Stage

The Hume formation contains a rich coral-brachiopod fauna in outcrops in many areas, which has been listed by name in Crickmay (1960a, his "*adoceta*" and "*verrilli*" zones) and Bassett (1961), and has been figured as from the Hare Indian River shale by Warren and Stelck (1956, their "*Radiastraea arachne*" fauna, Pls. I and II). Many of the fossils described by Meek (1867) are from this fauna from the Anderson River region.

Elements of this fauna that may be significant in assigning an age, include:

Billingsastraea verrilli (Meek)

Digonophyllum ("*Glossophyllum*") *rectum* (Meek)

Microcyclus? *kirkbyi* (Meek)

Zonophyllum robertsense (Stumm)

Of these, the species of *Billingsastraea* is almost certainly conspecific with *B. arachne* (Stumm) from the *Spirifer pinyonensis* zone of the lower Nevada formation of Nevada (Merriam, 1940). Meek's *Zaphrentis rectum* undoubtedly belongs to the genus *Digonophyllum* sensu lato, but is difficult to assign to a subgenus in terms of Wedekind and other European workers. The coral is probably not correctly assigned to *D. (Glossophyllum)*; it is, however, closely similar to forms referred to *Glossophyllum* by Soshkina, from beds of Eifelian age in the Urals (1952).

The generic assignment of *Microcyclus kirkbyi* is in some doubt, but longitudinal sections show that the coral is correctly classified with the Hadrophyllidae.

Zonophyllum robertsense also occurs in the lower Nevada formation, and the genus is reported from the Lower and early Middle Devonian of Europe.

Similarities between some of the brachiopods from the Hare Indian and the lower Nevada formation also suggest correlation. The overlying faunas—in Nevada the "*Martinia kirki* zone" (Merriam, op. cit.) with *Leiorhynchus* sp. a (probably a small variant of *L. awokanak*) and *M. kirki*, and in the Mackenzie a horizon with *L. castanea* and a *Warrenella* very close to "*M. kirki*", are also correlated, and believed to be of early Givetian age.

Based on the admittedly somewhat tenuous evidence furnished by the similarity between the "*Glossophyllum*" sp. and similar Eifelian Ural corals, and the recognition of *Zonophyllum*, the Hume fauna is considered of Eifelian age. A similar fauna is found in the Headless formation in the Nahanni River region, but has not yet been recognized elsewhere on the mainland. In the Arctic Islands, Eifelian faunas appear to be widespread and further correlation with northern Mackenzie and Yukon will probably be possible.

Givetian Stage

Most of the formations assigned a Givetian age either contain, or are stratigraphic equivalents of beds that contain *Dendrostella*, *Stringocephalus*, *Mastigospira* and various digonophyllid corals. In the Great Slave Lake area *Stringocephalus* occurs in the lower part of the Pine Point and in the Presqu'île and Sulphur Point formations. The Slave Point, which is poorly fossiliferous, is considered of Middle Devonian age on the basis of species of *Atrypa* and *Emanuella* (Norris, *in press*). Elsewhere in the Mackenzie basin beds correlated with the Great Slave Lake succession contain comparable faunas although *Stringocephalus* appears to be restricted to the Kee Scarp formation (*see* discussion p. 7 and p. 9).

Stringocephalus has not been collected, so far as is known, from the Nahanni formation; although *Dendrostella* and *Mastigospira* are known. The formation is assigned to the Givetian pending a full examination of the faunas. In Germany, for instance, *Stringocephalus* occurs only in the Middle and Upper Givetian (Schmidt, 1960).

Frasnian Stage

The Middle-Upper Devonian boundary in Western Canada continues to be a matter of some uncertainty. Beds that contain Givetian type digonophyllid corals, abundant *Emanuella* spp., and characteristic *Atrypa* spp., are assigned to the Givetian, whether *Stringocephalus* is present or not. The lower Waterways formation, however, contains many new elements which bear little resemblance to the faunas of underlying units. Unfortunately an important facies change at this horizon makes it difficult to be certain that the faunal change is not entirely facies controlled.

The fossiliferous beds of the underlying units are essentially carbonate with, very largely, a coral fauna. The Waterways, and its equivalents, the Beaverhill, the "Flume" north of Athabasca River, and basal Hay River formations, are devoid of rugose corals and contain a stromatoporoid-tabulate-brachiopod fauna most of which is new. Among the brachiopods, species of *Ladogioides*, *Allanaria*, *Eleutherokomma*¹, and "*Cyrtina*" (a form with costate fold and sulcus, possibly a new genus) make their first appearance. There are definite Middle Devonian elements such as *Spinocyrtia* sp. and many species of *Schizophoria*, *Stropheodonta*, and *Atrypa* which suggest affinities with forms found in the Cedar Valley formation of Iowa. The Waterways was so correlated by McLaren (1954).

The Waterways fauna, however, may perhaps be better correlated with the Snyder Creek formation of Missouri, which also contains relict Middle Devonian elements (Cooper, and others, 1942, p. 1782 and Cooper, 1944a). This correlation was first suggested by Warren (1933), and has recently been argued by Norris (*in press*). Closely similar species of the following genera occur in the two formations: *Eostrophalosia*, *Ladogioides*, *Atrypa*, *Spinatrypa*, *Allanaria*, *Athyris*, *Cyrtina*. The Snyder Creek is considered of early Upper Devonian age, Cooper (*op. cit.*), and post-Cedar Valley.

The faunas of the Waterways, and of the overlying beds that outcrop on Hay River, as well as the Maligne and Cooking Lake formations, form a broad faunal unit, or substage, which may be characterized by the presence of *Allanaria*, *Eleutherokomma*, late species of *Leiorhynchus*, and early *Calvinaria*. Throughout the Cordillera this substage has been commonly referred to the "*Spirifer argentarius* fauna" (discussion in Merriam, 1940, and Warren, 1942), and may be correlated

¹The genus *Eleutherokomma* Crickmay cannot easily be separated from *Mucrospirifer* Grabau, which is abundant in the Middle Devonian of eastern North America. Specimens of *Mucrospirifer thedfordensis* Shimer and Grabau from the Hungry Hollow formation of Ontario, and *Eleutherokomma reidfordi* Crickmay from the Hay River shale of Hay River, N.W.T., were sectioned and the interiors found to be indistinguishable. The only differences between the two species that might be considered of generic importance is stronger radial costellation and weaker concentric lamellae on *E. reidfordi* than on *M. thedfordensis*. The genus *Lamellispirifer* Nalivkin is a junior objective synonym of *Mucrospirifer*, but, as used by some Russian workers, embraces Upper Devonian forms that would be called *Eleutherokomma* in Western Canada (e.g. Nalivkin, 1941, 1947; Rzhonsnitskaya, 1952). A revision of the group might lead to the merging of the two genera, but *Eleutherokomma* is retained for the present.

with the Finger Lakes stage of New York (Cooper, and others, 1942). Its upper limit is transitional to a second substage characterized by the appearance of *Cyrtospirifer*, and which may be correlated with the Chemung stage of New York, and Merriam's *Phillipsastraea* zone in Nevada (1940). The faunas characteristic of this substage are abundant in the Escarpment to Kakisa formations on Hay River and to the west and in the Mount Hawk and Southesk formations in the Alberta Rockies.

The upper limit of the Frasnian occurs at a sharp faunal break that sees the final extinction of stromatoporoids¹, *Hypothyridina*, *Atrypa*, *Theodossia*, and the disappearance of compound rugose corals for the remainder of the Devonian (Crickmay, 1957; McLaren, 1959). The Famennian faunas contain many new elements, the most characteristic being *Cyrtopsis* and several new genera of rhynchonelloid brachiopods (Sartenaer, *in press*).

Zonal Subdivisions

Zonal schemes have been proposed for all or parts of the Western Canadian Devonian by several workers (Warren, 1949; Warren and Stelck, 1950; McLaren, 1954; Warren and Stelck, 1956; Raasch, 1956; Crickmay, 1957 and 1960a). The most difficult problem in the palæontology of shelly faunas is to establish the true biozone (range-zone) of a species, once its full morphological limits are understood. Similarly, faunizones (assemblage-zones) are equally difficult to relate to a relative time-scale consistent within the region over which they are recognized. A succession of faunules from one section composed of shelly benthonic organisms does not constitute a zonal scheme.

The present work is concerned primarily with establishing morphological species which may be recognized widely thus allowing local or regional range-zones to be established for each, empirically. McLaren (1954) attempted a range-zone zonation based on rhynchonelloids for the Upper Devonian. More is now known of the ranges of the species there proposed as zonal indicators and of their morphological expression. The present known time-ranges of the species and subspecies dealt with in this report are shown on Figure 1, and, although correlation between columns is inevitably interpretive, these ranges may be taken as a zonal scheme to be developed as collecting continues and correlation improves.

No further zonation is proposed in this work but a few comments may be made on the zonal value of the rhynchonelloids described.

The Middle Devonian must await further work before a satisfactory zonal scheme is evolved in Western Canada. Local schemes have been proposed that are satisfactory in limited areas (Crickmay, 1954, 1960a). Corals, which are both abundant and well preserved, may offer the best solution to the problem. Among the Middle Devonian rhynchonelloids, *Leiorhynchus manetoe* occurs only in the

¹Rare specimens belonging to the genus *Labechia* have been collected from the Costigan member of the Palliser formation, of middle Famennian age, in the Alberta Rocky Mountains (Stearn, C.W., 1961, *J. Paleontology*, vol. 35, pp. 932-948).

western part of the North and South Nahanni Rivers region and its biozone is far from being established. In the Great Slave Lake region *L. castanea*, *L. awokanak*, and *Hadorhynchia sandersoni* together characterize the upper part of the Pine Point formation. *L. castanea* is very widespread in the central Mackenzie River region, commonly in the top few feet of the Hume or the lower Hare Indian formations, and was successfully employed as a zone fossil by Bassett (1961). In the Anderson River area it is accompanied at this horizon by *Cassidirostrum pedderi*.

L. castanea, however, ranges higher, into the Kee Scarp formation at some localities, e.g. Carcajou Ridge, accompanied by *L. awokanak* and *H. sandersoni*. It is commonly larger at this horizon than lower and this has prompted Warren and Stelck (1956) and Crickmay (1960a) to differentiate the two forms. But, as large specimens are known from the Pine Point and small specimens are not rare in the Kee Scarp, the separation cannot be justified morphologically and could well lead to attributing a greater accuracy to the species as a zone fossil than in fact appears to be so.

In contrast to those of the Middle Devonian, the Upper Devonian rhychonelloid species described here have proved of considerable value as zonal markers, and the lower four zones of Frasnian age proposed by McLaren (1954) may be retained with some modification and refinement.

The genus *Ladogioides* with the two species *L. pax* and *L. kakwaensis* may be taken as the basal Upper Devonian zone in place of McLaren's "*Pugnoides kakwaensis* zone". This is now known to be restricted stratigraphically to the lower Waterways, lower Beaverhill (in northern Alberta) and lower "Flume" in the Kakwa Lake area of the Rockies. The zone fossil is commonly accompanied by *Leiorhynchus russelli*. The *Ladogioides* zone thus constitutes one of the most valuable regional horizon markers in the whole succession, in northern Alberta, north-eastern British Columbia, and southern Northwest Territories.

McLaren's "*Nudirostra athabascensis* zone," now redesignated *Calvinaria variabilis athabascensis*, is not contiguous with the *Ladogioides* zone but is restricted in the Alberta Rockies to the Maligne and lower Perdrix formations and their equivalents and the Cooking Lake formation in the subsurface of Central Alberta. On Hay River the species has been collected at the base of the Escarpment member of the Hay River formation, at what is believed to be the top of its range. The subspecies *C. variabilis jobensis* is known from one section only in the Rockies, in the Maligne formation.

The "*Nudirostra insculpta* zone", now designated *Calvinaria variabilis insculpta* is found in the upper Perdrix formation and its equivalents, in the Alberta Rockies and the Duvernay of the Central Alberta subsurface. The lowest part of its range overlaps that of the *athabascensis* zone. The zone fossil is commonly accompanied by *Leiorhynchus carya*, the last occurrence of the genus *Leiorhynchus* in the whole region. On Hay River, the lower part of the Escarpment member contains two other forms of *Calvinaria* — *C. variabilis variabilis* and *C. albertensis opima*, which are believed to lie within the *insculpta* zone.

Rhynchonelloid Brachiopods from Western Canada

The "*Nudirostra albertensis* zone", now designated *Calvinaria albertensis albertensis* is widespread in the lower and middle Mount Hawk formation and its equivalents in the Alberta Rockies and in the Ireton formation of the Alberta subsurface. Its lower limit overlaps the upper part of the *insculpta* zone. On Hay River a subspecies named *C. albertensis feni* occurs in the upper part of the Escarpment member and is believed to lie within the *albertensis* zone.

Diagnostic rhynchonelloids are not found in the upper beds of the Frasnian of Western Canada. A small rare *Calvinaria* sp. has been found near the top of the Kakisa formation on Trout River and may prove to be a further subspecies of *C. albertensis*. The latest Frasnian rocks are best typified by a small species of *Hypothyridina* and the genus *Theodossia* (= *Vandergrachtella* Crickmay).

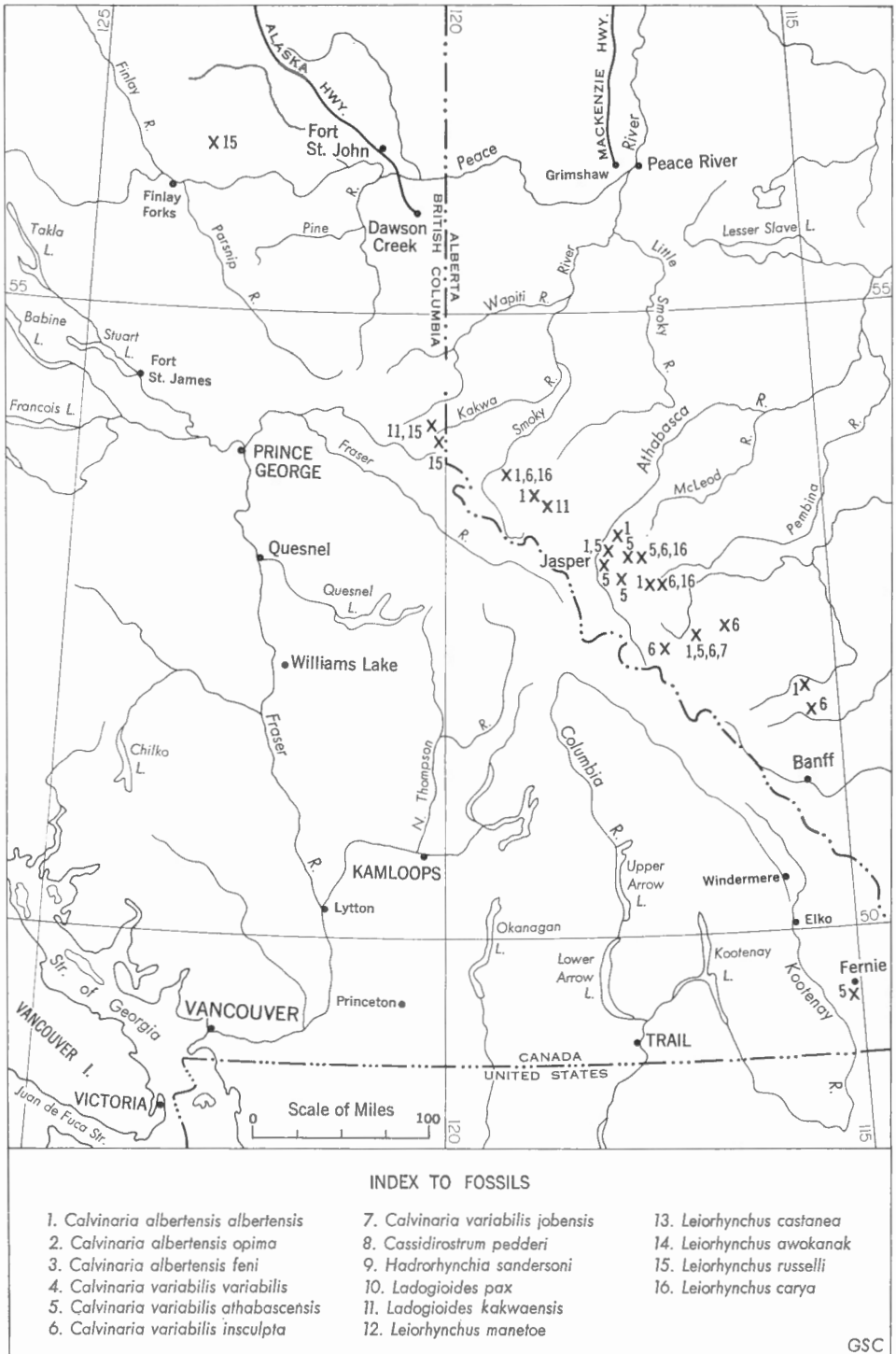


Figure 3. Index map of southern region.

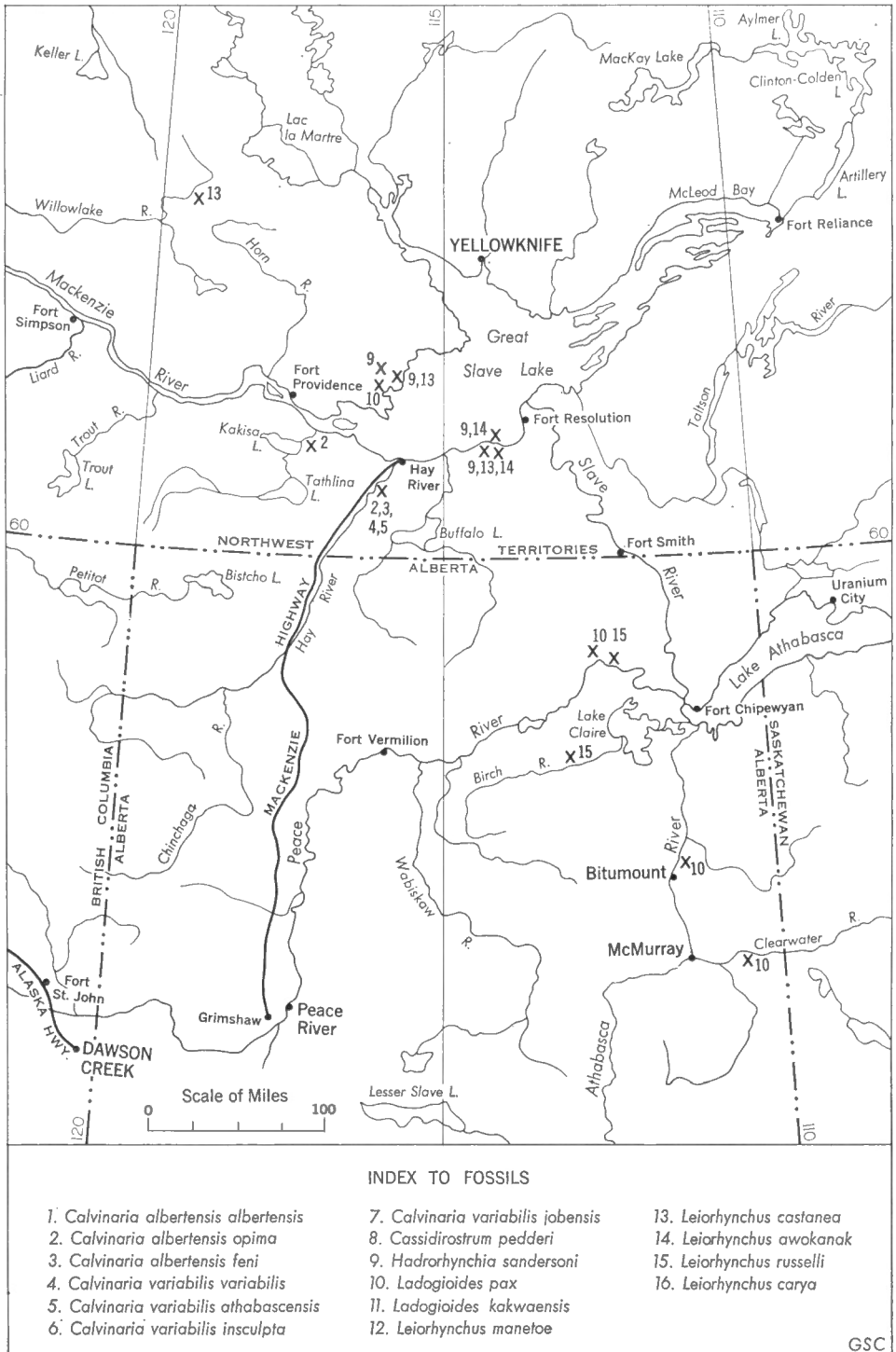
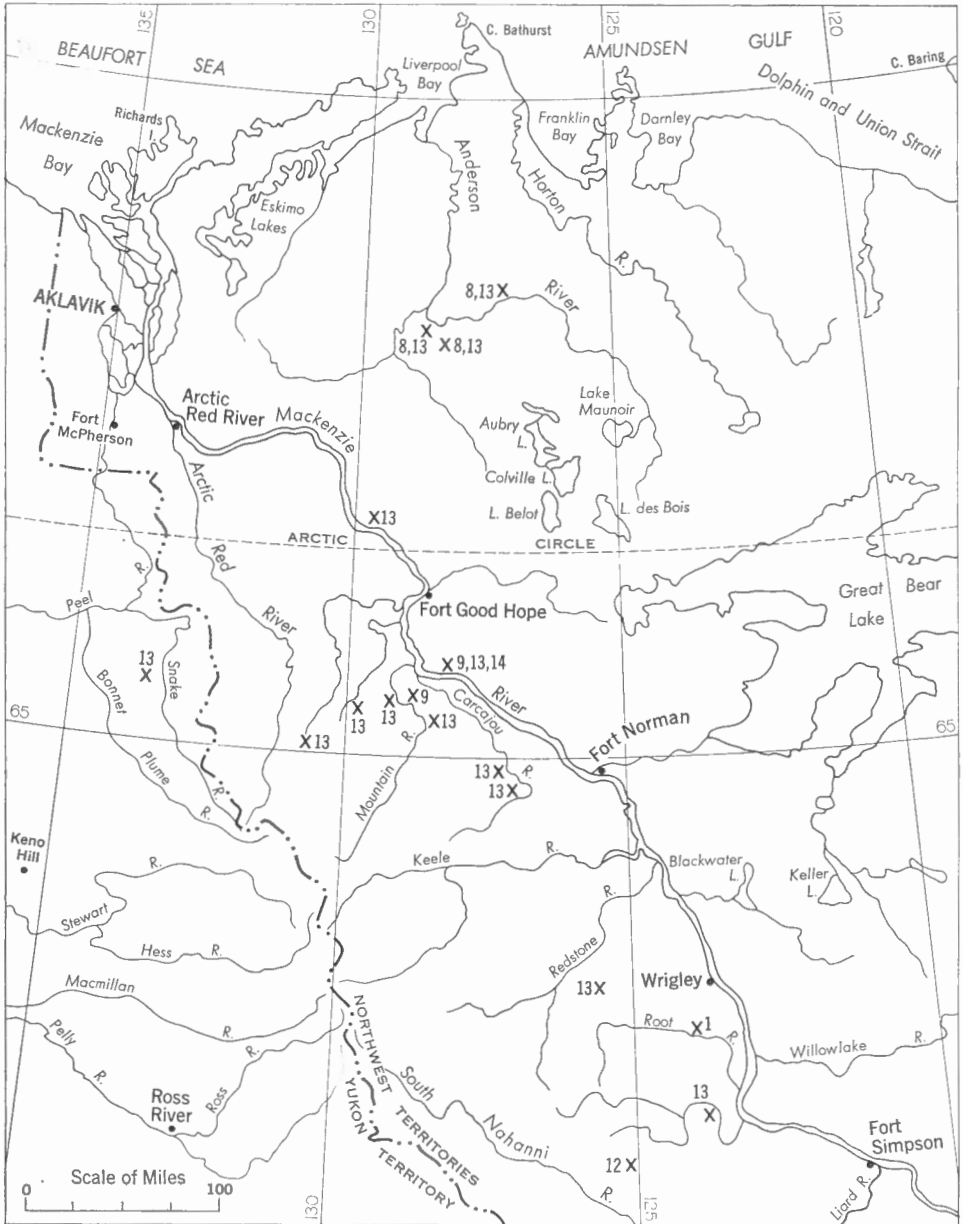


Figure 4. Index map of central region.



INDEX TO FOSSILS

- | | | |
|---|--|----------------------------------|
| 1. <i>Calvinaria albertensis albertensis</i> | 7. <i>Calvinaria variabilis jobensis</i> | 13. <i>Leiorhynchus castanea</i> |
| 2. <i>Calvinaria albertensis opima</i> | 8. <i>Cassidirostrum pedderi</i> | 14. <i>Leiorhynchus awokanak</i> |
| 3. <i>Calvinaria albertensis feni</i> | 9. <i>Hadorhynchia sandersoni</i> | 15. <i>Leiorhynchus russelli</i> |
| 4. <i>Calvinaria variabilis variabilis</i> | 10. <i>Ladogioides pax</i> | 16. <i>Leiorhynchus carya</i> |
| 5. <i>Calvinaria variabilis athabascensis</i> | 11. <i>Ladogioides kakwaensis</i> | |
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GSC

Figure 5. Index map of northern region.

DESCRIPTIVE PALÆONTOLOGY

Technique

The method of studying the interiors of brachiopods by serial grinding of roasted specimens was introduced by Buckman (1918) and developed by Muir-Wood (1934). It has recently been fully summarized by Ager (1956). In the present study about 40 to 70 drawings at 0.1 mm intervals were prepared of each specimen, using a camera lucida with a magnification of about 14 diameters. Selected drawings were inked in and reduced photographically for text-figure reproduction. It was found that a high degree of accuracy is achieved by this method. Hardened plaster replicas of the specimen sectioned were prepared and are numbered and listed as types, together with the residue (commonly more than half) of the specimen itself.

Classification

Cooper (1959) has discussed the history of rhynchonelloid classification in general and erected several new families and subfamilies for Tertiary and Recent forms. Subsequently, Rzhonsnitskaya (1959) has published a fuller account of her outline classification proposed in abstract in 1956. All the genera but one in the present study fall in the family Camarotoechiidae Schuchert, 1929. Subdivision of this family is not satisfactory as much remains to be learned about the interiors of many of the genera. Distribution of the genera in the present study into the subfamilies proposed by Rzhonsnitskaya is not easy. *Cassidirostrum* may fall within the Camarotoechiinae Schuchert, 1929, on the basis of its ornament, but the structure of the cardinalia suggests affinities with *Leiorhynchus*. The subfamily Leiorhynchinae Stainbrook, 1945 (which must once more replace Nudi-rostrinae Roger, 1952) contains *Calvinaria* and *Leiorhynchus*. *Ladogioides* may be assigned with some doubt to the Yunnanellinae Rzhonsnitskaya, 1956, together with *Ladogia*.

Hadrorhynchia by virtue of the internal grooving of its costae near the front margin may be classified with the family Uncinulidae Rzhonsnitskaya, 1956, but lack of a true cardinal process leaves its assignment in some doubt.

Growth and Variation

Some of the species in the present study occur over a wide area and are represented by large collections from many different localities. Statistics were used to test whether differences between such populations were significant for several species, but these were abandoned when it was found that significant differences between two populations did not necessarily agree with taxonomic judgment.

The statistics listed by Imbrie (1956, p. 242) were calculated for *Ladogioides pax*, *L. kakwaensis*, and *Leiorhynchus russelli*. Imbrie (op. cit.) shows how by use of length, width, and thickness measurements, the patterns of relative growth for any pair of measurements may be compared between populations. In the species in question, populations with different mean sizes sometimes also displayed different relative growth patterns. This led to a statistically significant difference between the populations which, however, appeared to be unreal taxonomically.

The reason for the disagreement between statistical tests and reality (albeit subjective!) became apparent when the populations were examined. The absolute size at which certain changes in relative growth proportions occurred, as well as appearance or development of certain non-quantitative characters, varied widely between populations. Thus, a small shell might develop mature features while a shell more than twice its size remains youthful.¹ This is well illustrated by the great range in size of mature forms of *Ladogioides pax* and *Hadorrhynchia sandersoni*, as well as many of the other species described, and is considered further as needed in the discussion on each species.

The causes of such variation is presumably related to environment — if it is assumed that disparate populations may in fact belong to the same species. There are few data on rate of growth of living brachiopods and what there are give little indication of possible variation with environment (e.g. Percival, 1944, p. 5). Du Bois (1916) has described changes in shell shape due to varying environmental conditions in a recent brachiopod.

Many brachiopods presumably grow throughout life. Before other factors such as preservation and selective forces operating on dead shells can take effect (Boucot, 1953), the frequency of occurrence of a shell of a certain size varies inversely as to the size. Despite this principle, which would appear to apply to most marine invertebrates, it is, nevertheless, still common to read diagnoses of species that give size as a prime distinguishing character (e.g. Pettitt, 1950).

Morphology

The number of terms employed to describe brachiopod morphology is increasing rapidly, but basic terminology depends on the work of Davidson, Hall and Clarke, Buckman, Thomson, Schuchert, Cooper, Herta Schmidt, Muir-Wood, and Cloud. Muir-Wood (1934) gives a useful account of terminology for Mesozoic Telotremata which is also of value for Palæozoic forms, and a concise summary of brachiopod morphology may be found in Cooper (1944b).

There has been a tendency among workers on Mesozoic brachiopods to coin terms that give great precision to details of shape or ornament (e.g. Buckman, 1918; Ager, 1956). This practice has not been followed in the present work and descriptions of both shape and ornament must be supplemented by reference to

¹The terms youthful and mature are purely relative and do not, of course, refer to development of sexual maturity. Presumably most or all the specimens described in this report were sexually mature.

figures in the plates. Certain descriptive terms require comment, because the terminology has not yet become fully stabilized or because the structures are of special interest.

Apical angle. The angle between the two postero-lateral margins of the ventral valve, measured in a horizontal plane.

Crura. Cooper (1959) has recently given an account of five types of crura recognized in Tertiary rhynchonelloids. In the genera described in the present work two types of crura are recognized: (1) In *Calvinaria*, *Ladogioides*, and *Leiorhynchus* the crura arise from the inner margins of the hinge plates and are initially round, triangular, or wedge-shaped in section becoming dorsally grooved or trough-shaped forwards into the shell; they plunge towards the floor of the ventral valve and may be recurved. They do not extend more than about a quarter of the length of the shell forward of the beak. The crura of *Cassidirostrum* are similar but are proximally heavily enclosed in shell material that fills the septalium. (2) In *Hadorrhynchia* the crura also arise from the inner margins of the hinge plates and are slender and triangular, becoming vertically flattened lamellae anteriorly that plunge ventrally and are slightly recurved. They are dorsally grooved and carry a small lateral projection anteriorly on each of their exterior surfaces.

Hinge plates. The term is used in the plural, as in all the genera under discussion there is a median division caused by the development to a greater or less extent of a septalium. Morphologically the hinge plates correspond to "outer plates" as defined by Cooper (1944b) and "inner plates" are not present. In *Hadorrhynchia* the septalium is filled by broad rounded longitudinal ridges developed on the inner margin of each hinge plate and separated by a narrow median groove. This development may represent the inner hinge plates of other genera but is more of a general thickening of the cardinalia medianly than true development of discrete plates.

Median septum. The septa of all genera described here are duplex structures which may be looked on as being the dorsal continuation of the septalial plates united medianly. The "true median septum" of Muir-Wood (1934, pp. 528-9) does not appear to be present in any forms. The structure has a certain analogy with the duplex cruralium of some pentameroids.

Plane of articulation. As the interiors of the species in this study are described largely from examination of serial transverse sections, the "plane of articulation" (Ager, 1956, p. vii) makes a useful reference plane in descriptions. As used here, it is a plane passing through the teeth and sockets at the point of their maximum development, at right angles to the length dimension of the specimen.

Septalium. Cooper (1959, pp. 9-10) discussed the camera or chamber formed between the crural bases and ventral end of the median septum in some rhynchonelloids. He considered that this chamber in Tertiary and Recent genera, and similarly in Mesozoic genera (Wiśniewska, 1932, p. 6), is formed by internal

inflection of the hinge plate to meet the median septum, and is formed differently in certain Palæozoic genera, e.g. *Camarotoechia*. Leidhold (1921, p. 354) defined the term "septalium" as a cavity formed by bifurcation of the median septum. This appears to describe the structure encountered in the present study, and the term is employed. The structure is certainly different from that described by Cooper for later forms of the family. Cloud (1942, pp. 10-11) employed the term "crural trough" for an analogous structure in terebratuloids suggesting that it was different from that of rhynchonelloids. The septum in Palæozoic terebratuloids and rhynchonelloids, however, appears to be exactly analogous and separation of this terminology appears unnecessary.

Genus *Calvinaria* Stainbrook, 1945

(Figure 8A)

STAINBROOK, 1945, pp. 43-45, Pl. 4, figs. 3-6, Fig. 2.

SARTENAER, 1955, pp. 1-12, Pl. 1, figs. 1-9.

Type species. By monotypy, *Rhynchonella ambigua* CALVIN, 1878, pp. 729-730.

Diagnosis. Medium to large transversely subelliptical shells, width always greater than length, hinge-line nearly straight, lateral margins smoothly rounded. Front margin strongly uniplicate. Pedicle valve smoothly curved longitudinally, shallow transversely; sulcus develops forward of umbō and extends into broad prominent tongue with flared margins, vertical or recurved in mature shells. Beak strongly incurved, interareas narrow. Brachial valve moderately to strongly convex, highest near or at front margin, falls sharply to lateral margins; fold prominent anteriorly, truncated by tongue of pedicle valve. Ornament highly variable, commonly two strong plications develop on fold which may increase by bifurcation in some species into weak costae; flanks smooth or feebly costate; umbones always smooth.

Weak, dorsally divergent, dental plates always present in pedicle interior, rarely persist to plane of articulation. May be hidden by secondary shell growth in large shells. Cardinalia typically consist of divided hinge plates and septalium supported by median septum; secondary thickening may obscure septalium and fill crural cavities nearly to front edges of hinge plates.

Discussion. The distinguishing characteristics of the genus *Calvinaria* consist of its highly transverse shell outline, prominent vertical tongue, and the maximum height of the brachial valve at or near the front margin. *Leiorhynchus*, a closely related genus, is commonly elongate or rarely more than slightly transverse, its tongue is low and inclined forward, and the maximum height of the brachial valve is at or posterior to mid-length.

Interiorly *Calvinaria* is somewhat similar to *Leiorhynchus* but its hinge plates are commonly more strongly developed and tend to be supported by the median

septum for a greater distance forward into the shell. The great variation between species of *Calvinaria* in the form of the cardinalia and degree of attachment of the septum to the hinge plates is a function of shell shape and amount of secondary shell deposition.

The type species of *Pseudocamarophoria* Wedekind 1926, *Terebratula micro-rhyncha* Roemer, possesses strongly developed and numerous costae on fold and flanks as figured by Roemer (1844), and is described and figured by Schmidt (1941, under the genus *Septalaria* Leidhold, 1928) as having an entire hinge plate. Schmidt's figures of the interior of *Terebratula subtetragona* Schnur, type species of the genus *Septalaria*, show a prominent cardinal process attached to the hinge plate. In *Calvinaria*, the weakly developed costae on the flanks, divided hinge plates, and lack of cardinal process distinguish it from these genera.

From *Nemesa* Schmidt, 1941, *Calvinaria* may be distinguished by its more transverse outline, straighter hinge-line, and the maximum height of the brachial valve at the front margin.

Stainbrook (1945) in his original description of *Calvinaria*, and Sartenaer (1955) in his revision of the genus, both illustrate serial sections of *C. ambigua* in which dental plates are not developed. This is a common feature in large shells in which secondary shell growth has filled the umbonal cavities. Sartenaer indicates "cavités umbonales résiduelles" on his figures (Pl. I). As umbonal cavities and well-developed dental plates are present on smaller specimens of the type species, their absence cannot be named as a characteristic of the genus (see Fig. 8A). In fact, in most species, they are invariably present, except in specimens exhibiting extreme gerontic characters.

Sartenaer (1955) indicated that *Calvinaria* is congeneric with *Nudirostra* Cooper and Muir-Wood, a junior homonym for *Leiorhynchus* (see Sartenaer, 1959), but, for the reasons given above, the genera are here considered distinct.

Occurrence. In North America, the following species and subspecies are included in *Calvinaria*:

Rhynchonella ambigua Calvin from the Independence Shale, and the "Amana beds" of Iowa. (Stainbrook, 1942, reports this species from the High Point Sandstone, New York.)

Calvinaria bransoni Stainbrook from the Sly Gap formation, New Mexico.

Leiorhynchus albertense Warren, from the Mount Hawk formation of the Alberta Rocky Mountains.

Calvinaria albertensis opima n. subsp., and *C. albertensis feni* n. subsp. from the Escarpment member of the Hay River formation, Hay River, Northwest Territories.

Eatonia variabilis Whiteaves from the Hay River Shale, Hay River, Northwest Territories.

Leiorhynchus athabascense Kindle, here designated *Calvinaria variabilis athabascensis* (Kindle), and *C. variabilis jobensis* n. subsp. from the upper Flume (=Maligne) formation of the Alberta Rocky Mountains.

Nudirostra insculpta McLaren, here designated *Calvinaria variabilis insculpta* (McLaren), from the Perdrix formation of the Alberta Rocky Mountains.

Of foreign species of *Calvinaria* the following may be considered:

Terebratula (Atrypa D'Orb) megistana LeHon from the Frasnian Stage of Belgium is considered conspecific with *C. ambigua* by Sartenaer (1955, p. 3). If this is substantiated then this species becomes the type for *Calvinaria*. Sartenaer suggests that *T. megistana* may in turn be conspecific with *Terebratula rhomboidea* Phillips. This species is reported by Phillips (1841, p. 88) from the Devonian of Devonshire but was first named by him from the Carboniferous of Yorkshire (1836). Whatever the affinities of the specimen figured by him (1841, Pl. 35, fig. 158) from Devonshire, the Yorkshire species is almost certainly not congeneric with *T. megistana*.

Terebratula formosa Schnur, as pointed out by Stainbrook (1945, p. 44), may belong to *Calvinaria*, and the similarity of its internal morphology to that of *C. ambigua* has been demonstrated by Sartenaer (1955, Pl. III). The species occurs in the Frasnian Stage of Germany, Belgium and elsewhere.

Sartenaer (1955) also considers *Camarophoria crenulata* Gosselet from the lower Famennian of Belgium to be congeneric with *Calvinaria ambigua*. This would appear to be the latest occurrence of the genus.

In the absence of descriptions of interiors, it is difficult to form conclusions on other species. *Camarophoria (Liorhynchus) medioplicata* Nalivkin from the Upper Devonian of Turkestan may be congeneric with *Calvinaria*.

Calvinaria albertensis (Warren)

The species was described by Warren (1928) from beds of Mount Hawk age in Crowsnest Pass, Alberta. Large collections of similar forms from the Alberta Rocky Mountains, and the Hay River region and westwards into the Mackenzie Mountains, Northwest Territories, show a degree of variability that appears related to both horizon and geographic region and the species is here subdivided into three subspecies.

C. albertensis albertensis occurs widely in the mountains and extends into the Northwest Territories, and, although extremely variable, is consistently recognizable in collections of a few individuals.

A form known from Hay River is described as *C. albertensis opima*. Its range of variation overlaps that of *C. albertensis albertensis* but the means of small populations are consistently different and most individuals may be assigned without difficulty to one or the other.

At a higher horizon on Hay River, another more poorly preserved subspecies is described as *C. albertensis feni*. Its relationship with *C. albertensis albertensis* is more obscure but it is assigned to the same species for the present.

The differences between *C. albertensis* and *C. variabilis* are discussed under the latter species. *C. bransoni* Stainbrook, a somewhat similar form, is considered in the discussion of *C. albertensis albertensis*.

Calvinaria albertensis albertensis (Warren)

Plate I, figures 1-11; Figures 6B, C

1928. *Leiorhynchus albertense* WARREN, pp. 117-8, Pl. I, figs. 1-5.
1954. *Nudirostra albertensis* (Warren), McLAREN, p. 179, Pl. I, figs. 14-18.
1956. *Calvinaria albertensis* (Warren), WARREN and STELCK, Pl. XVII, figs. 26-34; [non] Pl. XVIII, figs. 26-29.
1958. *Nudirostra albertensis* (Warren), McLAREN, Pl. VI, figs. 13, 14, 15.

Material. Here chosen as lectotype, U. of A. syntype Dv633. Figured by Warren (1928, Pl. I, figs. 3, 5). Warren collected his specimens from the basal beds of the Crowsnest section which occur "west of Coleman, extending from the east end of Crowsnest Lake westward a little past the station of Crowsnest" in Crowsnest Pass, Alberta (p. 109). These beds were referred to the Minnewanka limestone (lower part). From the associated fauna together with Warren's description of the section it is clear that the fossils in question come from beds equivalent to the Mount Hawk formation of the Jasper region.

Syntype, U. of A. No. Dv631. Figured by Warren (1928, Pl. I, figs. 1, 4). Same horizon and locality as lectotype.

Syntype, U. of A. No. Dv632. Figured by Warren (1928, Pl. I, fig. 2). Same horizon and locality as lectotype.

Hypotype A, GSC No. 14944. Argillaceous limestone member of the Mount Hawk formation, 316 feet above base, northeast flank of Roche Miette, Jasper Park, Alberta. GSC loc. 18202; collector D. J. McL., 1949.

Hypotype B, GSC No. 11237. Figured by McLaren (1954 and 1958). Same formation and locality as hypotype A, about 410 feet above base. GSC loc. 18163.

Hypotype C, GSC No. 14945. Same formation and locality as hypotype A, about 400 feet above base. GSC loc. 18208.

Hypotype D, GSC No. 14946. Same horizon and locality as hypotype B.

Hypotype E, GSC No. 14947. Same horizon and locality as hypotype B.

Hypotype F, GSC No. 11241. Figured by McLaren (1954). Same horizon and locality as hypotype B.

Hypotype G, GSC No. 14948. Same horizon and locality as hypotype B.

Hypotype H, GSC No. 14949. Argillaceous limestone member of the Mount Hawk formation, 18 feet above base of exposure, south end of Idlewilde Mountain, Clearwater River valley, Alberta. GSC loc. 16996; collector D. J. McL., 1949.

Hypotype I, GSC No. 14950. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figure 6C). Same horizon and locality as hypotype B.

Hypotype J, GSC No. 14951. Plaster replica and anterior half of specimen; remainder serial sectioned (illustrated, Figure 6B). In argillaceous and silty limestone, 150 feet below massive limestone reef, forming cliff on north side of Root River, 10 miles west of Gap in Camsell Range, Northwest Territories. GSC loc. 33254; collector D.J.McL., 1957.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Lectotype	10.4	9.9	12.4	6.8	138°
Syntype	12.2	11.5	14.1	(6.7)	120°
Syntype	11.7	10.9	(13.7)	7.2	117°
Hypotype A	17.6	17.0	23.3	14.0	150°
Hypotype B	15.0	14.6	20.2	12.2	146°
Hypotype C	14.3	13.7	18.2	6.2	144°
Hypotype D	13.1	11.9	19.8	9.7	150°
Hypotype E	13.1	11.9	16.8	9.6	142°
Hypotype F	(12.6)	12.2	16.2	8.2	140°
Hypotype G	11.9	11.0	13.7	7.5	137°
Hypotype H	10.0	9.2	10.3	5.3	121°
Hypotype I (sectioned)	(13.8)		20.4	12.7	142°
Hypotype J (sectioned)	11.9	10.6	14.9	7.9	133°

Description. Shell small to medium sized for the genus, transversely sub-elliptical, much wider than long, inflate; hinge-line nearly straight to straight; apical angle between 140 and 150 degrees in larger individuals; lateral margins rounded, front margin truncate; greatest width of shell at or posterior to mid-length. Fold commonly with two rounded costae, sulcus with one, umbones and flanks smooth; a few shells show additional development of costae on fold and sulcus, and more rarely on flanks. Anterior commissure uniplicate. Shell of medium thickness to thick.

The convex pedicle valve is shallower than the brachial. It is smoothly curved longitudinally from beak to anterior commissure and more weakly curved transversely. There is a tendency for the flanks to flatten in the less inflate shells. The sulcus develops well forward of the umbo from near the mid-length and extends into a broad flattened tongue which is vertical in large shells.

The beak is small, suberect to incurved and inconspicuous. There are narrow interareas with weak beak ridges. The foramen is small and extends onto the umbo by resorption of the beak. Deltidial plates are rarely seen and appear to be vestigial.

The brachial valve is strongly inflate with maximum height forward of the mid-length. The fold is only developed anteriorly and is sharply truncated by the tongue. The flanks are gently convex becoming almost flat in shells with high width-length ratio. The beak is incurved below that of the pedicle valve.

The ornament is commonly developed only on the anterior half of the shell; the umbones are always smooth. Most shells have two simple rounded costae on the fold and one in the sulcus and the flanks are smooth. Where additional costae develop, the commonest mode of increase is by intercalation of a small low ridge between the two first formed costae. Costae rarely bifurcate. Some shells show weakly developed costae on the flanks.

In the pedicle interior dental plates are stout, short and dorsally divergent. They become detached from the floor of the valve considerably posterior to the teeth, their dorsal ends remaining as stout processes merging with the teeth. The

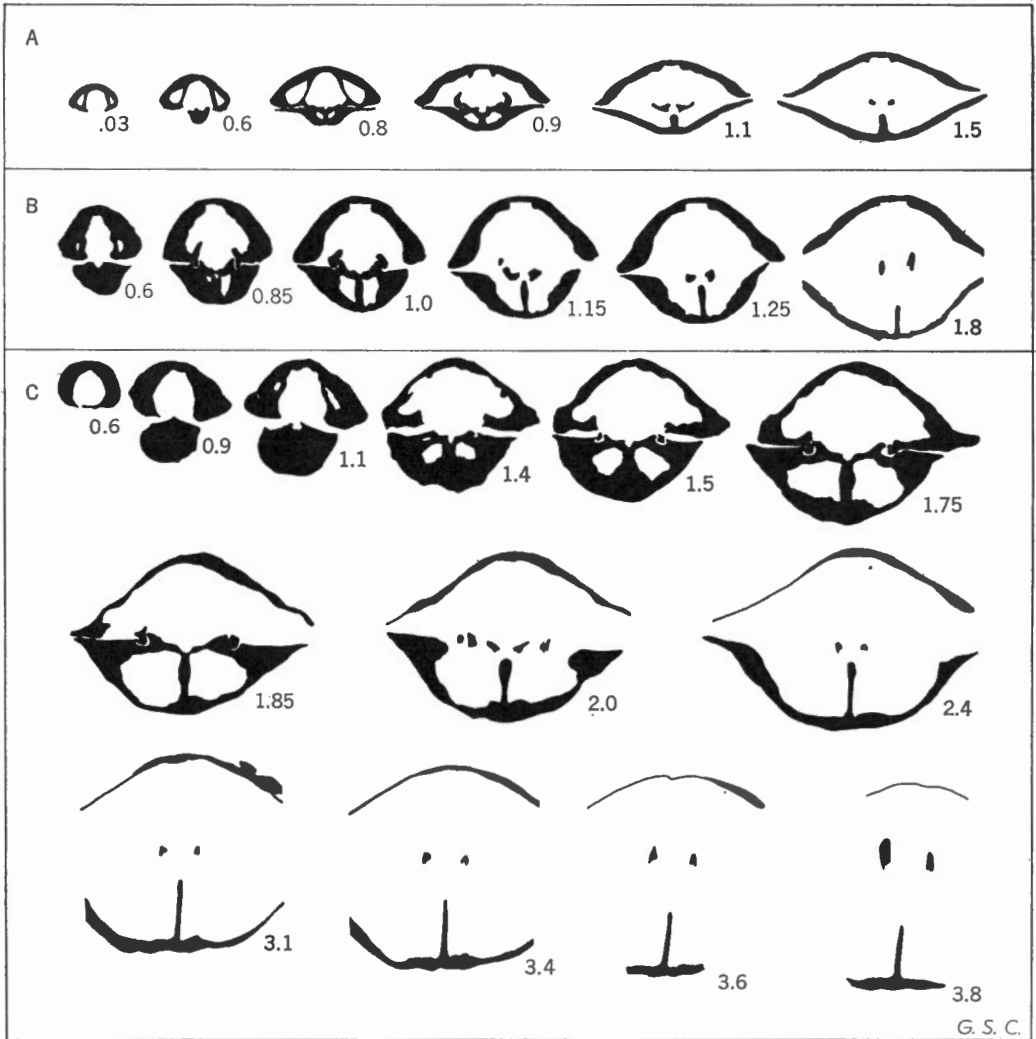


Figure 6A. *Calvinaria bransonii* Stainbrook. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype, GSC No. 15953; specimen with dimensions (in mm): length 12.4, width 11.6, thickness 6.3; from the Sly Gap formation, Indian Wells Canyon, Alamogordo, New Mexico.

Figures 6B, C. *Calvinaria albertensis albertensis* (Warren). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; 6B, hypotype J, GSC No. 14951; 6C, hypotype I, GSC No. 14950.

teeth are stout, quadrate to rounded in section, and recurved posteriorly. They are supported up to articulation by the lateral margins of the shell and may persist forwards into the shell as peg-like processes in contact with the socket ridges. There is a narrow undivided adductor track extending forward from the delthyrial cavity.

The cardinalia consist of wide, gently concave divided hinge plates joined by a moderately deep, U-shaped septalium which may be filled by secondary shell material. There is a stout, club-shaped median septum in contact with the septalium up to or beyond the plane of articulation, and which persists forward for at least a third of the total length of the shell. The inner socket ridges are prominent and protrude above the ventral surface of the hinge plates; they persist a short distance forward of articulation, parallel with the crural bases. The crura arise from bases at the inner margins of the hinge plates where they join the septalium. They are initially triangular to wedge-shaped and slender, becoming thicker curved laths anteriorly, which descend towards the floor of the pedicle valve. In section they appear U-shaped with a concave dorsal surface. They end about a quarter of the shell length forward of the beak.

Growth and Variation (55 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 11 mm		11.0 to 12.9 mm		13.0 to 14.9 mm		15 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.12	0.92-1.27	1.28	1.15-1.52	1.33	1.17-1.48	1.34	1.17-1.57
Thickness/length	0.48	0.37-0.53	0.62	0.48-0.80	0.70	0.43-0.86	0.71	0.43-0.86
Apical angle	118°	109°-121°	140°	120°-144°	144°	138°-150°	148°	140°-152°

The species is widespread and there are large collections from many localities. Consideration of growth is based on material from the Mount Hawk formation on Roche Miette. Externally the most variable character is the shape of the shell. In large shells, the width varies from 1.17 to 1.57 times the length and the thickness/length ratio from 0.43 to 0.86. The means of these ratios may vary sharply between populations from different localities. The position of the maximum width of the shell varies from about mid-length to within one fifth of the length forward of the beak. There is a general tendency for the maximum width to be posterior to the mid-length in the largest shells. The costation is more constant than for other species of the genus; only one third of the shells develop more than two costae on the fold and a quarter show some costation on flanks. There is no correlation between costation on the flanks and that on the fold. Rare specimens occur which are entirely smooth. The maximum number of costae developed at the front margin is five each on fold and flank.

Internal variation is largely due to degree of secondary shell thickening. Variation in shell thickness is considerable between collections from different localities. Shells from black calcareous shales tend to be thinner than those from limestones and there is evidence to suggest that depth of water was partly a controlling factor—the thicker shells occurring in shallower water than the thin-shelled forms. Thick shells are correlated with secondary thickening on the

dental plates and cardinalia. Extreme development results in the disappearance of lateral cavities in the pedicle valve and heavy hinge plates with a very shallow septalium in the brachial. Other internal differences are due to the width and gibbosity of the shells sectioned.

Discussion. The three cotypes described and figured by Warren are small examples of the species; he gives the dimensions of an average specimen as length, 10 mm, width, 12 mm, thickness, 7 mm. Hypotypes F and G in the present discussion are close to the original types in size and form. As the original description was based on an assemblage of small individuals, the full size range and variation of the species has not been described previously.

The specimen figured by Warren and Stelck (1956) on Plate XVIII, figures 26-29, although conspecific with *C. albertensis*, belongs to the subspecies described herein as *C. albertensis opima*.

Calvinaria bransonii Stainbrook, from the Sly Gap formation of New Mexico is similar in appearance to *C. albertensis albertensis*. From Stainbrook's description (1948, pp. 774-5) and limited collections from the type area in New Mexico, *C. bransonii* appears to differ in being less transverse, more inflated, with more pronounced angular costae on fold, and with costae on the flanks nearly always well developed towards the front margin. It is considered likely that *C. bransonii* belongs to the same species group as *C. albertensis* but is certainly subspecifically distinct (see Fig. 6A).

Occurrence. *Calvinaria albertensis albertensis* is widespread throughout the Front Ranges of the Alberta Rocky Mountains between the Red Deer and the Smoky Rivers. It occurs most commonly in the lower and middle beds of the Mount Hawk formation and, when shaly tongues occur within it, in the lower part of the Southesk formation. It ranges down into the Perdrix formation in some sections and may overlap in the lowest part of its range with *Calvinaria variabilis insculpta*. It is unknown in the upper member of the Mount Hawk or its equivalent, the Arcs Member of the Southesk formation. Its occurrence at the top of the Mount Hawk formation at Deception Creek (GSC loc. 24554), immediately below the fossiliferous Alexo formation (McLaren, 1956, p. 29), strongly suggests erosion of the upper beds of the Mount Hawk prior to the deposition of the Alexo in this area.

Specimens have been examined from many localities including the following: GSC loc. 16996, 18163, 18202, 18208, 19936, 24183, 24554, 24563, 31352, 36919, 36949, 40194, 40212.

In the Nahanni Rivers region of the southern Mackenzie Mountains, the subspecies has been found in shales and shaly limestones 100 to 200 feet below a horizon of reefoid biostrome and bioherm development which contains an Arcs member coral fauna. Specimens have been examined from GSC loc. 33254.

In the subsurface of Alberta specimens have been collected from cores at GSC loc. 24396, 26840, 28105.

Calvinaria albertensis opima n. subsp.

Plate II, figures 1-6; Figure 7A

1956. *Calvinaria albertensis* (Warren), WARREN and STELCK, Pl. XVIII, figs. 26-29; [non] Pl. XVII, figs. 26-34.

Material. Holotype, GSC No. 14952. Base of Escarpment member of Hay River formation on Hay River, left bank, one third of a mile east of junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, Northwest Territories. GSC loc. 31298; collector P. Harker, 1957.

Paratype A, GSC No. 14953. Same horizon and locality as holotype.

Paratype B, GSC No. 14954. "Limestone bed in Hay River shale;" from associated fauna this specimen is probably from the same horizon as the holotype. GSC loc. 17409; collector W. I. Wright, Socony Vacuum Exploration Company, 1950.

Paratype C, GSC No. 14955. Same formation and locality as holotype, 415 feet above base of exposure on Hay River, GSC loc. 31265.

Paratype D, GSC No. 14956. "Hay River shale, High Banks, Hay River." GSC loc. 6748; collector A. H. Low, Imperial Oil Ltd., 1920.

Paratype E, GSC No. 14957. Same horizon and locality as holotype.

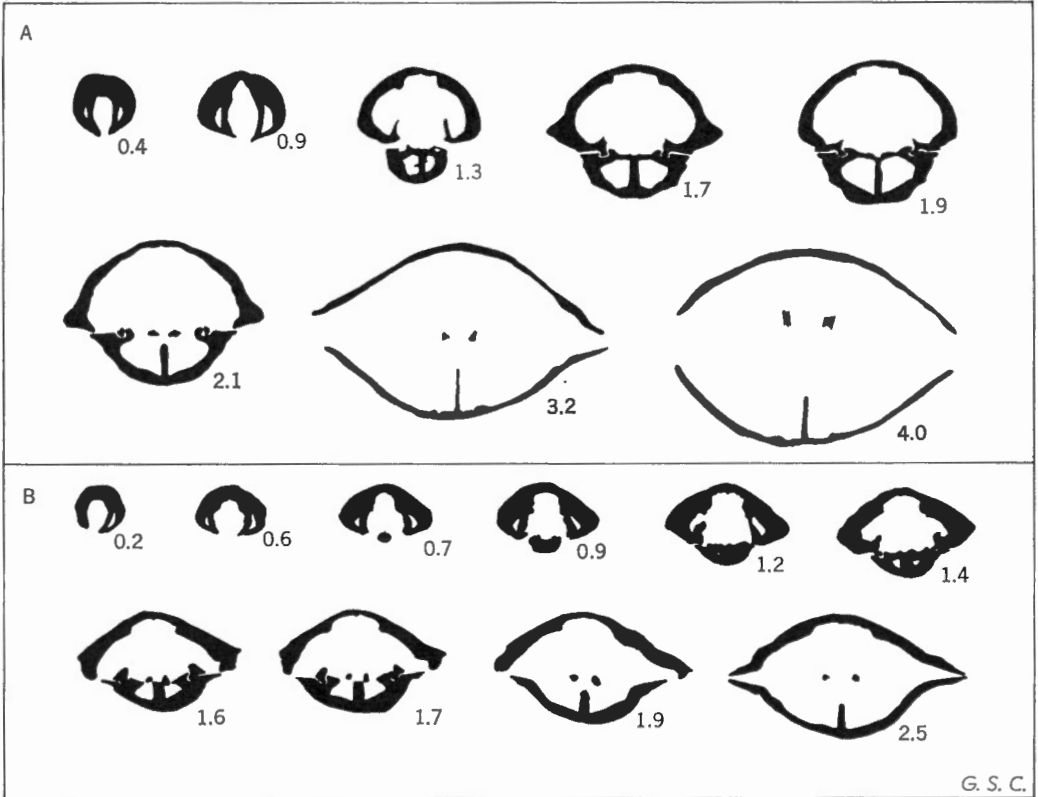
Paratype F, GSC No. 14958. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figure 7A). "Hay River shale, mile 24.6, Hay River." GSC loc. 24322; collector L. Vigrass, 1952.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	15.6	14.8	19.2	10.4	130°
Paratype A	15.8	15.0	20.8	10.9	136°
Paratype B	15.5	14.9	19.4	12.5	133°
Paratype C	12.0	11.6	15.4	6.8	134°
Paratype D	12.0	11.6	13.5	7.6	115°
Paratype E	10.6	9.9	11.3	6.0	114°
Paratype F (sectioned)	15.8	14.8	(20.0)	10.3	139°

Description. Shell is similar in shape and size to *C. albertensis albertensis* but differs in being less transverse with a more acute apical angle, ranging from 125 to 135 degrees in larger individuals; the greatest width of the shell is commonly at mid-length and not posterior to it. The ornament is very similar. Both valves tend to be smoothly rounded transversely and there is no tendency towards a flattening of the flanks. Beak, foramen and interareas are similar.

Internally the subspecies is identical in all respects with *C. albertensis albertensis*.



G. S. C.

Figure 7A. *Calvinaria albertensis opima* n. subsp. Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; paratype F, GSC No. 14958.

Figure 7B. *Calvinaria albertensis feni* n. subsp. Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; paratype D, GSC No. 15203.

Growth and Variation (46 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 11 mm		11.0 to 12.9 mm		13.0 to 14.9 mm		15 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.11	1.07-1.20	1.17	1.11-1.29	1.29	1.22-1.36	1.24	1.19-1.32
Thickness/length	0.54	0.44-0.60	0.60	0.56-0.69	0.62	0.58-0.70	0.75	0.67-0.81
Apical angle	118°	113°-121°	124°	115°-134°	130°	122°-136°	131°	127°-136°

All the specimens used in consideration of growth are from the Escarpment member on Hay River. The smallest shells cannot be distinguished from specimens of *C. albertensis albertensis* of comparable size, but the smaller width/length ratio and apical angle normally allow separation of larger shells.

Few shells have an apical angle of more than 135 degrees. The variation in these characters is therefore not so great, and the range overlaps that of the more variable *C. albertensis albertensis*. There are very few shells, however, that cannot be assigned with confidence to one or other subspecies on the basis of shape and general proportions. The ornament is similarly less variable. Few shells have more than two costae on the fold and only one specimen has four. About a quarter show weak or incipient costation on the flanks.

Discussion. The specimen figured by Warren and Stelck (1956) on Plate XVIII, figures 26-29, as *C. albertensis* is a typical example of this subspecies.

Calvinaria bransoni Stainbrook resembles *C. albertensis opima* in proportions and apical angle but differs in its more pronounced and angular costation on fold and flanks.

The subspecies is named from the Latin "opimus" well fed, fattened.

Occurrence. The subspecies occurs in the lower 16 feet of the Escarpment member of the Hay River formation, which outcrops in Hay River gorge from the junction of the Mills Lake road with Hay River highway for several miles downstream. Its range overlaps that of *Calvinaria variabilis athabascensis* at the base and *C. variabilis variabilis* at the top. It has been found elsewhere only on lower Kakisa River in beds assigned to the Escarpment member.¹ Specimens have been examined from the following localities: GSC loc. 5637, 5641, 6748, 17409, 24322, 30748, 31265, 31298.

Calvinaria albertensis feni n. subsp.

Plate II, figures 7-10; Figure 7B

Material. Holotype, GSC No. 14959. Escarpment member, 208 feet above base, Hay River formation, on Hay River, left bank, immediately below junction of Mills Lake road with Hay River highway, about 24½ miles above mouth of river, Northwest Territories. GSC loc. 30517; collector D. J. McL., 1957.

Paratype A, GSC No. 14960. A large specimen, front margin damaged. Same horizon and locality as holotype.

Paratype B, GSC No. 15201. Same horizon and locality as holotype.

Paratype C, GSC No. 15202. Same horizon and locality as holotype.

Paratype D, GSC No. 15203. Anterior part of specimen, remainder serial sectioned (illustrated, Figure 7B). Same horizon and locality as holotype.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	11.8	11.3	16.5	6.0	151°
Paratype A	(17.8)		25.6	9.4	153°
Paratype B	9.5	9.3	12.4	(4.3)	140°
Paratype C	7.6		8.8	3.4	112°
Paratype D (sectioned)	(14.4)		17.4	7.3	

¹This horizon may lie at the base of the Twin Falls formation (see Belyea and McLaren, 1962).

Description. Nearly every specimen in the collection is partly flattened and it is difficult to determine the full range in form and changes during growth. The shell resembles *C. albertensis albertensis* but differs in the hinge-line which is commonly straight and apical angle which is highly obtuse and appears to be about 150 degrees or more in larger specimens. The width/length ratio is greater and the thickness/length ratio less. The ornament is similar but possibly less pronounced, with a larger part of the posterior of the shell smooth. From two to five costae have been observed on the fold, with two being the most frequent; some shells are smooth. Costation on the flanks has not been observed. The beak, foramen, and interareas appear similar.

The internal structure is similar to that of *C. albertensis albertensis*, allowing for the proportionally reduced thickness. The shell near the beak is relatively thick but anteriorly it becomes very thin and fragile, and is nearly always broken.

About forty-five specimens at all stages of growth show that changes in proportion follow the normal pattern for the species, but the high width/length ratio and apical angle are apparent in all but the very smallest specimens.

Discussion. The more characteristic features of this subspecies are its straight hinge-line and obtuse apical angle. Better material may indicate that it is specifically distinct from *C. albertensis* but its similarity in general form and ornament warrant its inclusion in this species for the present. The shell bears some resemblance to *C. ambigua* (Calvin), from the Independence shale in Iowa, but the specimens illustrated by Stainbrook (1945) and the shells in a small collection from Iowa are all larger than any individual from Hay River.

The species is named from the Latin "fenum" hay, for Hay River, Northwest Territories.

Occurrence. The subspecies is known only from Hay River from the upper part of the Escarpment member, Hay River formation, GSC loc. 30517.

Calvinaria variabilis (Whiteaves)

The species has been well described by Whiteaves (1891, pp. 233-234) from Hay River, Northwest Territories. The description was based on a collection of a number of small individuals in a single block of shaly limestone made by R. G. McConnell who described their occurrence (1891, p. 70D). Additional collections from the same area have yielded specimens that vary more in size than those collected by McConnell and consequently the species merits redescription.

Two closely similar forms have been described from the Upper Devonian of the Alberta Rocky Mountains. These are *Leiorhynchus athabascensis* from the upper Flume formation and *Nudirostra insculpta* from the Perdrix formation. Careful consideration of growth series of these forms reveals a degree of overlap between them and *C. variabilis*. In each population, individual specimens occur that cannot be positively assigned to either species or separated from *C. variabilis*. Each form is however easily recognized in collections of several individuals and furthermore each has proved of stratigraphic significance in the Alberta Rockies.

Under these circumstances it is desirable that the names be retained to distinguish forms that are recognizably different and stratigraphically distinct although recognition must be accorded their close relationship to *C. variabilis*. *L. athabascensis* and *N. insculpta* are consequently designated subspecies of *C. variabilis*.

A fourth subspecies from the Alberta Rockies is described as new: *C. variabilis jobensis*.

The subspecies of *C. variabilis* differ from *C. albertensis*, which is equally widespread in Western Canada, primarily in the development of more complex ornament. Most specimens of *C. albertensis* have two simple rounded costae on the fold and the flanks are smooth. Bifurcation of the costae does occur occasionally but is longer delayed than in *C. variabilis*. Large specimens of *C. variabilis* are high with prominent vertical tongue, whereas *C. albertensis* tends to remain low, with a less prominent tongue, even in the largest specimens.

C. variabilis bears little resemblance to other species of *Calvinaria* so far described.

On Carcajou Ridge, Kindle in 1919 made a collection of small and medium-sized rhynchonelloids from soft grey to yellowish grey calcareous shale with limestone bands. These specimens, which bear a strong resemblance to *Calvinaria variabilis*, occur with an unusual *Emanuella*, a small *Productella*, and a thick-shelled *Schizophoria*.

Drs. H. Gordon Bassett and W. G. E. Caldwell of Shell Oil Company have made a similar collection on Carcajou Ridge near Lake Jan (personal communication). The associated fauna, in addition to the forms collected by Kindle, includes species of *Favosites*, *Paracyclas*, and *Schuchertella* and specimens of *Digonophyllum* (*Glossophyllum*?) *rectum* (Meek). This association suggests correlation with the upper Hume formation on Anderson River, and its age is probably Eifelian. A preliminary examination of the interior of the rhynchonelloid indicates that it is close to *Leiorhynchus* or *Calvinaria*, and may well be congeneric with the latter. From an isolated occurrence it is not yet possible or desirable to list similarities to or differences from Upper Devonian species of *Calvinaria*. The occurrence is recorded to draw attention to the existence of an Eifelian rhynchonelloid which, without further indications of age, would almost certainly be considered to belong to an Upper Devonian species. The species will be described in a later work.

Calvinaria variabilis variabilis (Whiteaves)

Plate III, figures 1-6; Figure 8B

1891. *Eatonia variabilis* WHITEAVES, pp. 233-234, Pl. XXIX, figs. 6, 6a, 7, 9; [non] figs. 8, 8a.

Material. Lectotype, GSC No. 4272. The specimen figured by Whiteaves (1891) on Pl. XXIX, figs. 6 and 6a, is selected as lectotype. This is not an average example of the species but from the numbering of the cotypes in the Survey collections it was plainly intended by Whiteaves to be the holotype. The locality is given by Whiteaves as "Hay River, forty miles above its mouth [collected] by R. G. McConnell, 1887". This locality, which is given by Whiteaves

for all of the species he describes from Hay River, is incorrect. The collections were made from the Escarpment member of the Hay River formation where it outcrops some 24 miles above the mouth of Hay River and for several miles downstream.

Syntype, GSC No. 4272b, figured by Whiteaves (1891) on Pl. XXIX, fig. 7.

Hypotype A, GSC No. 14927, a larger specimen from the McConnell collection.

Hypotype B, GSC No. 14928, Escarpment member, 16 feet above base, Hay River formation on Hay River, left bank, one third of a mile east of the junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, Northwest Territories. GSC loc. 31261; collector P. Harker, 1957.

Hypotype C, GSC No. 14929, same horizon and locality as hypotype B.

Hypotype D, GSC No. 14930, same horizon and locality as hypotype B.

Hypotype E, GSC No. 15207. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Figure 8B). Same horizon and locality as lectotype.

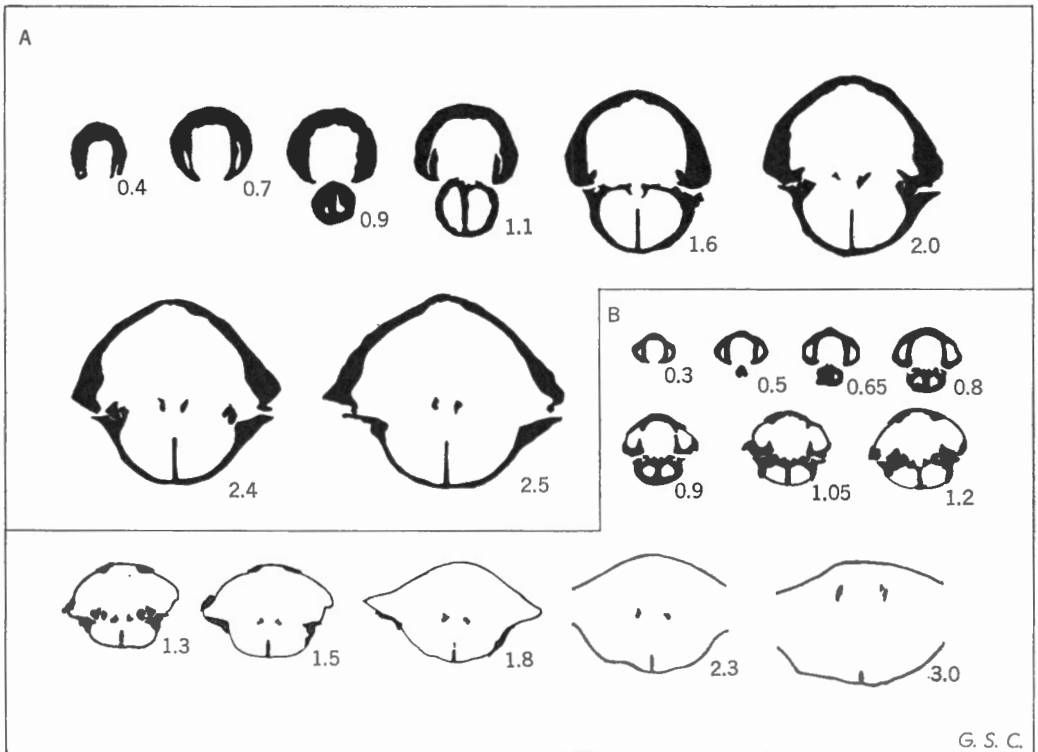
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Lectotype	11.9	11.7	14.6	6.8	122°
Syntype	12.2	11.2	14.6	6.1	127°
Hypotype A	14.7	13.8	16.7	7.6	127°
Hypotype B	13.4	12.8	15.0	7.2	120°
Hypotype C	16.4	15.7	24.3	12.8	143°
Hypotype D	19.2	18.3	27.0	15.0	139°
Hypotype E (sectioned)	12.5	11.5	15.3	8.2	132°

Description. Shell small to medium-sized for the genus, transversely sub-elliptical, width greater than length; hinge-line nearly straight in small specimens to straight in large; apical angle varies with size from about 120 to 140 degrees; lateral margins smoothly rounded, front margin truncate. Fold and sulcus costate, umbones smooth, flanks commonly costate. Anterior commissure uniplicate. Shell thin.

Pedicle valve strongly convex at umbo and smoothly curved longitudinally, shallow transversely with flanks nearly flat. Sulcus begins close to umbo and extends into broad and prominent tongue with widely flared margins, which is nearly vertical in large shells. The beak is suberect in small shells to strongly incurved in large. The interareas are narrow and the beak ridges weak. The small foramen extends onto the umbo by resorption of the beak. The deltidial plates are vestigial.

The brachial valve is convex with maximum height at the front margin in large shells. In smaller specimens the maximum height is near the middle of the shell. The fold is prominent anteriorly and truncated by the tongue of the pedicle valve. The beak is incurved below the pedicle beak.



G. S. C.

Figure 8A. *Calvaria ambigua* (Calvin). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype, GSC No. 15954; specimen with dimensions (in mm): length 18.8, width 27.0, thickness 12.9; from the Amana shale, Amana, Iowa.

Figure 8B. *Calvaria variabilis variabilis* (Whiteaves). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype E, GSC No. 15207.

The ornament consists of strong costae on the fold and sulcus that increase by bifurcation and become less prominent after division. Initially there are commonly two costae on the fold and one in the sulcus. The beaks are smooth. The flanks are weakly costate anteriorly, smooth posteriorly. There are fine close-set concentric growth lines on well-preserved specimens.

In the pedicle valve dental plates are well developed, parallel, becoming divergent anteriorly. They become detached dorsally at about where the teeth develop and continue forward a short distance as low ridges on the floor of the shell. The teeth are stout, rounded and recurved posteriorly. They are supported by the shell margin to the plane of articulation and persist forward as rectangular processes in contact with the inner socket ridges. A narrow undivided adductor track extends a short distance forward from the delthyrial cavity.

In the brachial valve the cardinalia consist of concave divided hinge plates supported to the plane of articulation by a stout medium septum which becomes increasingly long and slender forwards. The shallow rounded septalium may be

filled with secondary shell material. The hinge plates divide into prominent socket ridges and crural bases forward of articulation. The crura arise from bases bordering the septalium and are initially wedge-shaped, becoming slender descending curved laths which extend into the shell about one third of its total length.

Growth and Variation (40 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 11 mm		11 to 12.9 mm		13.0 to 14.9 mm		15 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.17	1.04-1.40	1.18	0.98-1.31	1.15	1.10-1.19	1.41	1.32-1.48
Thickness/length	0.49	0.45-0.54	0.54	0.46-0.62	0.57	0.52-0.65	0.77	0.69-0.80
Apical angle	107°	102°-117°	124°	120°-128°	124°	119°-132°	140°	135°-143°

Most of the specimens examined were collected by McConnell (Whiteaves, 1891) and show very little range in size. More recent collecting has added several specimens in the same size range, but only four examples with a length greater than 15 mm have been found.

Externally the most variable feature of the species is the costation of the fold, sulcus, and flanks; this was well stressed by Whiteaves. The costae on the fold arise close to the beak and are commonly two in number. Development may follow two distinct lines: (1) either or both of the initial costae may remain simple or bifurcate or trifurcate forwards; (2) a third and smaller costa may develop symmetrically between the other two, in which event the two outer costae seldom bifurcate. The costae on the flanks are usually simple and there is no correlation between their number and the number developed on the fold.

Variation in shape is not pronounced among specimens of about the same size; the proportionate heights and widths vary independently. In growth the thickness to length ratio increases with size.

Internally there appears to be some range of variation in structure. The lengths of the dental plates and of the median septum are not constant proportions of the length of the shell and their heights are dependent on the gibbosity of the shell near the beaks. The relative position at which the dental plates become detached from the hinge-teeth and the median septum from the hinge plates are not fixed.

Discussion. The specimen figured by Whiteaves (1891), Plate XXIX, figures 8 and 8a, is not conspecific with *C. variabilis*. It is probably a small specimen of *Calvinaria albertensis opima* which is found at the same locality.

Occurrence. The subspecies is known only from near the base of the Escarpment member of the Hay River formation on Hay River, near the junction of the Mills Lake road with Hay River highway. GSC loc. 5637, and 31261.

Calvinaria variabilis athabascensis (Kindle)

Plate IV, figures 3-8; Plate V, figures 1-3. Figure 9

1924. *Leiorhynchus athabascense* KINDLE, pp. 217-218, Pl. XIV, figs. 1, 2, 3.
 1931. [non] *Leiorhynchus athabascense* BURGESS, p. 197, Pl. I, fig. 2.
 1954. *Nudirostra athabascensis* (Kindle), McLAREN, p. 178, Pl. I, figs. 25, 26, 27.
 1956. *Nudirostra athabascensis* Kindle, WARREN and STELCK, Pl. XIV, figs. 20-25.
 1958. *Nudirostra athabascensis* (Kindle), McLAREN, Pl. VIII, figs. 4-10.

Material. Lectotype, GSC No. 5819. The specimen figured by Kindle (1924) on Plate XIV, figures 1 and 2 is chosen as lectotype. This is designated as holotype on the label with the specimen but Kindle made no mention of this in his original description. The locality printed in the description (p. 218) is "upper part of Banff limestone, on the north side of Folding Mountain, 1½ miles southeast of Sulphur Springs station, Jasper Park, Alberta" but in Kindle's own copy of the paper this is corrected in his handwriting to read ". . . on the north side of Roche à Perdrix, 1½ miles southeast of Miette Hot Springs station . . .". The specimen is very large and somewhat distorted with much of the right posterior margin broken away.

Syntype, GSC No. 5819a. The specimen figured by Kindle (1924, Pl. XIV, fig. 3); large distorted specimen with left posterior margin broken.

Hypotype A, GSC No. 14931. Upper few feet of upper Flume (Maligne) formation, near highway, Morro Peak, Jasper Park, Alberta. GSC loc. 16541; collector R. deWit, 1948.

Hypotype B, GSC No. 14932. Same horizon and locality as hypotype A.

Hypotype C, GSC No. 13820. Figured by McLaren (1958, Pl. VIII, figs. 8, 9, 10). Same horizon and locality as hypotype A.

Hypotype D, GSC No. 14933. Upper beds of upper Flume (Maligne) formation, saddle immediately south of Morro Peak, Jasper Park, Alberta. GSC loc. 17378; collector R. A. C. Brown, 1944.

Hypotype E, GSC No. 14934. Same horizon and locality as hypotype D.

Hypotype F, GSC No. 11232. Figured by McLaren (1954, Pl. I, figs. 25, 26, 27, and 1958, Pl. VIII, figs. 4-7). Same horizon and locality as hypotype A.

Hypotype G, GSC No. 14935. Escarpment member, basal bed, Hay River formation, on Hay River, left bank, one third of a mile east of the junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, Northwest Territories. GSC loc. 31275; collector P. Harker, 1957.

Hypotype H, GSC No. 15204. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figure 9). Same horizon and locality as hypotype D.

Dimensions (all measurements are in mm).

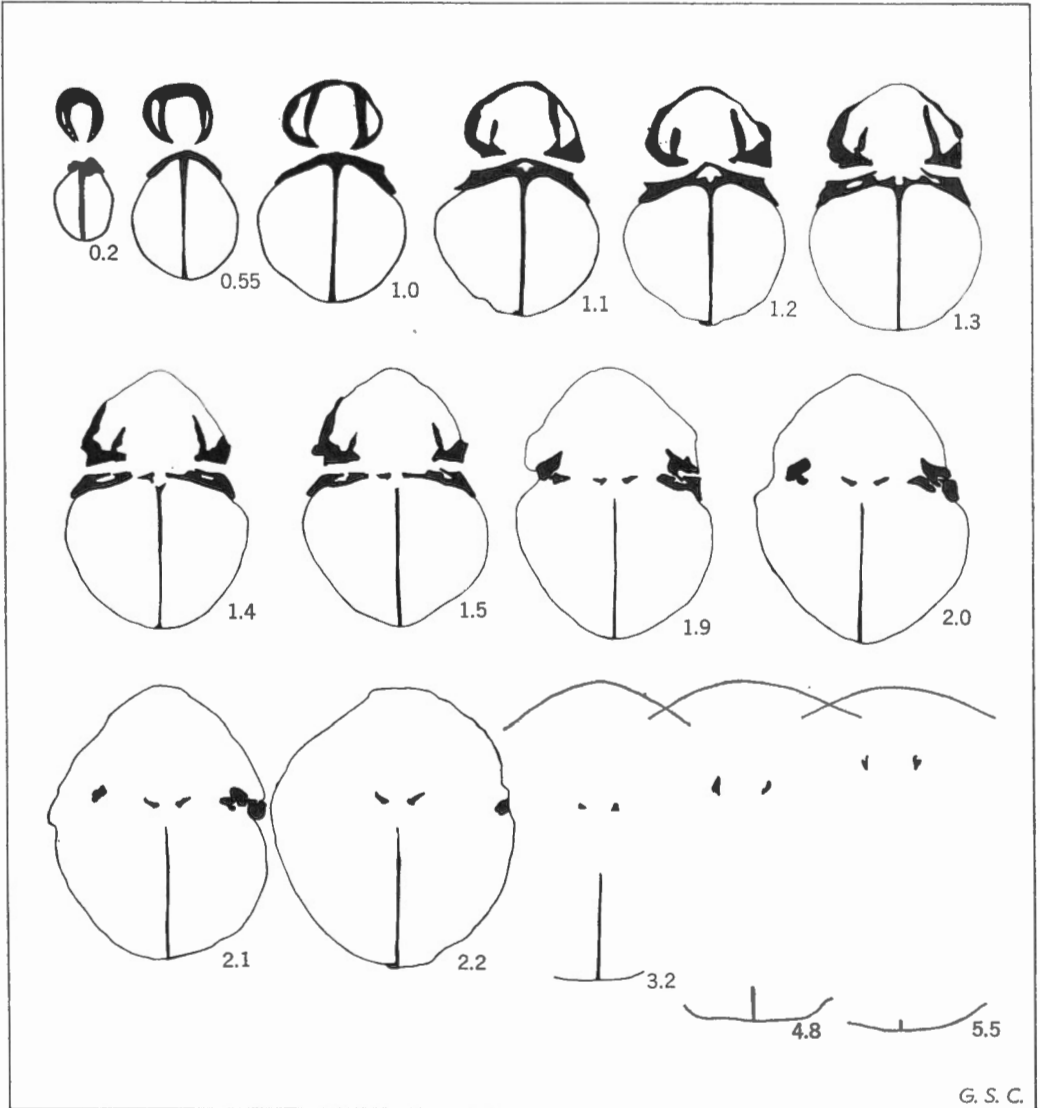
	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Lectotype	(33)		(50)	27	
Sytype	32	32	(42)	22.5	160°
Hypotype A	10.5	9.7	11.2	5.2	125°
Hypotype B	11.7	10.6	12.7	6.7	124°
Hypotype C	14.5	13.7	18.2	9.0	140°
Hypotype D	18.0	18.0	26.5	17.5	151°
Hypotype E	20.5	20.5	28.0	15.0	155°
Hypotype F	18.5	18.5	31.4	18.6	152°
Hypotype G	21.2	21.2	33.2	17.1	150°
Hypotype H (sectioned)	21.6		(27)	16.8	137°

Description. Shell medium to large size, differing from *C. variabilis variabilis* in attaining a greater maximum size with a more obtuse apical angle. The shell is proportionally thinner. The pedicle valve is more shallow, the convexity decreasing anteriorly and the lateral and postero-lateral margins almost flat. The tongue is high and flat. The brachial valve is strongly arched with curvature decreasing forwards; the fold is high and pronounced. The sides of the valve are steep and sinusoidally curved, flattening towards the lateral margin. In large specimens the postero-lateral slopes may become concave.

The ornament is less marked. The costae on fold and sulcus follow a similar development but are lower and more rounded. A larger part of the umbones is smooth. Costae on the flanks are much less common but traces are present near the anterior margin in some specimens.

Internally the differences from *C. variabilis variabilis* are partly the result of the greater convexity of the brachial valve near the beak, but internal plates and structures are thinner with less secondary shell growth even in large shells. In the pedicle valve an unusual early developmental stage of the dental plates was observed in sections of some shells. Close to the beak the dental plates appear as thin plates arising from the floor of the valve and curving inwards approximately parallel with the sides of the shell. Dorsally they are not joined to the shell directly, but each is supported by three slender, horizontal plates that lie between the sides of the shell and the dental plates near to their dorsal ends. These supporting plates do not persist, but coalesce upwards farther into the shell where the dental plates are joined directly to the dorsal margin of the valve.

In the brachial valve the cardinalia are similar but more slender, and the rounded cruralium consequently more open. The median septum is very long and thin, as a consequence of the height of the valve.



G. S. C.

Figure 9. *Calvinaria variabilis athabascensis* (Kindle). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype H, GSC No. 15204.

Growth and Variation (30 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 16.0 mm		16.0 to 17.9 mm		18.0 to 19.9 mm		20 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.22	1.07-1.39	1.33	1.24-1.47	1.39	1.32-1.70	1.40	1.20-1.54
Thickness/length	0.60	0.50-0.74	0.73	0.64-0.97	0.80	0.67-1.00	0.76	0.69-0.83
Apical angle	130°	119°-142°	142°	129°-148°	151°	132°-157°	152°	137°-160°

The collections include specimens at all stages of growth from a length of 10.5 mm upwards. The height and shape of the fold is one of the most variable features of the subspecies, the extremes being from relatively low and broad to high and rounded. The costae are markedly irregular. In some specimens the three first formed on the fold remain large and merely put off small branches anteriorly. In others, two initial costae branch equally to form up to about nine at the front margin of equal size and regularity. Kindle's types are unusually large and no other specimens of their size have been collected in the region.

Discussion. The subspecies occurs in black argillaceous limestones and calcareous mudstones suggestive of deeper water and more tranquil bottom conditions than obtained for *C. variabilis variabilis*. To this may be attributed the thinner shell and more slender cardinalia and internal plates. The unusual lateral supports for the developing dental plates are seen only in especially thin-shelled specimens. It is not considered likely that this structure has any intrinsic taxonomic significance but may be either a feature present in the whole species group, but not normally seen, or possibly a modification only developed in thin-shelled forms and a direct response to a special environment. No other morphological features in the subspecies suggest that it should be separated from the *C. variabilis* group.

Leiorhynchus athabascense Burgess (1931) is not readily recognized from Burgess' plate or description but is with little doubt different from Kindle's species. Burgess subsequently recognized that the name was a homonym and renamed his species *L. jasperensis* (1932).

Occurrence. The subspecies occurs widely in the Front Ranges of the Alberta Rocky Mountains from North Saskatchewan River to beyond Athabasca River, in the upper Flume or Maligne formation and in the basal beds of the Perdrix. Specimens have been examined from many localities including: GSC loc. 16541, 17378, 18889, 19608, 24171, 36853, 36868, 41896.

The subspecies has been collected on the east side of the Rocky Mountain Trench in southern British Columbia in Fernie map-area, west half, from beds low in the Fairholme group; GSC loc. 38964.

It occurs also in the Hay River section in the basal bed of the Escarpment member, Hay River formation; GSC loc. 31275.

The species has been collected from subsurface cores in Alberta and Saskatchewan at GSC localities 20135, 20198, 21288, 24588, 26810, 26819.

Calvinaria variabilis inculpta (McLaren)

Plate III, figures 7-10; Plate IV, figures 1, 2. Figure 10

1954. *Nudirostra inculpta* McLAREN, p. 178, Pl. I, figs. 22, 23, 24.

1958. *Nudirostra inculpta* McLAREN, Pl. VII, figs. 25, 26, 27.

Material. Holotype, GSC No. 11245. Figured by McLaren (1954 and 1958). Perdrix formation, 25 feet above base of outcrop, ridge on south side of Winnifred Pass (latitude 53°40', longitude 119°15'), Alberta. GSC loc. 19908; collector D. J. McL., 1951.

Hypotype A, GSC No. 14936. A small specimen showing ribbing at an early stage. Talus from Perdrix formation, 40 feet above base, Job Creek, eastern fault block (unit 11 in McLaren, 1956, p. 57), Alberta. GSC loc. 35520; collector D. J. McL., 1953.

Hypotype B, GSC No. 14937. Perdrix formation, in place, same horizon and locality as hypotype A. GSC loc. 24169.

Hypotype C, GSC No. 14938. A specimen closely similar in form to *C. variabilis variabilis*. Black shale and argillaceous dolomite member in upper part of Cairn formation, 600 feet above base, Front Range at Red Deer River gap, north side, (section 13 in McLaren, 1956), Alberta. GSC loc. 37833; collector D. J. McL., 1953.

Hypotype D, GSC No. 14939. A strongly sculptured specimen showing mode of bifurcation of ribs on fold and sulcus. From "top of *Martinia* zone, about 600 feet down from top of Fairholme in Nigel Peak Section" (section I in Severson, 1950), Sunwapta Pass area, Alberta. GSC loc. 35519; collector J. L. Severson, 1949.

Hypotype E, GSC No. 14940. Same horizon and locality as hypotype B.

Hypotype F, GSC No. 15208. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Figure 10). Same horizon and locality as hypotype B.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	17.4	15.7	25.6	15.8	128°
Hypotype A	8.3	7.9	10.4	6.3	124°
Hypotype B	11.0	10.7	13.5	7.9	133°
Hypotype C	12.6	12.2	16.4	7.3	144°
Hypotype D	(14.4)		18.6	11.1	136°
Hypotype E	15.9	15.5	22.9	11.4	147°
Hypotype F (sectioned)	(15.8)		20.6	13.6	137°

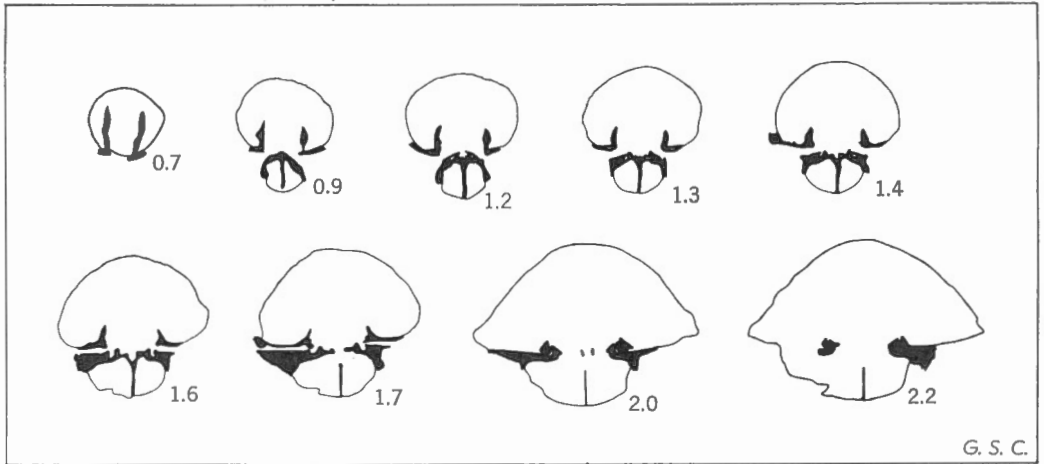


Figure 10. *Calvinaria variabilis insculpta* (McLaren). Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; hypotype F, GSC No. 15208.

Description. Shape, and size range is similar to *C. variabilis variabilis*, but proportionally wider and more inflate at all stages of growth; the apical angle tends to be greater. The ornament develops in a similar way but is more marked, costae are higher and more angular and the intervening furrows more impressed. The flanks, fold, and sulcus are commonly fully costate with the exception of a small smooth area on the umbones.

Internally the dental plates are similar in form to those of *C. variabilis variabilis* but are very weakly developed, the teeth are supported by the shell margin. The cardinalia tend to be relatively slender and the cruralium is moderately deep and prominent. There is little deposition of secondary shell material. The crura are not known.

Growth and Variation (30 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 11 mm		11.0 to 12.9 mm		13.0 to 14.9 mm		15 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.31	1.23-1.40	1.34	1.21-1.41	1.41	1.27-1.47	1.42	1.31-1.50
Thickness/length	0.68	0.58-0.76	0.70	0.55-0.85	0.77	0.59-0.90	0.83	0.70-0.91
Apical angle	134°	124°-144°	136°	122°-142°	143°	130°-149°	141°	128°-147°

Owing to poor preservation only thirty specimens were sufficiently complete to measure but about another sixty specimens among the collections display characteristic features of the subspecies. As with other subspecies in the *C.*

variabilis species group, the ornament is the most variable feature. The costation of the fold and sulcus follows the same pattern of development as *C. variabilis* but from their inception the costae are strongly impressed and do not weaken after bifurcation. Those on the flanks of the shell are commonly equally strong and may bifurcate also. The ratio of the thickness to the length of the shell is also highly variable and the tongue is vertical or even recurved in the most inflated shells.

As with the other subspecies, variation in the interior appears to be related largely to shell shape. Secondary thickening on the cardinalia was not observed.

Discussion. The subspecies approaches *C. variabilis athabascensis* more closely in form and proportions than *C. variabilis variabilis* but is readily separated by the deeply impressed ornament which is apparent even in very small specimens.

Occurrence. The subspecies is widespread throughout the Front Ranges of the Alberta Rocky Mountains from Red Deer River to Smoky River, in the Perdrix formation or shaly beds within the upper part of the Cairn formation. It occurs at a similar horizon in the Fairholme group as far west as Sunwapta Pass. The lowest part of its range overlaps *Calvinaria variabilis athabascensis* which extends into the lower part of the Perdrix or where the upper Flume or Maligne formation thickens at the expense of the Perdrix. The highest part of its range overlaps the lower occurrences of *C. albertensis albertensis*. Specimens have been examined from the GSC localities 19908, 19910, 24169, 24181, 25170, 25194, 35519, 35520, 36868, 37833.

The species is widespread in the subsurface of Alberta and has been collected from cores from GSC localities 20111, 20346, 20354, 22582, 22623, 22647, 22677, 24221, 26811, 28110.

Calvinaria variabilis jobensis n. subsp.

Plate V, figures 4-6; Figures 11A, B

1956. *Nudirostra athabascensis* (Kindle), McLAREN, p. 57.

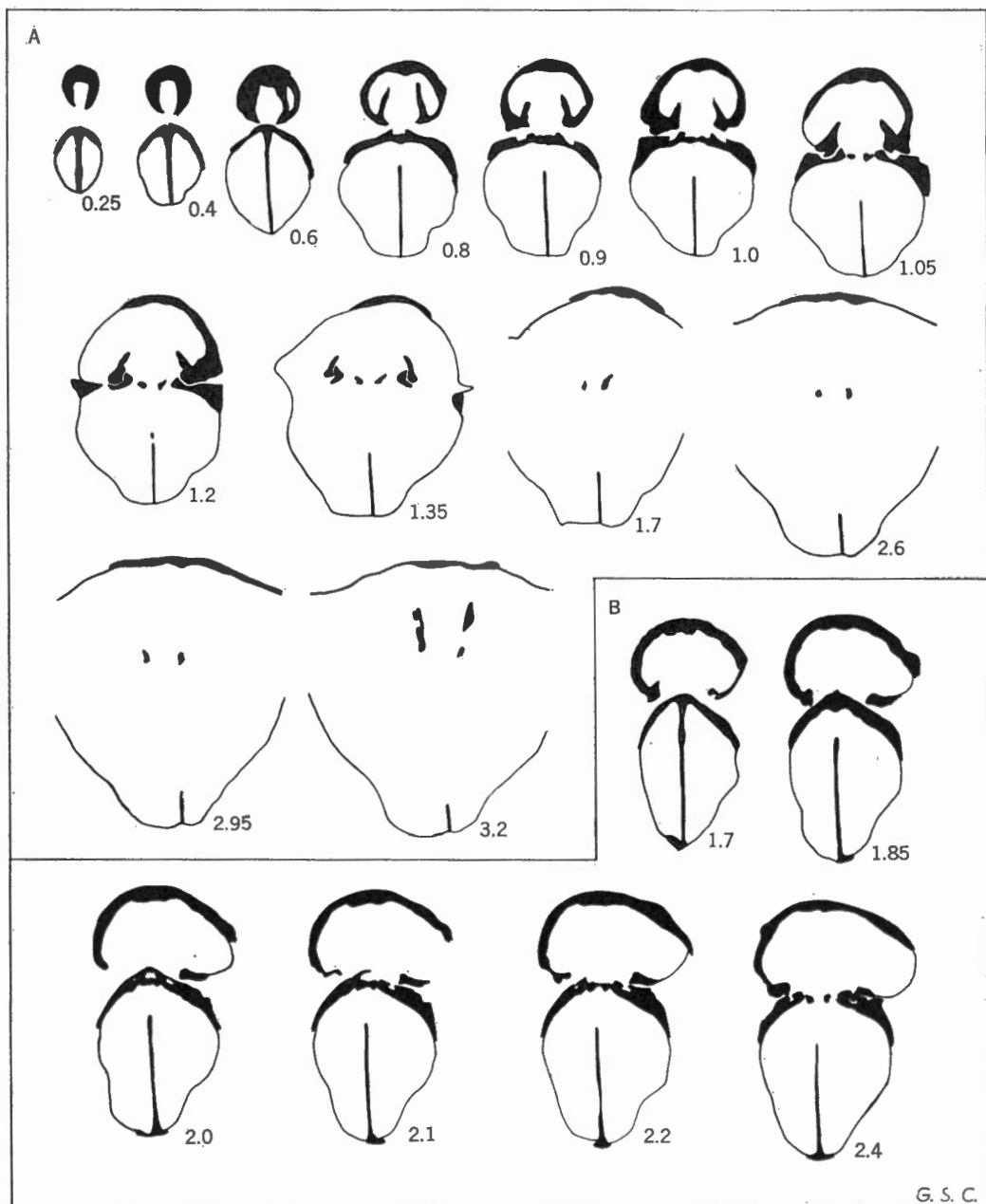
Material. Holotype, GSC No. 14941. Perdrix formation, 4 feet above base, Job Creek, eastern fault block (unit 11 in McLaren, 1956, p. 57), Alberta. GSC loc. 24180; collector D. J. McL., 1953.

Paratype A, GSC No. 14942. Same horizon and locality as holotype.

Paratype B, GSC No. 14943. Same horizon and locality as holotype.

Paratype C, GSC No. 15209. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 11A). Same horizon and locality as holotype.

Paratype D, GSC No. 15210. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 11B). Same horizon and locality as holotype.



G. S. C.

Figures 11A,B. *Calvinaria variabilis jobensis* n. subsp. Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; 11A, paratype C, GSC No. 15209; 11B, paratype D, GSC No. 15210.

Dimensions (all measurements are in mm).

	Length of		Width	Thickness	Apical Angle
	Length	Brachial Valve			
Holotype	17.2	17.2	24.8	17.0	150°
Paratype A	12.1	11.9	15.1	7.3	144°
Paratype B	17.2	17.2	19.9	17.3	136°
Paratype C (sectioned)	16.7	16.7	22.5	15.8	146°
Paratype D (sectioned)	16.9	16.9	21.2	17.1	125°

Description. The shell is similar in form to *C. variabilis athabascensis* but considerably more inflate in all but the smallest specimens. The height is approximately equal to the length. The tongue is high and vertical to recurved; in some shells its maximum width is nearly equal to the width of the shell. The brachial valve is very strongly arched with the flanks very steep, the fold is prominent from close to the beak.

The ornament is similar, with weak rounded costae on fold and sulcus which increase by bifurcation up to a maximum of nine on the fold at the front margin. The flanks of the shell show very weak but persistent costation. The shell is very thin and commonly exfoliated.

Internally the pedicle valve is closely similar to *C. variabilis athabascensis*. Lateral supports between the developing dental plates and the side of the valve were noted in one of the individuals sectioned. The dorsal interior, however, is different. The long thin median septum becomes detached from the hinge plates at a very early stage. The hinge plates are joined axially and divided only by a shallow furrow. They separate posterior to the plane of articulation and break up into crural bases and socket ridges which persist into the shell in contact with the teeth as in *C. variabilis athabascensis*, the interior of which it resembles in all other respects.

Growth and Variation (16 specimens). The collection contains specimens at all stages of growth from a length of 12.1 to 18.8 mm. The ratio of width to length remains approximately constant in shells with a length of 14 mm upwards, the mean being 1.39. The ratio of thickness to length increases from about 0.70 in the smaller shells to a mean of 0.98 in the larger. In some specimens the thickness is greater than the length.

The ornament is variable as with the other subspecies of *C. variabilis*. The width of the tongue is highly variable and ranges from less than half to nearly equal to the shell width. In some shells it is recurved posteriorly where it meets the anterior commissure.

Discussion. The bizarre character of the cardinalia of this subspecies might lead to the conclusion that these shells belong to a different species or even genus from *C. variabilis*, and that their similarity to *C. variabilis athabascensis* is a case of homeomorphy. This is not considered likely, however, as the similarities of both external form and ornament and internal structure are otherwise too close to be

explained away in this manner. It seems probable that the unusual height of the brachial valve, coupled with the slender shell and cardinalia have led to a morphological modification which is not of great taxonomic significance.

Sections show that the hinge plates are essentially similar to those normally found in *C. variabilis*. After the septum has become detached, a thin growth inwards from the crural bases unites them. It is not possible to determine if this growth corresponds to an "inner hinge plate" attached to each crural base, but it appears to be a single plate continuous with the "outer hinge plates" and presumably had the same function for muscle attachment as the cruralium in more normal shells. Subsequent development forward into the shell is normal. The crural bases are separated axially and become detached from the socket ridges in a manner precisely similar to that of *C. variabilis athabascensis*. This might be considered a good example of the plasticity of form possible among rhynchonelloids and may be an adaptation to a special environment.

Although the subspecies is known only from one collection it is worth naming and describing because of the unusual development of the cardinalia.

The species is named after Job Creek, Alberta.

Occurrence. The subspecies is known only from the basal beds of the Perdrix formation, at Job Creek; GSC loc. 24180.

Genus *Cassidirostrum* McLaren, 1961

Type species: Cassidirostrum pedderi McLAREN, 1961, pp. 2-3, Pl. I, figs. 1-3.

Diagnosis. Medium-sized, uniplicate rhynchonelloids, subpentagonal in outline; inflate brachial valve; width and length approximately equal; greatest thickness at or forward of mid-length. Pedicle valve shallow, sulcus begins forward of mid-length, weakly developed; tongue broad, flattened, vertical to recurved. Beak prominent, erect to strongly incurved; large concave interareas and strong beak ridges. Brachial valve high, domed, with steep lateral slopes. Fold begins forward of mid-length, inconspicuous. Shell wholly costate; costae angular, simple, very rarely bifurcate, interspaces V-shaped. Anterior and antero-lateral commissures crenulate.

Teeth supported by slightly divergent dental plates nearly to plane of articulation. Muscle impressions small, oval, lightly impressed. Hinge plates stout, septalium shallow; septum duplex, stout, supports septalium to plane of articulation. Heavy secondary growth almost fills septalial cavity; a plug of secondary material fills septalium and extends ventrally over crural bases in mature shells. Crural bases deeply enclosed in shell. Crura round proximally, slender, trough-shaped distally. Adductor impressions narrow and long.

Discussion. The distinguishing characters of the genus *Cassidirostrum* are: (1) the inflate uniplicate shell with strong angular costae; (2) the stout hinge plates with shallow open septalium and strong septum; (3) the heavy secondary

thickening of the cardinalia which fills the septalial cavity and may extend ventrally over the deeply enclosed crural bases.

Cassidirostrum resembles many forms of brachiopods loosely assigned to *Camarotoechia* Hall and Clarke, 1894. *C. congregata* (Conrad, 1841), the type species, however, as presently understood, possesses a deep covered septalium. *Nekhoroshevia* Bublichenko, 1956 also differs in possessing a covered septalium. *Ferganella* Nikiforova, 1937 differs in the undivided hinge plates with a "septal process" inside the septalial cavity. *Machaeraria* Cooper, 1955 possesses a cardinal process and lacks a median septum. The genera *Obturamentella* Amsden, 1958 and *Glossinotoechia* Havlíček, 1959 both possess plugs of shell material filling the septalium in a marked degree but differ considerably from *Cassidirostrum* in their shell form and in other features of their interiors. Other genera which may bear a superficial resemblance to *Cassidirostrum* possess marked differences in ornament, e.g. costae grooved on the interior at the front margin, as well as differing in internal structure.

The only species referred to *Cassidirostrum* is the type — *C. pedderi*, which is known only from the area of the Anderson River and its tributaries, Northwest Territories. Its age is early late Middle Devonian (early Givetian).

The genus is named from the Latin "cassida" a helmet, and "rostrum" a beak.

Cassidirostrum pedderi McLaren

Plate VI, figures 1-6; Figures 12, 13, 14A, B

1867. *Rhynchonella*, (sp. undt.) MEEK, p. 94, Pl. XIII, figs. 10a, b.

1961. *Cassidirostrum pedderi* McLAREN, pp. 2-3, Pl. I, figs. 1-3.

Material. Holotype, GSC No. 15350. Calcareous shale and shaly limestone in the lowest 15 feet of the Hare Indian formation, Anderson River, between latitude 68°28' and 68°32' and longitude 127°04' and 127°24', Northwest Territories. GSC loc. 41319; collector A. E. H. Pedder, Triad Oil Company Limited, 1959.

Paratype A, GSC No. 15351. "Interbedded shale and nodular limestone, lower Ramparts formation", Andrew River, latitude 68°20', longitude 128°56', Northwest Territories. GSC loc. 41327; collector G. V. Lloyd, J. C. Sproule and Associates, 1959.

Paratype B, GSC No. 15352. "lower Ramparts formation, 0 to 3 feet below top of formation", Andrew River, latitude 68°08', longitude 128°33', Northwest Territories. GSC loc. 41083; collector G. P. E. White, J. C. Sproule and Associates, 1959.

Paratype C, GSC No. 15353. Same horizon and locality as holotype.

Paratype D, GSC No. 15354. Same horizon and locality as holotype.

Paratype E, GSC No. 15355. Internal mould; shell removed to show internal structure. Same horizon and locality as holotype.

Rhynchonelloid Brachiopods from Western Canada

Paratype F, GSC No. 15356. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figs. 12, 14A). Same horizon and locality as holotype.

Paratype G, GSC No. 15357. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figs. 13, 14B). "lower Ramparts formation" (?), Anderson River, Northwest Territories. GSC loc. 39480.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	19.8	18.6	19.1	14.3	104°
Paratype A	22.2	21.7	23.4	18.2	118°
Paratype B	21.1	20.2	21.2	19.5	104°
Paratype C	20.6	19.0	19.8	18.3	109°
Paratype D	19.0	17.7	19.3	13.6	109°
Paratype E (interior)	20.7	19.5	21.6	15.1	108°
Paratype F (sectioned)	18.6	17.2	18.4	13.5	106°
Paratype G (sectioned)	20.0	18.3	19.4	18.4	93°

Description. Shell of medium size, subpentagonal in outline with rounded antero-lateral margins; high, uniplicate; width and length approximately equal, greatest width at or forward of mid-length; greatest thickness at or forward of mid-length; hinge-line angle greater than 90 degrees; apical angle about 110 degrees. Shell strongly costate.

The pedicle valve is shallowly convex, with greatest curvature on the umbo, decreasing anteriorly. The sulcus begins at about mid-length and is shallowly concave or flat bottomed; in inflate shells it scarcely develops. It extends forwards into a broad flattened tongue which is vertical to slightly recurved in most shells; its crest is gently arched and strongly crenulate. The beak is prominent, erect to strongly incurved. The interareas are wide and concave and marked with fine growth-lines; the beak ridges are prominent. The foramen is probably small and submesothyrid or mesothyrid. The delthyrium is open, flanked by discrete triangular deltidial plates.

The brachial valve is high and domed with steep lateral slopes that become vertical in inflate shells. The fold begins forward of mid-length and is inconspicuous on inflate shells. The antero-lateral sides of the fold are smooth. The beak is incurved.

The shell is ornamented with strong, angular, simple, costae; the interspaces between costae are V-shaped. Costation begins at the beak but is faint on the umbones and is commonly worn off in the specimens in the collection. There are from five to nine costae on the fold, commonly six or seven, and between seven and twelve on each flank. Very rarely a costa may bifurcate near the front of the fold or two costae may merge on the lateral slopes of the fold. The costae alternate between valves and produce strongly crenulate front and antero-lateral commissures. Some well-preserved shells show very weak flattened costellae super-

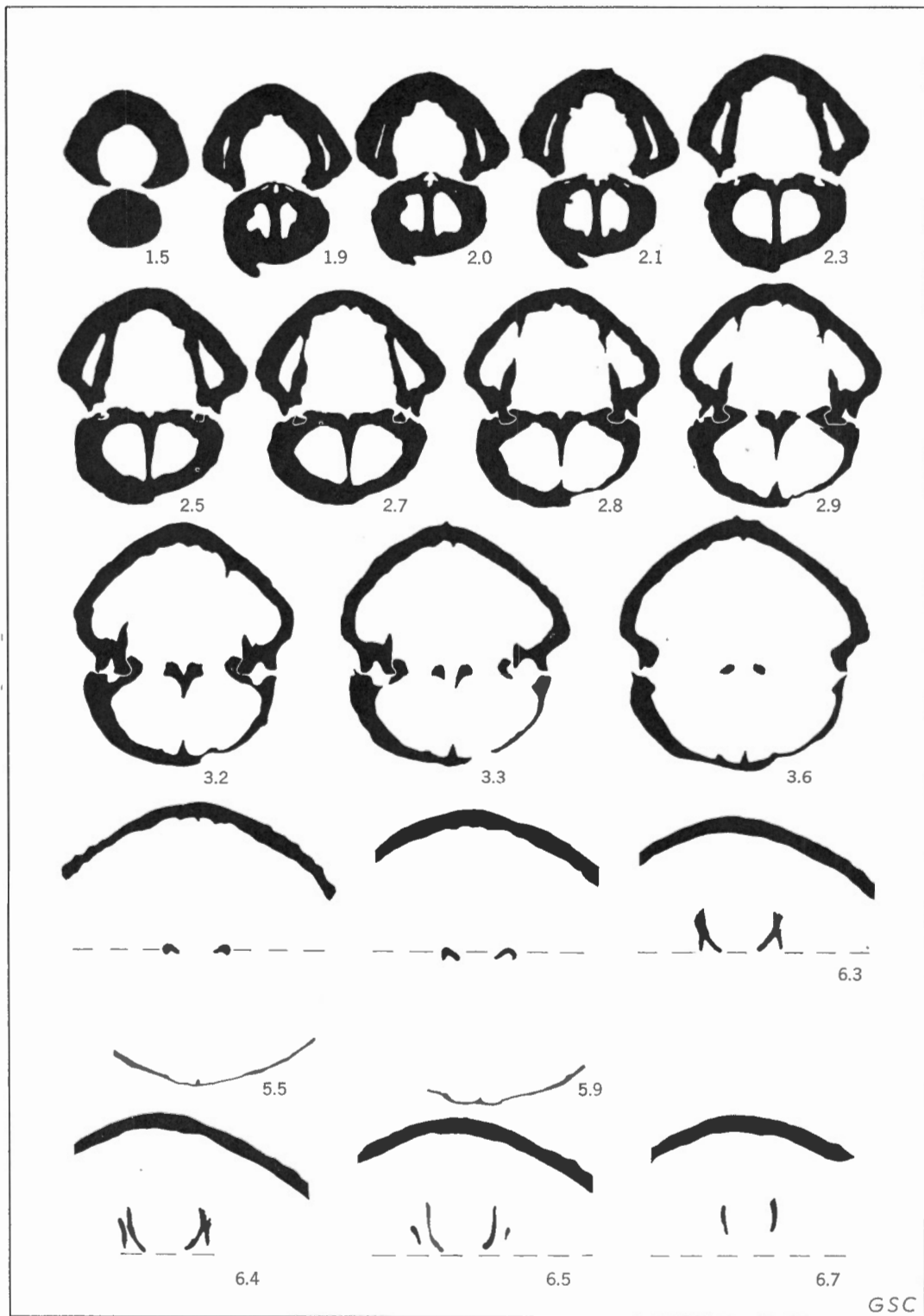


Figure 12. *Cassidirostrum pedderi* McLaren. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; paratype F, GSC No. 15356.

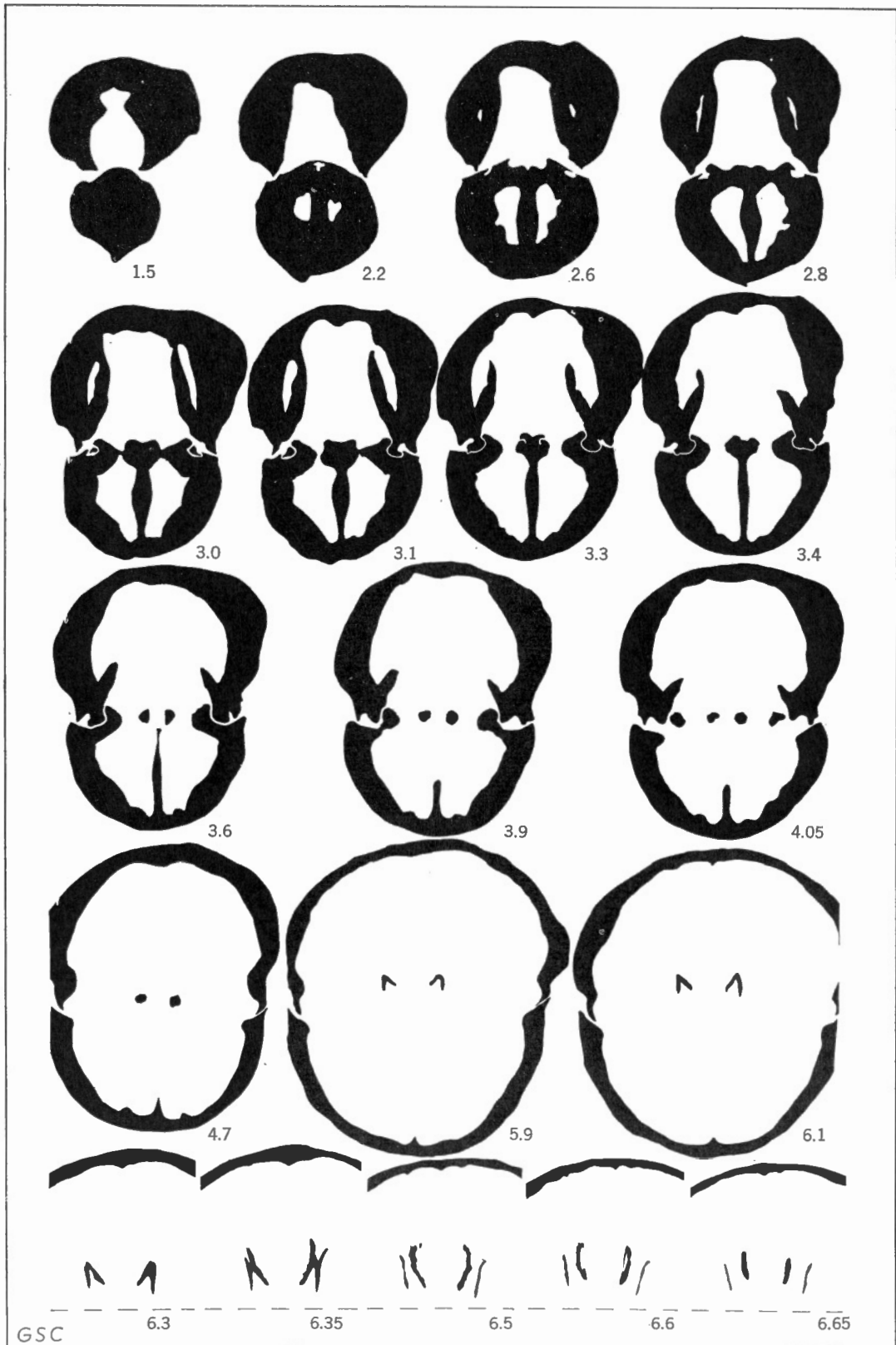
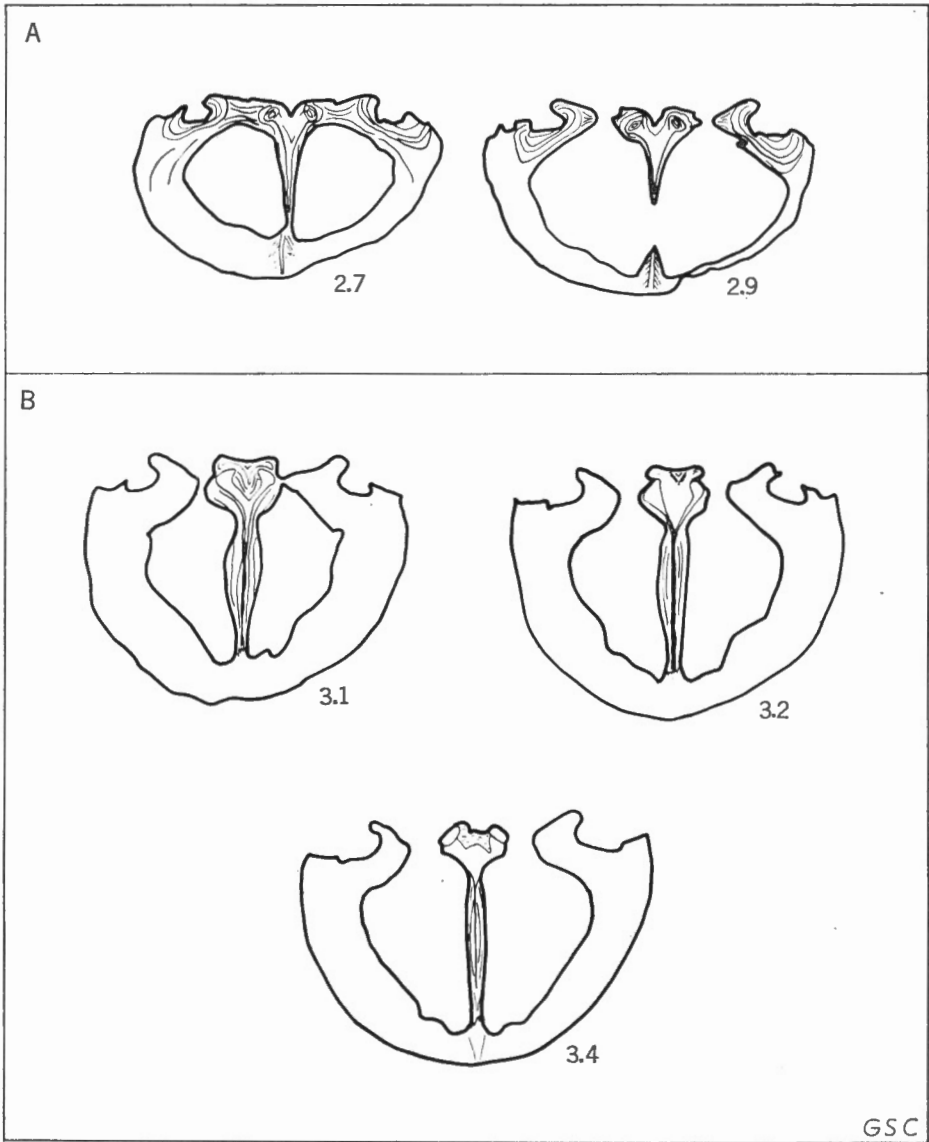


Figure 13. *Cassidirostrum pedderi* McLaren. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; paratype G, GSC No. 15357.



Figures 14 A, B. *Cassidirostrum pedderi* McLaren. Camera lucida drawings of serial transverse sections of brachial valves to show details of construction of the cardinalia $\times 5$; distances are in mm forward from the crest of the umbo; 14A, paratype F, GSC No. 15356; 14B, paratype G, GSC No. 15357.

imposed on the coarser costation and fine concentric growth-lines which become close-set at the front margin.

In the pedicle interior there are strong, slightly divergent dental plates that are in contact with the floor of the valve almost up to the plane of articulation. The delthyrial cavity is wide; the lateral cavities are more narrow and may be

filled with secondary shell material. The teeth are moderately developed and outwardly curved with a narrow neck. A U-shaped groove runs parallel with the teeth, between them and the margin of the shell. The muscle impressions are small, oval-shaped and lightly impressed. Costae are strongly marked on the interior. Pallial markings were not observed.

The cardinalia broadly resemble those of *Leiorhynchus*. The hinge plates are stout and the septalium is shallow. A stout septum supports the septalium to the plane of articulation where the hinge plates break into stout inner socket ridges and crural bases. The septum is duplex and bifurcates to form the septalium, the distal ends of which form the crural bases. Shell growth around the cardinalia obscures the true form of the septalium, filling the septalial cavity almost completely and deeply enclosing the crural bases. In mature shells a plug of secondary material fills the septalium completely and extends laterally over the crural bases. The crura are stout and round proximally, becoming slender and trough-shaped distally. They plunge vertically towards the ventral valve at their extremities. The adductor impressions are narrow and long; they extend over half the length of the shell. The septum persists as a low ridge to their anterior ends. Pallial markings were not observed.

Growth and Variation (31 specimens).

Changes in mean proportion during growth:

	Length					
	Less than 20 mm		20.0 to 21.9 mm		22 mm and more	
	mean	range	mean	range	mean	range
Width/length	1.03	0.97-1.12	1.04	0.91-1.26	1.01	0.92-1.09
Thickness/length	0.80	0.62-1.00	0.83	0.73-0.93	0.77	0.68-0.82
Apical angle	108°	101°-115°	106°	93°-121°	108°	102°-122°

The smallest specimen in the collections has a length of 18.3 mm, the largest 23.8 mm. Young and immature individuals are therefore unknown. Within the size range represented there are no significant changes in proportions of the shell. Both the width/length and thickness/length ratios show a range in variation normal in rhynchonelloids. The species does not appear to be greatly variable in other respects, but as all specimens come from the same area and occur in rocks of similar lithology the full potential of variation may not be realized.

Discussion. Small specimens of *C. pedderi* show a superficial resemblance to large specimens of a camarotoechiid that occurs widely in the late Middle Devonian Bird Fiord formation on Bathurst Island. This species was identified and figured by Meyer (1913) as "*Rhynchonella (Wilsonia) princeps* Barrande". Sections reveal a wide, deep, trigonal septalium with a strong covering plate that

supports a stalked Y-shaped cardinal process. The species may belong to an undescribed genus but is quite unrelated to *Cassidirostrum*.

The specimen figured by Meek (1867, Pl. XIII, figs. 10a, b) as "*Rhynchonella* (sp. undt.)" is preserved in the U.S. National Museum (No. 24424). It is a typical although slightly damaged specimen of *C. pedderi*. Meek's figures of this specimen show a greater resemblance to his species *Leiorhynchus castanea* with which it occurs than is in fact the case. The locality is given as "Lockhart River, lat. 67 deg. 15 min. N., long. 126 deg. W." but the coordinates are incorrect. Lockhart River is now known as Carnwath, a tributary of Anderson River, consequently Meek's specimen is from the same area and presumably the same horizon as the collections described here.

The species is named for A. E. H. Pedder of Triad Oil Company Limited, Calgary.

Occurrence. The species is known only from Anderson River and its tributaries, the Carnwath (=Lockhart) and Andrew. It occurs in beds variously described as highest Hume and basal Hare Indian or top lower Ramparts and lowest middle Ramparts. It is associated throughout this area with *Leiorhynchus castanea*. Specimens have been examined from GSC localities 39480, 41076, 41083, 41319, 41327.

Genus *Hadrorbynchia* McLaren, 1961

Type species: *Pugnoides sandersoni* WARREN, 1944, pp. 115-116, Pl. II, figs. 5, 6.

Diagnosis. Medium to large, uniplicate rhynchonelloids, subpentagonal to transversely elliptical; inflate brachial valve; greatest thickness forward of mid-length. Pedicle valve shallow, tongue broad and prominent, vertical to recurved; lateral margins of valve bent dorsally, raising the lateral commissure. Beak suberect to erect, large interareas and prominent beak ridges. Brachial valve high, fold inconspicuous, but bent down anteriorly to meet tongue at commissure below the crest of the shell. Shells costate anteriorly, umbones smooth; costae broad and rounded, never bifurcate. Where costae on fold bend downwards to meet anterior commissure they are thickened at point of inflexion. Near commissures, anterior and lateral, costae are flattened, and interspaces between them strongly ridged on interior of shell. Some shells covered with fine, flattened, branching costellae.

Teeth supported by widely spaced dental plates; lateral cavities narrow. Hinge plates in brachial valve divided proximally by small U-shaped septalium but filled anteriorly by two broad rounded longitudinal ridges developed on the inner part of each hinge plate, separated by a narrow V-shaped median groove. Septum slender and in contact with hinge plates to plane of articulation; beyond, the hinge plates are discrete and flat; crura arise from their inner margins. Crura vertical flattened lamellae anteriorly, plunging ventrally, and slightly recurved; dorsally grooved with lateral projection on each external surface anteriorly.

Discussion. The distinguishing characters of the genus *Hadorrhynchia* are: (1) the dorsal geniculation of the ventro-lateral slopes of the pedicle valve and the downward bending of the fold at the front margin of the brachial valve; these features having the effect of raising the lateral commissures above the ventro-lateral margins of the pedicle valve and depressing the anterior commissure below the crest of the brachial valve; (2) the flattened costae in the vicinity of the anterior and lateral commissures and the narrow ridging in the interspaces between costae in shell interior; (3) the longitudinal ridges developed at the inner margins of the hinge plates that prevent the formation of a true septalium except proximally; (4) the vertically flattened, recurved lamellae of the forward part of the crura.

Hadorrhynchia may be differentiated from many rhynchonelloid genera with somewhat similar external form on the basis of the modifications to its ornament at the front and lateral margins of the shell. The depression of the costae and internal ridging of the interspaces for a short distance above and below the commissure suggest development of marginal spines, although none has been seen. *Sphaerirhynchia* Cooper and Muir-Wood 1951 possesses spines formed by out-growths from the anterior and antero-lateral shell margins. The genus differs from *Hadorrhynchia*, however, in general external form and in possessing a "roofed-over cruralium" (see Amsden, 1958, p. 95). *Uncinulus* Bayle 1878, another form with marginal spines, possesses a well-developed cardinal process. Mailleux described the genus *Straelenia* (1935, p. 10) as possessing an entire hinge plate without a cardinal process, but with a median furrow and bounding ridges. Schmidt (1955, pp. 115-7) described the interior of the genus and referred to a rounded elevation in the centre of the hinge plate; in this it resembles *Dinapophysia* Mailleux 1935, which Schmidt placed in subjective synonymy with *Straelenia*. The interior of *Straelenia* as described by Mailleux may bear some resemblance to *Hadorrhynchia*, but not as described by Schmidt. The external ornament of Mailleux's genus is multicostate and the shell shallow with poorly defined fold, sulcus, and tongue; there is no mention of grooving at the front margin. These features are sufficient to distinguish the two genera.

The only species referred to *Hadorrhynchia* is the type — *H. sandersoni*, from beds of late Middle Devonian age (Givetian) of Great Slave Lake and Mackenzie River areas.

The genus is named from the Greek "hadros" stout, strong, and "rhynchos" a beak.

Hadorrhynchia sandersoni (Warren)

Plate VII, figures 1-7; Plate VIII, figures 1-3. Figures 15, 16

1867. *Rhynchonella*—? MEEK, p. 95, Pl. XV, fig. 4.
1944. *Pugnoides sandersoni* WARREN, pp. 115-116, Pl. II, figs. 5, 6.
1956. *Pugnoides sandersoni* Warren, WARREN and STELCK, Pl. VIII, figs. 16-21.
1961. *Hadorrhynchia sandersoni* (Warren), McLAREN, pp. 3-4, Pl. I, figs. 4, 5.

Material. Here chosen as lectotype, U. of A. syntype Dv853-2. Figured by Warren (1944, Pl. II, fig. 5) and by Warren and Stelck (1956, Pl. VIII, figs.

19-21). In Warren's original description the geological horizon is given as "lower part of the Upper Devonian below the *Cyrtospirifer* Zone" (1944, p. 116). Warren and Stelck, however, figure the species as occurring in the *Cyrtina panda* fauna of the Beavertail formation and the locality is given as "Carcajou rock, below Norman Wells" (1956, explanation to Pl. VIII).

Syntype, U. of A. Dv853-1. Figured by Warren (1944, Pl. II, fig. 6), and by Warren and Stelck (1956, Pl. VIII, figs. 16-18). Same horizon and locality as lectotype.

Hypotype A, GSC No. 15331. From Hume's field notebooks for 1922 (p. 84), the specimen was collected from heavy-bedded limestone 20 to 30 feet below the contact of the Beavertail formation with the overlying Fort Creek on the Wolverine anticline, Carcajou Ridge, Mackenzie River, right bank. The horizon appears to be below the section given by Hume (1923, p. 57B) at the "north end of Wolverine anticline". Hume (1954, pp. 25-34) has revised the formational terminology in the region and would include these beds in the upper Ramparts Limestone member of the Ramparts formation. Bassett (1961) has further discussed the section at Carcajou Rock and seems to suggest that this horizon lies within the upper part of the Kee Scarp formation. This is discussed more fully on page 10. GSC loc. 7237k; collector G. S. Hume, 1922.

Hypotype B, GSC No. 15332. Same horizon and locality as hypotype A.

Hypotype C, GSC No. 15333. From black bituminous limestones of the Pine Point formation, half a mile west of Pine Point, south shore of Great Slave Lake. In their field notebooks for 1917 (Kindle, p. 23, and Whittaker, p. 11), both Kindle and Whittaker mention collecting from this locality. Whittaker makes specific mention of rhynchonelloids in his collection but the same GSC locality number was assigned to both collections. GSC loc. 5675; collectors E. J. Whittaker and E. M. Kindle, 1917.

Hypotype D, GSC No. 15334. From the bituminous limestone member of the Pine Point formation, in the upper part of the formation. Dawson Landing wharf area, south shore of Great Slave Lake. GSC loc. 31068; collector A. W. Norris, 1957.

Hypotype E, GSC No. 15335. Black shales of Pine Point formation. Northwest side of eastern island of Pine Point Islands (Green Islands). GSC loc. 5672; collector E. J. Whittaker, 1917.

Hypotype F, GSC No. 15336. Same horizon and locality as hypotype D.

Hypotype G, GSC No. 15337. Pine Point formation, 150 feet east-northeast of Dawson Landing wharf, south shore of Great Slave Lake. GSC loc. 19263; collector R. deWit, 1950.

Hypotype H, GSC No. 15338. Pine Point formation, 800 feet west-southwest of Dawson Landing wharf, south shore of Great Slave Lake. GSC loc. 19264; collector R. deWit, 1950.

Hypotype I, GSC No. 15339. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 15). Same horizon and locality as hypotype A.

Hypotype J, GSC No. 15340. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 16). Same horizon and locality as hypotype D.

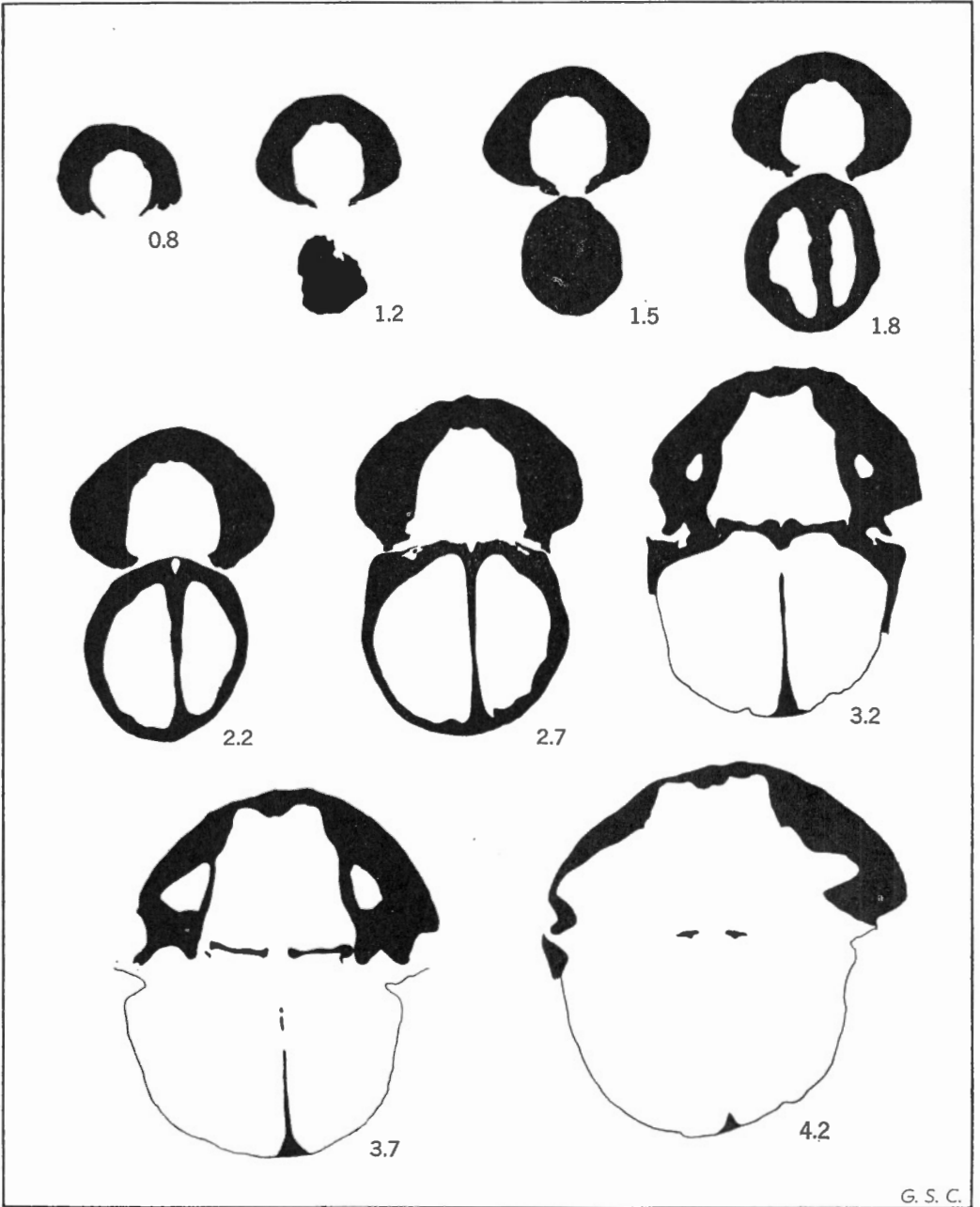
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Lectotype Dv853-2	29.1	28.0	32.6	22.3	121°
Syntype Dv853-1	29.0	26.7	29.9	26.9	114°
Hypotype A	27.0	26.2	33.2	24.8	119°
Hypotype B	22.8	22.4	25.0	23.8	113°
Hypotype C	20.6	19.3	22.4	16.0	109°
Hypotype D	18.1	17.2	23.6	15.0	127°
Hypotype E	14.6	13.8	16.6	10.5	117°
Hypotype F	14.5	13.9	18.2	13.5	122°
Hypotype G	11.9	11.2	13.0	9.3	105°
Hypotype H	11.3	10.2	11.0	9.3	95°
Hypotype I (sectioned)	24.8	23.6	27.7	25.7	121°
Hypotype J (sectioned)	14.7	14.0	18.1	12.2	117°

Description. Shell medium to large size, subpentagonal to transversely elliptical; uniplicate; width greater than length, greatest width at mid-length; greatest thickness commonly forward of mid-length, brachial valve strongly inflate, pedicle valve less inflate; hinge-line obtuse angled, less than half shell width; apical angle commonly between 110 and 120 degrees. Shell finely costellate, costate anteriorly.

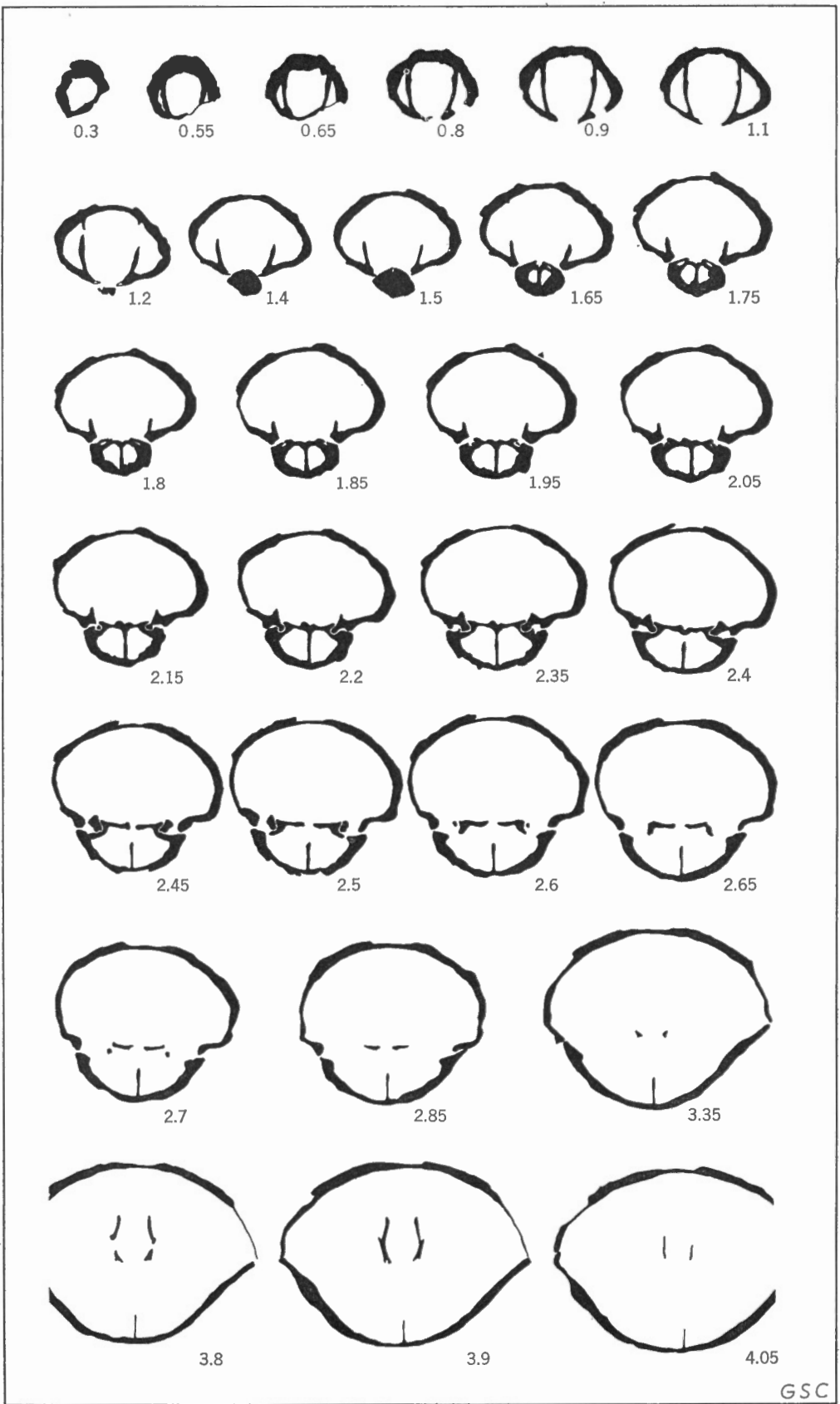
Pedicle valve is moderately convex on umbo, becoming weakly convex forward and laterally. It is smoothly and decreasingly curved from beak to anterior commissure. The sulcus is moderately deep to shallow and begins posterior to or at mid-length; its greatest depth is in line with the antero-lateral commissures. It extends forward to a broad flattened tongue which is vertical to recurved. On mature shells the lateral commissure is raised above the level of the ventro-lateral margins of the valve which bend abruptly upwards at right angles to the plane of the rest of the valve. The height of the commissure above the angle formed by this bend rises anteriorly to the lateral margin of the tongue. The lateral and anterior commissures are strongly crenulate. The beak is prominent and suberect to erect. The interareas are large, broadly elliptical and concave. Beak ridges are prominent. The foramen is large, elliptical, and submesothyrid. Narrow, discrete, deltidial plates are visible in section.

The brachial valve is high and domed. The fold is inconspicuous except on the anterior one third of the shell. The front of the fold on mature shells is bent sharply downwards to meet the tongue, so that the anterior commissure is below the crest or highest point of the valve by as much as one fifth of the height. The beak is incurved and inconspicuous.



G. S. C.

Figure 15. *Hadorhynchia sandersoni* (Warren). Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; hypotype I, GSC No. 15339.



GSC

Figure 16. *Hadrorynchia sandersoni* (Warren). Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; hypotype J, GSC No. 15340.

Well-preserved shells, which are rare among the collections, are marked with fine flattened costellae which increase by bifurcation. Some shells show fine closely set concentric lines. All shells are costate anteriorly, with strong rounded costae that never bifurcate. Costation begins from about 10 to 20 mm forward of the beak. There are three to five costae on the fold and four to six on each flank. On shells on which the fold is bent downwards anteriorly the costae are thickened at the point of inflexion, beyond the inflexion they are medianly depressed. The costae on the tongue show a similar depression near the commissure. On internal moulds the interspaces between the costae on both valves carry narrow, parallel-sided ridges that extend from the geniculate inflexion on the fold to the anterior commissure on the brachial valve and downwards from the commissure for as much as 10 mm on the pedicle valve. Similar ridges may be present above and below the lateral commissures. These ridges may be the trace of spines formed as outgrowths from the margins of the opposite valve (as described by Schmidt, 1937), but it proved impossible to find traces of such spines in longitudinal or tangential sections.

In the pedicle interior, widely spaced dental plates enclose an elliptical to quadrate delthyrial cavity. They may persist in contact with the floor of the valve to the plane of articulation or beyond, but commonly become detached posterior to articulation and persist forwards as ventrally directed ridges below the teeth. The lateral cavities are narrow and may be filled with secondary shell material in mature shells. The adductor impression is broad and longitudinally striated. The costae are strongly marked on the interior. Pallial sinuses are impressed, radiating, and bifurcate forwards.

In the brachial interior the cardinalia are highly distinctive. Proximally a small U-shaped septalium divides the hinge plates, but becomes filled anteriorly by two broad rounded longitudinal ridges which develop on the inner part of each hinge plate. These ridges or swellings persist to the plane of articulation and are separated by a narrow V-shaped median groove. The septum is slender and remains in contact with the hinge plates to articulation. It persists forward up to a quarter of the length of the valve. After the septum has become detached from the hinge plates they divide and continue forward of articulation as flat plates from the inner margins of which the crura arise. The inner socket ridges are scarcely raised above the level of the surface of the hinge plates. The crura are slender and triangular, becoming vertically flattened lamellae anteriorly that plunge ventrally and are slightly recurved. They are dorsally grooved and carry a small lateral projection anteriorly on each of their exterior surfaces. The adductor impressions are poorly distinguished, narrow, and lenticular; they do not extend beyond the median septum. Radiating and branching pallial sinuses are strongly impressed.

Growth and Variation (44 specimens).

Changes in mean proportion during growth:

	Length							
	Less than 14 mm		14.0 to 17.9 mm		18.0 to 21.9 mm		22 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.15	0.97-1.33	1.18	1.00-1.29	1.14	1.06-1.30	1.12	1.03-1.23
Thickness/length	0.84	0.60-0.98	0.80	0.70-1.00	0.78	0.60-0.86	0.94	0.77-1.05
Apical angle	109°	95°-126°	116°	107°-123°	113°	102°-127°	117°	113°-121°

Despite the wide range in size among the collections (from a length of 10.0 mm to 29.2 mm), there is no significant change in mean shell proportions during growth as expressed by width/length, and thickness/length ratios, and the apical angle. The variation in these proportions between individual shells, however, is high and due to a considerable range in the shell size at which "mature" characters are developed, i.e. recurved tongue, geniculate bending upwards of lateral margins of the pedicle valve and downwards of the anterior margin of the brachial fold, and the full development of costation. Very few shells show youthful characteristics such as hypotype E (Pl. VII, figs. 4a-c) which is at an earlier stage of development than the much smaller hypotype H (Pl. VII, figs. 1a-f).

That this variation is related to environment is suggested by the discrepancy in mean size between collections from the Great Slave Lake area and those from Carcajou Ridge on Mackenzie River. The former are smaller and their upper size limit just overlaps the smallest Carcajou forms. There is however great variation within one region and a similar developmental form may be reached at widely disparate absolute size. For example hypotype G (length 11.9 mm, Pl. VII, figs. 2a-c) is almost identical in shape, proportions, and ornament with hypotype C (length 20.6 mm, Pl. VII, figs. 6a-f). Their width/length ratio is 1.09 and their thickness/length ratios respectively 0.79 and 0.78. Yet owing to changes in direction of growth during development, hypotype G could not grow into a form resembling hypotype C in shape and size. Similarly hypotype C at a growth stage when it was the same size as hypotype G, was a thinner shell with no ornament yet developed.

It is probable that the development of fine costellae over the whole shell is a variable feature. Several specimens from Great Slave Lake appear to be sufficiently well preserved to show fine ornament if present, but only a few shells from Carcajou Ridge show this feature.

Discussion. *Hadrorhynchia sandersoni* is the only species of the genus yet recognized and it is not easily confused with other forms. Small specimens of *Ladogioides pax* may appear remarkably similar externally to juvenile forms of *H. sandersoni*. If the characteristic depressed anterior commissure and laterally geniculate pedicle valve together with the anteriorly depressed and grooved costae

of *H. sandersoni* have not developed, it may be necessary to examine their internal structures to separate the two forms. Mature or adult forms of the two species are quite dissimilar.

The specimen figured by Meek (1867, Pl. XV, fig. 4) and described as "*Rhynchonella*—?" is the internal mould of the dorsal valve of a specimen of *H. sandersoni* (USNM No. 24423).

Occurrence. *Hadrorhynchia sandersoni* is present in the upper part of the Pine Point formation in the vicinity of Great Slave Lake, both on the north and south of the lake. Its range appears to overlap almost exactly that of *Leiorhynchus awokanak*. Specimens in this region have been examined from GSC localities 5672, 5675, 5682, 17390, 17405, 19263, 19264, 31068, 31189, 33568, 33577.

In the Middle Mackenzie River region the species is common on Carcajou Ridge from beds variously reported as Lower Fort Creek formation, Beavertail formation, upper Ramparts formation, and Kee Scarp formation. Specimens have been examined from GSC localities 6872, 7237h, 7237k, 1287l.

In the Imperial Range, the species has been collected in the "upper Ramparts" and the "middle Ramparts" formations; GSC loc. 31582, 31610.

The species has been collected from the base of the McDame group near the mouth of French River in McDame map-area, British Columbia; GSC loc. 32418.

Genus *Ladogioides* McLaren, 1961

Type species: *Ladogioides pax* McLAREN, 1961, pp. 4-5, Pl. I, figs. 6, 7.

Diagnosis. Medium to large "*Pugnoides*"-like rhynchonelloids with inflate brachial valve and high, sometimes recurved, tongue in pedicle valve. Pedicle valve shallow, with sulcus beginning at or posterior to mid-length, and extending forward to broad and prominent tongue. Beak erect to incurved with prominent interareas and beak ridges. Foramen large, elliptical, hypothyrid to submesothyrid. Discrete, narrow deltidial plates. Brachial valve high to acuminate, highest point at anterior commissure in median line. Fold poorly differentiated. Ornament of abundant close-set, flattened, costellae over whole shell and strong angular costae developed only on anterior part of most shells on both fold and flanks; some shells without costae.

Teeth supported to plane of articulation by dorsally divergent dental plates; delthyrial cavity wide. Hinge plates flat, divided by deep narrow septalium supported proximally by thin impersistent median septum. Crura arise from inner margins of hinge plates at point of attachment to septalial plates; they are straight, dorsally grooved and plunge abruptly towards pedicle floor distally, becoming trough-shaped and slightly recurved.

Discussion. The distinguishing characters of the genus *Ladogioides* are: (1) the high acuminate form in "mature" shells; (2) the prominent beak, interareas, and beak ridges; (3) the wholly costellate surface ornament and variably delayed,

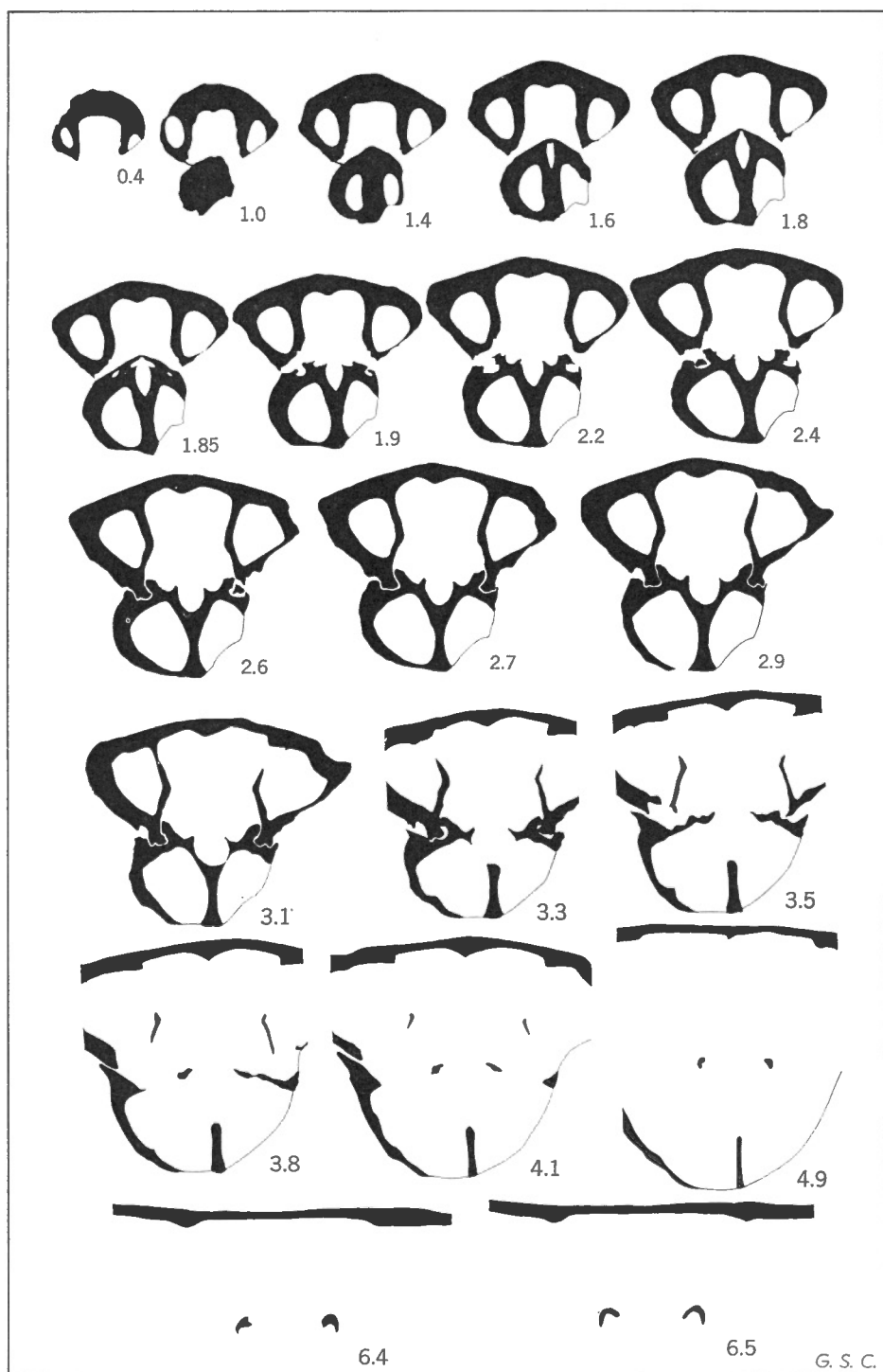


Figure 17. *Ladogia meyendorfi* (de Verneuil). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype GSC No. 15720; a specimen with the following dimensions (in mm): length 27.2, width 31.4, thickness 19.7; from the Pskov Stage, Pskov, Velikaja River, Estonia.

angular costation developed distally; (4) the deep narrow septalium, weak septum, and flat hinge plates; (5) the recurved, trough-shaped crura.

The external form of the genus *Ladogia* Nalivkin 1941, is closely similar in many characters to *Ladogioides*. *Ladogia meyerendorfi* (de Verneuil), the type species, shows the same high acuminate shell form, the same prominent beak and beak ridges, and identical ornament of flattened costellae over the whole shell surface. A specimen of *L. meyerendorfi* from the Pskov Stage (early Frasnian) of Estonia is figured on Plate VIII, figures 4a-f. Costation does not appear on *Ladogia* but may be absent from large specimens of *Ladogioides pax*.

One specimen of *Ladogia meyerendorfi* from the Pskov Stage of Estonia was sectioned in detail (Fig. 17). It agrees with the description of the interior given by Bekker (1924, p. 53), but shows radical differences in internal structure from *Ladogioides*. These differences may be summarized as follows:

<i>Ladogia</i>	<i>Ladogioides</i>
(1) Dental plates with geniculate bend inwards at about half their height, as seen in section.	Dental plates straight, slightly divergent.
(2) Lateral cavities large and wide.	Lateral cavities narrow.
(3) Hinge plates concave ventrally.	Hinge plates flat.
(4) Septalium V-shaped proximally, U-shaped distally; remains attached to septum up to plane of articulation.	Septalium narrow and deep, becomes detached from septum close to beak, well posterior to plane of articulation.
(5) Median septum stout, persists into shell well forward of articulation.	Median septum slender and scarcely persists forward of articulation.

There can be no doubt that the two genera are distinct and that similarities in external form are due to homeomorphy.

The genus *Yunnanellina* Grabau 1931 from the Upper Devonian of China (Upper Frasnian according to Chang, 1958), bears some resemblance externally to *Ladogioides*. It is a small to medium *Pugnoides*-like shell with angular costation developed on the anterior part of each valve. It is entirely covered with fine costellae which increase by bifurcation. Grabau (1932, p. 95) figures diagrammatically two sections of the type species, *Rhynchonella hanburii* Davidson, which suggest that there is an open septalium supported by a median septum at about the plane of articulation. The interior is further figured by Tien (1938, p. 44) in a series of serial sections that show a well-developed U- to V-shaped septalium supported by a stout median septum in the plane of articulation. The septum persists forward into the shell. Dental plates are well developed and the lateral cavities wide. The internal structure as thus described separates the genus from *Ladogioides*.

Yunnanella Grabau 1923 as described by him (1932) and Tien (1938) differs from *Ladogioides* in external ornament in that the costellae are present only

on the part of the shell devoid of costation. Its interior is closely similar to *Yunnanellina*.¹

Porostictia Cooper 1955, with type species *Paraphorhynchus perchaensis* Stainbrook from the Percha Shale of New Mexico, has some similarity in general form to *Ladogioides*. The striations between the fine costellae, however, possess rows of fine pits, and internally the septalium is supported by the median septum, which is long and slender.

The only species assigned to *Ladogioides* are *L. pax* and *Pugnoides kakwaensis* McLaren, both of early Upper Devonian (early Frasnian) age, from Alberta and southern Northwest Territories.

The genus is named for its resemblance to the genus *Ladogia* Nalivkin 1941.

Ladogioides pax McLaren

Plate IX, figures 1-8; Plate X, figures 1-3. Figure 18

1961. *Ladogioides pax* McLAREN, pp. 4-5, Pl. I, figs. 6-7.

Material. Holotype, GSC No. 15216. Peace Point member of Waterways formation, sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, 1.1 miles east-northeast of east end of island just below Boyer Rapids, Alberta, 24 to 30 feet above water level. GSC loc. 29157; collector A. W. Norris, 1956.

Paratype A, GSC No. 15217. Firebag member of Waterways formation, west bank of Edwin Creek near junction with Clearwater River, Alberta. A. W. Norris states that specimens from this locality were probably collected from thin beds of green argillaceous limestone interbedded with green shale that are exposed at low water, near the mouth of Edwin Creek. GSC loc. 35106; collector H. D. Curry, Shell Oil Company, 1945.

Paratype B, GSC No. 15218. Same horizon and locality as paratype A.

Paratype C, GSC No. 15219. Peace Point member of Waterways formation. Sink-hole filling in Slave Point formation, Gypsum Cliffs, north bank of Peace River, opposite unnamed island immediately below Boyer Rapids, Alberta. GSC loc. 29432; collector A. W. Norris, 1956.

Paratype D, GSC No. 15220. Peace Point member of Waterways formation, near base of green shale overlying Slave Point formation, Gypsum Cliffs, north bank of Peace River, opposite mid-point of island just below Boyer Rapids, Alberta. GSC loc. 29441; collector A. W. Norris, 1956.

Paratype E, GSC No. 15221. Same horizon and locality as paratype A.

Paratype F, GSC No. 15222. Same horizon and locality as paratype A.

Paratype G, GSC No. 15223. Same formation and locality as holotype, 35 to 55 feet above river level. GSC loc. 29151.

¹Sartenaer (1961a) has recently shown that *Yunnanellina* Grabau 1931 is an objective synonym of *Yunnanella* Grabau 1923, *Rhynchonella hanburii* having originally been proposed as type species for both. He proposes the name *Nayunnella* to replace Grabau's 1931 usage of *Yunnanella* (type species *Yunnanella symplicata* Grabau 1931).

Paratype H, GSC No. 15224. Same horizon and locality as paratype G.

Paratype I, GSC No. 15225. Same horizon and locality as paratype C.

Paratype J, GSC No. 15226. Same horizon and locality as paratype G.

Paratype K, GSC No. 15227. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 18). Same horizon and locality as holotype.

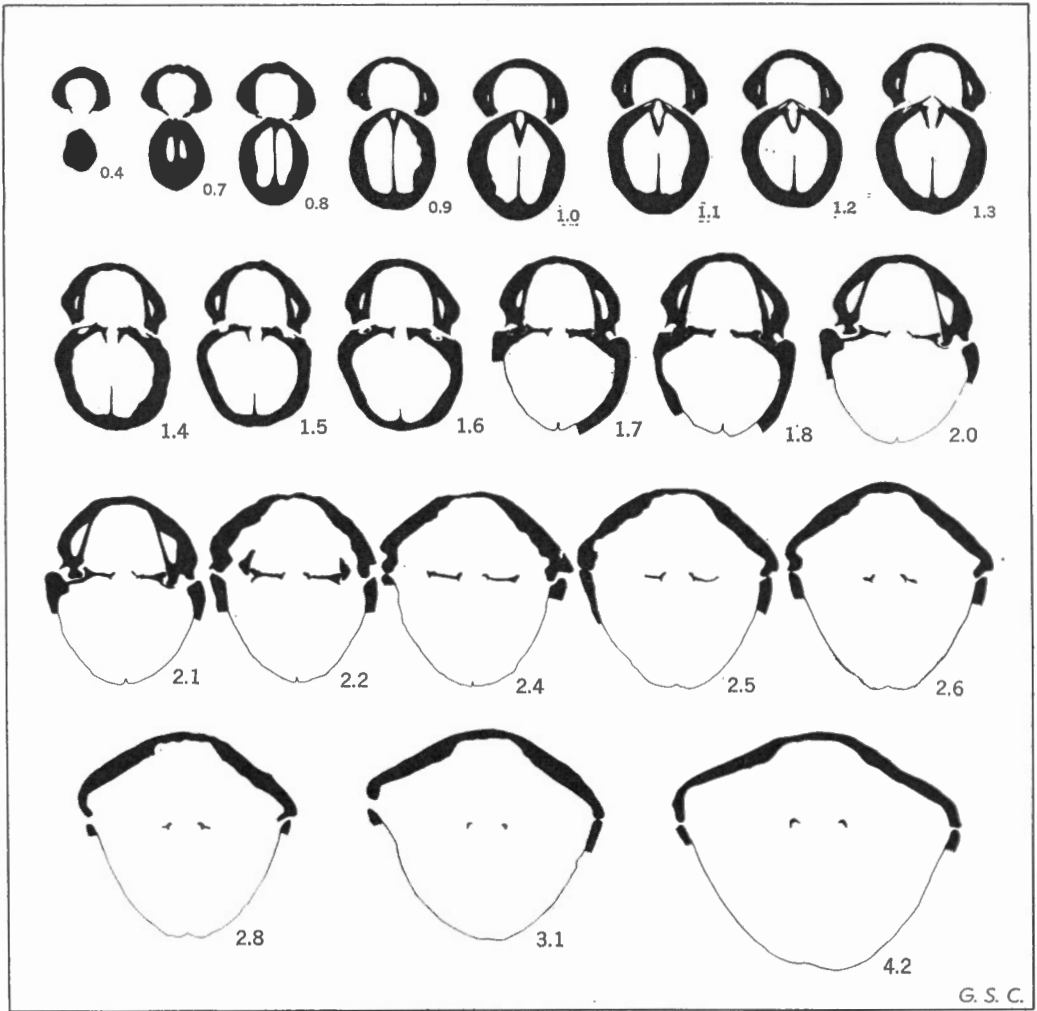
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	16.0	15.2	18.3	11.0	119°
Paratype A	27.2	25.7	31.8	16.7	129°
Paratype B	25.2	24.6	30.7	27.8	135°
Paratype C	24.1	23.5	28.7	19.1	127°
Paratype D	21.7	21.2	24.4	18.3	116°
Paratype E	20.8	20.1	22.5	12.5	120°
Paratype F	20.4	19.7	24.3	13.9	133°
Paratype G	15.8	15.0	18.4	8.7	127°
Paratype H	15.2	14.5	17.7	10.9	118°
Paratype I	15.1	14.2	16.2	10.1	104°
Paratype J	10.5	9.6	11.1	4.4	107°
Paratype K (sectioned)	16.7	15.6	18.3	11.9	116°

Description. Shell medium to large size, transversely subelliptical to sub-pentagonal, *Pugnoides*-like; width greater than length, greatest width at or forward of mid-length; greatest thickness at front margin, valves of unequal depth, brachial valve having greater depth; hinge-line nearly straight, less than half shell width; apical angle between 115 and 130 degrees, rarely more. Shell finely costellate, otherwise smooth or weakly costate at anterior margin.

Pedicle valve is shallow, weakly convex transversely, smoothly and regularly curved longitudinally from beak to anterior commissure. Sulcus begins at or a little posterior to mid-length, shallow and ill-defined, extending forwards into broad and prominent tongue which becomes vertical or even recurved in fully developed shells. Antero-dorsal end of tongue at the front margin tends to narrow to a sharply acuminate crest which in most shells is the highest point of the valve. The crest may be modified by costae which, because they alternate in development between the valves, cause the commissure to become crenulated. The beak is nearly straight to erect. The interareas are broadly triangular, narrow, slightly concave in a longitudinal direction, and weakly striated transversely. Beak ridges are present and may be prominent. The foramen is large, longitudinally elliptical, and hypothryid to submesothryid. Discrete deltidial plates are present on either side of the foramen, but are never in contact medianly.

The brachial valve is high and acuminate at front margin. The fold is inconspicuous and not differentiated from the lateral slopes of the shell. The beak is incurved and inconspicuous.



G. S. C.

Figure 18. *Ladogioides pax* McLaren. Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; paratype K, GSC No. 15227.

The whole shell is covered with fine, flattened costellae that increase by bifurcation. There are fifteen to twenty in 5 mm at the front margin of average shells. They are crossed by yet finer concentric growth lines which are not always present but increase in abundance peripherally. Most shells are weakly costate anteriorly both medianly and on flanks. The angular costae commonly appear well forward of mid-length close to anterior and antero-lateral margins. Some shells are smooth. The costae alternate between valves, and when developed cause strong angular crenulation of the commissure. There are commonly three or four on the fold with a maximum of six, and three to five on the flanks.

In the pedicle interior dorsally divergent, widely spaced dental plates are developed close to the beak and support the teeth up to and beyond the plane of articulation. The delthyrial cavity is wide and U-shaped, the lateral cavities are narrow and deep. The adductor track is broad and weakly striated longitudinally; it extends forward of the delthyrial cavity for about one third of the length of the shell and is bluntly rounded at its anterior margin. Pallial sinuses are poorly impressed, radiating, and weakly branching.

In the brachial valve the cardinalia consist of divided hinge plates, a deep septalium supported proximally by a slender median septum. The septum becomes detached from the septalial plates within about one millimetre of the beak and scarcely persists forward of the plane of articulation. The septalium is formed by bifurcation of the duplex septum and encloses a high narrow chamber close to the beak which opens dorsally and ventrally after becoming detached from the septum. The two septalial plates are attached to the inner edges of the hinge plates; the point of attachment becomes the crural bases. The hinge plates are wide and prominent and are almost flat to slightly concave. The inner socket ridges are scarcely raised above the level of their ventral surfaces. The crura are small, slender, and dorsally grooved. The adductor impressions are poorly distinguished, narrow, lenticular and weakly striated and confined to the posterior half of the shell; the remains of the median septum serves as a myophragm in the muscle area. Pallial sinuses are very weakly impressed and appear to be similar to those in the pedicle valve.

Growth and Variation (100 specimens).

Changes in mean proportion during growth of 90 specimens, all from Gypsum Cliffs area:

	Length									
	Less than 13 mm		13.0 to 14.9 mm		15.0 to 16.9 mm		17.0 to 18.9 mm		19 mm and more	
	mean	range	mean	range	mean	range	mean	range	mean	range
Width/length	1.13	1.00-1.39	1.20	1.09-1.31	1.11	0.96-1.24	1.12	1.01-1.24	1.12	1.07-1.19
Thickness/length	0.56	0.42-0.78	0.66	0.57-0.79	0.62	0.52-0.73	0.65	0.55-0.76	0.75	0.62-0.85
Apical angle	114°	97°-127°	116°	108°-125°	117°	104°-127°	117°	105°-130°	123°	116°-128°

Ten specimens from Clearwater River (size range from length 18.1 to length 28.5):

	mean	range
Width/length	1.15	1.02-1.30
Thickness/length	0.72	0.50-0.76
Apical angle	127°	122°-135°

Examination of the above tables shows the rather surprising fact that, except for very small and very large specimens, there is little change in mean proportions during growth. The width of specimens with a length of about 10 mm or less is equal to or less than their length, their height less than half the length, and their apical angle about 100 degrees. Otherwise the means in proportions of size groups up to a length of about 20 mm differ little. Above this size there is a tendency for proportionate thickness and apical angle to increase, but it is not marked and not significantly demonstrable owing to scarcity of large specimens.

That these proportions should prove to vary so little is surprising because the species is a typical acuminate rhynchonelloid in which the direction of growth changes from forward to upward in the pedicle valve during growth, producing a shell with a vertical tongue and a high front margin (in Rudwick's terminology (1959, p. 4) the anterior component of growth rate (x) gives way to the vertical component (z)). Although forward growth does not stop at any stage, nevertheless the net result in a high-tongued shell is an increase in the thickness/length ratio during growth — a normal pattern for many rhynchonelloids including many discussed in the present work.

An examination of the individuals comprising the sample furnishes an answer. It is clear that the high-tongued stage is reached at widely different sizes. The species is unusually variable in that a mature or adult shape may be reached by shells varying from a length of 10 mm to 20 mm or more.

This conclusion is reinforced by the appearance of costation on individual shells. Costation, which may also be considered a mature feature in this species, shows a tendency to be restricted to shells with a high tongue and acuminate form. There is no correlation between first appearance of costation and absolute size except at the outside extremes of size range, but there is good visual correlation between height of tongue and degree of development of costation.

The holotype (Pl. IX, figs. 5a-e) with a length of 16 mm, a moderately high tongue (thickness/length = 0.70), and anterior costation, may be considered a more "mature" shell than, for instance, paratype A (Pl. X, figs. 3a-e) which has a length of 27.2 mm, a relatively low tongue (thickness/length = 0.61), and costation scarcely beginning to appear at the front margin. Paratype A cannot have passed through a stage in its growth when it resembled the holotype. On the other hand, the holotype must closely resemble a younger stage of growth of paratype B (Pl. X, figs. 2a-d) which has a length of 25.2 mm, a high acuminate tongue which is recurved dorsally (thickness/length = 0.91), and well-developed anterior costation. The costation on the fold on both the holotype and paratype B begins about 13 mm forward of the beak.

This range in size over which "mature" features may be developed is exhibited by small populations collected from a number of localities along Peace River for a distance of some 6 miles, from beds of remarkably consistent lithology (*vide* A. W. Norris) and of unquestionably similar stratigraphic horizon. A similar but possibly even more pronounced variation is exhibited by the relatively few specimens from Edwin Creek on Clearwater River.

Discussion. *L. pax* bears a superficial resemblance to many *Pugnoides*-like rhynchonelloids common at higher horizons in the Upper Devonian, but may be readily separated on external morphology, including beak characteristics and micro-ornament. No species of the genus *Ladogioides* are as yet known at horizons above the lowest beds of the Upper Devonian. Differentiation from *L. kakwaensis* is discussed under the latter species.

The species is named from the Latin "pax" peace, for Peace River, Alberta.

Occurrence. *Ladogioides pax* is abundant in the Peace Point member of the Waterways formation exposed in the vicinity of Gypsum Cliffs on Peace River over a distance of about 6 miles. It also occurs in the stratigraphically equivalent Firebag member of the Waterways formation on Clearwater River and on Athabasca River downstream from Fort McMurray. It is commonly associated with *Leiorhynchus russelli*. Specimens have been examined from many localities, including GSC loc. 29151, 29154, 29157, 29202, 29432, 29441, 35106, 41889. A few specimens have been collected from the basal beds of the Hay River formation near Sulphur Bay on the north shore of Great Slave Lake, GSC loc. 31082. The species has been collected from subsurface cores in northern Alberta from GSC loc. 31473, 37501, 41919.

Ladogioides kakwaensis (McLaren)

Plate X, figures 4, 5; Plate XI, figures 1-4; Plate XII, figures 1-4. Figures 19, 20, 21

1954. *Pugnoides kakwaensis* McLAREN, p. 176, Pl. I, figs. 28-32.

1958. *Ladogia kakwaensis* (McLaren), McLAREN, Pl. VIII, figs. 1, 2, 3.

Material. Holotype, GSC No. 11246. Figured by McLaren (1954 and 1958). Cairn formation ("Flume equivalent"), 44 to 66 feet above base, from slightly argillaceous, grey limestone unit; southeast end of the Ancient Wall, Jasper Park (lat. 53°22', long. 118°39'), Alberta. GSC loc. 19971; collector D. J. McL., 1951.

Paratype, GSC No. 11247. Figured by McLaren (1954). Same horizon and locality as holotype.

Hypotype A, GSC No. 13819. Figured by McLaren (1958). "Flume formation", 186 to 205 feet above base of Devonian section, from argillaceous, nodular, grey limestone; below the saddle at the northeast end of the mountain on the northwest side of Kakwa Lake (lat. 54°03', long. 120°10'), British Columbia. GSC loc. 35100; collector D. J. McL., 1952.

Hypotype B, GSC No. 15229. Same horizon and locality as hypotype A.

Hypotype C, GSC No. 15230. From talus collection, same formation and locality as hypotype A. GSC loc. 35102.

Hypotype D, GSC No. 15231. Same horizon and locality as hypotype A.

Hypotype E, GSC No. 15232. Same horizon and locality as hypotype A.

Hypotype F, GSC No. 15233. From same formation and locality as hypotype A, in lithologically similar beds, 205 to 220 feet above base of Devonian section. GSC loc. 35101.

Rhynchonelloid Brachiopods from Western Canada

Hypotype G, GSC No. 15234. Internal mould of specimen; shell removed to show internal structure. Same horizon and locality as hypotype A.

Hypotype H, GSC No. 15235. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figs. 19, 21). Same horizon and locality as hypotype A.

Hypotype I, GSC No. 15236. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 20). Talus collection, as for hypotype C.

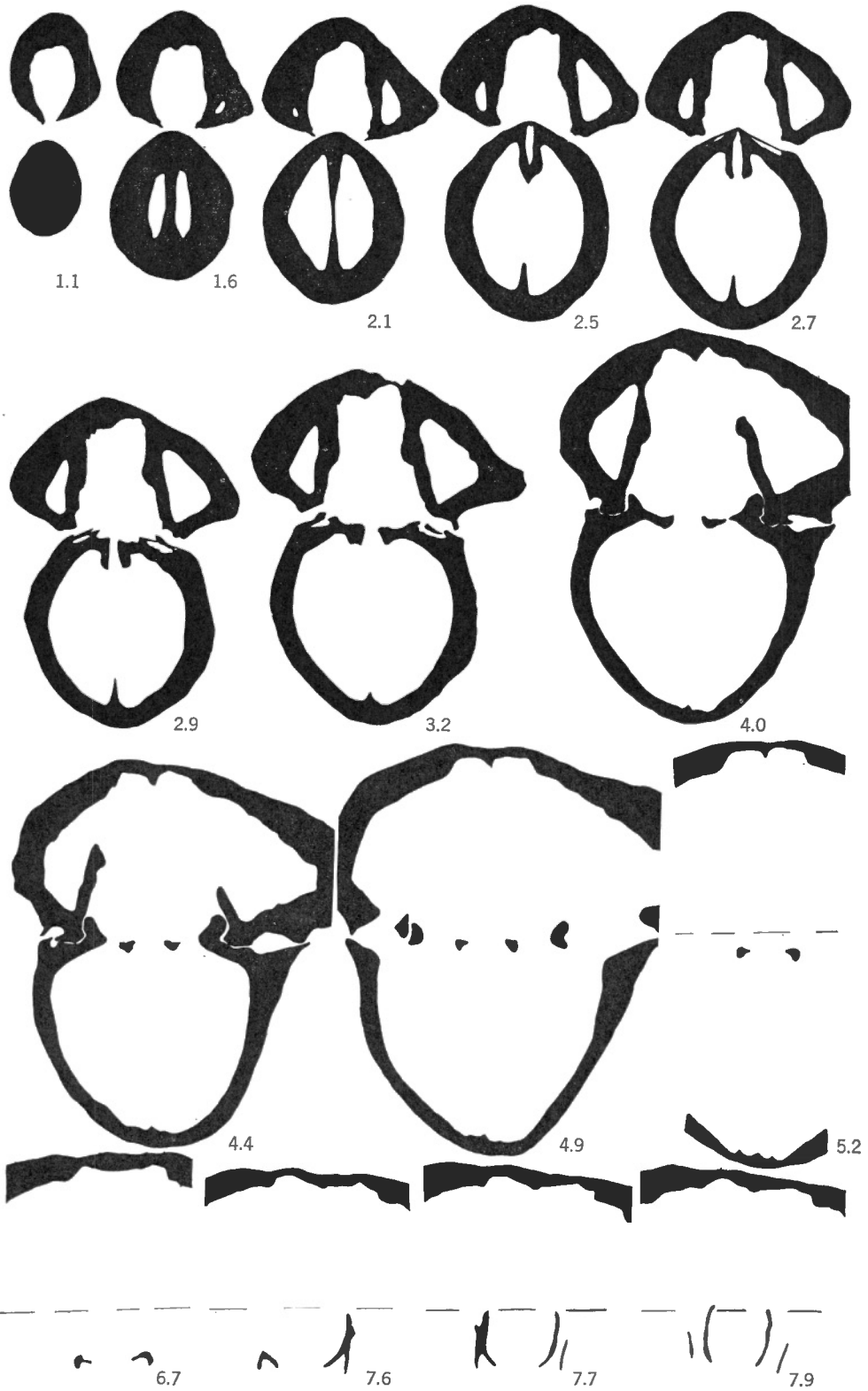
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	27.0	27.0	32.5	24.4	137°
Paratype	(21.2)		25.3	21.2	130°
Hypotype A	31.6	31.6	38.8	29.7	139°
Hypotype B	28.0	27.7	35.2	25.3	137°
Hypotype C	27.6	27.6	35.1	31.8	147°
Hypotype D	27.1	25.7	30.0	29.5	124°
Hypotype E	21.0	20.7	26.6	22.2	135°
Hypotype F	19.4	18.8	21.9	14.7	119°
Hypotype G (internal mould)	24.6	24.2	29.9		128°
Hypotype H (sectioned)	30.6	30.6	(35.4)	30.2	130°
Hypotype I (sectioned)	15.9	14.8	16.1	10.9	102°

Description. Shell large, subpentagonal in outline; width greater than length, greatest width at or posterior to mid-length; brachial valve strongly inflate and acuminate; greatest thickness of shell at front margin or at crest of recurved tongue; hinge-line nearly straight, less than half shell width; apical angle in large shells between 130 and 140 degrees. Anterior part of shell strongly costate with angular costae, smooth posteriorly; whole shell finely costellate.

The pedicle valve is shallow, almost flat transversely just forward of the sharply convex beak, smoothly curved longitudinally from beak to anterior commissure, the curvature decreasing regularly forward. Postero-lateral flanks tend to become concave in some shells but are normally gently convex. The sulcus begins posterior to mid-length, 10 to 15 mm forward of the beak and deepens and widens rapidly to a maximum in line with the antero-lateral commissures. From there it extends into a broad prominent tongue which narrows upwards and may end in a rounded and crenulated or a sharply acuminate commissure. In large shells the tongue is recurved, so that the maximum height of the whole shell, which is normally at the crest of the tongue, may be at or even posterior to mid-length. The beak is erect to incurved. The interareas are narrowly elliptical and concave; beak ridges are prominent and angular. The foramen may be concealed or damaged, apparently large and possibly submesothyrid. Discrete deltidial plates are seen only in section.

The brachial valve is very high and acuminate at front margin. The fold is poorly differentiated from the remainder of the valve but is sharply ridged axially and may be modified by costation. The beak is incurved. Narrow inter-



GSC

Figure 19. *Ladogioides kakwaensis* (McLaren). Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; hypotype H, GSC No. 15235.

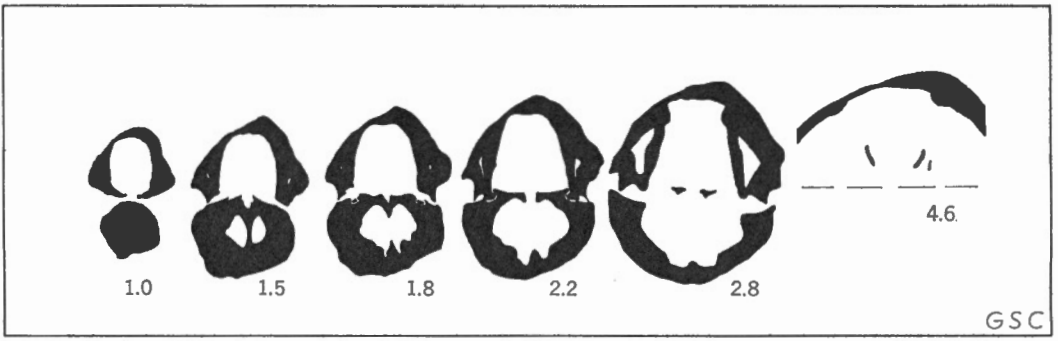


Figure 20. *Ladogioides kakwaensis* (McLaren). Camera lucida drawings of serial transverse section: x3; distances are in mm forward from the crest of the umbo; hypotype I, GSC No. 15236.

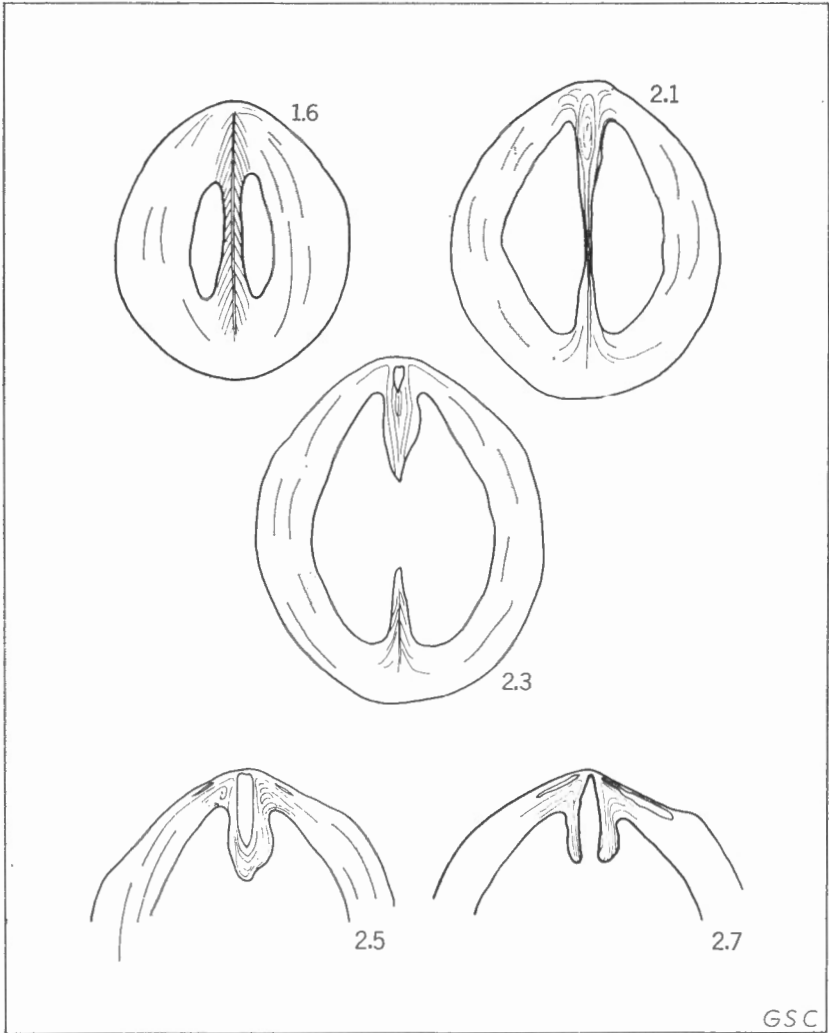


Figure 21. *Ladogioides kakwaensis* (McLaren). Camera lucida drawings of serial transverse sections of brachial valve to show details of the developing septum and cardinalia x5; distances are in mm forward from the crest of the umbo; hypotype H, GSC No. 15235.

areas may be seen on some shells set off by angular beak ridges that meet those of the pedicle valve at the nick point.

The whole shell is covered by fine flattened costellae that increase by bifurcation. There are about twenty in 5 mm near the front of an average specimen. Very fine concentric growth lines are sometimes visible; they are very irregularly developed but always increase in number towards the shell margins. Strong angular costae are developed from about 10 to 15 mm forward of the beaks. Alternation of the costae between the valves causes the anterior and antero-lateral commissures to be strongly crenulated. There are two to six costae on the fold, and up to six on the flanks. The costellae are quite independent of the costae and are developed equally on costate and non-costate parts of the shell.

The interior of both valves is similar to that of *Ladogioides pax*, although the muscle impressions and pallial sinuses are much more strongly impressed on the inner shell surface. The costae are strongly marked on the interior and the shell is thicker. The crura are better known and are dorsally grooved, becoming trough-shaped distally. They plunge abruptly towards the pedicle floor at about a quarter of the shell length forward of the umbo, and may become slightly recurved. The antero-dorsal margins of the trough give the appearance of twin lamellae in each crus in section.

Growth and Variation (80 specimens).

Changes in mean proportion during growth:

	Length									
	Less than 17 mm		17.0 to 19.9 mm		20.0 to 22.9 mm		23.0 to 25.9 mm		26 mm and more	
	mean	range	mean	range	mean	range	mean	range	mean	range
Width/length	1.19	1.01-1.45	1.16	1.08-1.30	1.21	1.02-1.40	1.26	1.16-1.37	1.24	1.11-1.47
Thickness/length	0.72	0.60-0.93	0.77	0.68-0.82	0.93	0.58-1.09	1.02	0.92-1.15	1.00	<u>0.73-1.18</u>
Apical angle	115°	102°-127°	116°	108°-125°	132°	117°-144°	134°	119°-146°	136°	116°-147°

Most of the specimens in the collections (seventy) are from Kakwa Lake but the specimens from the Ancient Wall (ten) show no difference in size range or proportions. There are very few specimens with a length less than 15 mm among the collections and the largest specimen has a length of 32.1 mm. There is a definite tendency for the width and the thickness to increase proportionately to the length with increasing size; the apical angle shows a similar increase. There is very much less tendency for the degree of inflateness of a shell to vary independently from size and there is less variation in the growth stage at which costation begins than in *Ladogioides pax*. Nevertheless the development of an acuminate shell with recurved tongue is not entirely dependent on size. For instance hypotype A (Pl. XII, figs. 3a-e) with a length of 31.6 mm, has a moderately high tongue which is scarcely recurved and cannot have passed through a stage in its growth when it resembled hypotype D (Pl. XI, figs. 3a-f), length 27.1,

with a highly acuminate form and strongly recurved tongue. The two specimens, hypotypes B and C, have almost identical widths and lengths (*see* table of dimensions) yet their heights differ by more than 20 per cent. The shape of the tongue of hypotype B (Pl. XII, figs. 2a-d) is low, rounded and scarcely recurved, whereas that of hypotype C (Pl. XI, figs. 4a-c, and Pl. XII, figs. 1a, b) is high, acuminate and strongly recurved.

These observations reinforce the belief that conclusions drawn from comparisons of means of populations or size groups may mask an inherent variability which in itself may be a meaningful taxonomic character.

Discussion. *L. kakwaensis* may be distinguished from *L. pax* by the following features: (1) Shells of comparable length are wider and more inflate with a larger apical angle. (2) Appearance of costation is less variable and there are no large shells that are smooth or almost smooth as in *L. pax*. (3) The interareas and beak ridges are more prominent. (4) The muscle impressions and pallial sinuses are much more strongly impressed. Pallial markings are noticeable on every internal mould among the collections, whereas they are rarely seen in *L. pax*. (5) There is much less variation in shape in relation to size increase and in length of shell at which costae first appear.

The species is not easily confused with any other known species of rhynchonelloid. Some specimens bear a superficial resemblance to *Hypothyridina cameroni* Warren but they are easily seen to be generically distinct on external as well as internal characters.

McLaren (1958) assigned the species to the genus *Ladogia* on the basis of close similarity in external form between *L. kakwaensis* and *Ladogia meyendorfi* (de Verneuil), the type species of that genus. As has been shown above, the genera are quite distinct internally.

Occurrence. *Ladogioides kakwaensis* occurs abundantly in beds assigned to the Flume formation at Kakwa Lake in the Rocky Mountains of British Columbia and in the lower Cairn formation, at the Ancient Wall, Jasper Park, Alberta. Specimens have been examined from numerous localities within these two areas, including: GSC loc. 19971, 35100, 35101, 35102.

Genus *Leiorhynchus* Hall, 1860

Type species: *Orthis quadracostata* Vanuxem, 1842. (For full synonymy and description *see* Sartenaer, 1961b.)

Discussion. Sartenaer's full description and discussion of the type species allows this important genus to be used with a confidence hitherto lacking. Large numbers of species have been assigned to it on somewhat slender evidence, and more than one genus erected for species which may now be assigned to *Leiorhyn-*

chus. The genus may be characterized by its inflate elongate oval to subpentagonal form, strongly incurved beak, maximum thickness at or posterior to mid-length, low fold of medium to narrow width, smooth umbones, and relatively weak bifurcating costae developed on fold and flanks. Internally there are weak, ventrally approximating dental plates, narrow teeth, divided impersistent hinge plates, shallow septalium, and strong median septum.

Of these characters, the most variable are (1) the degree of development of dental plates, which persist forward to articulation only as small ridges below the developing teeth, and which may be very weakly developed or absent as fully formed plates extending to the floor of the valve; (2) the hinge plates, which may be well formed and persist forward almost to the plane of articulation or which may break up close to the posterior end of the valve into inner socket ridges and strong crural bases; (3) the degree of secondary thickening of the shell and cardinalia both between species and between individuals of one species, and which is at least partly dependent on size.

Nudirostra Cooper and Muir-Wood, 1951 is an objective synonym of *Leiorhynchus* (see Sartenaer, 1959).

Five species are recognized in the region under study. These are, in stratigraphic order of occurrence:

L. carya

L. russelli

L. castanea, *L. awokanak*

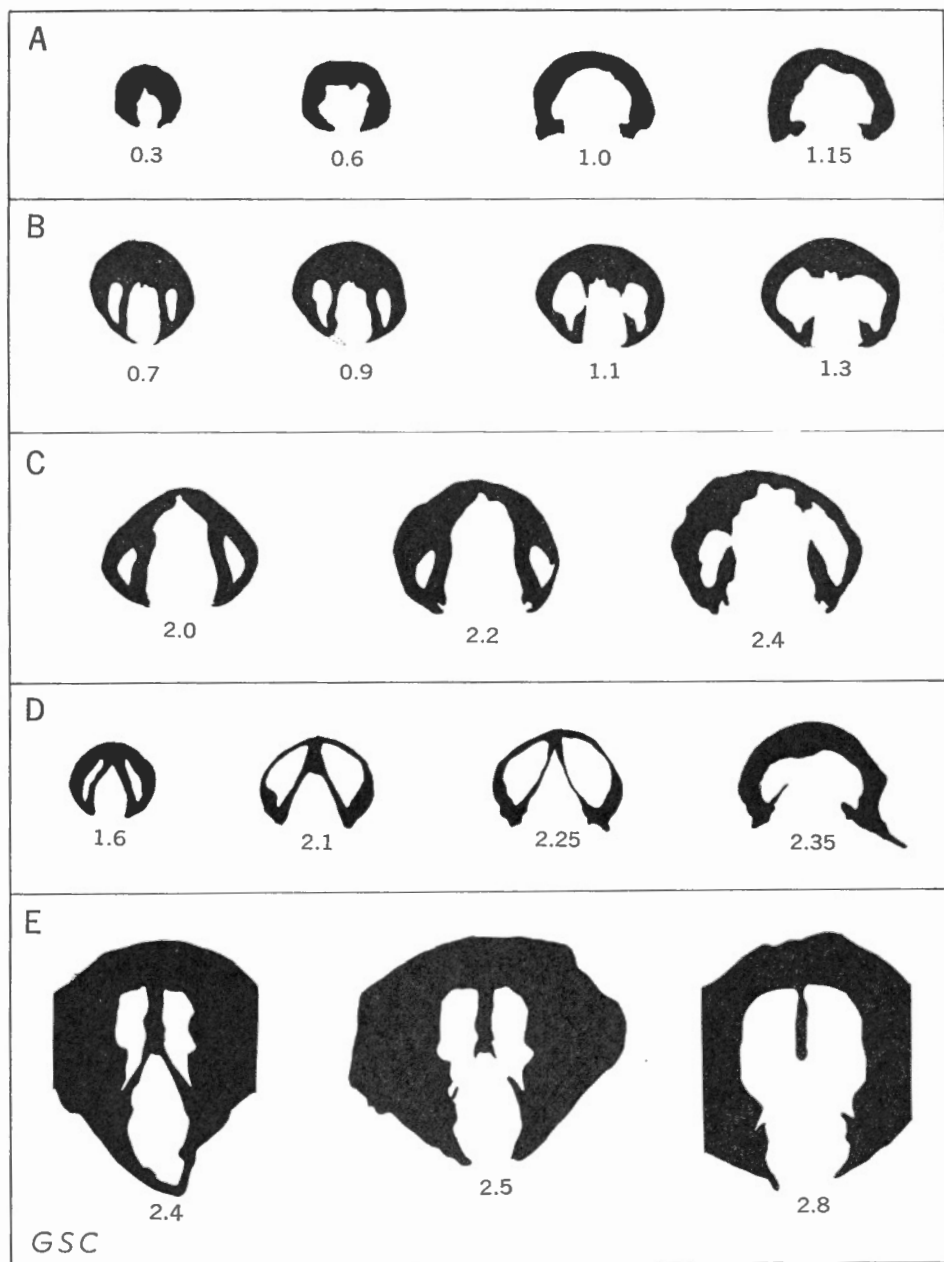
L. manetoe

These species display a morphological series of changes affecting the dental plates and summarized on the accompanying diagram (Fig. 22). In *L. manetoe*, the earliest species in the region, the dental plates join ventrally to form a strong bifid septal process which persists a short distance into the shell after the plates have become detached from it. In *L. castanea* a similar but lower and more weakly developed process is formed which ends at the point where the dental plates become detached. In *L. awokanak*, a species which occurs with *L. castanea*, no such process is formed, the dental plates approximate ventrally, but do not join.

In *L. russelli*, a basal Upper Devonian species, the dental plates approximate ventrally more weakly and show a tendency to break up closer to the beak than in the previous species. Finally in *L. carya*, the youngest species, true dental plates do not appear to be developed and are represented only by ridges on the side of the shell beneath the teeth.

It is of interest to note that *L. quadracostatus*, a basal Upper Devonian species, displays approximately the same development of dental plates as *L. awokanak* (late Middle) or *L. russelli* (early Upper Devonian).

The range of the genus in Western Canada, therefore, is from late-early Middle Devonian (upper Eifelian) to mid-early Upper Devonian (middle Frasnian).



Figures 22A-E. *Leiorhynchus*. Camera lucida drawings of serial transverse sections of pedicle valves to show morphological series of changes affecting the dental plates, $\times 4$ (approximately); distances are in mm forward from the crest of the umbo.

22A. *L. carya* Crickmay, hypotype F, GSC No. 15215.

22B. *L. russelli* n. sp., paratype J, GSC No. 15205.

22C. *L. awokanak* n. sp., paratype G, GSC No. 15349.

22D. *L. castanea* (Meek), hypotype R, GSC No. 15375.

22E. *L. manetoe* n. sp., paratype H, GSC No. 15719.

Leiorhynchus manetoe n. sp.

Plate XIII, figures 1-7; Plate XIV, figure 1; Figure 23

Material. Holotype, GSC No. 15711. "Nodular weathering beds between 800 and 810 feet below the top of the Nahanni formation in the southern Manetoe Range, approximately latitude $61^{\circ}49'$ and longitude $125^{\circ}05'$, N.W.T." GSC loc. 42016; collector A. E. H. Pedder, Triad Oil Company Limited, 1960.

Paratype A, GSC No. 15712. Headless formation talus, from between 1,007 and 1,367 feet below the top of the Nahanni formation, in creek flowing through western part of Iverson Range, about 8 miles south of West Iverson Lake; latitude $62^{\circ}10'$, longitude $124^{\circ}44'$. GSC loc. 32652; collector P. Harker, 1957.

Paratype B, GSC No. 15713.

Paratype C, GSC No. 15714.

Paratype D, GSC No. 15715.

Paratype E, GSC No. 15716.

Paratype F, GSC No. 15717.

Paratype G, GSC No. 15718. Internal mould, shell removed to show internal structure.

Paratype H, GSC No. 15719. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Figs. 22E, 23).

Paratypes B to H inclusive are from the same horizon and locality as the holotype.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	33.4	33.4	37.8	27.9	130°
Paratype A		19.8	26.5	14.7	
Paratype B		24.5	30.4	18.0	
Paratype C	28.2	27.3	29.6	22.2	121°
Paratype D	29.3	28.0	30.3	19.2	128°
Paratype E	32.1	32.1	34.0	24.4	122°
Paratype F	37.0	37.0	38.9	30.4	125°
Paratype G (internal mould)	31.9	31.9	35.0	27.8	128°
Paratype H (sectioned)			29.0	23.6	122°

Description. Medium to large-sized *Leiorhynchus*; rounded subpentagonal to elliptical, width greater than length to subequal in large specimens; greatest width forward of mid-length; hinge-line nearly straight, less than half shell width, apical angle about 125 degrees. Inflate, greatest thickness at or posterior to mid-length. Most of shell irregularly costate, umbones smooth.

The pedicle valve is shallow, smoothly convex, but nearly flat as posterolateral margins. The sulcus is broad and shallow, beginning about mid-length, and

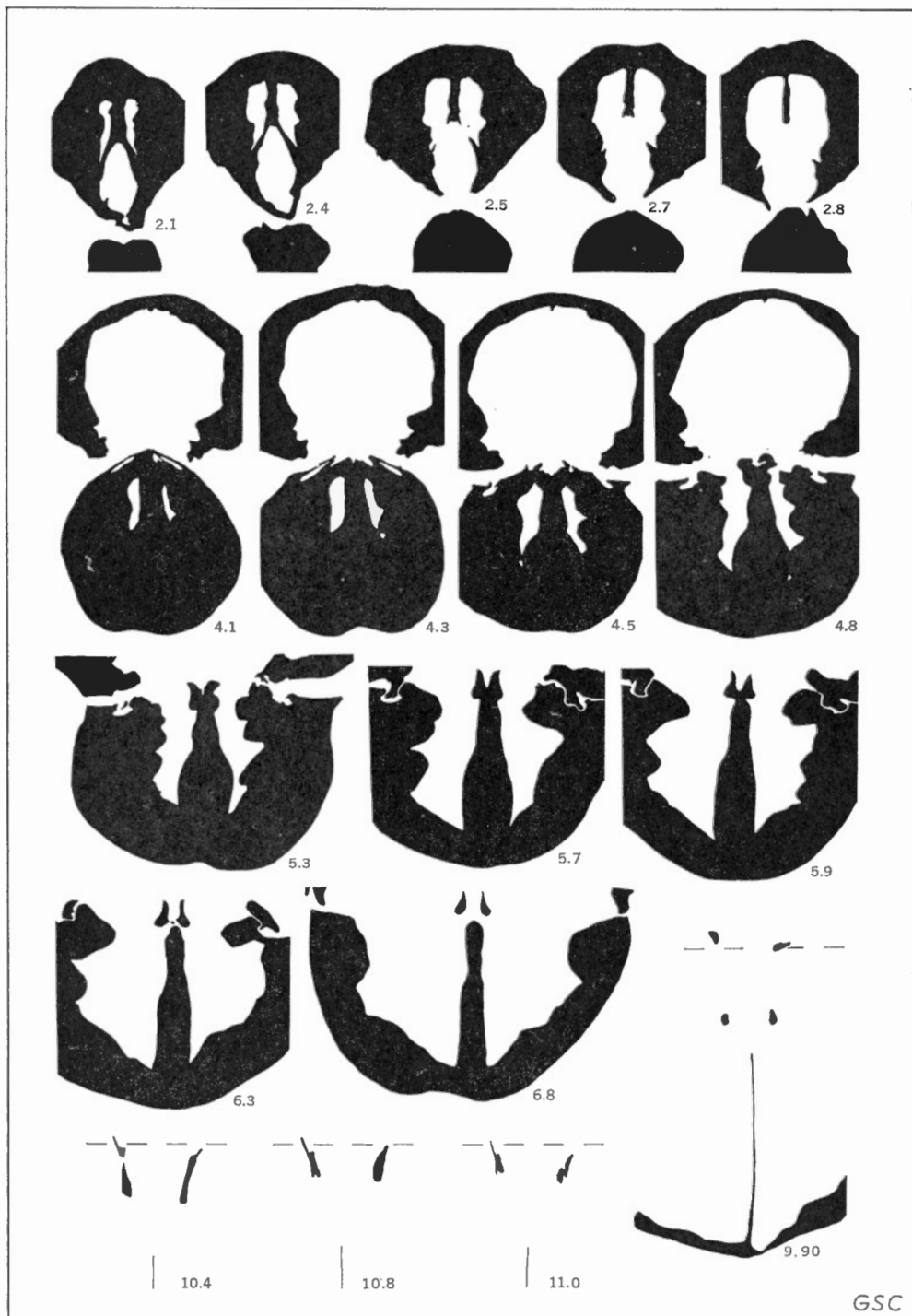


Figure 23. *Leiiorhynchus manetoe* n. sp. Camera lucida drawings of serial transverse sections x3; distances are in mm forward from the crest of the umbo; paratype H, GSC No. 15719.

ending in a broad flat tongue with a rounded anterior margin. The beak is strongly incurved and the interareas entirely concealed.

The brachial valve is inflat and domed. On large shells it projects posteriorly to overhang the pedicle beak. The fold is broad and low and develops only forward of mid-length. It falls anteriorly to meet the tongue of the pedicle valve approximately at right angles. The beak is incurved and hidden by the pedicle beak.

The ornament consists of well-developed rounded costae that are broader than the interspaces between. The umbones are smooth but costation begins a short distance forward and most of the shell is ornamented. The costae commonly bifurcate on fold, rarely on flanks. There are four to seven costae on the fold at the front margin and between five and nine on each flank. They commonly alternate between valves at the anterior margin and produce a weakly crenulate commissure. Closely spaced fine growth lines are visible near the front of well-preserved specimens. The costae are strongly impressed on the interior of the shell.

In the pedicle interior weak dental plates enclose a wedge-shaped delthyrial cavity proximally, but persist forward to articulation only as sharp ridges on the lateral wall of the shell below the developing teeth. The dental plates unite ventrally close to the apex of the beak and form a stout bifid septal process which persists after the plates have become detached dorsally. This process appears high in section due to the angle at which the incurved beak is cut (*see* paratype G, Pl. XIII, fig. 7). It ends close to the beak and a low ridge persists on the floor of the valve forward of the plane of articulation. The teeth are small, slender, and outwardly directed, they are supported by the shell margin. The muscle impressions form a broad longitudinally striated, rounded, pentagonal area, pointed posteriorly and truncated anteriorly, ending just posterior to shell mid-length.

In the brachial interior, hinge plates are scarcely developed and break up into stout inner socket ridges and crural bases posterior to the plane of articulation. The shallow cruralium is almost entirely filled with secondary material. It is supported by a stout bifid median septum which remains in contact with the heavy wedge-shaped crural bases up to articulation. The septum thins abruptly forward of the disappearance of the teeth and continues as a slender high lamella nearly to shell mid-length. The crura are weakly trough-shaped and develop forwards into stout, slightly recurved, vertical, lamellae. There is considerable secondary thickening of the interior of the shell wall and of the cardinalia in the mature specimens that were sectioned. Adductor impressions are weakly impressed, but appear to be elongate and narrow on either side of the median septum. They terminate forwards at about shell mid-length. Pallial markings are weakly developed on the brachial valve and appear to parallel the internal trace of the costae.

Growth and Variation (20 specimens).

Changes in mean proportion during growth:

	Length					
	Less than 28 mm		28.0 to 31.9 mm		32 mm and more	
	mean	range	mean	range	mean	range
Width/length	1.14	1.08-1.17	1.10	1.04-1.18	1.04	0.94-1.13
Thickness/length	0.82	0.69-0.97	0.82	0.66-0.96	0.80	0.71-0.84
Apical angle	122°	118°-124°	126°	120°-131°	124°	118°-130°

The smallest specimen in the collection has a length of 25.0 mm, and the largest 37.0 mm. Young and immature individuals are therefore unknown. Within the size range represented, the smaller specimens are more transversely elliptical than the large, in which the width/length ratio approximates unity. There appear to be no appreciable changes in thickness/length proportions, nor in the apical angle. The large shells are, however, considerably more inflate than the smaller, and the thickness/width ratio increases with size.

The most variable feature of the species is the development of costation. Costae on the fold may be wide and unbranched, normally totalling four. On other shells one or more may bifurcate at or posterior to mid-length, producing a maximum of seven at the front margin. Costae on the flanks bifurcate more rarely but vary considerably in size between shells of equal dimensions. On a few specimens the costae on one flank are smaller and more numerous than those on the other and the number developed on each flank is commonly unequal.

Discussion. The species is characterized by its inflate subpentagonal shell, and the strong development of irregular bifurcating costae, which begin close to the beak. Internally, in section, the appearance of a stout septal process formed by the ventral confluence of the dental plates, close to the beak in the pedicle valve may be characteristic, but it is essentially an extreme development of a tendency observable in other species of *Leiorhynchus*, (see, for instance, *L. castanea*, hypotype R, Fig. 22D). The height of the process is at least partly due to the oblique angle of section of the incurved beak, but is, nevertheless, a prominent feature on an internal mould (paratype G, Pl. XIII, fig. 7).

L. manetoe may be distinguished from other species of *Leiorhynchus* by its large size, robust subpentagonal shell, and strongly developed ornament. The smallest specimens in the collection are strongly transverse, an unusual feature in the genus, although the juvenile form is unknown. *L. castanea*, a species which occurs in the same region at a higher horizon, is readily distinguished by its more elongate form and weakly developed costation.

Apart from one poorly preserved specimen from near West Iverson Lake, the species is known only from the Headless formation of the southern Manetoe Range; GSC loc. 32652, 42016.

The species is named from the Manetoe Range, Northwest Territories.

Leiorhynchus castanea (Meek)

Plate XIV, figures 2-7; Plate XV, figures 1-11; Plate XVI, figure 1;
 Figures 24, 25A, B

1867. *Rhynchonella castanea* MEEK, pp. 93-95, Pl. XIII, figs. 9a-c.
 1884. *Rhynchonella castanea* Meek, WALCOTT, pp. 153-155, Pl. XV, figs. 1, 1a, 4, 4a.
 1952a. *Leiorhynchus castanea* Meek, CRICKMAY, Pl. 70, figs. 6, 7.
 1952b. *Caryorhynchus castanea* Meek, CRICKMAY, p. 1.
 1956. *Caryorhynchus castanea* (Meek) (var.), WARREN and STELCK, Pl. VIII, figs. 29-31.
Caryorhynchus castanea (Meek), WARREN and STELCK, Pl. IX, figs. 12-16.
 1960. *Caryorhynchus hippocastanea* CRICKMAY, p. 13, Pl. IX, figs. 10-17.

Material. Here chosen as lectotype *Rhynchonella castanea* Meek, USNM No. 5890, the specimen figured by Meek (1867) on Plate XIII, figures 9a, b, and c. In his description, Meek gave the dimensions of a medium-sized specimen (p. 94) as length, 0.96 inch [24.0 mm]; breadth, 0.79 inch [17.5 mm]; and convexity, 0.60 inch [15.0 mm]. The dimensions of the lectotype (measured from a plaster cast of the U.S. National Museum specimen) are length 20.6 mm, width 19.5 mm, thickness 15.2 mm.

Hypotype A, GSC No. 15358. "Upper 2 feet of Lower Ramparts or Hume formation, from grey argillaceous limestone on east bank of Andrew River, 4 miles south of junction with Carnwath River, N.W.T." GSC loc. 41060; collector R. deWit, J. C. Sproule and Associates, 1959.

Hypotype B, GSC No. 15359. "Same locality as Hypotype A, from lower beds of middle Ramparts or Hare Indian formation." GSC loc. 41327; collector G. V. Lloyd, J. C. Sproule and Associates, 1959.

Hypotype C, GSC No. 15360. Calcareous shale and shaly limestone in the lowest 15 feet of the Hare Indian formation, Anderson River, between latitude 68°28' and 68°32', and longitude 127°04' and 127°24', Northwest Territories. GSC loc. 41319; collector A. E. H. Pedder, Triad Oil Company Limited, 1959.

Hypotype D, GSC No. 15361. Same horizon and locality as hypotype A. GSC loc. 41076; collector G. P. E. White, J. C. Sproule and Associates, 1959.

Hypotype E, GSC No. 15362. "From a 2-foot limestone bed in the Fort Creek shale about 25 feet above the contact with the Beavertail limestone, east side of mouth of canyon on Carcajou River"; approximately latitude 64°58', longitude 127°12', Northwest Territories. GSC loc. 7240; collector G. S. Hume, 1922.

Hypotype F, GSC No. 15363. "Beavertail limestone, 20 to 30 feet below contact with Fort Creek shale, north end of Wolverine anticline, Carcajou Ridge, N.W.T." (from section described by Hume, 1923, p. 57B). GSC loc. 7237k; collector G. S. Hume, 1922.

Hypotype G, GSC No. 15364. "Eleven to twelve feet above base of Fort Creek formation, in interbedded limestone and shale in Dodo Canyon, along east side of Canol Road where it leaves Mackenzie Mountains front"; approximately latitude 65°01', longitude 127°18', N.W.T. GSC loc. 39675.

Hypotype H, GSC No. 15365. "In shale . . . underlying Hare Indian and Ramparts formations at Gayna River, tributary of Mountain River, N.W.T." GSC loc. 38687; collector Alfred Lenz, 1959.

Hypotype I, GSC No. 15366. Highest bed exposed of the Nahanni formation, in a 15-foot unit of grey, well-bedded limestone, exposed in creek flowing through the western part of the Iverson Range, about 8 miles south of West Iverson Lake, latitude $62^{\circ}10'$, longitude $124^{\circ}44'$, Northwest Territories. GSC loc. 32644; collector P. Harker, 1957.

Hypotype J, GSC No. 15367. Same horizon and locality as hypotype I.

Hypotype K, GSC No. 15368. Same horizon and locality as hypotype I.

Hypotype L, GSC No. 15369. Upper foot of Nahanni formation, in tributary to north fork of Root River, latitude $63^{\circ}08'$, longitude $125^{\circ}44'$, Northwest Territories. GSC loc. 33982; collector B. R. Pelletier, 1957.

Hypotype M, GSC No. 15370. Same horizon and locality as hypotype L.

Hypotype N, GSC No. 15371. Black bituminous limestone of Pine Point formation, half a mile west of Pine Point, south shore of Great Slave Lake, Northwest Territories. GSC loc. 5675; collectors E. J. Whittaker and E. M. Kindle, 1917.

Hypotype O, GSC No. 15372. Brown nodular argillaceous limestone of the Horn River formation (upper part of Unit 13, Douglas and Norris, 1960), on Clive River, tributary to Willowlake River, latitude $62^{\circ}50'$, longitude $119^{\circ}48'$, Northwest Territories. GSC loc. 30641; collector D. J. McL., 1957.

Hypotype P, GSC No. 15373. Drift boulder of Pine Point formation, Windy Point, north shore of Great Slave Lake, Northwest Territories. GSC loc. 12801; collector Imperial Oil Limited, 1919.

Hypotype Q, GSC No. 15374. Same horizon and locality as hypotype N.

Hypotype R, GSC No. 15375. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 24). Same horizon and locality as hypotype C.

Hypotype S, GSC No. 15376. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 25B). Brown nodular argillaceous limestone of the Horn River formation (upper part of Unit 13, Douglas and Norris, 1960), on Clive River, tributary to Willowlake River, latitude $62^{\circ}50'$, longitude $119^{\circ}43'$, Northwest Territories. GSC loc. 30656; collector D. J. McL., 1957.

Hypotype T, GSC No. 15377. Plaster replica and anterior part of specimen, remainder serial sectioned (illustrated, Fig. 25A). Same horizon and locality as hypotype S.

Hypotype U, GSC No. 15378. Natural internal mould. "Basal Fort Creek sandstone, 135 feet above upper Ramparts limestone, in small stream cut one mile northeast of northeast bank of Mackenzie River, latitude $66^{\circ}46'30''$, longitude $129^{\circ}52'$, N.W.T." GSC loc. 41154; collector D. L. Campbell, J. C. Sproule and Associates, 1959.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
<i>Anderson River region</i>					
Hypotype A	18.6	17.9	18.7	11.0	123°
Hypotype B	20.1	20.1	21.4	14.0	124°
Hypotype C	21.5	21.5	18.4	16.3	114°
Hypotype D	23.3	23.3	21.4	17.5	109°
<i>Central Mackenzie River region</i>					
Hypotype E	21.5	20.5	21.0	15.3	110°
Hypotype F	24.3	24.3	21.6	19.2	108°
Hypotype G	24.7	24.7	22.4	20.2	125°
Hypotype H	26.2	26.2	26.5	18.6	113°
<i>Nahanni Rivers region</i>					
Hypotype I	15.7	15.0	16.2	9.1	110°
Hypotype J	18.6	18.2	19.0	12.0	127°
Hypotype K	21.4	21.0	20.3	13.7	123°
Hypotype L	23.6	23.2	20.6	18.0	106°
Hypotype M	25.8	25.8	25.6	19.8	117°
<i>Great Slave Lake region</i>					
Hypotype N	19.9	18.6	17.9	13.6	99°
Hypotype O	21.4	20.8	21.6	15.0	119°
Hypotype P	23.5	23.5	21.8	17.4	118°
Hypotype Q	30.8	30.8	29.3	21.4	121°
<i>Specimens serial sectioned</i>					
Hypotype R	18.1	18.1	17.3	14.0	114°
Hypotype S			20.0	(15.2)	126°
Hypotype T	23.6	23.4	22.2	19.1	117°
<i>Internal mould</i>					
Hypotype U	23.0	21.8	20.0	14.8	111°

Description. Medium to large sized *Leiorhynchus*; rounded subpentagonal to longitudinally elliptical in outline, length greater than width to subequal; greatest width at or forward of mid-length; hinge-line obtuse angled, less than half shell width, apical angle between about 115 and 120 degrees. Strongly inflate with posteriorly protruding dorsal umbo, greatest thickness posterior to mid-length. Fold and sulcus weakly costate, flanks smooth to weakly costate.

The pedicle valve is strongly convex near the umbo, becoming more weakly curved anteriorly and towards the flanks. The sulcus begins about mid-length. It is commonly less than half shell width at its broadest, flat-bottomed, and extends into a low, truncated, anteriorly directed tongue. The beak is strongly incurved, and the interareas small and narrow or concealed.

The brachial valve is strongly inflate and domed. In mature shells it projects posterior to the pedicle beak. Its maximum height lies increasingly posterior to mid-length with increase in size. The fold is of narrow to medium width and develops only forward of mid-length. It falls anteriorly and meets the tongue

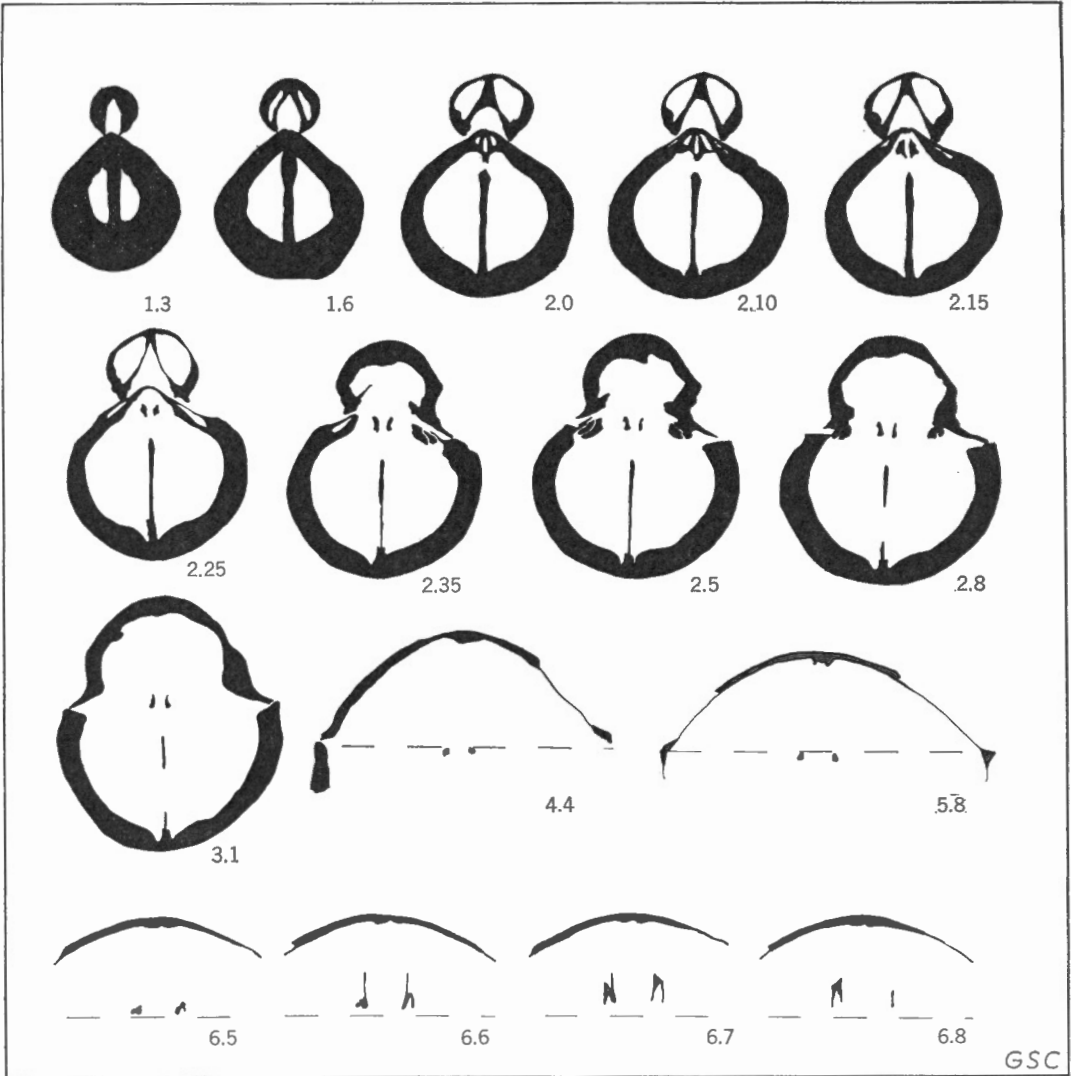
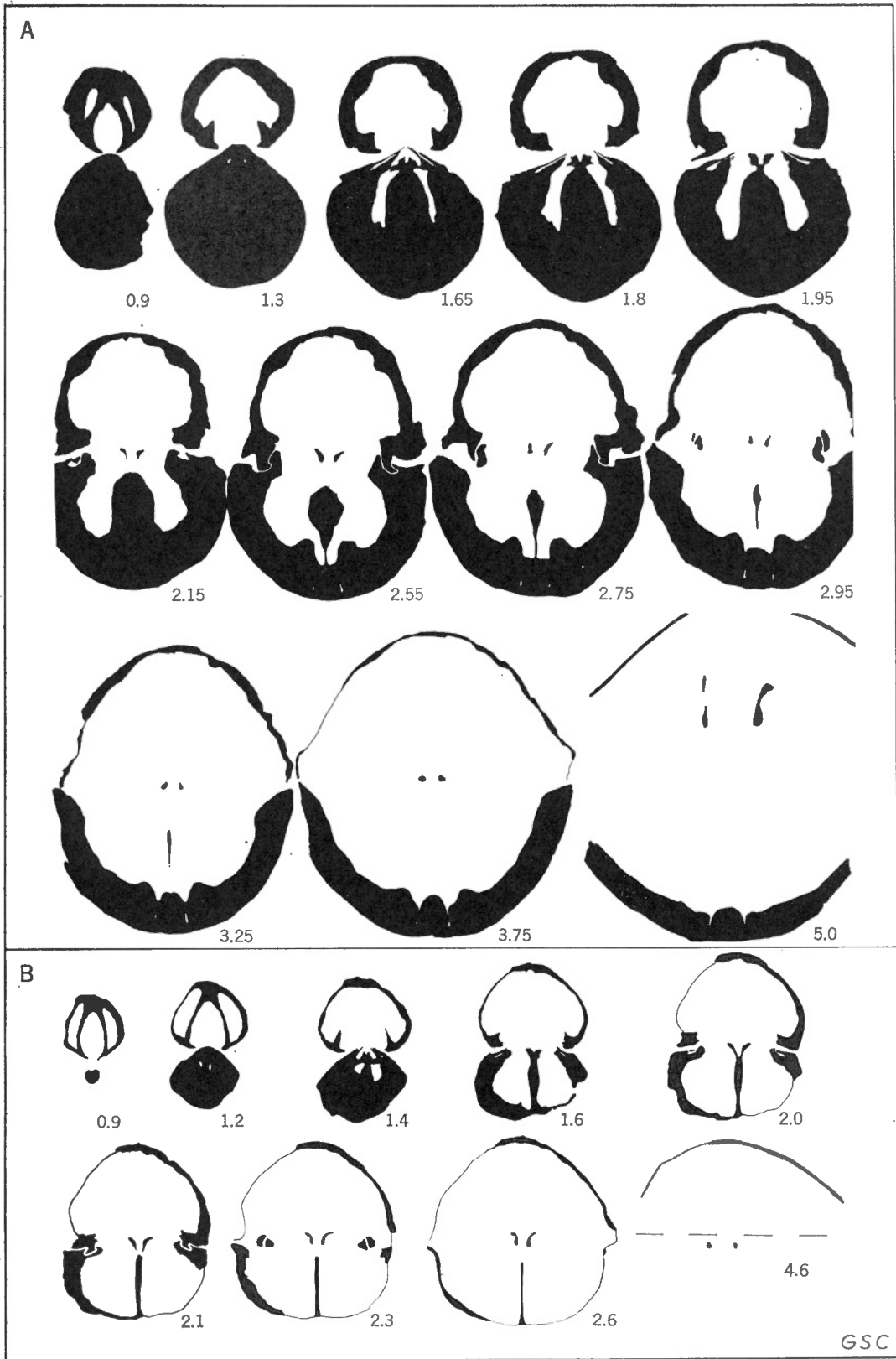


Figure 24. *Leiorhynchus castanea* (Meek). Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; hypotype R, GSC No. 15375.

approximately at right angles. The beak is incurved and hidden by the beak of the pedicle valve.

The shell is smooth posteriorly. The fold is weakly costate anteriorly, the costae, beginning at about mid-length, may bifurcate; there are from three to seven at the front margin, commonly four or five. About half the shells are smooth on the flanks; on the remainder there are four to seven weak costae anteriorly, which may occasionally bifurcate. The costae are low and convex with narrow interspaces and are of irregular size. The anterior commissure is



Figures 25 A, B. *Leiiorhynchus castanea* (Meek). Camera lucida drawings of serial transverse sections $\times 3$, distances are in mm forward from the umbo; 25A, hypotype T, GSC No. 15377; 25B, hypotype S, GSC No. 15376.

Rhynchonelloid Brachiopods from Western Canada

weakly and irregularly crenulate. Fine growth lines are rarely seen on the anterior part of the shell. The costae are weakly impressed on the interior of the shell.

In the interior of the pedicle valve, weak dental plates enclose a V- or U-shaped delthyrial cavity close to the beak but become detached from the floor of the valve well posterior to the plane of articulation. They persist forward as ventrally directed ridges on the lateral wall of the shell below the developing teeth. Near the beak the dental plates unite ventrally to form a raised process slightly elevated above the valve floor. The teeth are slender and outwardly directed and supported by the inner margin of the shell. The muscle impressions form an elongate oval area, pointed posteriorly and rounded anteriorly, that extends about one quarter of the shell length forward of the beak.

In the brachial interior the hinge plates break up early into inner socket ridges and crural bases. The crural bases may remain in contact with the median septum to form a V-shaped septalium. The median septum is long, bifid, and slender in small specimens. It becomes heavily invested with secondary material in larger shells and is broad based posteriorly, club-shaped anteriorly. It persists a short distance forward of articulation. The crura are slender, rounded posteriorly, trough-shaped and ventrally curved anteriorly. The posterior adductor impressions are elongate oval and strongly impressed on each side of the median septum. Anteriorly they enclose the posterior end of a smaller pair of impressions just forward of the septum, and separated medianly by a low rounded ridge. The anterior impressions end forward at about mid-length of the shell. Pallial markings are weak or obscure on both valves.

Growth and Variation (112 specimens).

Changes in mean proportion during growth:

Anderson River Region (28 specimens from loc. 41327)

	Length							
	Less than 19 mm		19.0 to 20.9 mm		21.0 to 22.9 mm		23 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.03	0.98-1.10	1.01	0.93-1.08	0.91	0.78-1.04	0.93	0.86-0.99
Thickness/length	0.68	0.63-0.73	0.69	0.59-0.79	0.76	0.64-0.83	0.73	0.61-0.82
Apical angle	114°	108°-118°	116°	111°-124°	115°	109°-124°	118°	113°-122°

Central Mackenzie River Region (22 specimens from loc. 39709)

	Length					
	Less than 23 mm		23.0 to 24.9 mm		25 mm and more	
	mean	range	mean	range	mean	range
Width/length	0.96	0.87-1.11	0.94	0.88-0.98	0.91	0.82-1.01
Thickness/length	0.76	0.67-0.81	0.74	0.66-0.91	0.73	0.70-0.76
Apical angle	116°	110°-122°	116°	108°-128°	115°	99°-131°

Nahanni Rivers Region (41 specimens from loc. 32644)

Length										
	less than 17 mm		17.0 to 18.9 mm		19.0 to 20.9 mm		21.0 to 22.9 mm		23 mm and more	
	mean	range	mean	range	mean	range	mean	range	mean	range
Width/length	1.01	0.94-1.05	1.03	0.99-1.11	1.00	0.89-1.12	0.96	0.84-1.02	0.95	0.87-1.00
Thickness/length	0.55	0.50-0.60	0.63	0.59-0.74	0.68	0.62-0.75	0.70	0.63-0.76	0.71	0.65-0.79
Apical angle	112°	104°-118°	118°	103°-127°	120°	113°-126°	117°	110°-125°	117°	112°-124°

Great Slave Lake Region (21 specimens from loc. 30656)

Length						
	Less than 21 mm		21.0 to 22.9 mm		23 mm and more	
	mean	range	mean	range	mean	range
Width/length	0.96	0.89-1.05	0.99	0.90-1.12	0.98	0.88-1.06
Thickness/length	0.80	0.66-0.95	0.72	0.66-0.80	0.71	0.66-0.82
Apical angle	122°	119°-129°	120°	108°-130°	122°	116°-130°

The collections from the four main regions listed above total about 500 specimens. The mean sizes of collections from different localities vary widely. As the type specimen of Meek's species, from Carnwath River (Lockhart River in Meek's 1867 report), is small relative to many specimens from other areas, it has been necessary to examine the growth of representative populations from each of the main regions of occurrence in the Northwest Territories, in order to confirm that the same species is present in each region.

The mean pattern of growth in each region is closely similar. The proportionate width decreases with increasing length, the thickness/length ratio increases in specimens up to about 21 mm long and then remains approximately constant, and the thickness relative to width increases with growth. The apical angle remains approximately constant.

Every population varies within wide limits, two main variants or end members being distinguishable. Some shells become increasingly transverse and sub-pentagonal in outline with almost straight postero-lateral margins, e.g. hypotypes, B, E, H, M, O, and Q. Others become longitudinally oval with smaller proportional width and strongly inflate brachial valves which protrude posteriorly, e.g. hypotypes C, F, G, L, and P. The lectotype tends towards this type of development. Smaller shells, with a length of about 20 mm or less do not show this variability, and all tend to be transverse, subpentagonal or rounded, with brachial valves weakly or moderately inflate, and protruding pedicle beaks, e.g. hypotypes A, I, J, N. The transverse subpentagonal variant is presumably a shell that

retains youthful features while attaining normal adult size; the oval inflate variant is the normal mature form of the species which may be reached at widely differing sizes.

In common with many rhynchonelloid brachiopods, mature form is only weakly correlated with size and, as in other species, shells of the same size may differ widely in their "maturity". Although in each region both variant forms commonly occur in the same fossil population, a few collections show a preponderance of one or the other. This phenomenon may be related to environment, rapid growth tended to prolong youthful features, whereas slow growth led to smaller shells possessing mature outlines.

Environment also controls absolute size and from some localities in the middle Mackenzie River region very large specimens are known with lengths of 30 to 35 mm, notably Carcajou Ridge (GSC locs. 3991 and 7237k), Ontarotue River (GSC loc. 41158), and Upper Hume River (GSC loc. 39826). Poorly preserved specimens of comparable size are also known from the Pine Point formation in the Great Slave Lake area (GSC locs. 5682 and 12801). The proportions of these specimens fall within the developmental growth ranges outlined above.

Discussion. The distinguishing characters of *Leiorhynchus castanea* may be summarized: (1) the highly domed brachial valve which protrudes beyond the pedicle beak; (2) the weak bifurcating costae, developed only towards the front of the shell; (3) the development, in mature shells, of an elongate oval outline; (4) the narrow steep-sided fold which falls to the front margin and meets the tongue of the sulcus approximately at right angles. Internally, most shells possess a low process formed by the ventral joining of the dental plates with secondary shell growth between.

The species is comparable with *L. quadracostatus* (Vanuxem) in general outline (see Sartenaer, 1961b). It differs primarily in the more weakly developed ornament present only on the anterior part of the shell, and more weakly developed costation on the flanks. Internally *L. quadracostatus* has better developed and more persistent hinge plates but is otherwise closely similar. There is nothing in *L. castanea* to suggest generic difference from the type species of the genus (cf. *Caryorhynchus* Crickmay, 1952b).

Caryorhynchus castanea (Meek) (var.) of Warren and Stelck 1956 and *Caryorhynchus hippocastanea* Crickmay (1960a) are large variants of *L. castanea* from Carcajou Ridge and vicinity, and fall well within the normal range of variation of the species.

The differences from *L. manetoe*, *L. awokanak*, *L. russelli*, and *L. carya* are summarized in the discussion of those species.

Occurrence. *Leiorhynchus castanea* occurs in the upper few feet of the lower Ramparts or Hume formation and basal beds of the middle Ramparts, or Hare Indian formation in the Anderson River area and in its tributaries, Carnwath and Andrew Rivers. In this area it is associated with *Cassidirostrum pedderi*. Specimens have been examined from GSC localities 41060, 41076, 41083, 41319, 41327.

The species is widespread in the central Mackenzie River region in the upper beds of the Hume (lower Ramparts) formation and the Hare Indian (middle Ramparts). Localities from which specimens have been examined include GSC loc. 38687, 39826, 39843, 39856, 40334, 40342, 40402. In the Carcajou River area south of Norman Wells the species has been reported from the highest beds of the "upper Ramparts" and "lower Fort Creek" formations. It is probable, however, that these beds represent the upper Hume and lower Hare Indian, and that the "upper Ramparts" or Kee Scarp formation (of Bassett, 1961) is there not present or poorly developed, as suggested by Bassett. These localities include GSC loc. 7240, 39675, and 39709. On Carcajou Ridge the species has been reported from the Beavertail formation by several workers (Hume, 1954; Bassett, 1961; and Parker in Canol Report Assignment 6, 1944). This formation was included in the upper Ramparts formation by Hume (1954) and the Kee Scarp formation by Bassett (1961). In at least one collection (GSC loc. 7237k), *L. castanea* occurs with *L. awokanak* and *Hadorhynchia sandersoni*. Other localities include GSC loc. 7237b, and 7237h. The possible interpretation of the occurrence is discussed elsewhere (p. 11). The species has also been collected in beds considered by the collector to be basal Fort Creek, overlying the "upper Ramparts formation" on Mackenzie River near the mouth of Ontaratue River, GSC loc. 41154.

Leiorhynchus castanea is found in black shaly limestones of the upper few feet of the Nahanni formation in the Nahanni Rivers region of the southern Mackenzie Mountains. Specimens have been examined from several localities including GSC loc. 26736, 26741, 32644, 33982.

In the Great Slave Lake region *Leiorhynchus castanea* occurs in the upper part of the Pine Point formation on the south and northwest sides of the lake and in the correlative Horn River formation on Clive River. Specimens have been examined from many localities including GSC loc. 5675, 5682, 12801, 30641, 30656, 31190.

The species has been collected from the base of the McDame group near the mouth of French River in McDame map-area, British Columbia; GSC loc. 32418.

In Nevada, *L. castanea* is reported (Nolan and others, 1956) to occur in the Woodpecker limestone member of the Nevada formation in the *Martinia kirki* zone (Merriam, 1940). This is overlain by the *Stringocephalus* zone which extends from the upper beds of the Woodpecker limestone through the overlying Bay State dolomite member.

Leiorhynchus awokanak n. sp.

Plate XVI, figures 2-7; Figures 26A, B

1940. [?] *Leiorhynchus* sp. a MERRIAM, Pl. 8, figs. 18, 19.

1956. *Nudirostra* sp. (= *Leiorhynchus* sp. A Merriam, 1940), WARREN and STELCK, Pl. IV, figs. 28-33.

Material. Holotype, GSC No. 15342. Pine Point formation; half a mile west of Pine Point, south shore of Great Slave Lake, Northwest Territories. GSC loc. 5675; collectors E. M. Kindle and E. J. Whittaker, 1917.

Rhynchonelloid Brachiopods from Western Canada

Paratype A, GSC No. 15343. Same horizon and locality as holotype.

Paratype B, GSC No. 15344. Pine Point formation; Pine Point, opposite centre island of Green Island group, south shore Great Slave Lake, Northwest Territories. GSC loc. 17391; collector J. A. Wallace, Socony-Vacuum Exploration Company, 1950.

Paratype C, GSC No. 15345. Pine Point formation; 2½ miles east of Pine Point, south shore of Great Slave Lake, Northwest Territories. GSC loc. 5681; collector E. J. Whittaker, 1917.

Paratype D, GSC No. 15346. Same horizon and locality as paratype B.

Paratype E, GSC No. 15347. Same horizon and locality as paratype C.

Paratype F, GSC No. 15348. Anterior part of specimen; remainder serial sectioned (illustrated, Fig. 26A). Pine Point formation, Pine Point, south shore of Great Slave Lake, Northwest Territories. GSC loc. 31061; collector A. W. Norris, 1957.

Paratype G, GSC No. 15349. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 26B). Same horizon and locality as holotype.

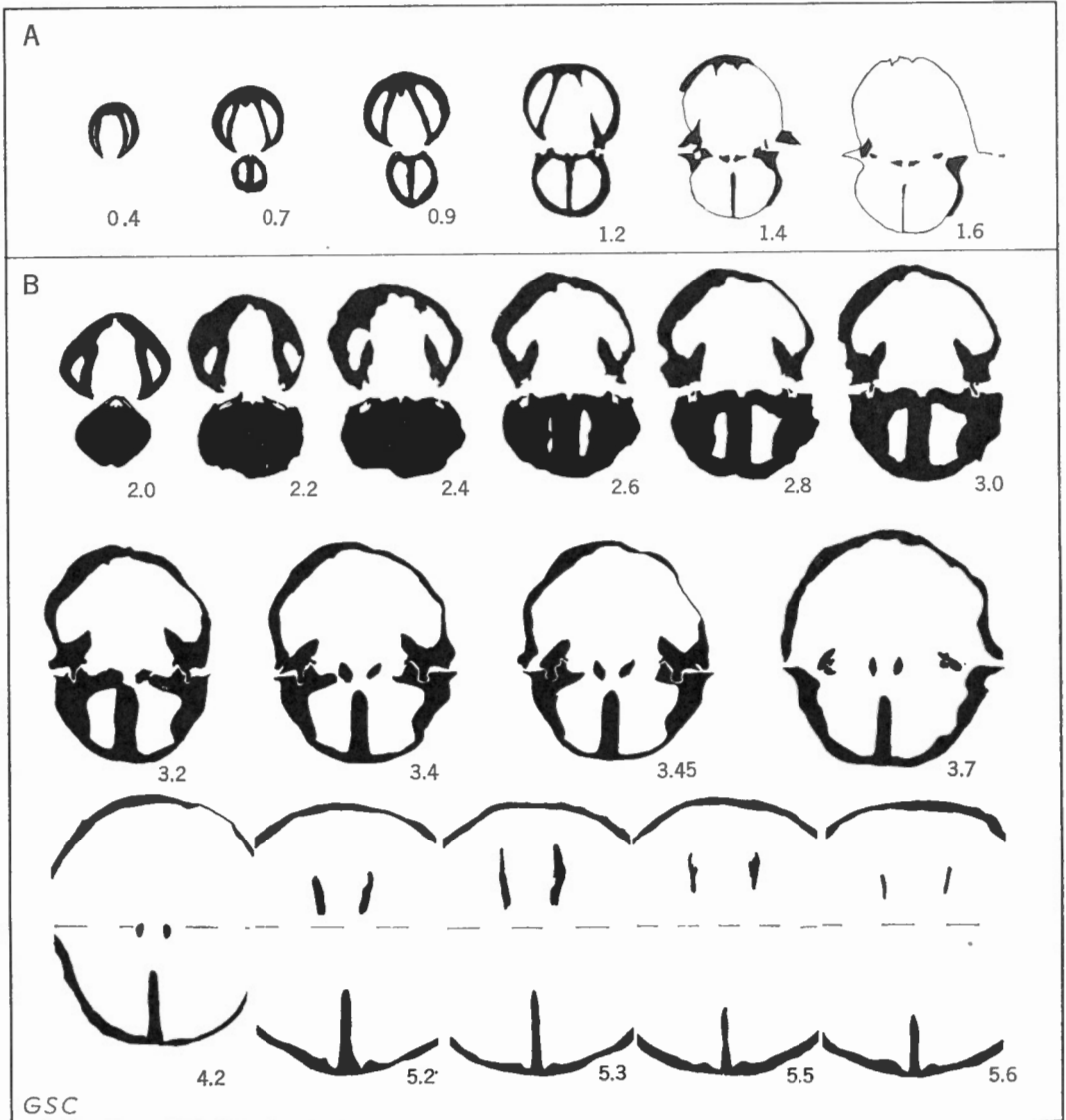
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	19.9	18.8	21.0	13.1	120°
Paratype A	(20.2)	20.0	23.1	15.0	116°
Paratype B	(17.4)	17.2	20.3	15.2	125°
Paratype C	16.8	15.9	19.1	11.4	119°
Paratype D	14.2	13.7	15.2	7.7	114°
Paratype E	9.2	8.5	8.7	3.6	97°
Paratype F (sectioned)	partly crushed small specimen				
Paratype G (sectioned)	20.1	18.9	20.3	13.9	109°

Description. Shell of medium size, transversely elliptical to subpentagonal, uniplicate; width greater than length; greatest width at mid-length; both valves convex, brachial valve more inflates than pedicle, to subequal; greatest thickness at or posterior to mid-length; hinge-line nearly straight; fold and sulcus developed anteriorly, narrow; variably costate, flanks commonly weakly costate.

Pedicle valve is weakly to moderately convex, strongly convex on umbo. The sulcus is narrow and shallow, and develops only on the front half of the shell. It extends into a low flat-topped tongue which protrudes forwards and is far from reaching the vertical on most shells. Its flanks are steep and weakly flared. The beak is strongly incurved and the interareas are narrow or concealed. As far as known, the foramen is small to minute and submesothyrid. Deltoidal plates were not seen.

Brachial valve is moderately to strongly convex with maximum height at or posterior to mid-length. It falls in a smooth curve towards the anterior commissure which it meets at a right angle or less. The fold is developed only on the anterior



Figures 26 A, B. *Leiorhynchus awokanak* n. sp. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; 26A, paratype F, GSC No. 15348; 26B, paratype G, GSC No. 15349.

third or half of the shell. It is low, flat topped, and steep sided. The beak is incurved and hidden by the pedicle beak. The umbo is inflatè but rarely protrudes behind the ventral beak.

The shell is smooth posteriorly, costate anteriorly, the costae develop from one quarter to three quarters of the shell length forward of the beaks. There are four or five low and broad, rounded, slightly irregular costae on the fold, with a

maximum of seven; some of them bifurcate; the interspaces are narrow. Each flank may have up to eight weak costae, with an average of about five. On some shells the costae are so weak as to be scarcely discernible. Growth lines are apparent near the anterior margin of some shells.

In the pedicle interior there are strong dorsally divergent dental plates which become detached from the floor of the valve posterior to the plane of articulation. The teeth are weak and supported up to articulation by the shell margin. The remnants of the dental plates persist as stout rectangular processes which support the teeth ventrally. A narrow adductor track is impressed on the shell as far as articulation; posteriorly it may be divided by a low stout ridge.

In the brachial interior the divided hinge plates are supported by a stout median septum which becomes detached at or just posterior to the plane of articulation. The septum persists forward for at least one third of the length of the shell. The thick hinge plates are persistent and divided by a shallow septalium; they are ventrally concave. They break up into strong inner socket ridges and crural bases beyond articulation. The crura are slender lamellae which plunge ventrally at about a quarter of the shell length forward. The narrow adductor impressions are bounded laterally by low ridges. The cardinalia, septum, and dental plates are characteristically very stout and the shell thick in mature shells; lateral cavities may be entirely filled posteriorly by secondary material.

Growth and Variation (23 specimens).

Changes in mean proportion during growth:

	Length					
	Less than 16 mm		16 to 19.9 mm		20 mm and more	
	mean	range	mean	range	mean	range
Width/length	1.01	0.95-1.07	1.09	0.99-1.19	1.09	0.98-1.18
Thickness/length	0.46	0.39-0.54	0.67	0.55-0.77	0.68	0.62-0.74
Apical angle	105°	97°-114°	113°	99°-123°	117°	103°-126°

Most of the specimens are large and thick shelled. There appears to be considerable variation between populations from different localities, some being relatively thin shelled and strongly ornamented, but invariably crushed. A few specimens are unusually inflat, e.g. paratype B, in which the tongue becomes almost vertical.

The development of costation is the most variable character. It is commonly restricted to the anterior one third of the shell although it may develop close to the beak, especially in thin-shelled specimens. The number of costae on both fold and flanks varies widely, three to seven on fold, zero to eight on each flank.

Discussion. The most characteristic features of the species are: (1) the transverse shell; (2) the narrow flattened fold developed only anteriorly; (3) the

steep-walled shallow sulcus with low flat-topped tongue; (4) the variable anterior costation.

It differs from *Leiorhynchus russelli* which it resembles in general form, in the narrow fold, the more steeply walled sulcus and the development of costation on the flanks, a feature relatively uncommon in *L. russelli*.

The species may be distinguished from *L. castanea* by its more transverse shell outline, and smaller, more numerous costae on the flanks. Internally hinge plates are more strongly developed and persist nearly to the plane of articulation.

The species is named from the Cree "awokanak" slaves, after Great Slave Lake, Northwest Territories.

Occurrence. *Leiorhynchus awokanak* occurs in the middle part of the Pine Point formation in the Great Slave Lake region, having almost exactly the same range as *Hadorrhynchia sandersoni*. The upper part of its range overlaps that of *Leiorhynchus castanea*. Specimens have been examined from many localities including GSC loc. 5669, 5675, 5681, 5682, 17391, 19265, 31061, 31069, 31078, 31514.

One locality has yielded the species on Carcajou Ridge in the middle Mackenzie River region, where it occurs with *Hadorrhynchia sandersoni* and *Leiorhynchus castanea* in the "Beavertail formation" (but see discussion on this area above, p. 11); GSC loc. 7237k.

The species also occurs in the subsurface of southern Northwest Territories, and has been collected from cores from GSC localities 28379, 28396, 28423.

Leiorhynchus russelli n. sp.

Plate XVII, figures 1-10; Figures 27, 28

Material. Holotype, GSC No. 14917. Peace Point member of Waterways formation, sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, about 1.13 miles east-northeast of east end of island just below Boyer Rapids, Alberta. GSC loc. 29228; collector A. W. Norris, 1956.

Paratype A, GSC No. 14918. Same horizon and locality as holotype.

Paratype B, GSC No. 14919. Peace Point member of Waterways formation, sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, 1.1 miles east-northeast of east end of island just below Boyer Rapids, 24 to 30 feet above water level, Alberta. GSC loc. 29157; collector A. W. Norris, 1956.

Paratype C, GSC No. 14920. Peace Point member of Waterways formation, sink-hole filling, in Slave Point formation, Gypsum Cliffs, north bank of Peace River, opposite unnamed island immediately below Boyer Rapids, Alberta. GSC loc. 29432; collector A. W. Norris, 1956.

Paratype D, GSC No. 14921. An unusual specimen possessing weakly costate flanks. Same horizon and locality as paratype C.

Paratype E, GSC No. 14922. A specimen almost circular in plan view. Same horizon and locality as paratype C.

Rhynchonelloid Brachiopods from Western Canada

Paratype F, GSC No. 14923. A large specimen with strongly costate fold and sulcus and weakly costate flanks. Peace Point member, Waterways formation, sink-hole filling in brecciated Slave Point formation, Gypsum Cliffs, northeast bank of Peace River, about 4 miles northwest of the Ranger cabin, Alberta. GSC loc. 29154; collector A. W. Norris, 1956.

Paratype G, GSC No. 14924. Part of a silicified brachial valve showing the cardinalia, with one tooth of pedicle valve still in dental socket. Two hundred and thirty feet above base of Devonian, northeast flank of Wallbridge Mountain, Cecilia Lake, British Columbia Rockies. GSC loc. 35103; collector D. J. McL., 1952.

Paratype H, GSC No. 14925. Same horizon and locality as paratype G.

Paratype I, GSC No. 14926. Same horizon and locality as paratype G.

Paratype J, GSC No. 15205. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 27). Same horizon and locality as paratype C.

Paratype K, GSC No. 15206. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 28). Same horizon and locality as paratype G.

Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	20.7	19.7	23.6	12.8	112°
Paratype A	11.5	10.8	11.9	5.2	117°
Paratype B	12.7	11.8	13.6	6.5	108°
Paratype C	18.3	17.6	19.2	10.6	122°
Paratype D	20.8	19.7	24.0	12.4	122°
Paratype E	22.3	21.2	22.6	13.0	122°
Paratype F	24.0	23.2	28.8	17.4	114°
Paratype H	12.5	11.8	13.7	8.1	116°
Paratype I	21.5	20.4	25.0	14.7	122°
Paratype J (sectioned)	22.4	21.9	24.0	14.2	116°
Paratype K (sectioned)	20.2	19.6	25.0	15.3	117°

Description. Shell of medium size for the genus, subpentagonal to rounded in outline, width greater than length to subequal; hinge-line nearly straight, apical angle about 120 degrees; lateral margins smoothly rounded. Fold and sulcus weakly costate to smooth anteriorly, umbones smooth, costae rare on flanks. Anterior commissure weakly uniplicate. Shell moderately thin.

The pedicle valve is weakly convex, nearly flat at the lateral margins, and forms an acute angle with the adjacent dorsal valve. The sulcus is broad and variable in development, commonly only apparent in the anterior half of the shell, ending in a shallow, rounded tongue bounded by outwardly flared flanks. The beak is strongly incurved and the interareas narrow or concealed. In small shells the beak is suberect with narrow interareas bounded by weak beak ridges.

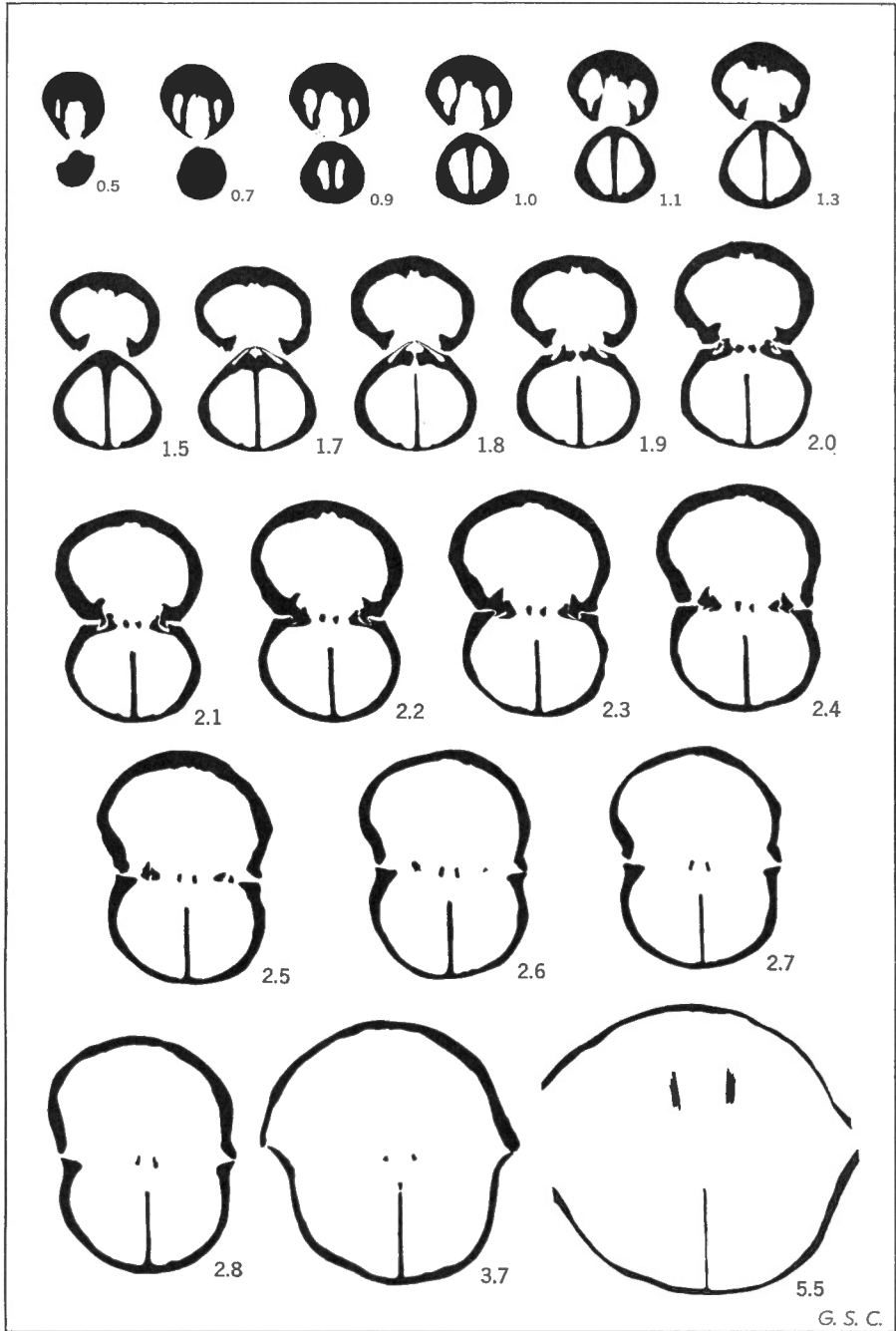
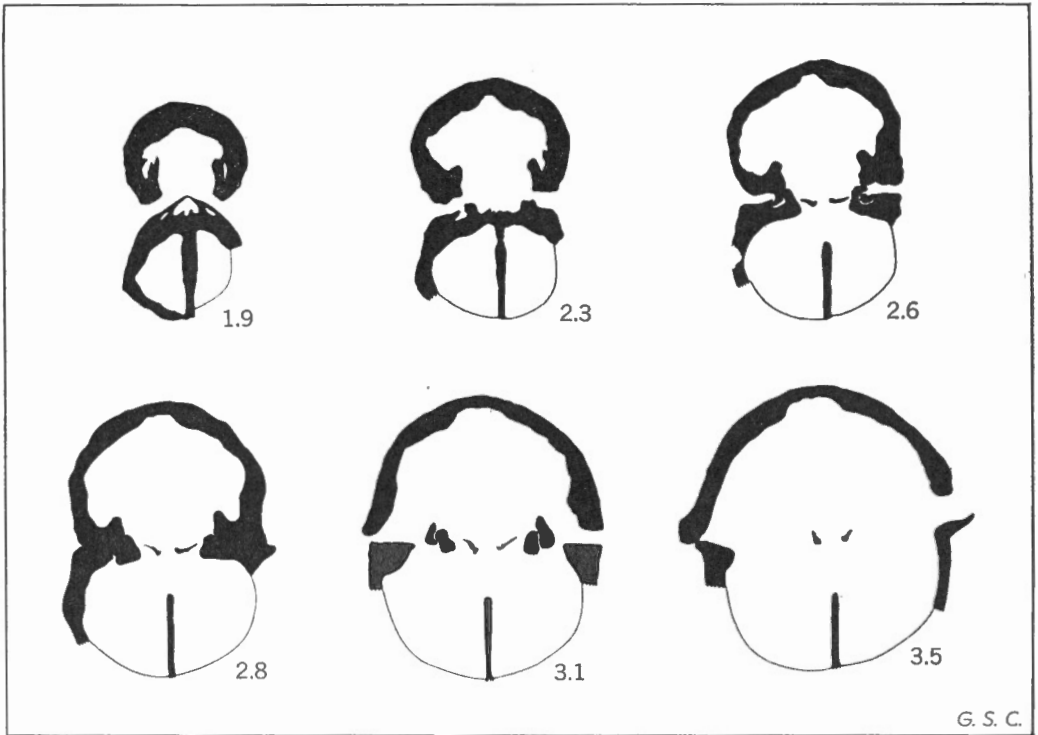


Figure 27. *Leiorhynchus russelli* n. sp. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; paratype J, GSC No. 15205.



G. S. C.

Figure 28. *Leiorhynchus russelli* n. sp. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; paratype K, GSC No. 15206.

The foramen is prominent, parallel sided, and rounded posteriorly; normally it extends onto the umbo by resorption of the beak. Vestigial deltidial plates are apparent in some sections.

The brachial valve is moderately convex with maximum height posterior to the mid-length. Anteriorly it falls gently to meet the tongue of the pedicle valve at an acute angle. The broad, low fold is present only near the front margin and is lacking on some shells. The beak is incurved and hidden by the pedicle valve.

The ornament is highly variable. Many shells are smooth. In others three or four, with a maximum of seven, low, rounded, irregular costae, some of which may bifurcate, are developed in the anterior part of the fold and sulcus. Traces of costae are rarely present on the flanks. Fine, close-set concentric growth lines are apparent on well-preserved specimens.

In the pedicle interior the delthyrial cavity is bounded by weak dorsally divergent dental plates which do not persist forward to support the teeth. The teeth are stout and supported up to the plane of articulation by the shell margin. They persist forward as unsupported rectangular processes in contact with the inner socket ridges of the brachial valve. A narrow adductor track beginning near the front of the delthyrial cavity and continuing forward at least as far as the plane

of articulation is visible in serial sections of some shells. It is divided medianly by a low ridge.

In the brachial interior the cardinalia consist of divided hinge plates supported posteriorly by a median septum which becomes detached posterior to the plane of articulation. A shallow septalium is weakly developed and the hinge plates divide into stout socket ridges and crural bases within about 2 mm of the beak. The socket ridges persist forward as stout processes in contact with the teeth after they have become detached from the shell margins. The crura are slender and curved. The septum thins anteriorly and persists to about the middle of the valve. The adductor impressions are long and lenticular on either side of the septum; they are bounded laterally by low ridges.

Growth and Variation (200 specimens).

Changes in mean proportions during growth:

	Length							
	Less than 12 mm		12 to 15.9 mm		16 to 19.9 mm		20 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.01	0.88-1.12	1.08	1.02-1.15	1.08	0.94-1.24	1.14	1.01-1.36
Thickness/length	0.52	0.42-0.64	0.55	0.49-0.62	0.61	0.45-0.71	0.63	0.58-0.72
Apical angle	110°	99°-117°	115°	105°-123°	118°	105°-129°	118°	108°-125°

The collections include specimens at all stages of growth from a length of 8.5 mm to a maximum of 26.0 mm. Small specimens are subrounded and depressed biconvex, without fold and sulcus and with suberect beaks. The fold and anterior plication develop in specimens larger than about 15 mm although their appearance varies.

In general the species is not highly variable with the exception of the costation. About half of the specimens examined show obvious costation in the fold and sulcus and faint signs of one or more costae are discernible on many others. Very few (less than 5 per cent) show any costation on the flanks. The appearance of costation is only poorly correlated with size, although without exception the umbones are smooth. In many shells costation begins within 10 mm of the beak, but many large specimens are smooth.

The collections from the Cecilia Lake region are closely similar to those from Gypsum Cliffs although more poorly preserved. The larger specimens show a tendency to become more inflat than those from the type area although there is overlap in form at all stages of growth.

Four specimens were serial sectioned in detail. Apart from differences due to size there was little variation between them. A large specimen showed a tendency for secondary shell thickening around the dental plates, median septum, and cardinalia to the extent that the lateral cavities in the pedicle valve and the

septalium in the brachial are nearly filled. Large or gerontic specimens would probably be without lateral cavities and would thus appear to lack dental plates.

Discussion. This species is characterized by its smoothly subpentagonal to rounded outline, the poorly developed costation, many shells being nearly smooth, and by the prominent foramen which extends onto the umbo by resorption. Internally the cardinalia are slender and less thickened than in most species of *Leiorhynchus*. It is much less inflates and more transverse than *Leiorhynchus castanea* (Meek). *Leiorhynchus kelloggi* Hall, which it resembles, is more finely costate, more inflates, and develops ornament on fold and sulcus at an earlier stage of growth.

Small specimens may resemble small *Ladogioides pax* which occur in the same beds, but are readily distinguished by the lack of micro-ornament and the structure of the beak.

The species is named for Dr. L. S. Russell of the National Museum of Canada.

Occurrence. *Leiorhynchus russelli* is abundant in the Peace Point member of the Waterways formation exposed in the vicinity of Gypsum Cliffs on Peace River over a distance of about 6 miles. It also occurs in the stratigraphically equivalent Firebag member of the Waterways on Birch River in the same region. It is commonly associated with *Ladogioides pax*. Specimens have been examined from many localities, including GSC loc. 20851, 29151, 29154, 29157, 29228, 29432, 29441. It also occurs 230 feet above the base of the Devonian on the northeast flank of Wallbridge Mountain, near Cecilia Lake in the British Columbia Rockies, GSC loc. 35103, and, in association with *Ladogioides kakwaensis*, in the Flume formation, at Kakwa Lake in the same region, GSC loc. 35102. Farther north in British Columbia, the species has been found on Nabesche River in beds assigned to the "Flume formation equivalent", GSC loc. 41321.

Leiorhynchus carya Crickmay

Plate XVIII, figures 1-6; Figures 29A-C

1952a. *Leiorhynchus carya* CRICKMAY, pp. 599-600, Pl. 70, figs. 1-5, 8-11.

1952b. *Caryorhynchus carya* (Crickmay), CRICKMAY, p. 1.

1954. *Calvinaria? inelegans* McLAREN, pp. 178-179, Pl. I, figs. 19, 20, 21.

1956. *Caryorhynchus carya* (Crickmay), WARREN and STELCK, Pl. XVI, figs. 4, 5, 6.

1958. *Calvinaria? inelegans* McLaren, McLAREN, Pl. VII, figs. 22, 23, 24.

Material. Holotype; preserved in the collections of Imperial Oil Limited, Calgary, Alberta. The specimen figured by Crickmay (1952a, Pl. 70, figs. 1-5) and reported by him (pp. 599-600) to occur in "Upper 100 feet of Perdrix shale and in succeeding limestone, early Upper Devonian (lower Frasnian) on mountain north of Mt. Cheviot, Alberta". Collected by F. Glenn Fox.

Hypotype A, GSC No. 11248. The specimen figured by McLaren (1954 and 1958) as holotype of *Calvinaria? inelegans*. Perdrix formation, 170 feet above base of outcrop, ridge on south side of Winnifred Pass (approximately latitude

53°40', longitude 119°15'), Alberta. GSC loc. 19888; collector D. J. McL., 1951.

Hypotype B, GSC No. 15211. Same formation and locality as hypotype A, from talus collection. GSC loc. 19885.

Hypotype C, GSC No. 15212. Same formation and locality as hypotype A, 132 feet above base of exposure. GSC loc. 19887.

Hypotype D, GSC No. 15213. Same horizon and locality as hypotype A.

Hypotype E, GSC No. 15214. Same horizon and locality as hypotype A.

Hypotype F, GSC No. 15215. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 29A). Same horizon and locality as hypotype A.

Hypotype G, GSC No. 15228. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 29B). Talus from Perdrix formation, northeast flank of Mount Mackenzie, near Mountain Park, Alberta. GSC loc. 25194; collector D. J. McL., 1953.

Hypotype H, GSC No. 15955. Plaster replica and anterior part of specimen; remainder serial sectioned (illustrated, Fig. 29C). From mountain north of Mount Cheviot, Alberta. Specimen donated by C. H. Crickmay.

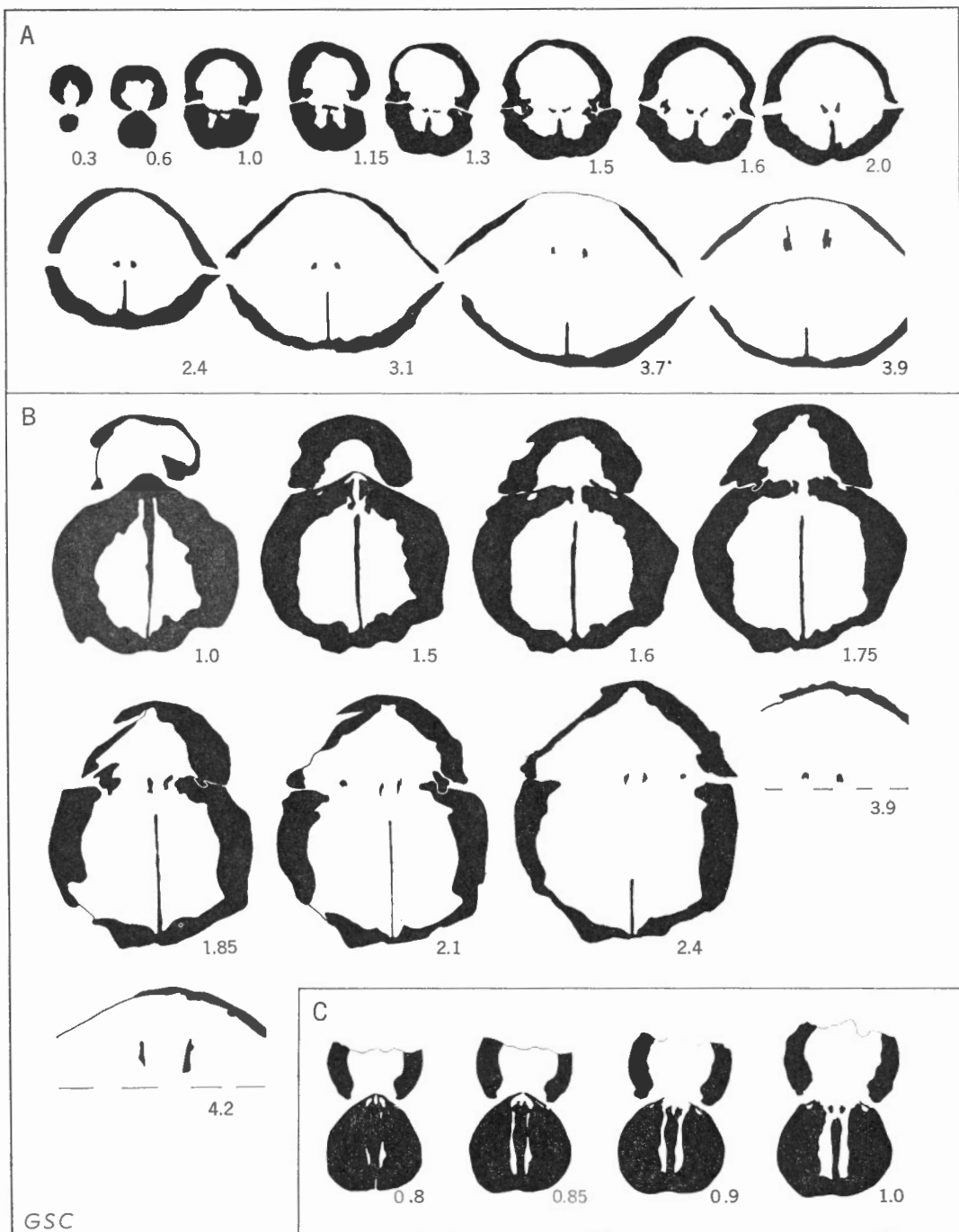
Dimensions (all measurements are in mm).

	Length	Length of Brachial Valve	Width	Thickness	Apical Angle
Holotype	20.6	20.6	21.1	18.6	(118°)
Hypotype A	20.7	20.5	25.0	15.4	134°
Hypotype B	23.0	22.6	25.9	18.0	118°
Hypotype C	(21.9)	(21.6)	25.0	17.9	121°
Hypotype D	19.6	19.2	21.1	14.3	124°
Hypotype E	14.7	14.3	15.5	9.0	113°
Hypotype F (sectioned)	15.5	15.1	(17.8)	9.3	123°
Hypotype G (sectioned)	(15.9)		(20.7)	18.0	
Hypotype H (sectioned)	(14.0)		(17.3)	(13.0)	115°

Description. Shell medium to large size, transversely subelliptical to sub-pentagonal, width greater than length to subequal; inflate; hinge-line nearly straight, apical angle 120 to 130 degrees or more; greatest width forward of mid-length. Fold and sulcus irregularly costate, flanks smooth to weakly costate. Anterior commissure weakly to strongly uniplicate. Shell thick.

The pedicle valve is shallow, its convexity decreasing forwards; the flanks are almost flat. The sulcus is shallow, beginning just posterior to mid-length and extending forward into a broad, low tongue. The beak is strongly incurved at all stages of growth represented in the collections; interareas concealed. The foramen is minute, and is developed at the point of the beak by resorption.

The brachial valve is moderately to strongly convex with well-rounded flanks. The maximum height is approximately at mid-length. Anteriorly it descends to the anterior commissure to meet the tongue of the pedicle valve at about the mid-



Figures 29 A-C. *Leiiorhynchus carya* Crickmay. Camera lucida drawings of serial transverse sections $\times 3$; distances are in mm forward from the crest of the umbo; 29A, hypotype F, GSC No. 15215; 29B, hypotype G, GSC No. 15228; 29C, hypotype H, GSC No. 15955.

height of the shell. The fold is low to moderately high and is developed only on the anterior two thirds to one half of the valve. The umbo is inflated and the beak incurved and hidden by the pedicle valve.

Ornament consists of two broad smoothly rounded costae which begin close to the beak in the brachial valve and are confined to the fold. These costae commonly bifurcate independently and more rarely trifurcate in a highly irregular manner. In some shells a low inconspicuous costa may develop medianly between the larger primary costae. In the sulcus there are commonly three costae of which the middle one is the largest. The flanks are commonly smooth, but may bear up to three weakly developed costae.

In the pedicle interior dental plates are not developed. The teeth are stout and supported by the lateral margins of the shell to the plane of articulation. A short, ventrally directed ridge underneath each tooth suggests the detached remnant of a dental plate, but complete plates are developed in none of the specimens sectioned (compare similar ridges below teeth in *Leiorhynchus russelli*, Fig. 27, sections 2.1, 2.2, 2.3, and 2.4).

In the brachial valve the cardinalia are typical of the genus. The hinge plates are scarcely developed, breaking up early into socket ridges and crural bases. The crural bases show a tendency to remain attached to the median septum after the hinge plates have disappeared, forming a T- or Y-shaped process at the end of the septum. The socket ridges persist forward of articulation in contact with the teeth. The septum is very thick and club-shaped posteriorly, thinning anteriorly and persisting forward for about one third of the length of the valve. The crura are triangular to round in section posteriorly, becoming dorsally grooved forwards. They persist for about one quarter of the length of the valve.

Growth and Variation (20 specimens).

Changes in mean proportion during growth:

	Length							
	Less than 16 mm		16.0 to 17.9 mm		18.0 to 19.9 mm		20 mm and more	
	mean	range	mean	range	mean	range	mean	range
Width/length	1.17	1.05-1.30	1.17	1.10-1.25	1.21	1.04-1.39	1.12	1.01-1.21
Thickness/length	0.67	0.60-0.79	0.81	0.74-0.93	0.83	0.73-1.00	0.80	0.74-0.90
Apical angle	123°	113°-128°	119°	113°-132°	125°	120°-130°	122°	118°-134°

Only twenty of the approximately eighty specimens among the collections studied are sufficiently undeformed to allow measurement. From the above table it may be seen that there is apparently little change in proportion during growth between the size limits represented (from shell length of 14.7 to 21.9 mm), but the number of specimens is scarcely sufficient to allow definite conclusions. There is probably an increase in proportionate thickness with growth. The width/length ratio and the apical angle are too variable to show a trend. It is apparent from

damaged and incomplete specimens that the proportionate shell width is unusually variable. Among specimens of comparable size the width/length ratio varies from 1.04 to 1.34. Specimens from the same bed display this variability which is apparently not ecologically controlled.

In other respects the species is not highly variable. The number of costae at the front margin varies from two to six on the fold but they always develop by branching from two prominent initial costae. The size of individual costae varies greatly, there commonly being one larger and more prominent than the others in each pair or triplet developed from one of the primary costae.

Although very small specimens are not present in the collections, the smallest that there are show a strongly incurved pedicle beak with no sign of interareas or beak ridges.

Discussion. The species is characterized by the moderate to strongly inflate brachial valve combined with a transverse shell outline and depressed anterior commissure; by the developmental pattern of the costation on fold and sulcus; and by the strongly incurved pedicle beak and minute foramen.

Internally the lack of dental plates, except as vestigial ridges underneath the teeth is characteristic and serves to separate the species from other *Leiorhynchus* species whose interiors are adequately known. The degree of taxonomic importance to be given to this feature is problematical. Crickmay (1952b) makes his species type of a new genus — *Caryorhynchus* — in which he includes *Rhynchonella castanea* Meek (1867). He gives the following diagnosis for the genus:

Rotund, tumid, leiorhynchidae. Apical callus, abundant, extensive. Anterior commissure, strongly uniplicate (to episulcate). Fold and sulcus, from umbo to anterior. Lateral slopes, short, steep. Plication, confined to fold and sulcus. Dental lamellae, short, never reaching floor of valve, much abbreviated at maturity.

None of the characters listed serve to distinguish *Caryorhynchus* from *Leiorhynchus* except the "short dental lamellae." (Crickmay's terms clearly refer to a similar feature to that described here; i.e. fully formed dental plates are not developed.) At the time at which Crickmay described his genus and species, full details of the interior of *Leiorhynchus quadracostatus* (Vanuxem), the type species of the genus *Leiorhynchus*, were unknown, or at least in some doubt. Sartenaer (1961b) has shown that *L. quadracostatus* does possess dental plates.

Throughout the species assigned to *Leiorhynchus* that have yet been fully described, and among species of the closely related genus *Calvinaria*, the development of dental plates is variable even within the range of a single species. They may be short, losing their connection with the floor of the valve very close to the beak, or they may persist up to the plane of articulation of the valves. Similar variation in development of dental plates is known in other rhynchonelloid genera.

It seems inadvisable at present to rely on such a character in defining a genus especially when it is recognized that in all other respects, e.g. external form, ornament, and development of the cardinalia, no valid or consistent distinction can be made from *Leiorhynchus*. *Caryorhynchus* is therefore considered synony-

mous. The name will remain available should *L. carya* be shown to differ consistently on other grounds and other species of the genus are described.

Rhynchonella castanea possesses well-marked dental plates, and may be assigned with assurance to *Leiorhynchus*.

L. carya differs from *L. castanea* externally in its more transverse outline, the more prominent fold and sulcus, and strongly impressed ornament. It differs from *L. russelli* in the more inflate shell, more strongly developed ornament, lack of exposed interareas on the pedicle valve and minute foramen. The species differs from any species of *Calvinaria*, whose range it overlaps, by its less transverse outline, the maximum height of the shell at or near mid-length, and the depressed anterior commissure.

Occurrence. *Leiorhynchus carya* occurs in the Perdrix formation, commonly associated with *Calvinaria variabilis insculpta*, in the Alberta Rocky Mountains between Brazeau and Smoky Rivers. It has also been collected from the upper Flume (or Maligne) when this formation thickens at the expense of the overlying Perdrix. In the lower part of its range it may overlap *Calvinaria variabilis ahabascensis*. Specimens have been examined from GSC localities 19885, 19887, 19888, 19910, 25194, 36868. The species has been collected from a subsurface core in Alberta at GSC loc. 22573.

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APPENDIX

Locality Index

- 5637 Hay River shale, loose, from 2 miles below first island below Alexandra Falls, Hay River, N.W.T. E. J. Whittaker, 1917:
Calvinaria albertensis opima
Calvinaria variabilis variabilis
- 5641 Hay River shale, at water level at foot of first island below Alexandra Falls, Hay River, N.W.T. E. J. Whittaker, 1917:
Calvinaria albertensis opima
- 5669 Pine Point formation; west side of most westerly of Pine Point Islands, Great Slave Lake, N.W.T. E. J. Whittaker, 1917:
Leiorhynchus awokanak
- 5672 Black shales of Pine Point formation; northwest side of eastern island of Pine Point Islands (Green Islands), N.W.T. E. J. Whittaker, 1917:
Hadorrhynchia sandersoni
- 5675 Black bituminous limestone of Pine Point formation; half a mile west of Pine Point, south shore of Great Slave Lake, N.W.T. E. J. Whittaker and E. M. Kindle, 1917:
Hadorrhynchia sandersoni
Leiorhynchus castanea
Leiorhynchus awokanak
- 5681 Pine Point formation; 2½ miles east of Pine Point, south shore of Great Slave Lake, N.W.T. E. J. Whittaker, 1917:
Leiorhynchus awokanak
- 5682 Pine Point formation; small point 3 miles east of Pine Point, Great Slave Lake, N.W.T. E. J. Whittaker, 1917:
Hadorrhynchia sandersoni
Leiorhynchus castanea
Leiorhynchus awokanak
- 6748 "Hay River shale, High Banks, Hay River." A. H. Low, Imperial Oil Ltd., 1920:
Calvinaria albertensis opima
- 6872 (Formation not specified.) Carcajou Rock, Mackenzie River, N.W.T. J. W. Beede, 1920:
Hadorrhynchia sandersoni
- 7237b "Two-inch thin shaly bed, 17 feet 3 inches below probable contact between Fort Creek formation above and Beavertail limestone below, north end of Wolverine anticline, Carcajou Ridge, Mackenzie River, right bank, N.W.T." (from section described by Hume, 1923, p. 57B). G. S. Hume, 1922:
Leiorhynchus castanea
- 7237h "Vertical beds of Beavertail formation; north end of Wolverine anticline, Carcajou Ridge, Mackenzie River, N.W.T." G. S. Hume, 1922:
Hadorrhynchia sandersoni
Leiorhynchus castanea
- 7237k "From heavy-bedded limestone 20 to 30 feet below the contact of the Beavertail formation with the overlying Fort Creek shale, north end of the Wolverine anticline, Carcajou Ridge, Mackenzie River, right bank." G. S. Hume, 1922:
Hadorrhynchia sandersoni
Leiorhynchus castanea
Leiorhynchus awokanak
- 7240 "From a 2-foot limestone bed in the Fort Creek shale about 25 feet above the contact with the Beavertail limestone, east side of mouth of canyon on Carcajou River;" approx. lat. 64°58', long. 127°12', N.W.T. G. S. Hume, 1922:
Leiorhynchus castanea

- 12801 Drift boulder of Pine Point formation, Windy Point, north shore of Great Slave Lake, N.W.T. Imperial Oil Limited, 1919:
Leiorhynchus castanea
- 12871 "Lower Fort Creek; central part of Carcajou Ridge, Mackenzie River, N.W.T." J. M. Parker, 1943. (Canol Report Assignment No. 6, Accession No. 42178, Suite No. 8517):
Hadorrhynchia sandersoni
- 16541 Upper few feet of upper Flume (Maligne) formation; near highway, Morro Peak, Jasper Park, Alberta. R. deWit, 1948:
Calvinaria variabilis athabascensis
- 16996 Argillaceous limestone member of the Mount Hawk formation; 18 feet above base of exposure, south end of Idlewilde Mountain, Clearwater River valley, Alberta. D. J. McLaren, 1949:
Calvinaria albertensis albertensis
- 17378 Upper beds of upper Flume (Maligne) formation; saddle immediately south of Morro Peak, Jasper Park, Alberta. R. A. C. Brown, 1944:
Calvinaria variabilis athabascensis
- 17390 Pine Point formation; most easterly of Pine Point Islands (Green Islands), Great Slave Lake, N.W.T. J. A. Wallace, Socony Vacuum Exploration Company, 1950:
Hadorrhynchia sandersoni
- 17391 Pine Point formation; Pine Point, opposite centre island of Pine Point Islands (Green Islands), south shore Great Slave Lake, N.W.T. J. A. Wallace, Socony Vacuum Exploration Company, 1950:
Leiorhynchus awokanak
- 17405 Pine Point formation; Consolidated Mining and Smelting Company landing, east of Pine Point, Great Slave Lake, N.W.T. J. A. Wallace, Socony Vacuum Exploration Company, 1950:
Hadorrhynchia sandersoni
- 17409 "Limestone bed in Hay River shale;" 400 feet above base of exposure on Hay River, left bank, one third of a mile east of junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, N.W.T. W. I. Wright, Socony Vacuum Exploration Company, 1950:
Calvinaria albertensis opima
- 18163 Argillaceous limestone member of the Mount Hawk formation; about 410 feet above base, northeast flank of Roche Miette, Jasper Park, Alberta. D. J. McLaren, 1949:
Calvinaria albertensis albertensis
- 18202 Argillaceous limestone member of the Mount Hawk formation; 316 feet above base, northeast flank of Roche Miette, Jasper Park, Alberta. D. J. McLaren, 1949:
Calvinaria albertensis albertensis
- 18208 Argillaceous limestone member of the Mount Hawk formation; 400 feet above base, northeast flank of Roche Miette, Jasper Park, Alberta. D. J. McLaren, 1949:
Calvinaria albertensis albertensis
- 18889 Upper Flume (Maligne) formation; about 40 feet from top, northeast shoulder of Roche Miette, Jasper Park, Alberta. D. J. McLaren, 1948 (see McLaren, 1956, p. 26):
Calvinaria variabilis athabascensis
- 19263 Pine Point formation; 150 feet east-northeast of Dawson Landing wharf, south shore of Great Slave Lake. R. deWit, 1950:
Hadorrhynchia sandersoni
- 19264 Pine Point formation; 800 feet west-southwest of Dawson Landing wharf, south shore of Great Slave Lake. R. deWit, 1950:
Hadorrhynchia sandersoni
- 19265 Pine Point formation; Pine Point, 550 feet east-northeast of Dawson Landing wharf, south shore of Great Slave Lake, N.W.T. R. deWit, 1950:
Leiorhynchus awokanak

- 19608 Upper 6 feet of upper Flume (Maligne) formation; on northeast side of ridge that separates Medicine and Beaver Lakes, Jasper Park, Alberta. D. J. McLaren, 1951 (unit 17, p. 49, McLaren, 1956):
Calvinaria variabilis athabascensis
- 19885 Perdrix formation; talus collection, ridge on south side of Winnifred Pass (approx. lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951:
Leiorhynchus carya
- 19887 Perdrix formation; 132 feet above base of exposure, ridge on south side of Winnifred Pass (approx. lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951:
Leiorhynchus carya
- 19888 Perdrix formation; 170 feet above base of outcrop, ridge on south side of Winnifred Pass (approx. lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951:
Leiorhynchus carya
- 19908 Perdrix formation; 25 feet above base of outcrop, ridge on south side of Winnifred Pass (lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951.
Calvinaria variabilis insculpta
- 19910 Perdrix formation; 100 feet above base of outcrop, ridge on south side of Winnifred Pass (lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951:
Calvinaria variabilis insculpta
Leiorhynchus carya
- 19936 Mount Hawk formation, lower part; on mountain to southeast of ridge on south side of Winnifred Pass (approx. lat. 53°40', long. 119°15'), Alberta. D. J. McLaren, 1951:
Calvinaria albertensis albertensis
- 19971 Cairn formation ("Flume equivalent"), 44 to 66 feet above base, from slightly argillaceous, grey limestone unit; southeast end of the Ancient Wall, Jasper Park (lat. 53°22', long. 118°39'), Alberta. D. J. McLaren, 1951:
Ladogioides kakwaensis
- 20111 California Standard Winterburn Province No. 1, 5,505 feet to 5,530 feet; ls. 10, sec. 4, tp. 53, rge. 25, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 20135 Bear Beaumont, 1,817 feet; ls. 14, sec. 25, tp. 77, rge. W4th mer., Alberta:
Calvinaria variabilis athabascensis
- 20198 Bear Beaumont, 1,838 feet; ls. 14, sec. 25, tp. 77, rge. 18, W4th mer., Alberta:
Calvinaria variabilis athabascensis
- 20346 Husky Phillips Pine Lake No. 1, 7,798 feet; ls. 13, sec. 14, tp. 35, rge. 25, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 20354 Husky Phillips Pine Lake No. 1, 7,751 feet; ls. 13, sec. 14, tp. 35, rge. 25, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 20851 Firebag member of Waterways formation; Birch River between long. 113° and 113°12', northeastern Alberta. D. Merrill, 1956:
Leiorhynchus russelli
- 21288 Superior Dodsland No. 1, 4,070 feet; ls. 9, sec. 16, tp. 32, rge. 22, W3rd mer. Saskatchewan:
Calvinaria variabilis athabascensis
- 22573 Gulf-William E. Porter No. 16, 5,217 feet; ls. 16, sec. 31, tp. 41, rge. 18, W4th mer., Alberta:
Leiorhynchus carya
- 22582 California Standard Stettler Province, 5,620 feet; ls. 11, sec. 18, tp. 39, rge. 18, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 22623 Crown Gabruck, 4,354 feet; ls. 16, sec. 11, tp. 46, rge. 16, W4th mer., Alberta:
Calvinaria variabilis insculpta

- 22647 Imperial Labyrinth Lake, 5,641 feet; ls. 15, sec. 14, tp. 48, rge. 23, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 22677 Imperial Roundhill, 4,670-4,680 feet; ls. 9, sec. 2, tp. 49, rge. 19, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 24169 Perdrix formation; 40 feet above base, Job Creek, eastern fault block, Alberta. D. J. McLaren, 1953 (unit 11, p. 57, McLaren, 1956):
Calvinaria variabilis insculpta
- 24171 Upper Flume (Maligne) formation; 24 feet above base, Job Creek, eastern fault block, Alberta. D. J. McLaren, 1953 (unit 9, p. 58, McLaren, 1956):
Calvinaria variabilis athabascensis
- 24180 Perdrix formation; 4 feet above base, Job Creek, eastern fault block, Alberta. D. J. McLaren, 1953 (unit 11, p. 57, McLaren, 1956):
Calvinaria variabilis jobensis
- 24181 Perdrix formation; 250 feet above base, Job Creek, eastern fault block, Alberta. D. J. McLaren, 1953 (unit 16, p. 57, McLaren, 1956):
Calvinaria variabilis insculpta
- 24183 Grey calcareous mudstone and limestone member of Mount Hawk formation, basal beds, Job Creek, eastern fault block, Alberta Rocky Mountains. D. J. McLaren, 1953 (unit 20, p. 57, McLaren, 1956):
Calvinaria albertensis albertensis
- 24221 Socony Three Hills No. 1, 7,764 feet; ls. 8, sec. 35, tp. 31, rge. 25, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 24322 "Hay River shale, mile 24.6, Hay River." L. Vigrass, 1952:
Calvinaria albertensis opima
- 24396 Seaboard Hudson's Bay Sunnyslope 7-11, 7,985-7,995 feet; ls. 7, sec. 11, tp. 31, rge. 27, W4th mer., Alberta:
Calvinaria albertensis albertensis
- 24554 Argillaceous limestone member of Mount Hawk formation; 12 feet below top, east side of Deception Creek, Alberta Rocky Mountains. D. J. McLaren, 1953 (unit 22, p. 29, McLaren, 1956):
Calvinaria albertensis albertensis
- 24563 Banded grey mudstone and limestone member, Mount Hawk formation, at base, east side of Deception Creek, Alberta Rocky Mountains. D. J. McLaren, 1953 (unit 10, p. 30, McLaren, 1956):
Calvinaria albertensis albertensis
- 24588 Imperial Eastgate, 4,570-4,575 feet; ls. 1, sec. 22, tp. 57, rge. 22, W4th mer., Alberta:
Calvinaria insculpta athabascensis
- 25170 Basal bed of grey calcareous mudstone member, Mount Hawk formation; southeast side of Wapiabi Gap, Bighorn Range, Alberta. D. J. McLaren, 1953 (unit 16, p. 43, McLaren, 1956):
Calvinaria variabilis insculpta
- 25194 Talus from Perdrix formation; north flank of Mount Mackenzie, 5 miles south-southeast of Mountain Park, Alberta. D. J. McLaren, 1953:
Calvinaria variabilis insculpta
Leiorhynchus carya
- 26736 Upper beds of Nahanni formation; North Nahanni River, right bank, lat. 62°19', long. 123°45', N.W.T. Mobil Oil of Canada, 1955:
Leiorhynchus castanea
- 26741 Upper beds of Nahanni formation; North Nahanni River, left bank, lat. 62°21', long. 123°47', N.W.T. Mobil Oil of Canada, 1955:
Leiorhynchus castanea

- 26810 Imperial-Canadian Superior Pendryl, 9,703-9,713 feet; ls. 4, sec. 22, tp. 45, rge. 5, W5th mer., Alberta:
Calvinaria variabilis athabascensis
- 26811 Imperial Westlock, 5,090 feet; ls. 14, sec. 24, tp. 59, rge. 26, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 26819 Imperial-Canadian Superior Buck Creek, 8,945 feet; ls. 14, sec. 29, tp. 48, rge. 6, W5th mer., Alberta:
Calvinaria variabilis athabascensis
- 26840 Imperial Cynthia, 8,665 feet; ls. 3, sec. 1, tp. 52, rge. 11, W5th mer., Alberta:
Calvinaria albertensis albertensis
- 28105 California Standard Gulf Kaybob, 8,675-8,680 feet; ls. 5, sec. 35, tp. 62, rge. 18, W5th mer., Alberta:
Calvinaria albertensis albertensis
- 28110 Imperial Smith, 3,902-3,910 feet; ls. 15, sec. 17, tp. 71, rge. 25, W4th mer., Alberta:
Calvinaria variabilis insculpta
- 28379 Imperial Island River No. 1, 7,385-7,390 feet; lat. 60°09'29", long. 121°08'16", N.W.T.:
Leiorhynchus awokanak
- 28396 Briggs Foetus Lake No. 1, 2,530 feet; lat. 60°55'13", long. 118°31'49", N.W.T.:
Leiorhynchus awokanak
- 28423 Briggs Rabbit Lake No. 1, 2,612-2,615 feet; lat. 60°55'51", long. 118°47'29", N.W.T.:
Leiorhynchus awokanak
- 29151 Peace Point member of Waterways formation; sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, 1.1 miles east-northeast of east end of island just below Boyer Rapids, 35 to 55 feet above river level, Alberta. A. W. Norris, 1956:
Ladogioides pax
Leiorhynchus russelli
- 29154 Peace Point member, Waterways formation; sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, northeast bank of Peace River, about 4 miles northwest of the Ranger cabin, Alberta. A. W. Norris, 1956:
Ladogioides pax
Leiorhynchus russelli
- 29157 Peace Point member of Waterways formation; sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, 1.1 miles east-northeast of east end of island just below Boyer Rapids, 24 to 30 feet above water level, Alberta. A. W. Norris, 1956:
Ladogioides pax
Leiorhynchus russelli
- 29202 Peace Point member of Waterways formation; east bank of Peace River, at upper end of Boyer Rapids, Alberta. A. W. Norris, 1956:
Ladogioides pax
- 29228 Peace Point member of Waterways formation; sink-hole filling, in brecciated Slave Point formation, Gypsum Cliffs, north bank of Peace River, about 1.13 miles east-northeast of east end of island just below Boyer Rapids, Alberta. A. W. Norris, 1956:
Leiorhynchus russelli
- 29432 Peace Point member of Waterways formation; sink-hole filling, in Slave Point formation, Gypsum Cliffs, north bank of Peace River, opposite unnamed island immediately below Boyer Rapids, Alberta. A. W. Norris, 1956:
Ladogioides pax
Leiorhynchus russelli

- 29441 Peace Point member of Waterways formation; near base of green shale overlying Slave Point formation, Gypsum Cliffs, north bank of Peace River, opposite mid-point of island just below Boyer Rapids, Alberta. A. W. Norris, 1956:
Ladogioides pax
Leiorhynchus russelli
- 30517 Escarpment member, 208 feet above base, Hay River formation, Hay River; left bank, immediately below junction of Mills Lake road with Hay River highway, about 24½ miles above mouth of river, N.W.T. D. J. McLaren, 1957:
Calvinaria albertensis feni
- 30641 Brown nodular argillaceous limestone of the Horn River formation; on Clive River, tributary to Willowlake River, lat. 62°50', long. 119°48', N.W.T. D. J. McLaren, 1957:
Leiorhynchus castanea
- 30656 Brown nodular argillaceous limestone of the Horn River formation; on Clive River, tributary to Willowlake River, lat. 62°50', long. 119°43', N.W.T. D. J. McLaren, 1957:
Leiorhynchus castanea
- 30748 In grey calcareous mudstone of Escarpment member of Hay River formation; right bank of Lower Kakisa River at small rapids immediately above Mills Lake road crossing, N.W.T. D. J. McLaren, 1957:
Calvinaria albertensis opima
- 31061 Pine Point formation; Pine Point, south shore of Great Slave Lake, N.W.T. A. W. Norris, 1957:
Leiorhynchus awokanak
- 31068 From the bituminous limestone member of the Pine Point formation; in the upper part of the formation, Dawson Landing wharf area, south shore of Great Slave Lake, N.W.T. A. W. Norris, 1957:
Hadorrhynchia sandersoni
- 31069 About middle of Pine Point formation; Dawson Landing, 3.6 miles east-southeast of Pine Point, south shore of Great Slave Lake, N.W.T. A. W. Norris, 1957:
Leiorhynchus awokanak
- 31078 Pine Point formation; near top of lower half; 0.88 mile southeast of tip of Pine Point, south shore of Great Slave Lake, N.W.T. A. W. Norris, 1957:
Leiorhynchus awokanak
- 31082 Basal beds of Hay River formation; overlying Presqu'île dolomite, 1.84 miles northwest of the mid-north shore of the most northern arm of Sulphur Bay, Great Slave Lake, N.W.T. A. W. Norris, 1957:
Ladogioides pax
- 31189 Pine Point formation; northwest shore of Caribou Bay, north shore of Great Slave Lake, N.W.T. A. W. Norris, 1957.
Hadorrhynchia sandersoni
- 31190 Near top of Pine Point formation; near mouth and northwest shore of Caribou Bay, north shore of Great Slave Lake, N.W.T. A. W. Norris, 1957:
Leiorhynchus castanea
- 31261 Sixteen feet above base of Escarpment member, Hay River formation; on Hay River, left bank, one third of a mile east of the junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, N.W.T. P. Harker, 1957:
Calvinaria variabilis variabilis
- 31265 Seventeen feet above base of Escarpment member, Hay River formation; on Hay River, left bank, one third of a mile east of junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, N.W.T. P. Harker, 1957:
Calvinaria albertensis opima

¹See footnote, page 33.

- 31275 Basal bed of Escarpment member, Hay River formation; on Hay River, left bank, one third of a mile east of the junction of Mills Lake road with Hay River highway, some 24 miles above mouth of River, N.W.T. P. Harker, 1957:
Calvinaria variabilis athabascensis
- 31298 Base of Escarpment member, Hay River formation; on Hay River, left bank, one third of a mile east of the junction of Mills Lake road with Hay River highway, some 24 miles above mouth of river, N.W.T. P. Harker, 1957:
Calvinaria albertensis opima
- 31352 Top of Perdrix or basal Mount Hawk formation; Roche à Perdrix, Miette map-area, west half, Alberta. E. W. Mountjoy, 1957:
Calvinaria albertensis albertensis
- 31473 Imperial West Prairie, 8,180 feet; ls. 11, sec. 18, tp. 72, rge. 17, W5th mer., Alberta.
Ladogioides pax
- 31514 Pine Point formation, middle of Pine Point Islands (Green Islands), Great Slave Lake, N.W.T. W. B. Brady, 1957:
Leiorhynchus awokanak
- 31582 "Middle Ramparts formation, shale unit, 40 feet from top; Imperial Range, N.W.T." Mobiloil Company, 1957:
Hadorrhynchia sandersoni
- 31610 "Ramparts formation, 200 feet down from top; Imperial Range, N.W.T." Mobiloil Company, 1957:
Hadorrhynchia sandersoni
- 32418 Well-bedded, fine-grained limestone with nodules; from base of section of McDame group, on south facing ridge, 1.2 miles southwest of peak 5011, 7.6 miles west-northwest of the mouth of French River, McDame map-area, B.C. H. Gabrielse, 1957:
Hadorrhynchia sandersoni
Leiorhynchus castanea
- 32644 Highest bed exposed of the Nahanni formation, in a 15-foot unit of grey, well-bedded, limestone, exposed in creek flowing through the western part of the Iverson Range, about 8 miles south of West Iverson Lake, lat. 62°10', long. 124°44', N.W.T. P. Harker, 1957:
Leiorhynchus castanea
- 32652 Headless formation, talus, from between 1,007 and 1,367 feet below the top of the Nahanni formation, in creek flowing through western part of Iverson Range, about 8 miles south of West Iverson Lake, lat. 62°10', long. 124°44'. P. Harker, 1957:
Leiorhynchus manetoe
- 33254 In argillaceous and silty limestone, 150 feet below massive limestone reef, forming cliff on north side of Root River, 10 miles west of Gap in Camsell Range, N.W.T. D. J. McLaren, 1957:
Calvinaria albertensis albertensis
- 33568 Near top of Pine Point formation; 5.2 miles north of middle north shore of Sulphur Bay, Great Slave Lake, N.W.T. D. K. Norris, 1957:
Hadorrhynchia sandersoni
- 33577 Near top of Pine Point formation; 5.1 miles north of middle of north shore of Sulphur Bay, Great Slave Lake, N.W.T. D. K. Norris, 1957:
Hadorrhynchia sandersoni
- 33982 Upper one foot of Nahanni formation; in tributary to north fork of Root River, lat. 63°08', long. 125°44', N.W.T. B. R. Pelletier, 1957:
Leiorhynchus castanea
- 35100 "Flume formation", 186 to 205 feet above base of Devonian section, from argillaceous, nodular, grey limestone; below the saddle at the northeast end of the mountain on the northwest side of Kakwa Lake (lat. 54°03', long. 120°10'), British Columbia. D. J. McLaren, 1952:
Ladogioides kakwaensis

- 35101 "Flume formation", 205 to 220 feet above base of Devonian section, from argillaceous, nodular, grey limestone; below the saddle at the northeast end of the mountain on the northwest side of Kakwa Lake (lat. 54°03', long. 120°10'), British Columbia. D. J. McLaren, 1952:
Ladogioides kakwaensis
- 35102 From talus collection, "Flume formation", 186 to 205 feet above base of Devonian section, from argillaceous, nodular, grey limestone; below the saddle at the northeast end of the mountain on the northwest side of Kakwa Lake (lat. 54°03', long. 120°10'), British Columbia. D. J. McLaren, 1952:
Ladogioides kakwaensis
Leiorhynchus russelli
- 35103 Two hundred and thirty feet above base of Devonian, northeast flank of Wallbridge Mountain, Cecilia Lake, British Columbia. D. J. McLaren, 1952:
Leiorhynchus russelli
- 35106 Firebag member of Waterways formation; west bank of Edwin Creek near junction with Clearwater River, Alberta. A. W. Norris states that specimens from this locality were probably collected from thin beds of green argillaceous limestone interbedded with green shale that are exposed at low water, near the mouth of Edwin Creek. H. D. Curry, Shell Oil Company, 1945:
Ladogioides pax
- 35519 "Top of *Martinia* zone, about 600 feet down from top of Fairholme formation, Nigel Peak section, Sunwapta Pass area, Alberta". J. L. Severson, 1949 (section I in Severson, 1950):
Calvinaria variabilis insculpta
- 35520 Talus from Perdrix formation, 40 feet above base, Job Creek, eastern fault block, Alberta. D. J. McLaren, 1953 (unit 11, p. 57, McLaren, 1956):
Calvinaria variabilis insculpta
- 36853 Maligne formation; southeast side of creek at lat. 53°02', long. 117°38', Miette map-area, east half, Alberta. E. W. Mountjoy, 1958:
Calvinaria variabilis athabascensis
- 36868 Upper Flume (Maligne) formation; headwaters of creek at lat. 53°04', long. 117°33', Miette map-area, east half, Alberta. E. W. Mountjoy, 1958:
Calvinaria variabilis athabascensis
Calvinaria variabilis insculpta
Leiorhynchus carya
- 36919 Mount Hawk formation; lower part, Ogre Canyon section, Miette map-area, west half, Alberta. E. W. Mountjoy, 1958:
Calvinaria albertensis albertensis
- 36949 Mount Hawk formation; 350 feet above base, Sulphur Creek, 1½ miles south of Miette Hot Springs, Miette map-area, west half, Alberta. E. W. Mountjoy, 1958:
Calvinaria albertensis albertensis
- 37501 Imperial Shell Burntwood, 9,325 feet; ls. 12, sec. 6, tp. 64, rge. 12, W5th mer., Alberta.
Ladogioides pax
- 37833 Black shale and argillaceous dolomite member in upper part of Cairn formation; 600 feet above base, Front Range at Red Deer River gap, north side, Alberta. D. J. McLaren, 1953:
Calvinaria variabilis insculpta
- 38687 "In shale . . . underlying Hare Indian and Ramparts formations at Gayna River, tributary of Mountain River, N.W.T." Alfred Lenz, 1959:
Leiorhynchus castanea
- 38964 Fairholme group; about 100 feet above base, in Sand Creek, Lizard Range, Fernie map-area, west half, B.C. H. R. Belyea, 1959. (This horizon is at about 4th unit from base of described section on p. 25 in Leech, 1958.)
Calvinaria variabilis athabascensis
- 39480 "Lower Ramparts formation" (?), Anderson River, N.W.T.:
Cassidirostrum pedderi

- 39675 "Eleven to twelve feet above base of Fort Creek formation, in interbedded limestone and shale in Dodo Canyon, along east side of Canol Road where it leaves Mackenzie Mountains front", approx. lat. 65°01', long. 127°18', N.W.T.
Leiorhynchus castanea
- 39709 "Uppermost beds of Ramparts formation on east side of Carcajou River, 3½ miles downstream from mouth of Rouge Mountain River, latitude 64°44', longitude 126°47'38", N.W.T." :
Leiorhynchus castanea
- 39826 "Middle Ramparts formation, 25-35 feet above base, Upper Hume River system, latitude 65°20', longitude 129°55', N.W.T." R. B. Nelson, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 39843 "Lower or middle Ramparts, 505 to 512 feet below base of reefal limestone in upper Ramparts formation, east bank of Gayna River, latitude 65°17', longitude 129°20', N.W.T." A. Reece, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 39856 "Middle or upper Ramparts formation, immediately underlying Fort Creek shale, in creek tributary to Snake River, latitude 65°26', longitude 133°44', Y.T." J. D. Aitken, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 40194 Middle Mount Hawk formation; Glacier Pass, Blue Creek map-area, west half, Alberta. E. W. Mountjoy, 1959:
Calvinaria albertensis albertensis
- 40212 Middle Mount Hawk formation; fault slice below Ancient Wall thrust, one mile north of Noonday Peak, Blue Creek map-area, west half, Alberta. E. W. Mountjoy, 1959:
Calvinaria albertensis albertensis
- 40334 "Upper 10 feet of lower Ramparts formation, on tributary to Mountain River, latitude 65°17', longitude 129°10', N.W.T." J. D. Aitken, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 40342 "Top 2 feet of lower Ramparts limestone, Mountain River at Mountain Front, latitude 65°15', longitude 128°30', N.W.T." J. D. Aitken, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 40402 "Lower Ramparts limestone member, 65 feet below top, in 'Rusty Creek', 2 miles east of Gaytic Divide, latitude 65°01', longitude 130°37', N.W.T." A. Reece, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 41060 "Upper 2 feet of lower Ramparts or Hume formation, from grey argillaceous limestone on east bank of Andrew River, 4 miles south of junction with Carnwath River, N.W.T." R. deWit, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea
- 41076 Same horizon and locality as GSC loc. 41060. G. P. E. White, J. C. Sproule and Associates, 1959:
Cassidirostrum pedderi
Leiorhynchus castanea
- 41083 "Lower Ramparts formation, 0 to 3 feet below top of formation, Andrew River, latitude 68°08', longitude 128°33', N.W.T." G. P. E. White, J. C. Sproule and Associates, 1959:
Cassidirostrum pedderi
Leiorhynchus castanea
- 41154 "Basal Fort Creek sandstone, 135 feet above upper Ramparts limestone, in small stream cut one mile northeast of northeast bank of Mackenzie River, latitude 66°46'30", longitude 129°52', N.W.T." D. L. Campbell, J. C. Sproule and Associates, 1959:
Leiorhynchus castanea

- 41319 Calcareous shale and shaly limestone in the lowest 15 feet of the Hare Indian formation, Anderson River, between lat. 68°28' and 68°32', and long. 127°04' and 127°24', N.W.T. A. E. H. Pedder, Triad Oil Company Limited, 1959:
 Cassidirostrum pedderi
 Leiorhynchus castanea
- 41321 Argillaceous limestone of "Flume formation equivalent" about 100 feet below shale unit ("Perdrix equivalent") near Nabesche River, lat. 56°17', long. 123°23', B.C. A. E. H. Pedder, Triad Oil Company Limited, 1960:
 Leiorhynchus russelli
- 41327 "Same locality as GSC loc. 41060, from lower beds of Middle Ramparts or Hare Indian formation." G. V. Lloyd, J. C. Sproule and Associates, 1959:
 Cassidirostrum pedderi
 Leiorhynchus castanea
- 41889 Firebag member of Waterways formation, east bank of Athabasca River, 63.75 miles north of No. 3 Wharf at Waterways, Alberta. A. W. Norris, 1956:
 Ladogioides pax
- 41896 Upper Flume (Maligne) formation, at Cold Sulphur Spring, Jasper Park, Alberta. R. A. C. Brown, 1944:
 Calvinaria variabilis athabascensis
- 42016 "Nodular weathering beds between 800 and 810 feet below the top of the Nahanni formation in the southern Manetoe Range, approximately latitude 61°49', and longitude 125°05', N.W.T." A. E. H. Pedder, Triad Oil Company Limited, 1960:
 Leiorhynchus manetoe
- 41919 Imperial Sikanni Chief No. 1, 7,810 feet; lat. 58°04'45", long. 121°53'30", Alberta:
 Ladogioides pax

PLATES I to XVIII

PLATE I

(All figures are natural size)

Calvinaria albertensis albertensis (Warren)

(Page 26)

- Figures 1a-e. Lectotype, U. of A. No. Dv633, dorsal, ventral, anterior, posterior, and side views.
- Figures 2a-c. Syntype, U. of A. No. Dv631, dorsal, anterior, and side views.
- Figures 3a-c. Syntype, U. of A. Dv632, dorsal, anterior, and side views.
- Figures 4a-c. Hypotype H, GSC No. 14949, dorsal, anterior, and side views.
- Figures 5a-c. Hypotype G, GSC No. 14948, ventral, anterior and side views.
- Figures 6a-e. Hypotype F, GSC No. 11241, dorsal, ventral, anterior, posterior, and side views.
- Figures 7a-e. Hypotype E, GSC No. 14947, dorsal, ventral, anterior, posterior, and side views.
- Figures 8a-e. Hypotype D, GSC No. 14946, dorsal, ventral, anterior, posterior, and side views.
- Figures 9a-d. Hypotype C, GSC No. 14945, dorsal, ventral, anterior, and side views.
- Figures 10a-e. Hypotype B, GSC No. 11237, dorsal, ventral, anterior, posterior, and side views.
- Figures 11a-e. Hypotype A, GSC No. 14944, dorsal, ventral, anterior, posterior, and side views.



1a



1b



1c



1d



1e



2a



2b



2c



3a



3b



3c



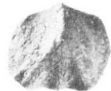
4a



4b



4c



5a



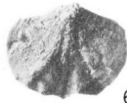
5b



5c



6a



6b



6c



6d



6e



7a



7b



7c



7d



7e



8a



8b



8c



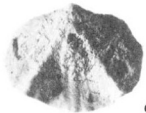
8d



8e



9a



9b



9c



9d



10a



10b



10c



10d



10e



11a



11b



11c



11d



11e

PLATE II

(Except where otherwise stated, all figures are natural size)

Calvinaria albertensis opima n. subsp.

(Page 31)

- Figures 1a-d. Paratype E, GSC No. 14957, dorsal, anterior, posterior, and side views.
Figures 2a-e. Paratype D, GSC No. 14956, dorsal, ventral, anterior, posterior, and side views.
Figures 3a-e. Paratype C, GSC No. 14955, dorsal, ventral, anterior, posterior, and side views.
Figures 4a-e. Paratype B, GSC No. 14954, dorsal, ventral, anterior, posterior, and side views.
Figures 5a-f. Holotype, GSC No. 14952, 5a-e, dorsal, ventral, anterior, posterior, and side views; 5f, detail of beak x3.
Figures 6a-e. Paratype A, GSC No. 14953, dorsal, ventral, anterior, posterior, and side views.

Calvinaria albertensis feni n. subsp.

(Page 33)

- Figures 7a-c. Paratype C, GSC No. 15202, dorsal, posterior, and side views.
Figures 8a-c. Paratype B, GSC No. 15201, ventral, posterior, and side views.
Figures 9a-f. Holotype, GSC No. 14959, 9a-e, dorsal, ventral, anterior, posterior, and side views; 9f, detail of beak x3.
Figures 10a-c. Paratype A, GSC No. 14960, ventral, posterior, and side views.

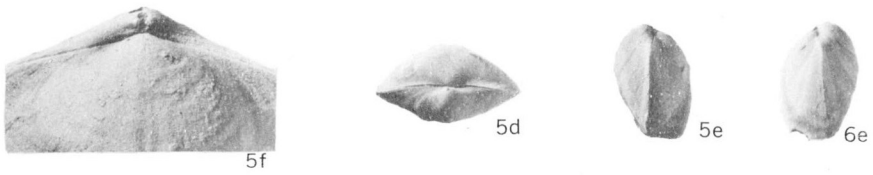
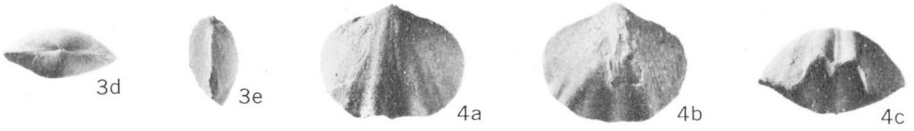
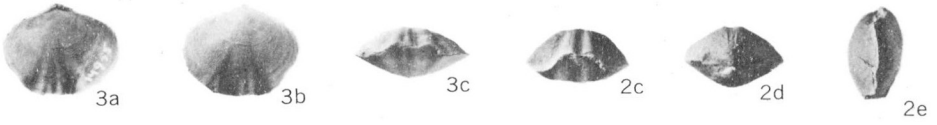


PLATE III

(Except where otherwise stated, all figures are natural size)

Calvinaria variabilis variabilis (Whiteaves)

(Page 35)

- Figures 1a-c. Lectotype, GSC No. 4272, dorsal, anterior, and side views.
Figures 2a-c. Syntype, GSC No. 4272b, dorsal, anterior, and side views.
Figures 3a-c. Hypotype A, GSC No. 14927, dorsal, anterior, and side views.
Figures 4a-c. Hypotype B, GSC No. 14928, dorsal, anterior, and side views.
Figures 5a-e. Hypotype C, GSC No. 14929, 5a-d, dorsal, anterior, posterior, and side views; 5e, detail of beak x3.
Figures 6a-e. Hypotype D, GSC No. 14930, dorsal, ventral, anterior, posterior, and side views.

Calvinaria variabilis insculpta (McLaren)

(Page 43)

- Figures 7a-c. Hypotype A, GSC No. 14936, dorsal, anterior, and side views.
Figures 8a-d. Hypotype B, GSC No. 14937, dorsal, anterior, posterior, and side views.
Figures 9a-f. Hypotype C, GSC No. 14938, 9a-e, dorsal, ventral, anterior, posterior, and side views; 9f, detail of beak x3.
Figures 10a-c. Hypotype D, GSC No. 14939, dorsal, ventral, and front views.



1a



1b



1c



2a



2b



2c



3a



3b



3c



4a



4b



4c



5a



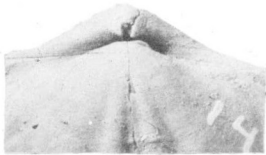
5b



5c



5d



5e



6a



6b



6c



6d



6e



8d



7a



7b



7c



8a



8b



8c



9a



9b



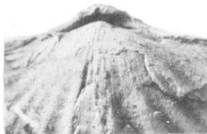
9c



9d



9e



9f



10a



10b



10c

PLATE IV

(All figures are natural size)

Calvinaria variabilis insculpta (McLaren)

(Page 43)

Figures 1a-d. Hypotype E, GSC No. 14940, dorsal, ventral, anterior, and side views.
Figures 2a-c. Holotype, GSC No. 11245, dorsal, anterior, and side views.

Calvinaria variabilis athabascensis (Kindle)

(Page 39)

Figures 3a-c. Hypotype A, GSC No. 14931, dorsal, ventral, and anterior views.
Figures 4a-c. Hypotype B, GSC No. 14932, dorsal, posterior, and side views.
Figures 5a-e. Hypotype C, GSC No. 13820, dorsal, ventral, anterior, posterior, and side views.
Figures 6a-c. Hypotype D, GSC No. 14933, dorsal, posterior, and side views.
Figures 7a-d. Hypotype E, GSC No. 14934, dorsal, ventral, posterior, and side views.
Figures 8a-e. Hypotype F, GSC No. 11232, dorsal, ventral, anterior, posterior, and side views.



1a



1b



1c



1d



2a



2b



2c



3a



3b



3c



4a



4b



4c



5a



5b



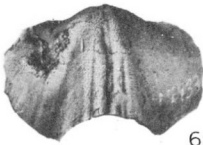
5c



5d



5e



6a



6b



6c



7a



7b



7c



7d



8a



8b



8c



8d



8e

PLATE V

(Except where otherwise stated, all figures are natural size)

Calvinaria variabilis athabascensis (Kindle)

(Page 39)

- Figures 1a-f. Hypotype G, GSC No. 14935, 1a-e, dorsal, ventral, anterior, posterior, and side views; 1f, detail of beak x3.
Figures 2a-c. Lectotype, GSC No. 5819, dorsal, anterior, and side views.
Figures 3a-c. Syntype, GSC No. 5819a, dorsal, ventral, and posterior views.

Calvinaria variabilis jobensis n. subsp.

(Page 45)

- Figures 4a-c. Paratype A, GSC No. 14942, ventral, anterior, and side views.
Figures 5a-c. Paratype B, GSC No. 14943, ventral, anterior, and side views.
Figures 6a-d. Holotype, GSC No. 14941, dorsal, ventral, anterior, and posterior views.

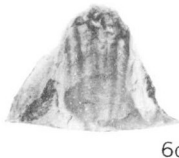
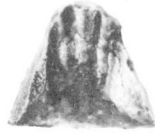
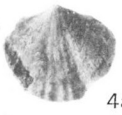
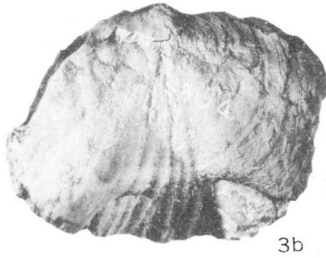
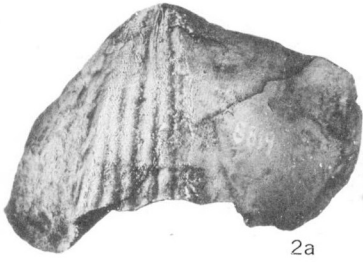
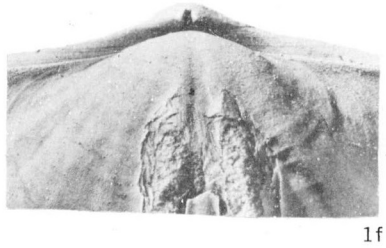


PLATE VI

(Except where otherwise stated, all figures are natural size)

Cassidirostrum pedderi McLaren

(Page 49)

- Figures 1a-c. Paratype D, GSC No. 15354, dorsal, anterior, and side views.
Figures 2a-f. Holotype, GSC No. 15350, 2a-e, dorsal, ventral, anterior, posterior, and side views; 2f, detail of posterior showing interareas and beak ridges x3.
Figures 3a-e. Paratype C, GSC No. 15353, dorsal, ventral, anterior, posterior, and side views.
Figures 4a-e. Paratype B, GSC No. 15352, dorsal, ventral, anterior, posterior, and side views.
Figures 5a-d. Paratype A, GSC No. 15351, dorsal, anterior, posterior, and side views.
Figures 6a, b. Paratype E, GSC No. 15355, 6a, ventral view of beak of internal mould x3; 6b, posterior view of internal mould x3.



1a



1b



1c



2f



2a



2b



2c



2d



2e



3a



3b



3c



3d



3e



4a



4b



4c



4d



4e



5a



5b



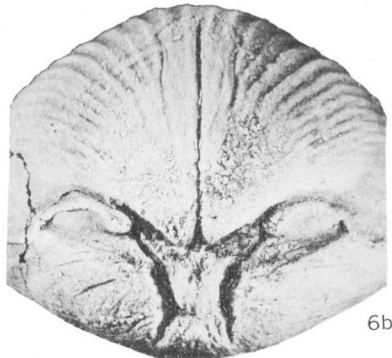
5c



5d



6a



6b

PLATE VII

(Except where otherwise stated, all figures are natural size)

Hadorrhynchia sandersoni (Warren)

(Page 56)

- Figures 1a-f. Hypotype H, GSC No. 15338, 1a-d, dorsal, ventral, posterior, and side views; 1e, detail of beak x3; 1f, anterior view x3.
- Figures 2a-c. Hypotype G, GSC No. 15337, dorsal, anterior, and side views.
- Figures 3a-c. Hypotype F, GSC No. 15336, dorsal, anterior, and side views.
- Figures 4a-c. Hypotype E, GSC No. 15335, dorsal, anterior, and side views.
- Figures 5a-f. Hypotype D, GSC No. 15334, 5a-e, dorsal, ventral, anterior, posterior, and side views; 5f, detail of beak x3.
- Figures 6a-f. Hypotype C, GSC No. 15333, 6a-e, dorsal, ventral, anterior, posterior, and side views; 6f, detail of side view to show interior ridges on interspaces between costae on each side of lateral commissure x3.
- Figures 7a-c. Hypotype B, GSC No. 15332, ventral, anterior, and side views.



1a



1b



1c



1d



1e



1f



2a



2b



2c



3a



3b



3c



4a



4b



4c



5f



5a



5b



5c



5d



6a



6b



6c



6e



6f



6d



6e



7c



7a



7b

PLATE VIII

(Except where otherwise stated, all figures are natural size)

Hadrorhynchia sandersoni (Warren)

(Page 56)

- Figures 1a-e. Hypotype A, GSC No. 15331, 1a-d, dorsal, anterior, posterior, and side views; 1e, detail of anterior view to show ridges between costae on interior on each side of commissure x3.
- Figures 2a-d. Syntype, U. of A. Dv853-1, dorsal, anterior, posterior, and side views.
- Figures 3a-d. Lectotype, U. of A. Dv853-2, dorsal, ventral, anterior, and side views.

Ladogia meyendorfi (de Verneuil)

- Figures 4a-f. Hypotype, GSC No. 15341, from the Pskov Stage, Pskov, Velikaja River, Estonia; 4a-e, dorsal, ventral, anterior, posterior, and side views; 4f, detail of ventral view to show ornament in sulcus x3.



1a



1c



1b



1d



1e



2a



2b



2c



2d



3a



3b



3c



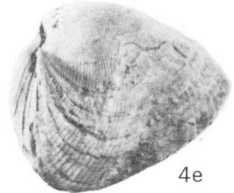
3d



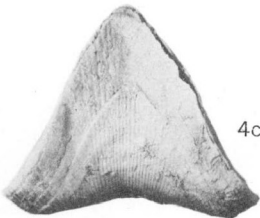
4a



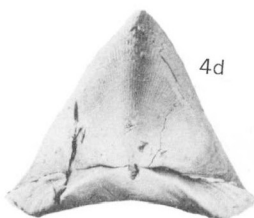
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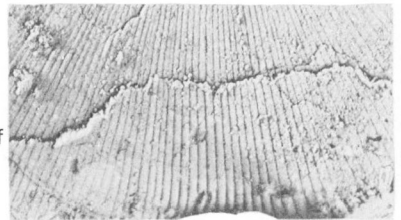
4e



4c



4d



4f

PLATE IX

(Except where otherwise stated, all figures are natural size)

Ladogioides pax McLaren

(Page 66)

- | | |
|---------------|--|
| Figures 1a-c. | Paratype J, GSC No. 15226, dorsal, posterior, and side views. |
| Figures 2a-e. | Paratype I, GSC No. 15225, dorsal, ventral, anterior, posterior, and side views. |
| Figures 3a-d. | Paratype H, GSC No. 15224, 3a-c, dorsal, anterior, and side views; 3d, detail of beak $\times 3$. |
| Figures 4a-c. | Paratype G, GSC No. 15223, dorsal, posterior, and anterior views. |
| Figures 5a-e. | Holotype, GSC No. 15216, dorsal, ventral, anterior, posterior, and side views. |
| Figures 6a-e. | Paratype F, GSC No. 15222, dorsal, ventral, anterior, posterior, and side views. |
| Figures 7a-c. | Paratype E, GSC No. 15221, ventral, anterior, and side views. |
| Figures 8a-e. | Paratype D, GSC No. 15220, dorsal, ventral, anterior, posterior, and side views. |

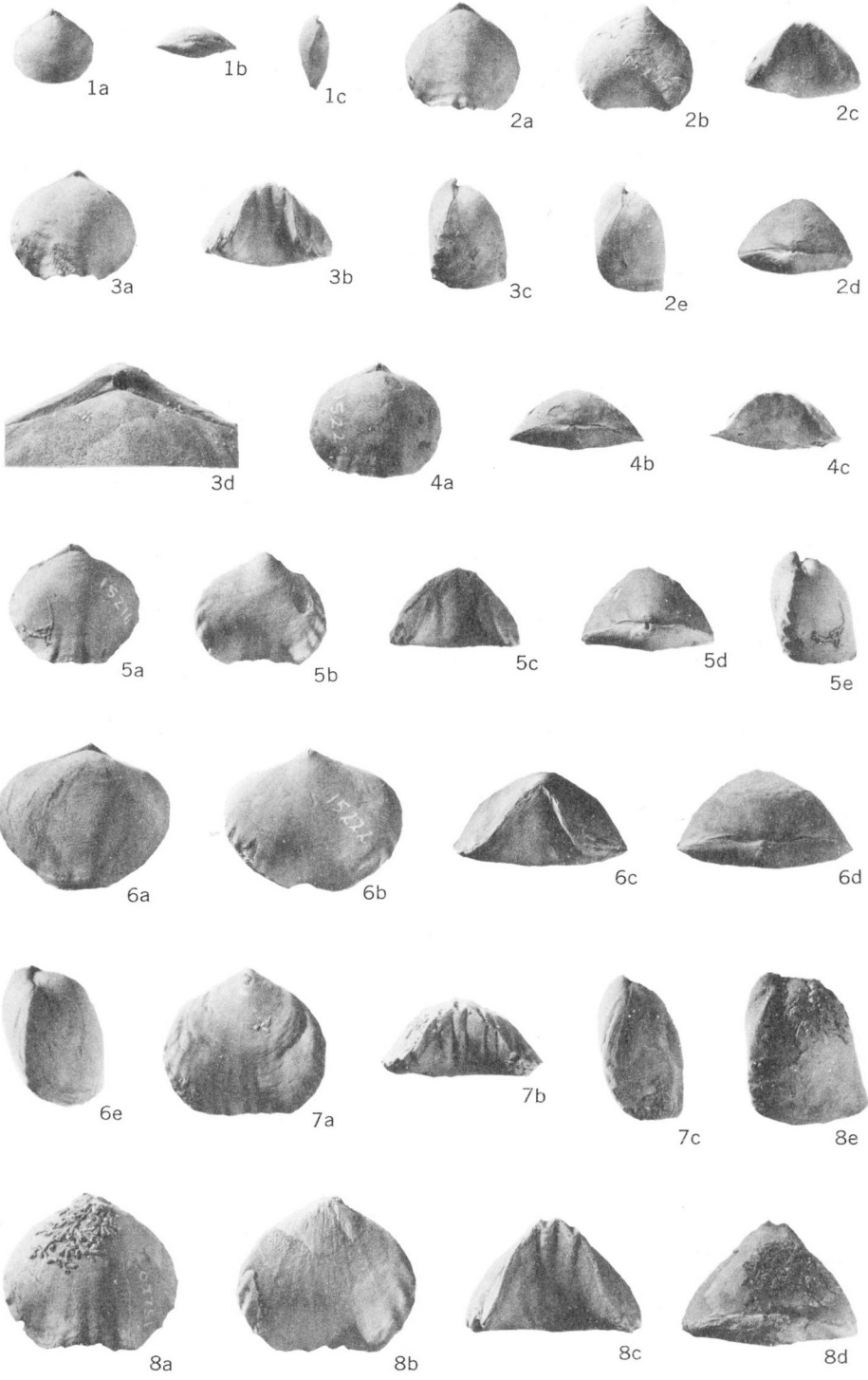


PLATE X

(Except where otherwise stated, all figures are natural size)

Ladogioides pax McLaren

(Page 66)

- Figures 1a-d. Paratype C, GSC No. 15219, 1a-c, dorsal, anterior, and side views; 1d, detail of anterior view to show ornament on tongue x3.
Figures 2a-d. Paratype B, GSC No. 15218, 2a-c, dorsal, posterior, and side views; 2d, detail of side view to show ornament x3.
Figures 3a-e. Paratype A, GSC No. 15217, dorsal, ventral, anterior, posterior, and side views.

Ladogioides kakwaensis (McLaren)

(Page 71)

- Figures 4a-d. Hypotype F, GSC No. 15233, dorsal, ventral, anterior, and side views.
Figures 5a-d. Hypotype E, GSC No. 15232, dorsal, anterior, posterior, and side views.



1a



1b



1d



1c



2a



2b



2c



3a



3b



2d



3c



3d



3e



4a



4b



4c



4d



5a



5b



5c



5d

PLATE XI

(Except where otherwise stated, all figures are natural size)

Ladogioides kakwaensis (McLaren)

(Page 71)

- Figures 1a-c. Paratype, GSC No. 11247, dorsal, anterior, and side views.
Figures 2a-c. Holotype, GSC No. 11246, dorsal, anterior, and side views.
Figures 3a-f. Hypotype D, GSC No. 15231, 3a-e, dorsal, ventral, anterior, posterior, and side views; 3f, detail of anterior view to show ornament on tongue x3.
Figures 4a-c. Hypotype C, GSC No. 15230 (continued on Pl. XII), dorsal, ventral, and anterior views.

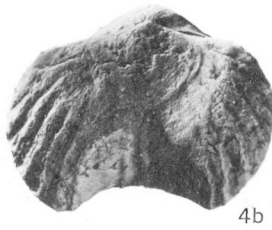
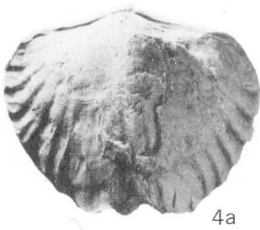
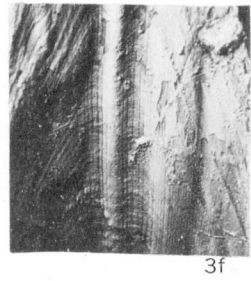
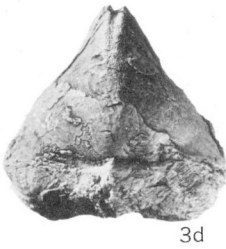
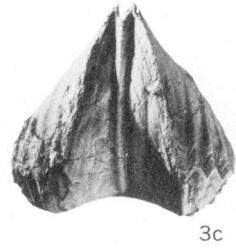
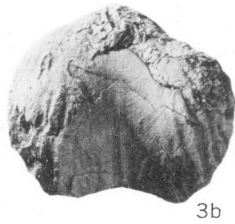
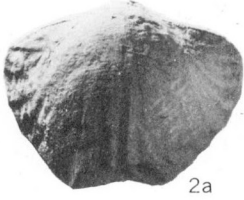


PLATE XII

(Except where otherwise stated, all figures are natural size)

Ladogioides kakwaensis (McLaren)

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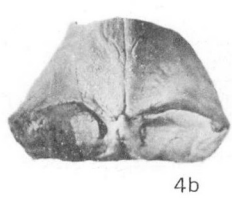
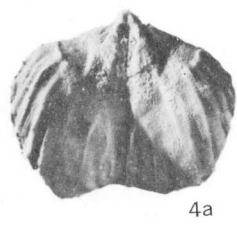
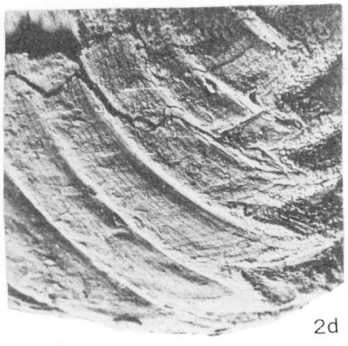


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(All figures are natural size)

Leiorhynchus manetoe n. sp.

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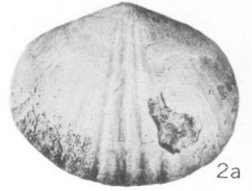
1a



1b



1c



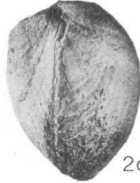
2a



3b



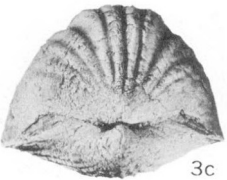
3a



2c



2b



3c



3d



4a



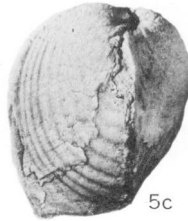
4b



5a



5b



5c



4c



6a



6b



6c



7



6d



6e

PLATE XIV

(All figures are natural size)

Leiorhynchus manetoe n. sp.

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Leiorhynchus castanea (Meek)

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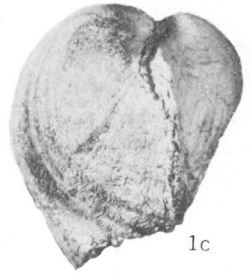
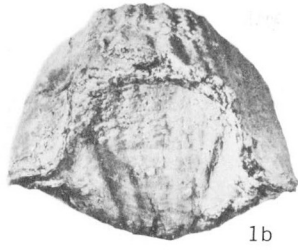
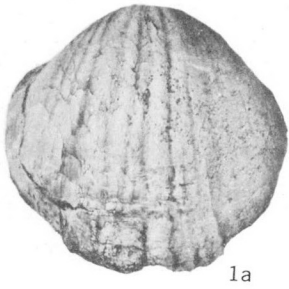


PLATE XV

(All figures are natural size)

Leiorhynchus castanea (Meek)

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(Except where otherwise stated, all figures are natural size)

Leiorhynchus castanea (Meek)

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Leiorhynchus awokanak n. sp.

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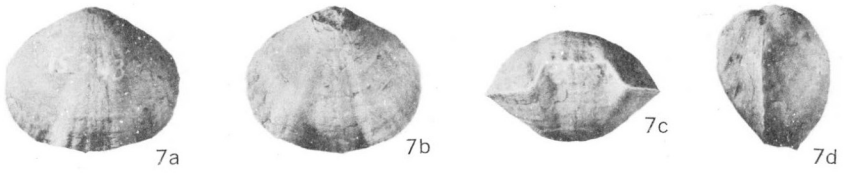
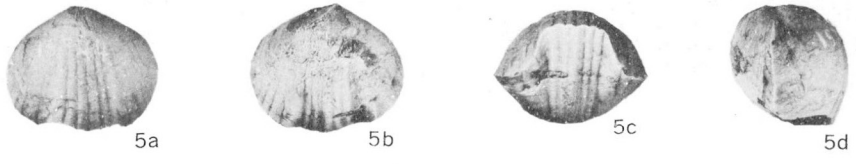
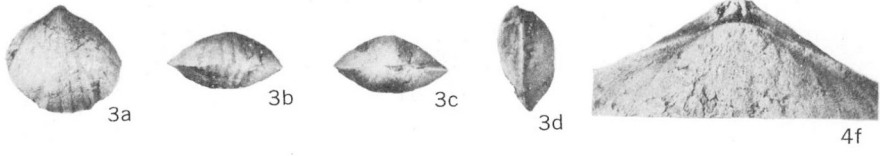
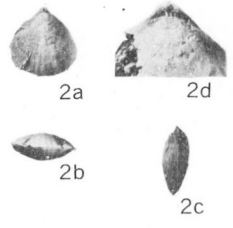
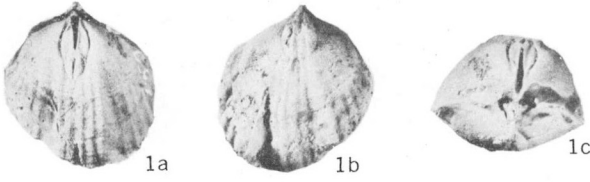


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(Except where otherwise stated, all figures are natural size)

Leiorhynchus russelli n. sp.

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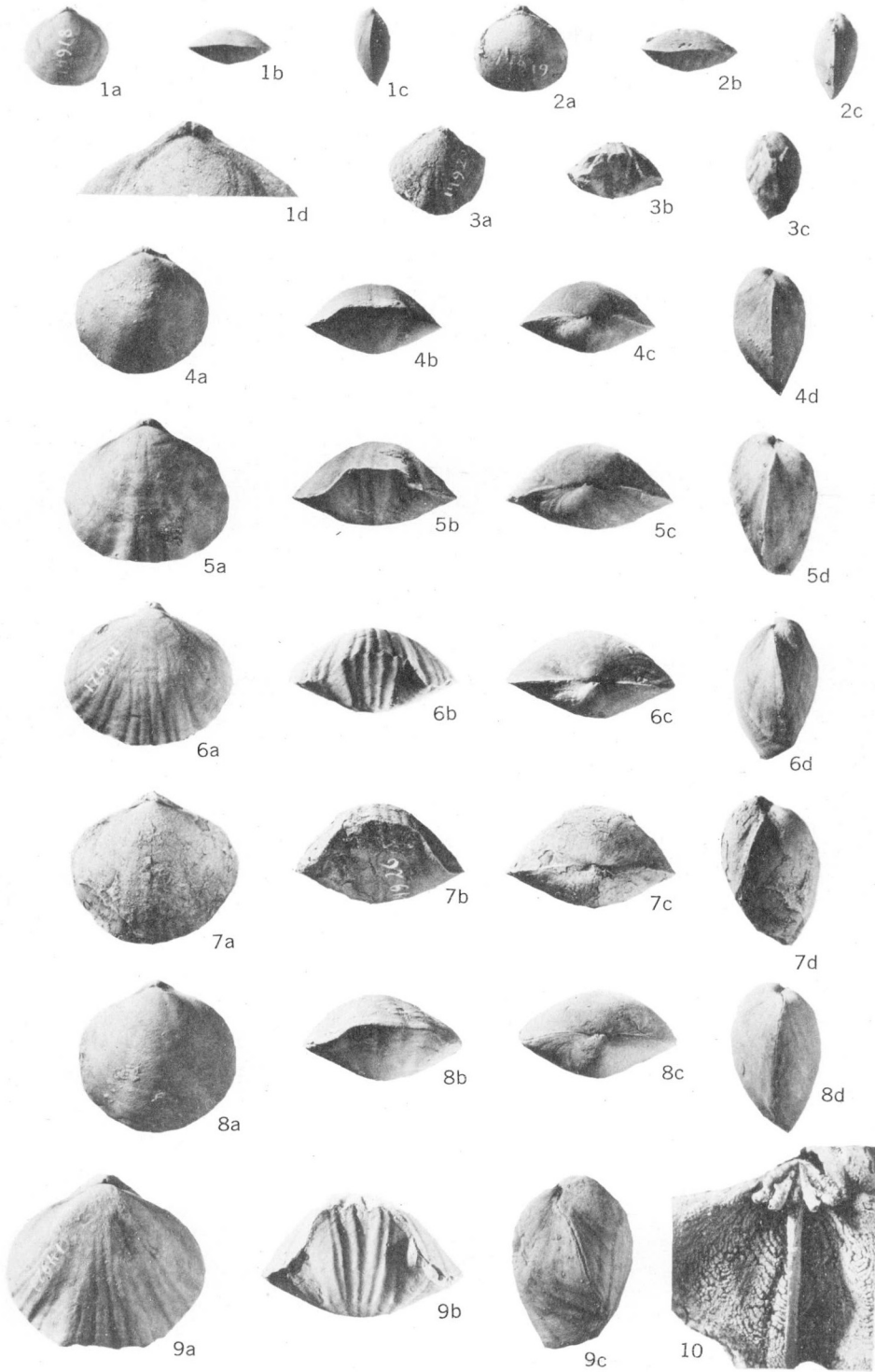


PLATE XVIII

(Except where otherwise stated, all figures are natural size)

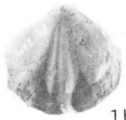
Leiorhynchus carya Crickmay

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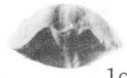
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1a



1b



1c



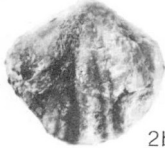
1d



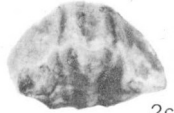
1e



2a



2b



2c



2d



2e



3a



3b



3c



4a



4b



4c



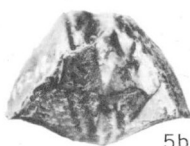
4d



4e



5a



5b



5c



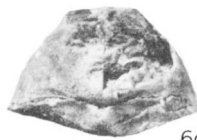
5d



6a



6b



6c



6d

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