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Rolf Ludvigsen

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MIDDLE ORDOVICIAN TRILOBITES, SOUTH NAHANNI RIVER AREA, DISTRICT OF MACKENZIE

by

Rolf Ludvigsen

Department of Geology

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of the requirements for the degree of
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ABSTRACT

Study of the Bathyuridae, Cheiruridae, and Encrinuridae of large, diverse, and well-preserved silicified trilobite faunas of Middle Ordovician age collected in eleven stratigraphic sections through the upper Sunblood, Esbataottine, and lower Whittaker Formations in the South Nahanni River area, southern Mackenzie Mountains, permits recognition of one faunal unit and eight assemblage zones - Orthidiella-"Goniotelina" Fauna (Whiterockian), Bathyurus granulosus and Ceraurinella nahanniensis Zones (Chazyan), Bathyurus ulu and Ceraurus gabrielsi Zones (Blackriveran), and Ceraurinella longispina, Ceraurinella necra, Ceraurus mackenziensis, and Whittakerites planatus Zones (Rocklandian to Edenian). The zonal sequence contains no apparent gaps and, as such, is unique in western North America.

The trilobites occur in thin to medium bedded, variably argillaceous and silty micrites that represent uniform, quiet, level-bottom carbonate mud environments which extended from the littoral zone to deeper sub-littoral zones on a broad marginal platform about 50-100 km wide. Four trilobite biofacies, based on recurrent generic associations, are recognized within the Chazyan/Blackriveran interval and appear to be distributed in belts parallel to the shoreline. From shallow to deeper water, these are; Bathyurus Biofacies (Bathyu-

rus and *Ceraurus gabrielsi* dominate), *Isotelus* Biofacies (*Isotelus* dominates), *Calyptaulax*-*Ceraurinella* Biofacies (*Calyptaulax*, *Ceraurinella*, *Cybeloides*, and *Sphaerexochus* dominate), and *Dimeropyge* Biofacies (*Dimeropyge*, *Dolichoharpes*, and *Acanthoparypha* dominate). Deep platform-edge faunas are dominated by trinucleid and olenid trilobites and graptolites. From the *Bathyurus* to the *Dimeropyge* Biofacies, the trilobite species diversity increases from fewer than 4 to as many as 25, the trilobite density increases from 12 to more than 100 individuals/kg of limestone, the average size of trilobites decreases, the relative proportion of spinose trilobites increases, and the number of associated suspension feeders (brachiopods, bryozoans) initially increases and then sharply decreases in the *Dimeropyge* Biofacies. The areal and stratigraphic distribution of the trilobite biofacies allows recognition of three transgressive/regressive couplets within the Chazyan/Rocklandian interval. In the Rocklandian to Edenian interval, an undifferentiated *Calyptaulax*-*Ceraurinella*-*Dimeropyge* Biofacies occurs in deeper water argillaceous limestones and a cryptolithid-asaphid-olenid-graptolite association in deep water shales. Shallower biofacies consist of brachiopod-coral-pelmatozoan-mollusk-algal associations (among them, the "Arctic Ordovician Fauna").

Phylogeny of selected genera shows that separate and distinct species groups of *Ceraurinella*, *Ceraurus*, and *Bathyurus* occur in northern and in eastern North America. The species differences indicate, either, a separate post-Whiterockian evolutionary history of taxa in these areas or the presence of generic morphologic clines in the Middle Ordovician.

Autecological analysis of *Bathyurus esbataottinensis* indicates a quasi-infaunal feeding position for this trilobite.

Forty-three species belonging to eighteen genera are described and illustrated - *Bathyurus* (four species), *Ceraurinella* (eight), *Remipyga* (one), *Ceraurus* (seven), *Whittakerites* n. gen. (one), *Borealaspis* n. gen. (three), cheirurinid indet. (one), *Acanthoparypha* (three), *Pandaspinapyga* (two), *Holia* (two), *Heliomeroides* (one), *Heliomera* (one), *Sphaerexochus* (two), *Kawina* (one), *Sphaerocoryphe* (two), *Encrinuroides* (one), *Cybeloides* (two), and *Cybellela*? (one). Twenty-four species and two genera are new.

ACKNOWLEDGEMENTS

The finances that enabled me to collect in the South Nahanni River area during the 1972 and 1973 field seasons came from a number of sources. I thank the Department of Indian and Northern Affairs, the Geological Survey of Canada, the National Research Council of Canada (through a grant to A.C. Lenz), and the Northern Research Group at the University of Western Ontario for providing this support. A number of important collections were acquired in 1971 and 1972 while I was employed by [illegible] Zay Smith Associates and I express my gratitude to this company, especially to the party chief, Mr. J. Frank Conrad, for allowing time out of a busy field program to collect these trilobites. The help and support of Dr. S.L. Blusson of the Geological Survey of Canada facilitated the field work in 1972 and 1973 from base camps at Macmillan Pass and Summit Lake. I also express thanks to Parks Canada for permission to collect within the Nahanni National Park.

Drs. B.S. Norford and T.E. Bolton arranged for the loan of collections made by the Geological Survey of Canada during Operations Mackenzie and Nahanni. Type specimens were examined through the courtesy of Drs. T.E. Bolton and M.J. Copeland of the Geological Survey of Canada, Ottawa; Mr. D.H. Collins of the Royal Ontario Museum, Toronto; Mr. J.P. Collier of the United States National Museum, Washington; Mrs. J.S.

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I express my gratitude to Dr. B.D.E. Chatterton of the University of Alberta who instructed me in the specialized photographic techniques of these fossils, helped to unravel taxonomic and morphologic problems, and, on a number of occasions, constructively criticised many of the ideas expressed in this thesis. I would also like to thank Mr. Ravindra S. Tipnis of the University of Alberta for providing preliminary biostratigraphic information on the conodonts of the collections studied herein and Dr. J.R.P. Ross of Western Washington State College for identifications of the bryozoans.

Special thanks go to my supervisor, Dr. A.C. Lenz, who provided an environment conducive for research and who has guided and supported this investigation for the past three years. He also identified the graptolite collections from Summit Lake.

Many colleagues took part in the field work and I acknowledge the help of Dave Perry, Brian Chatterton, Alf Lenz, John Harrington, Frank Conrad, Brian Skinner, and Dave Christie in collecting fossils and in interpreting field data.

I am grateful to Dr. D.B. Craig, Resident Geologist at

Whitehorse, who located and rescued about a quarter of a ton of silicified fossil samples that had been lost along the Ross River Road.

During his year at Western, Dr. P.M. Sheehan contributed stimulating discussion of Ordovician stratigraphy and paleoecology.

Finally, I express my deep gratitude and affection to my friend and lover, Kathleen MacKinnon, who has been a part of this project from its inception - taking part in many tasks including fossil picking, cataloguing, and typing - and who has shared its excitement and its momentary disappointments.

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INTRODUCTION

General remarks

Lower Paleozoic strata constitute most of the exposed rock in the southern Mackenzie Mountains. The well-exposed character of the rocks and the pronounced colour differentiation and contrasting weathering styles of many of the Cambrian to Devonian carbonate units has permitted compilation of remarkably detailed and accurate geological maps by members of the Geological Survey of Canada during Operation Mackenzie in 1957 (Douglas and Norris, 1960, 1961, 1963) and Operation Nahanni in 1963 and 1965 (Gabrielse *et al.*, 1973). The mapping was accomplished with comparative ease using information from air photographic coverage to tie together stratigraphic and structural data gathered from relatively widely spaced ground checks and stratigraphic sections. This has meant that the lithostratigraphy of the eastern carbonate belt is rather well known and the established formations can, with few exceptions, be recognized over large parts of this area.

Biostratigraphic studies of the Lower Paleozoic rocks in this area have lagged behind the lithostratigraphic studies. This is unfortunate because only by parallel effort in each of these fields and careful integration of the results does a satisfactory picture emerge about the stratigraphic history. To date, only two intervals of the extensive Lower Paleozoic column in this area have come under careful biostratigraphic scrutiny - the Early Cambrian (Fritz, 1972) and the Late Silurian-Early Devonian (Perry, 1974). The intervening strata comprise a thick succession of dominantly carbonate rock that records one of the most complete and continuously fossiliferous Cambrian to Silurian sequences in North America. This study focuses on some of the trilobites of the Middle Ordovician portion of this succession; specifically, the families Bathyuridae, Cheiruridae, and Encrinuridae of the upper Sunblood Formation, the Esbataottine Formation, and the lower Whittaker Formation in the South Nahanni River area of the Mackenzie Mountains.

The continuous succession of Middle Ordovician trilobites described in this thesis is one of the few documented in a single area on this continent and the only one from western North America. In completeness and in preservation, the faunal succession in the Nahanni area is only rivalled by the sequences of trilobite faunas of the same age in Virginia (Whittington, 1959). In other parts of western North America complete sequences of shelly faunas of Canadian and Whiterockian age, including abundant trilobites, are known from Nevada and Utah (Ross, 1951, 1967, 1970, 1972; Hintze, 1953; Hintze et al., 1972), but a large portion of the Chazyan to Trentonian interval is poorly known due to the absence of biostratigraphic information from the extensive quartzite units of late Middle Ordovician age. An apparently complete

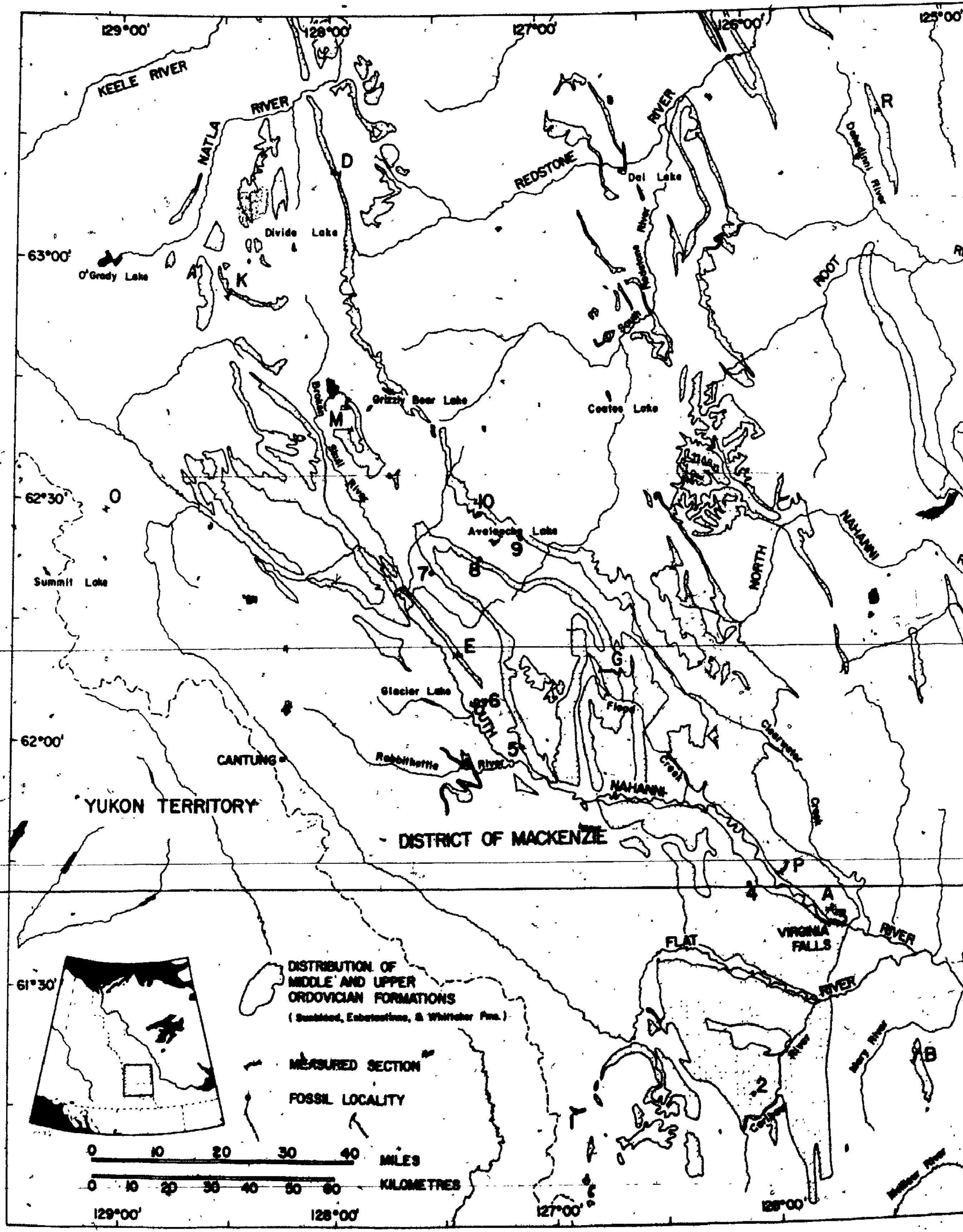
Middle Ordovician sequence of trilobite faunas is present in Oklahoma, but here the interval between the Whiterockian (Joins and Oil Creek Formations) and the late (?) Blackriveran (upper Bromide Formation) is sparsely fossiliferous (Shaw, 1974, Tab. 1).

In addition to providing information about the distribution of these trilobite faunas in a vertical or temporal sense; parts of the Nahanni sequence also contain alternating "shallow" and "deep" water trilobites and, thus, contribute towards an understanding of the lateral relationship of differing trilobite faunas of the same age in a community sense. Similar "shallow" and "deep" water trilobites occur in eastern North America, but here each is found in geographically separated areas in strata that have been classified according to different stadial schemes - Chazyan and Blackriveran in New York/Ontario/Quebec and Ashby, Marmor, Porterfield, and Wilderness in Tennessee/Virginia. The separate areas of development of these trilobite faunas and the application of discrete stage names have been effective in concealing their basic unity.

The purpose of this thesis is to document the presence of well preserved and diverse silicified trilobite faunas of Middle Ordovician age in the South Nahanni River area, to describe and illustrate some of the more important of these trilobites, to demonstrate their utility in biostratigraphy, to erect a zonation based on these trilobites that spans most of the Middle Ordovician, to provide evidence that the distribution of different trilobites is governed by specific sets of physical parameters, to isolate and describe four recurrent trilobite associations (or biofacies), and, in general, to elucidate the natural history of these fossils.

The remoteness and comparative inaccessibility of the study area presents special problems. These are, however, ameliorated by the propitious preservation of the fossils. The silicified state of most of the faunas allows rapid, yet rather complete, sampling of a fossiliferous section. Furthermore, the collecting is less subject to bias than is conventional sampling of non-silicified fossils and allows the retention of very small specimens that otherwise would have gone unnoticed. Large collections can be processed with a minimum of effort and these provide the sheer number of individuals necessary for any kind of quantitative analysis - either morphologic, ontogenetic, or paleoecologic. The apt term "dry-dredging", coined by G. Arthur Cooper, emphasizes the similarity of method and product between this technique and that employed by marine biologists.

In a recently published paper (Ludvigsen, 1975), I review and revise the Ordovician stratigraphy of the southern Mackenzie Mountains and propose a new formation. Much of the background information for the material presented herein will be found in this paper and frequent reference will eliminate needless repetition. The paper is included as an appendix and is considered an integral part of this thesis.


129°00'
128°00'
127°00'
126°00'
125°00'
KEELE RIVER
NATLA
RIVER
REDSTONE
RIVER
Redstone River
Dal Lake
Dahadinni River
R
D
Divide Lake
63°00'
O'Grady Lake
A
K
ROOT
M
Grizzly Bear Lake
Broken Skull River
Coates Lake
62°30'
O
10
Avalanche Lake
9
8
7
Summit Lake
NORTH
NAHANNI
E
G
Glacier Lake
6
Flood
SOUTH
5
62°00'
CANTUNG
Rabbitkettle River
Clearwater Creek
Creek
NAHANNI
YUKON TERRITORY
DISTRICT OF MACKENZIE
P
4
A
VIRGINIA FALLS
RIVER
FLAT
RIVER
61°30'
DISTRIBUTION OF MIDDLE AND UPPER ORDOVICIAN FORMATIONS
(Sunblood, Esbataottine, & Whittaker Fms.)
MEASURED SECTION
FOSSIL LOCALITY
Caribou River
Mary River
B
2
0 10 20 30 40 MILES
0 10 20 30 40 50 60 KILOMETRES
129°00'
128°00'
127°00'
126°00'
Meilleur River

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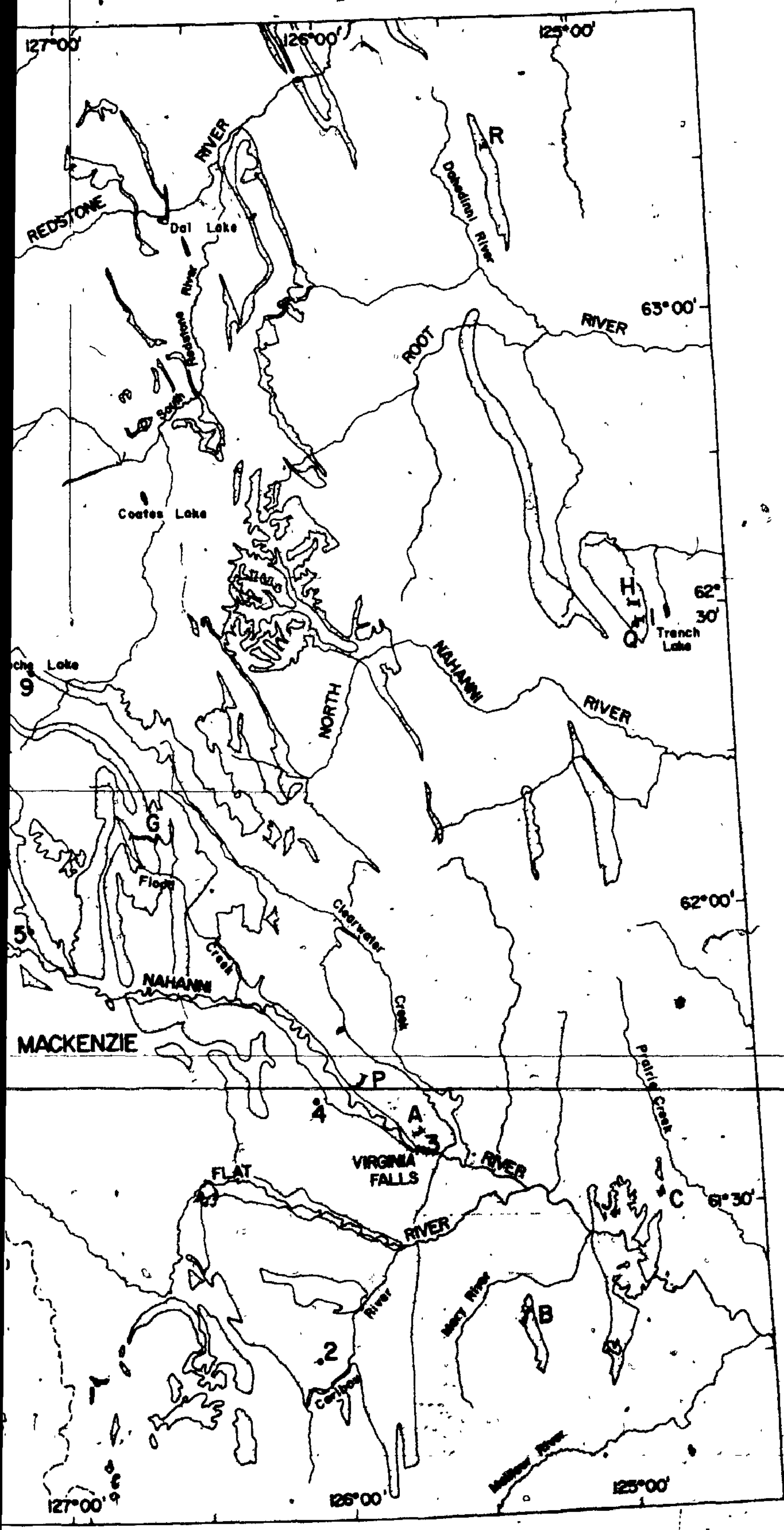


Text-figure 1.

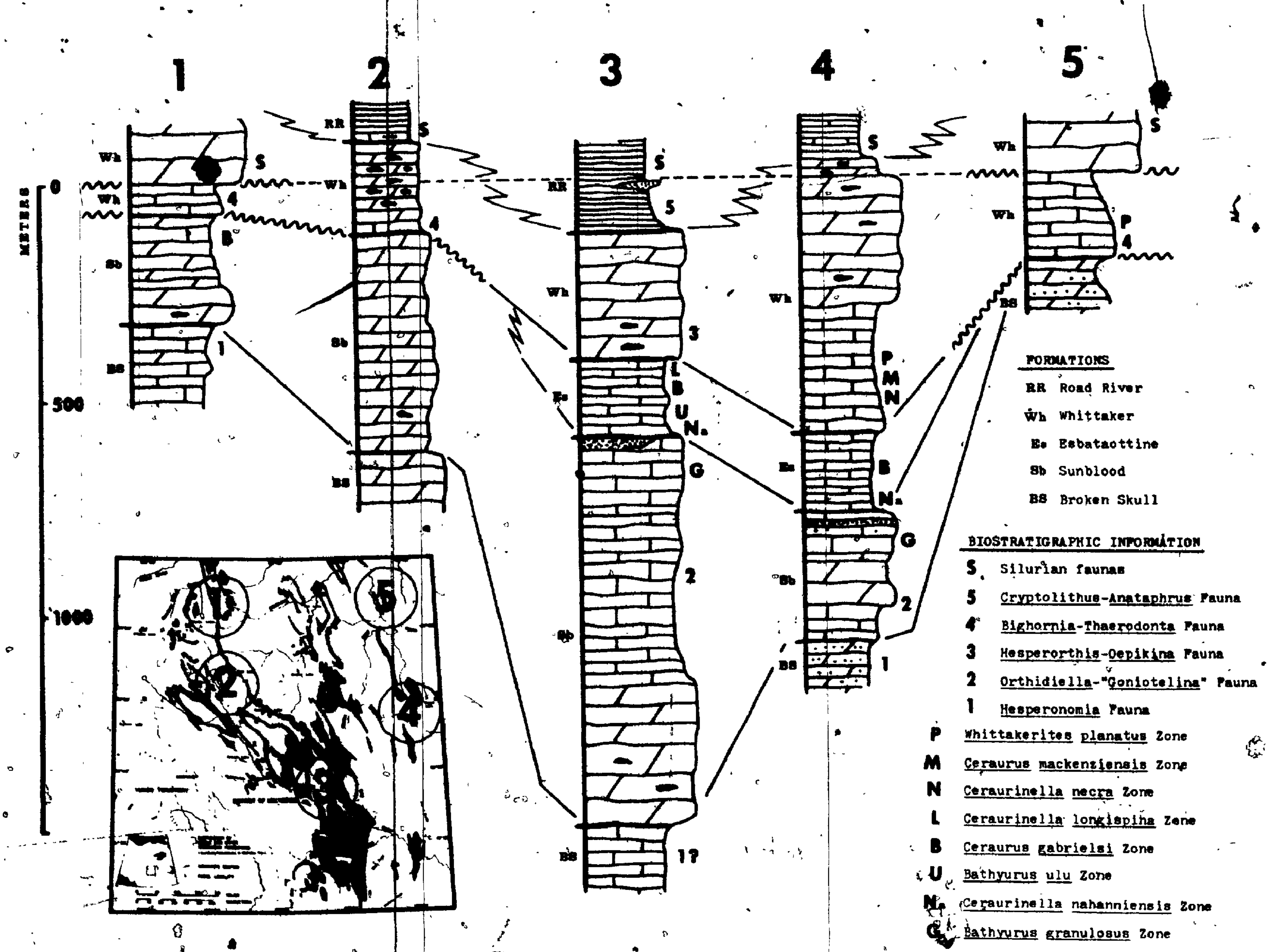
Locality map of the South Nahanni River area showing measured sections (capital letters) and fossil locations (numbers). The outcrop areas of the Sunblood, Esbataottine, and Whittaker Formations are indicated by stipple. Equivalent fine clastic rocks of the Road River Formation are not outlined. Geology modified from Douglas and Norris (1960, 1961, 1963), Blusson (1968, 1971) and Gabrielse et al. (1973). The following sections are shown:

Natla River	Section D
Broken Skull River	Section K
Grizzly Bear Lake	Section M
Glacier Lake	Section E
Flood Creek	Section G
Sunblood Range	Section P Section A
Mary Range	Section B
Funeral Range	Section J Section C
Whittaker Range	Section Q Section I Section H
Dusky Range	Section R

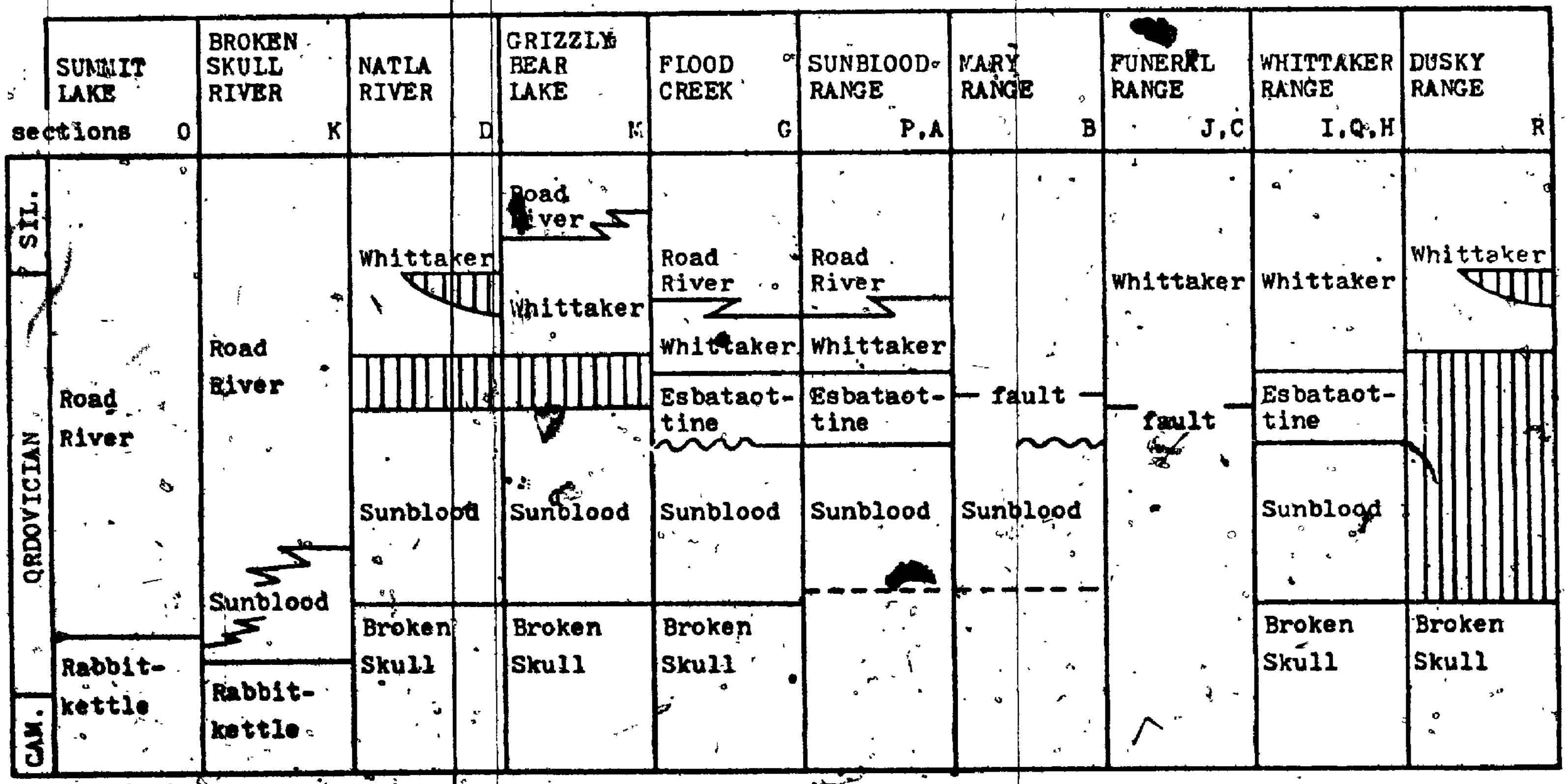
Diagrammatic lithology sections and detailed locality data are included in Appendix I.

Locality 4 is GSC loc. 58678

2 of 2



Text-figure 2. Cross-section of Ordovician rocks.



Text-figure 3. Correlation chart of Ordovician formations of the South Nahanni River area.

Field work

The isolation of the study area (Text-fig. 1) necessitates air support of any field effort. The nearest roads are at the Canada Tungsten Mine at Cantung to the west and at Fort Simpson, some 200 km to the east. A number of lakes in the area are suitable for use by small float-equipped fixed wing aircraft and the South Nahanni River, above Virginia Falls, is sufficiently wide to permit landing with such craft in many locations. The most effective method of carrying out stratigraphic and paleontologic field work in this area, and the approach used for the majority of the sections measured for the present study, is the judicious use of a helicopter for transportation to the sections and for ferrying the samples collected to the nearest point where they can be picked up later by a float plane.

Stratigraphy

The trilobites studied in this thesis were collected from the upper part of the Sunblood Formation, the Esbataottine Formation, and the lower part of the Whittaker Formation. The distribution, thicknesses, lithologies, and general faunal content of these and other Ordovician formations have been covered previously (Ludvigsen, 1975) and need not be repeated here.

Text-figure 2 is a generalized NW-S-NE cross-section of the study area that approximately parallels the edge of the Redstone Arch and shows the relationship of Ordovician formations, gross lithology, and location of the trilobite zones recognized herein and the informal biostratigraphic divisions recognized by Ludvigsen (1975). Text-figure 3 is a correlation chart of Ordovician formations of the study area.

Fossil nomenclature

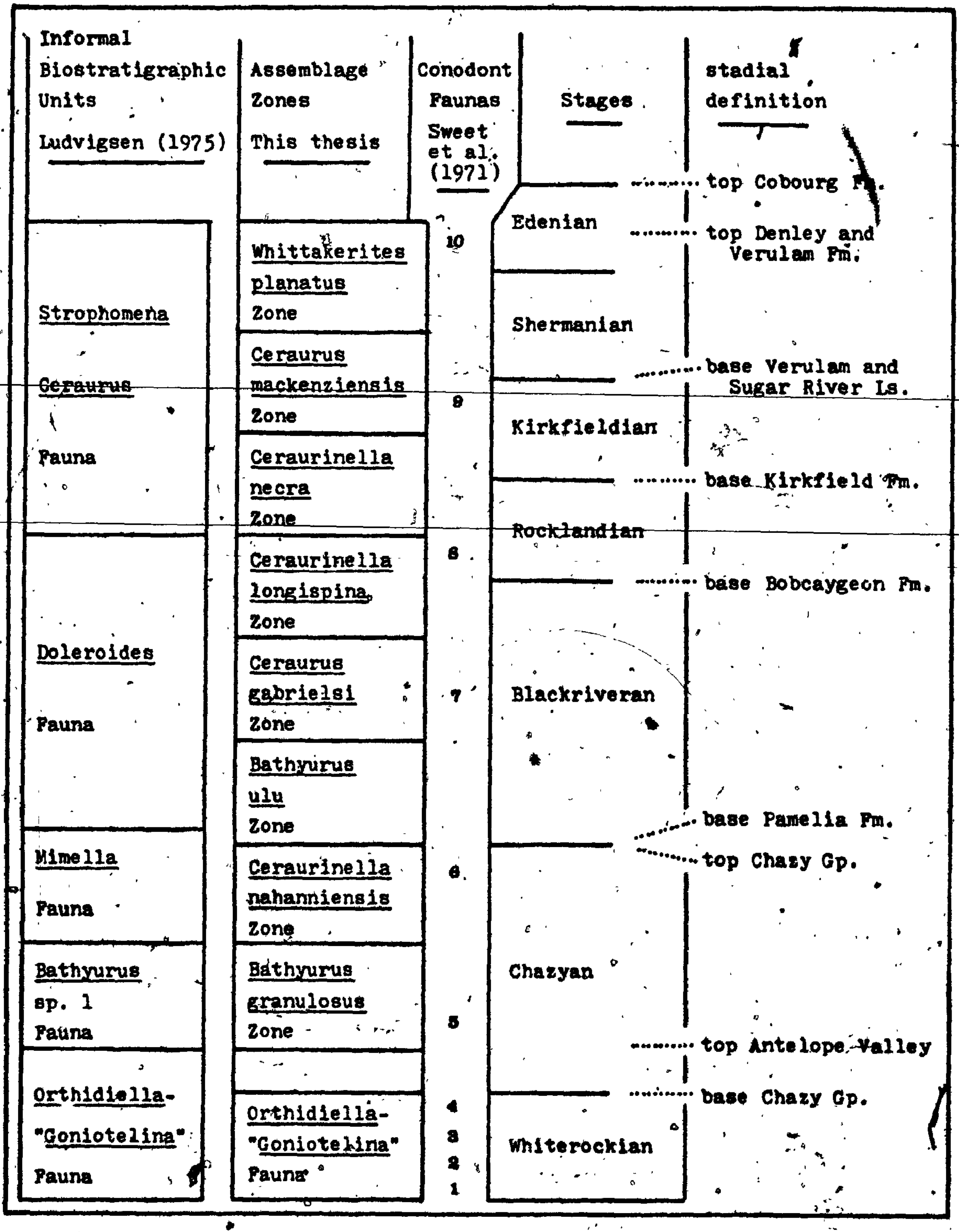
New taxa are introduced in this thesis with the full realization that the proposed names will be considered invalid manuscript names under the Code of Zoological Nomenclature. This procedure, however, eliminates such transcriptive monstrosities as "cheirurinid n. gen. and n. sp. (cf. Cheirurus numitor Billings, 1866)", which can be replaced by "Borealaspis biformis n. gen. and n. sp.", and continuing and confusing reference to Ceraurinella n. sp. 7 and Ceraurus n. sp. 4, which can be replaced by Ceraurinella arctica n. sp. and Ceraurus hirsuitus n. sp.

A portion of this thesis constitutes a part of a paper on the trilobite faunas of the lowest 50 m of the Esbataottine Formation from two sections in the Sunblood Range (Sections A and P). This paper, co-authored by Brian Chatterton of the University of Alberta, is in manuscript stage. Chatterton photographed many of the specimens included on Plates 6, 7, 21, 22, 23, 25, 27, and 29 (identified by University of Alberta type numbers) and critically read the parts of the section on Systematic Paleontology dealing with cheirurids and encrinurids from the lowest Esbataottine Formation. New taxa appearing in this paper are, in this thesis, attributed to Chatterton and Ludvigsen, ms.

Stadial nomenclature

Considerable time, effort, and printed space have been devoted to discussion of the relative merits of a number of parallel stadial schemes that have been proposed for Ordovician rocks of North America (Twenhofel et al., 1954; Cooper, 1956; Kay, 1960, 1968; Fisher, 1962; Sweet and Bergström, 1971, Bergström, 1971; among many others). The sad fact is that a satisfactory scheme is not yet available. The one adopted herein (Text-fig. 4) is largely an amalgam of Kay's and Cooper's stages; the individual choices were dictated by their utility from the point of view of correlation by trilobites.

Whiterockian Stage: The trilobites of this stage have been extensively studied from sequences in Newfoundland (Lower Head, Whittington, 1963; Table Head, Whittington, 1965a), Nevada (Antelope Valley, Ross, 1970), Oklahoma (Joins, Oil Creek, Shaw, 1974), and Yukon Territory (Dean, 1973), among others. In Nevada the type Whiterockian Stage comprises the lower Orthidiella Zone and the upper Anomalorthis Zone (Ross, 1970). The age of the upper part of the stage has been the subject of much discussion. Ross (1970) claimed that it extended as high as the Blackriveran of eastern North America, but Bergström et al. (1973) concluded that the youngest part of the Whiterockian is equivalent to the Chazyan, but is not as young as the type Porterfieldian. Herein, the name Whiterockian is applied to strata carrying the Orthidiella-"Goniotelina" Fauna (Ludvigsen, 1975) and conodonts of Fauna 1 to



Text-figure 4.

Relationship of trilobite zones, conodont faunas, and informal biostratigraphic units to stadial scheme.

Fauna 4 of Sweet et al., 1971 (Tipnis, personal communication, 1975).

Chazyan Stage: The study of trilobites from the Chazy Group of New York State by Shaw (1968) has, from the point of view of trilobite biostratigraphy, placed the Chazyan Stage on a firm foundation. The recognition, in the Nahanni area, of trilobite faunas highly similar to those from the Chazy Group has negated the suggestion in Twenhofel et al. (1954, p. 253) that "the Chazyan fauna has turned out to be a somewhat restricted and provincial facies not clearly recognizable elsewhere". The Lincolnshire Limestone of Virginia (Evitt, 1951; Whittington and Evitt, 1954) and the Upper Stinchar Limestone of Girvan, Scotland (Tripp, 1967) contribute other trilobite faunas of Chazyan age. Within the study area, the Chazyan Stage includes the Bathyurus granulosus Zone and the Ceraurinella nahanniensis Zone and/or strata carrying conodonts of Fauna 5 and Fauna 6 of Sweet et al. (1971). The base of the Chazyan is drawn to coincide with the first appearance of species of Bathyurus s.s. (that is, Bathyurus cf. nevadensis Ross and B. cf. angustus Ross). These occur below the B. granulosus Zone in collections with Fauna 5 conodonts (Tipnis, personal communication, 1975). The interval assigned to the Chazyan in the Nahanni area probably corresponds closely to the total time span of the Chazy Group (Raring, 1972) and appears to overlap somewhat with the upper part of the Whiterockian Stage (Bergström et al., 1973). The argument that the name Chazyan is invalid as a time-stratigraphic unit because it is based on a rock-stratigraphic unit seems picayune. Surely, an assemblage of fossils can be recognized as being of Chazyan age without the implication that the strata yielding the fossils belong to the Chazy Group. In any case, to pin the name of a local post office on a section of strata as a stage term (as Fisher, 1962 did when he applied the term Barneveld to the Trenton Stage of Cooper, 1956) changes neither the fossils nor the time span of the section, but it does introduce yet another name into an already confused terminology.

Blackriveran Stage: The exposures at Black River, New York, from the base of the Pamelia Formation to the base of the Selby Formation (including the Pamelia, Lowville, and Chaumont Formations; Walker, 1973) belong to the Black River Group (Kay, 1968) and constitute the type section of the Blackriveran Stage. In Ontario, this corresponds to the interval from the base of the Shadow Lake Formation to the base of the Bobcaygeon Formation (Kay, 1968; Winder and Sanford, 1972). Trilobites are sparse in the Blackriveran of New York and Ontario, but lists and illustrations in Wilson (1947) suffice to characterize this interval. Additional and more diverse trilobites from the Edinburg Limestone of Virginia (Whittington, 1959) and the Bromide Formation of Oklahoma (Shaw, 1974) appear to be largely of Blackriveran age. In terms of conodonts, the Blackriveran consists of Fauna 7 of Sweet *et al.* (1971). In the Nahanni area, the *Bathyurus ulu* Zone and the *Ceraurus gabrielsi* Zone are assigned to the Blackriveran Stage. The upper boundary with the Rocklandian Stage probably falls within the Ceraurinella longispina Zone.

Rocklandian, Kirkfieldian, and Shermanian Stages: The interval from the base of the Selby Formation to the base of the Hollowell Member of the Cobourg Formation constitute the Rocklandian to Shermanian Stages (Kay, 1968). In terms of well-studied trilobite faunas, these stadial intervals include the faunas from the upper part of the Platteville Group and the Decorah Formation of the upper Mississippi Valley (DeMott, 1963), the Kimmswick Formation of Illinois and Missouri (Foerste, 1920; Bradley, 1930), the shaly beds at Silliman's Fossil Mount, Baffin Island (Whittington, 1954), the "Trenton" fauna from the Shenandoah Valley, Virginia (Whittington, 1941), the Cape Calhoun Formation of northern Greenland (Troedsson, 1928), and the Rockland, Hull, Sherman Falls Formations of Ontario (Wilson, 1947; or Coboconk, Kirkfield, Verulam, and lower Cobourg Formations, Winder and Sanford, 1972). This interval includes conodonts of Fauna 8, Fauna 9, and lower Fauna 10 of Sweet et al. (1971). In the Nahanni area, the base of the Rocklandian falls within the Ceraurinella longispina Zone. The Ceraurinella necra, Ceraurus mackenziensis, and lower Whittakerites planatus Zones are included in the Rocklandian, Kirkfieldian, and Shermanian Stages. In this thesis, the term "Trentonian" is occasionally used to denote the approximate Rocklandian/Shermanian interval.

Edenian Stage: The lower part of the type Cincinnatian Series comprises the Clays Ferry and most of the Kope Formation in the Cincinnati region and constitute the Edenian Stage. In New York, that portion of the Trenton Group above the base of the Hollowell Member of the Cobourg Formation is included in the Edenian (Sweet and Bergström, 1971). Trilobites of this interval are generally poorly known, but include those from the upper part of the Cobourg Formation in Ontario (Wilson, 1947) and probably some of those from the Maquoketa Formation of Iowa (Slocum, 1913). The interval includes portions of conodont Faunas 10 and 11 of Sweet et al. (1971).

At the present time, one sees little hope that a stadial scheme, satisfactory to most Lower Paleozoic stratigraphers and paleontologists, can be derived from the much studied and much interpreted Ordovician successions of eastern North America. Perhaps the time has come to recognize that the use of any established stage name in the Ordovician of North America is strictly an interim measure until a new succession of stages can be defined - preferrably from an area far removed from the "classical" Ordovician areas of North America. The Ordovician succession of the South Nahanni River area would be admirably suited to serve as the type area for the Middle Ordovician part of a new stadial scheme (when the remaining trilobites and the conodonts, brachiopods, and bryozoans have received study).

TRILOBITE BIOSTRATIGRAPHY

Preliminary remarks

Chronostratigraphy (the study of geologic time based on fossils) must ultimately rest on biostratigraphy (the study of rock units and their contained fossils) carried out in a number of local sections. The value, nature, and meaning of these and allied terms have been extensively discussed in the literature. Particularly; if, and to what extent, biostratigraphic units carry temporal significance. Hedberg (1965, 1971) perceived a biostratigraphic unit to refer to a body of rock strata unified by its fossil content or paleontological character. This definition does not, necessarily, have any time meaning. Jeletzky (1956) proposed that this term be abandoned because it means essentially the same as "biofacies". Although chronostratigraphic units (time defined) are basically distinct from biostratigraphic units (rock and fossil defined); in practice, "biostratigraphic units frequently approximate the best chronostratigraphic units we can attain and ... they are often identified with each other" (Hedberg, 1971, p. 25).

The present study recognizes a series of assemblage zones based on trilobites from the upper Sunblood, Esbataottine, and lower Whittaker Formations in the southern Mackenzie Mountains (Text-fig. 4). Concurrently, the trilobites from the lower part of this sequence have been arranged into four biofacies defined by persistent recurrence of specified groups of critical genera. The biofacies reflect community structure and their boundaries must, necessarily cross those of the assemblage zones which are based on the phylogenetic grade within the genera. The reconnaissance nature of the collecting sometimes makes it impossible to separate a biofacies boundary from an assemblage zonal boundary. In many cases, however, the presence of adjoining biofacies can be recognized within a single assemblage zone and, because the two groupings are separately defined, the "facies" control of the zonal sequence can be minimized, but can never be eliminated. The assemblage zones used in this thesis can therefore be considered to be refined biostratigraphic units that do have time meaning. The zones, however, are a long way from being biochronological zones.

One important conclusion of this study is that biostratigraphy on faunal sequences similar to those studied herein cannot be carried out in the absence of parallel work on the biofacies aspect of the same faunas and, in fact, a grasp of the composition of, and inter-relationship between, contemporary biofacies is mandatory before a satisfactory zonal scheme can be established. This conclusion has been stated many times before, but it is one that, perhaps, requires periodic repetition. This study shows that a much greater diversity gradient exists between adjoining and contemporary biofacies than between faunas of different ages but of the same biofacies. Biofacies shifts are reflected in generic changes, to the extent that a near-shore *Bathyurus* Biofacies is completely dissimilar to a deeper-water *Calyptaulax*-*Ceraurinella* Biofacies of the same age. True zonal changes only become evident upon tracing relatively subtle intra-generic morphological changes of various taxa within a single biofacies. These concepts emphasize the unreliability of correlation based on generic composition and, further, caution against the unqualified use of generic data in biogeographical studies unless these studies are accompanied by biofacies analyses of the regions being compared. It is also suggested that a zone defined on taxa belonging to a single biofacies should be viewed with scepticism (including portions of the present zonal scheme) or should be recognized to be of restricted zonal utility within that biofacies.

The building blocks of the proposed zonal scheme are mainly phylogenetic series of species of *Bathyurus*, *Ceraurinella*, and *Ceraurus* (or its derivative, *Whittakerites*). *Bathyurus* is a shallow-water inhabitant in the upper Sunblood and Esbataottine Formations; *Ceraurinella* persistently occupied a moderately deep-water environment in the Esbataottine to lower Whittaker interval; and *Ceraurus* is a shallow-water inhabitant in the middle Esbataottine Formation and, higher in the formation, apparently started to migrate into deeper water where it becomes a significant element within the lower Whittaker Formation. The decision to place emphasis on species of these genera in erecting the zonal scheme was influenced, primarily, by their relatively common occurrence (every collection studied contains species of one or more of these genera), but also by their preference for different habitats which allows integration of zonal information derived from shallow and deeper water trilobites and tends to minimize the influence of the biofacies in the zonal scheme.

In a recent paper (Ludvigsen, 1975), I recognize seven broad biostratigraphic divisions of rocks of Canadian to ?Maysvillian age in the southern Mackenzie Mountains. Text-figure 4 shows the relationship of these divisions to the present zonal scheme. Text-figures 5 to 8 summarize the occurrences of species of Cheiruridae, Encrinuridae, and Bathyuridae in each of 72 collections from eleven measured sections (Sections A, B, C, D, G, H; I, J, P, Q, R; Text-fig. 1). Diagrammatic lithology sections are included as an appendix. A composite range chart showing zonal occurrences of all studied species is included as Text-figure 9.

The following discussion of each of the proposed assemblage zones is mainly based on the trilobite species studied in this thesis. Reference will also be made to taxa illustrated and discussed by Ludvigsen (1975) and to the biostratigraphic significance of the ostracods from the same collections (Copeland, 1974). A number of trilobites from the lower part of the Esbataottine Formation at Sections A and P are currently under study by Brian Chatterton and my-

A	Heliomeroides teres	Acanthoparypha evitti	Holia secristi	Sphaerexochus arenosus	Ceraurinella nahanniensis	Ceraurinella kingstoni	Cybeloides cimelia	Encrinuroides rarus	Acanthoparypha echinoderma	Sphaerocoryphe cf. pemphis	Pandaspinapyga dactyla	Ceraurinella seriata	Bathyurus ulu	Ceraurus gabrielsi	Ceraurinella media	Ceraurinella longispina	
A 615							○	○								○	C. LONGISPINA ZONE
A 385							○	○							○		CERAURUS GABRIELSI ZONE
A 365							○	○						○			
A 247				○			○	○				○	○				BATHYURUS ULU ZONE
A 240												○	○				
A 220												○	○				
A 160					○	○											CERAURINELLA NAHANNIENSIS ZONE
A 140		○			○	○	○										
A 125		○	○	○	○	○	○	○	○	○	○						
A 115	○	○	○	○	○	○	○	○									

B	Bathyurus granulosus	Ceraurus blussoni	Bathyurus platyparius	Cybeloides cimelia	Ceraurinella arctica	
B 1510-20				○	○	C. LONGISPINA ZONE
B 1450		○	○			C. GABRIELSI ZONE
B 1315	○					BATHYURUS GRANULOSUS ZONE
B 1295	○					
B 1265	○					

Text-figure 5. Distribution of trilobites from Sections A and B and zonal assignment of collections.

C	Ceraurinella necra	Borealaspis biformis	Holia anacantha	Ceraurus mackenziensis	Ceraurinella brevispina	Remipyga serrata	Borealaspis whittakerensis	Sphaerocoryphe robustus	Acanthoparypha? goniopyga	
C 655				○	○	○	○	○	○	CERAURUS MACKENZIENSIS ZONE
C 640				○						
C 570-90	○	○	○							CERAURINELLA NECRA ZONE

D	Bathyurus esbataottinensis	Ceraurus gabrielsi	Bathyurus sp.	
D 1375		○	○	CERAURUS GABRIELSI ZONE
D 1342	○			
GSC loc. 69001	○			

G	Bathyurus granulosus	Cybeloides cimelia	Ceraurinella arctica	Encrinuroides rarus	Ceraurus cf. hirsuitus	
G 3340				○	○	CERAURINELLA LONGISPINA ZONE
G 3195		○	○	○		
G 2795	○					B. GRANULOSUS ZONE

R	Ceraurinella brevispina	Ceraurus milleranus	Whittakerites planatus	Sphaerocoryphe robustus	Ceraurus maewectoides	Borealaspis cf. biformis	Remipyga serrata	cheirurinid gen. et sp. indet.	
R 655	○								WHITTAKERITES PLANATUS ZONE
R 625	○	○	○	○	○	○	○	○	

J	Ceraurus mackenziensis	Ceraurinella brevispina	Sphaerocoryphe robustus	Borealaspis cf. biformis	
J 220	○	?	○	○	CERAURUS MACKENZIENSIS ZONE

Q	Ceraurinella media	?Acanthoparypha evitti	?Ceraurus mackenziensis	Ceraurinella brevispina	Remipyga serrata	Borealaspis cf. biformis	Whittakerites planatus	
Q 530				○	○		○	W. PLANATUS ZONE
Q 430			○	○	○	○		C. MACKENZIENSIS ZONE
Q 130	○	○						C. GABRIELSI ZONE

Text-figure 6. Distribution of trilobites from Sections C, D, G, J, Q, and R and zonal assignment of collections.

H	Bathyurus granulosus	Ceraurinella nahanniensis	Acanthoparypha evitti	Ceraurus gabrielsi	Bathyurus esbataottinensis	Bathyurus platyparius	Acanthoparypha? goniopyga	Ceraurinella brevispina	Ceraurus mackenziensis	Remipyga serrata	Borealaspis cf. biformis	Sphaerocoryphe robustus	Borealaspis whittakerensis	
H 1975								O	O	O				CERAURUS MACKENZIENSIS ZONE
H 1920								O	O	O	O	O	O	
H 1850							O	O	O	O				
H 1300						O								CERAURUS GABRIELSI ZONE
H 1020				O	O									
H 900				O	?									
H 800-820		O	?											CERAURINELLA NAHANNIENSIS ZONE
H 410	?													BATHYURUS GRANULOSUS ZONE

I	Bathyurus esbataottinensis	Ceraurinella necra	Ceraurus tuberosus	Borealaspis biformis	Acanthoparypha? goniopyga	Sphaerocoryphe robustus	Ceraurinella sp.	Ceraurus mackenziensis	Ceraurinella brevispina	Borealaspis cf. biformis	Whittakerites planatus	Remipyga serrata	
I 1590									O	O	O	O	W. PLANATUS ZONE
I 1410					O			O	O	O			CERAURUS MACKENZIENSIS ZONE
I 1350-80					O	O	O	O	O				
I 1275		O	O	?	O	O							CERAURINELLA NECRA ZONE
I 780	O												CERAURUS GABRIELSI ZONE

Text-figure 7. Distribution of trilobites from Sections H and I and zonal assignment of collections.

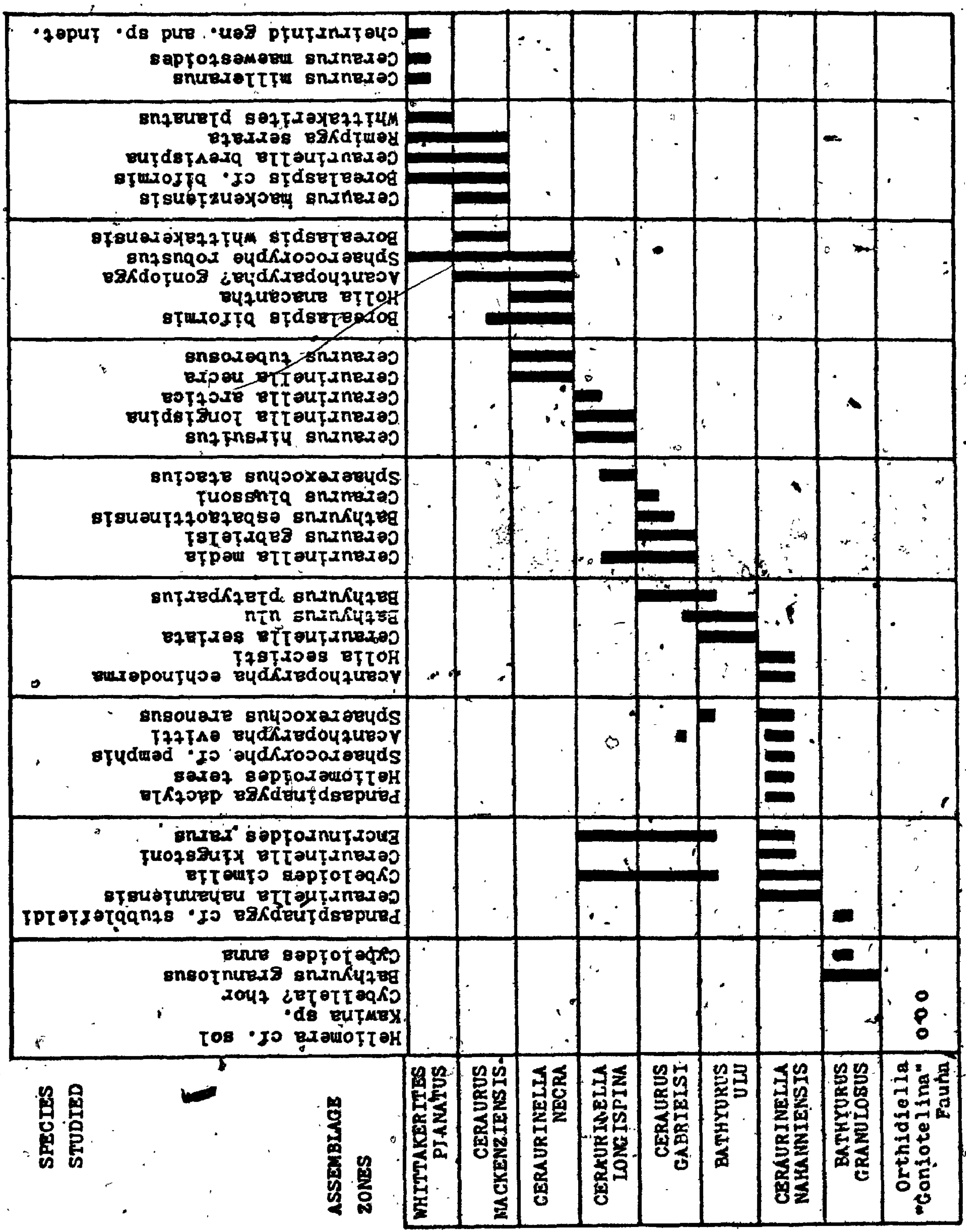
P	Bathyurus granulosus	Cybeloides anna	Pandaspinapyga cf. stubblefieldi	Ceraurinella nahanniensis	Cybeloides cimelia	Ceraurinella kingstoni	Pandaspinapyga dactyla	Heliomeroides teres	Acanthoparypha evitti	Encrinuroides rarus	Sphaerexochus arenosus	Holia secristi	Acanthoparypha echinoderma	Ceraurinella seriata	Bathyurus ulu	Bathyurus platyparius	Ceraurus gabrielsi	Ceraurinella media	Bathyurus esbataottinensis	Sphaerexochus atacius	Ceraurus hirsuitus	Ceraurinella longispina	Ceraurinella arctica	
P 2050					O																O		O	CERAURINELLA LONGISPINA ZONE
P 2038					O													O		O	O	O	O	
P 2010					O															O	O	O		
P 1945-55																	O		O					CERAURUS GABRIELSI ZONE
P 1931																	O		O					
P 1870																	O		O					
P 1785					O					O							O	O						
P 1665-85															O		O							
P 1625														O		O								BATHYURUS ULU ZONE
P 1595															O									
P 1585														O										
P 1575														O										
P 1520				O	O						O	O	O											CERAURINELLA NAHANNIENSIS ZONE
P 1512				O	O				O		O	O	O											
P 1497				O	O			O	O	O	O	O												
P 1485				O	O	O	O	O	O	O	O	O												
P 1440				O	O																			
P 1187	O	O	O																					BATHYURUS GRANULOSUS ZONE
P 1090-1130	O																							

Text-figure 8. Distribution of trilobites from Section P and zonal assignment of collections.

self and manuscript names of these are included in the faunal lists for completeness. Brief reference will also be made to some of the bryozoans being studied by J.R.P. Ross. An important segment of the discussion will be the preliminary results of a parallel study by Ravindra Tipnis on conodonts from these collections. Conodonts are superior to the shelly macrofauna in supplying biostratigraphic information to the extent that there is a greater probability of recovering these fossils from any given part of a Paleozoic carbonate sequence.

It is anticipated that, in the near future, a biostratigraphic synthesis of these formations can be presented based on trilobites, brachiopods, ostracods, conodonts, and bryozoans. The potential applicability of this synthesis would be significant in integrating zonal schemes based on each of these groups from areas outside of the study area because of the assurance of exact contemporaneity of various fossils from each collection.

It should be emphasized that the present study is reconnaissance in nature. Only a single part of the extensive Ordovician sequence has been sampled with relatively closely spaced collections, and that only in a single area - the Esbataottine Formation in the Sunblood Range. Widely spaced samples are at hand from the Sunblood Formation and relatively few and widely separated samples are available from the Whittaker Formation.



Text-figure 9.

Composite range chart of bathyurid, cheirurid, and encrinurid trilobites of the upper Sunblood, Esbataottine and lower Whittaker Formations related to trilobite zones.

ORTHIDIELLA-"*GONIOTELINA*" FAUNA (Whiterockian)

Within the context of this thesis, the *Orthidiella*-"*Goniotelina*" Fauna is important because it contains a few of the trilobites described; that is, *Heliomera* cf. *sol* (Billings), *Kawina* sp., and *Cybellela*? *thor* n. sp. The reassessment of species of the two similar genera, *Heliomera* and *Heliomeroides*, in this thesis suggests that *Heliomera* is confined to strata of Whiterockian age in Newfoundland (Whittington, 1963, 1965a) and in Nevada (Ross, 1972). In the study area at B 145, *H.* cf. *sol* occurs 50 m below a collection containing conodonts of Fauna 4 (late Whiterockian) of Sweet *et al.* (1971). *Kawina* sp. differs from most other species in possessing only three axial rings on the pygidium. In this respect, it is similar to species from the upper Antelope Valley Limestone, Nevada (Ross, 1970) and from the Oil Creek Formation, Oklahoma (Shaw, 1974). *Cybellela*? *thor* is of little value biostratigraphically. Its occurrence with a primitive species of *Calyptaulax* at GSC loc. 58678 (Text-fig. 1) suggests that it is definitely older than the *Ceraurinella nahanniensis* Zone and it is tentatively included in the *Orthidiella*-"*Goniotelina*" Fauna.

The remainder of the fauna from this unit is diverse and largely unstudied. A few of the trilobites and brachiopods were illustrated by Ludvigsen (1975) and the ostracods were described and illustrated by Copeland (1974). According to Tipnis, the conodonts of this unit constitute a complete sequence spanning the entire Whiterockian from

Fauna 1 to Fauna 4 of Sweet *et al*. (1971)

Maximum thickness: About 400 m at Section G.

Upper contact: The *Orthidiella*-"*Goniotelina*" Fauna is separated from the overlying *Bathyurus granulosus* Zone by a considerable interval of sparsely fossiliferous limestone (140 m at Section G, 230 m at Section P, and 270 m at Section B). This interval contains unstudied bathyurid trilobites (among them, *Bathyurus* cf. *nevadensis* Ross and *B*. cf. *angustus* Ross) and, according to Tipnis, conodonts assignable to Fauna 5 of Sweet *et al* (1971) that he evaluates as being early Chazyan in age.

Assigned collections: Sunblood Formation at Mary Range (B 145 to B 400), Glacier Lake East(E 1150 to E 1495), Flood Creek (G 1030 to G 2335), Whittaker Range (H 0 to H 130), Broken Skull North (K 2375), Sunblood Range (P 10 to P 330). Questionably assigned: GSC loc. 58678 (locality 4 on Text-fig. 1) and the fauna from the lower Sunblood Formation near the confluence of Caribou and Flat Rivers (Lenz and Jackson, 1964, p. 894).

Trilobites: "*Bathyurus*" sp. (Pl. 1, figs. 15-17), *Carolinites* sp., **Cybellela*? *thor* n. sp., "*Goniotelina*" sp. (Pl. 1, figs. 11-13), **Heliomera* cf. *sol* (Billings), *Ischyrotoma* sp. (Pl. 1, fig. 14), **Kawina* sp., *Nileus* sp., *Pseudomera* sp. (Pl. 1, fig. 10).

Brachiopods: *Anomalorthis* cf. *juabensis* Jensen (Pl. 1, figs. 7-9), *Orthambonites marshalli* (Wilson) (Pl. 1, figs. 1-3), *Orthidiella* cf. *extensa* Ulrich and Cooper (Pl. 1, figs. 4-6).

Conodonts (Tipnis): A number of taxa referrable to Faunas 1 to 4 of Sweet *et al*. (1971).

Ostracods (Copeland, 1974): "*Aparchites*" cf. *fimbriatus* (Ulrich), *Bairdiocypris* sp., *Cryptophyllus magnus* (Harris), *Eoleperditia bivia* (White), *Isochilina*? sp., *Leperdi-*

tella cf. *germana* (Ulrich), *Schmidtella*? cf. *subrotunda* Ulrich.

Bryozoans (Ross): *Stictopora* spp., Trepostomes.

Note, in this and in following lists, trilobites described and illustrated in this thesis are preceded by an asterisk (*). Unqualified references to illustrations are to those of Ludvigsen (1975), included as an appendix. Authorship quoted as "C and L" refers to Chatterton and Ludvigsen, ms.

BATHYURUS GRANULOSUS ZONE (early to middle Chazyan)

The upper part of the Sunblood Formation at a number of localities contains low diversity assemblages of trilobites dominated by *Bathyurus granulosus* n. sp. In only a single collection (P 1187) do other trilobites appear; that is, *Cybeloides anna* n. sp., *Pandaspinapyga* cf. *stubblefieldi* (Bancroft), and a few additional unstudied species.

The trilobites and ostracods of this zone are of little use biostratigraphically. The two ostracod species have ranges that span a large part of the Middle Ordovician in other areas (Copeland, 1974). *C. anna* may be a morphological intermediate between the Whiterockian (?) *Cybellela*? *thor* and the late Chazyan *Cybeloides cimelia*. *P.* cf. *stubblefieldi* differs only slightly from *P. stubblefieldi* from the Caradocian of Shropshire, but is probably appreciably older than this species. *B. granulosus* (*B.* sp. 1 in Ludvigsen, 1975) has not been recognized outside of the study area. I suggested previously (Ludvigsen, 1975) that *B. granulosus* was probably conspecific with *B.* cf. *extans* described by Ross (1970, p. 85, Pl. 15, figs. 16, 17) from the upper Antelope Valley Limestone of Nevada. An examination of the actual specimens revealed a number of features not described by Ross, nor evident in his published figures. These differences, listed in the section on Systematic Paleontology, negate my previous suggestion of affinity between these species. *B. granulosus* was derived from *B.* cf. *nevadensis* Ross or *B.* cf. *angustus* Ross; both of which occur below the first occurrence of *B. granulosus* in the post-*Orthidiella*-"*Goniotelina*" beds of the Sunblood Formation at Mary Range. This species was probably ancestral to the younger *B. ulu*.

The occurrence of this zone below the well-dated *Ceraurinella nahanniensis* Zone in the Sunblood Range provides a minimum age limit of late Chazyan for the *B. granulosus* Zone. Tipnis suggests that the conodonts from these collections are early to middle Chazyan in age.

The significance of the age of the *B. granulosus* Zone is that it supplies unequivocal evidence that *Bathyurus* made its first appearance in rocks considerably older than Blackriveran. This, in itself, is not new because Twenhofel (1938) described a species of *Bathyurus* (*B. eskimoensis*) from Chazyan-age strata on the Mingan Islands. More recent workers (Whittington, 1953, p. 653; Ross, 1970, p. D17) have implied that *Bathyurus* is a Blackriveran genus.

Maximum thickness: 45 m at Section P.

Upper contact: The *Bathyurus granulosus* Zone is recognized below the superjacent *Ceraurinella nahanniensis* Zone in only a single area. This is in the Sunblood Range at Section P where the highest collection assigned to the *B. granulosus* Zone (P 1245) is separated by about 35 m of silty and platy limestones of shallow water aspect (desiccation polygons) from the lowest collection (P 1405) assigned to the *C. nahanniensis* Zone. In the Whittaker Range at Section H, a collection questionably assigned to the *B. granulosus* Zone (H 410) is separated by 120 m of silty and arenaceous limestones from a collection (H 800-820) assigned to the *C. nahanniensis* Zone. In other areas on the margin of the basin, the *B. granulosus* Zone is separated by a disconformity from still younger zones - *Ceraurus gabrielsi* Zone in the Mary Range at Section B and the *Ceraurinella longispina* Zone in the Flood Creek area at Section G.

Assigned collections: Upper Sunblood Formation at Mary Range (B 1265 to B 1315), Whittaker Range (?H 410), Flood Creek (G 2795 to G 2910), Sunblood Range (P 1090 to P 1245 and a collection from about 30 m below the top of the Sunblood Formation at Sunblood Mountain).

Biofacies diversity: *Bathyurus* Biofacies (dominant) and *Calyptaulax*-*Ceraurinella* Biofacies.

Trilobites: **Bathyurus granulosus* n. sp., *Calyptaulax* sp., **Cybeloides anna* n. sp., illaenid, *Isotelus* sp., **Pandaspinapyga* cf. *stubblefieldi* (Bancroft).

Conodonts (Tipnis): Forms identified from these collections include *Phragmodus tortus*, *Erismodus radicans*, *Leptochirognathus*, and *Chirognathus*. Tipnis assigns these forms to Faunas 5 or 6 of Sweet *et al.* (1971) and suggests that they are early to middle Chazyan in age, based on the recent study of conodonts from the type Chazy Group of New York State (Raring, 1972).

Ostracods (Copeland, 1974): *Leperditella* cf. *germana* (Ulrich), *Schmidtella affinis* Ulrich.

CERAURINELLA NAHANNIENSIS ZONE (late Chazyan)

The lower part of the Esbataottine Formation in two areas, the Sunblood Range and the Whittaker Range, yields highly diverse faunas that are assigned to the *Ceraurinella nahanniensis* Zone. Significantly, this zone is developed only within the axial part of a large marginal basin which is bounded on the seaward side by the emergent Redstone Arch (Ludvigsen, 1975, Fig. 10-4). The zone is absent, or cannot be recognized, on the margins of this basin at Section G and B. The *C. nahanniensis* Zone is represented by taxa assignable to two relatively deep water faunas -- the *Ceraurinella*-*Calyptaulax* Biofacies and the *Dimeropyge* Biofacies. Forms characteristic of the *Bathyurus* Biofacies are completely absent in this zonal interval. This raises the question about the identity of this zone in a shallow water environment. A *Bathyurus* Biofacies of the *C. nahanniensis* Zone should include either *B. granulosus* or *B. ulu*, the nearshore facies representatives of the underlying and overlying zones, respectively, or an intermediate species. It is quite possible that the shallow water equivalent of the *C. nahanniensis* Zone is found in the upper part of the *B. granulosus* Zone in the Mary Range, but the resolution capacity of the zonal scheme of either trilobites or conodonts is not sufficiently refined to prove or disprove this.

The *C. nahanniensis* Zone is defined basally by the first occurrence of either *Ceraurinella nahanniensis* or *Cybeloides cimelia*, and extends upwards to the first occurrence of either *Bathyurus ulu* or *Ceraurinella seriata* (Text-fig. 9). In the three sections from which this zone is recognized, these strata are contained within the lower part of the Esbataottine Formation, with the exception of a single collection (P 1405), 6 m below the top of the Sunblood Formation at Section P. This collection did not yield trilobites, but the contained ostracods and conodonts show affinities with the *C. nahanniensis* Zone and not with the underlying *B. granulosus* Zone.

The *Mimella* Fauna as discussed in Ludvigsen (1975) is essentially synonymous with the *C. nahanniensis* Zone with one minor change. The upper boundary of the *C. nahanniensis* Zone is placed 6 m below that of the *Mimella* Fauna to shift two collections with *Ceraurinella seriata* into the *B. ulu* Zone. In the previous paper, the *Mimella* Fauna was concluded to be Chazyan in age and that assessment stands for the *C. nahanniensis* Zone. In particular, the presence in this zone of the following taxa previously known only from the Chazyan Lincolnshire Limestone of Virginia and/or the Chazy Group of New York State support this assignment: *Holia secristi* Whittington and Evitt, *Ceratocephala tricantheis* Whittington and Evitt, *Heliomeroides teres* Evitt (also known from the Stinchar Limestone, Scotland), and *Dimeropyge clintonensis* Shaw. To this list may be added the following species which, although distinct, are highly similar to Chazyan species from eastern North America: Acanthoparypha evitti Chatterton and Ludvigsen (cf. A. chiropyga Whittington and Evitt), Sphaerexochus arenosus Chatterton and Ludvigsen (compare with S. hapsidotus Whittington and Evitt), Remopleurides pattersoni Chatterton and Ludvigsen (compare with R. canadensis Billings), and Carrickia pinguimitra Chatterton and Ludvigsen (compare with C. setoni Shaw and C. pelagica Tripp from the Stinchar Limestone, Scotland). These comparisons are, of course, aided by similar preservation and biofacies position of the eastern North American material (Whittington and Evitt, 1954; Shaw, 1968), but the faunas are sufficiently distinctive to render age assignment certain.

The biostratigraphic significance of the brachiopods and ostracods from the C. nahanniensis Zone were discussed by Ludvigsen (1975) and Copeland (1974). The age information from both groups is in good agreement with that derived from the trilobites.

Tipnis notes that the distribution of conodont faunas in the upper Sunblood and lower Esbataottine is very similar to that of the Chazy Group of New York (Raring, 1972); especially evident in the consecutive changes in the morphology of Phragmodus. One important difference is the complete absence of "North Atlantic" type conodont faunas in the central part of the study area; suggesting that trilobites and conodonts did not respond in the same manner to the physical determinants of biofacies. It should be pointed out that, even though the similarity of trilobites from the C. nahanniensis Zone to those of Virginia, New York State, and Girvan in Scotland (all found in rocks carrying a "North Atlantic" type conodont fauna, Bergström, 1971) is striking, the Nahanni fauna differs at the family level in lacking agnostids, styginids, trinucleids, raphiophorids, proetids, and endymioniids. The physical parameters that exclude these types from the study area during deposition of the C. nahanniensis Zone may be the ones that exclude the "North Atlantic" biofacies conodonts, as well.

The age assignment of conodonts from the C. nahanniensis Zone strongly supports that of the trilobites and suggests further refinement. Tipnis considers these conodonts to be of late Chazyan age, transitional to early Blackriveran. Bergström et al. (1974) localized the Chazyan-Blackriveran boundary between Faunas 6 and 7 of Sweet et al. (1971). In this thesis, the Chazyan-Blackriveran boundary is placed at the base of the Bathyurus ulu Zone - a level that coincides with the first definite occurrences of Fauna 7 conodonts.

Maximum thickness: 40 m at Section P.

Upper contact: The contact of the C. nahanniensis Zone with the B. ulu Zone is fairly accurately defined at both Sections A and P. At Section P, it falls within 10 m of strata between P 1540 and P 1575 and at Section A, within 10 m of strata between A 160 and A 190. In the Whittaker Range at Section H, the Bathyurus ulu Zone is not recognized and a collection yielding C. nahanniensis Zone trilobites (H 800-

820) is followed 23 m upsection by one assigned to the C. gabrielsi Zone (H 900).

Assigned collections: Sunblood Range (A 115 to A 160, P 1405 to P 1540), Whittaker Range (H 800-820). All of these are from the lower Esbataottine Formation except the lower collection from Section P (P 1405) which was collected 6 m below the top of the Sunblood Formation.

Biofacies diversity: Calyptaulax-Ceraurinella Biofacies (dominant) and Dimeropyge Biofacies.

Trilobites: *Acanthoparypha echinoderma C and L, *Acanthoparypha evitti C and L, Amphilichas aff. aspratilis Bradley, Amphilichas conradi C and L (Pl. 3, fig. 15), Apianurus barbatus Whittington and Evitt (Pl. 3, figs. 3, 4), Bumastoides aff. milleri (Billings), Calyptaulax callirachis Cooper (Pl. 4, figs. 27-29), Carrickia pinguimitra C and L (Pl. 3, figs. 13, 14), Ceratocephala tricantheis Whittington and Evitt, *Ceraurinella kingstoni C and L, *Ceraurinella nahanniensis C and L, *Cybeloides cimelia C and L, Dimeropyge clintonensis Shaw (Pl. 3, figs. 11, 12), Dolichoharpes aff. reticulata Whittington (Pl. 3, fig. 29), *Encrinuroides rarus (Walcott), Failleana calva C and L, *Heliomeroides teres Evitt, Hemiarges turneri C and L, *Holia secristi Whittington and Evitt, Isotelus parvirugosus C and L, Nahannia mediocrisulcata C and L (Pl. 3, figs. 25, 26), Nanillaenus aduncus C and L, Nanillaenus mackenziensis C and L, *Pandaspinapyga dactyla C and L, Remopleurides pattersoni C and L (Pl. 3, figs. 9, 10), *Sphaerexochus arenosus C and L, *Sphaerocoryphe cf. pemphis Lane.

Brachiopods: Chaulistomella cf. nitens Cooper (Pl. 2, figs. 8-10), Glyptorthis cf. costellata Cooper (Pl. 2, fig. 7), ?Macrocoelia sp. (Pl. 1, fig. 37), Mimella aff. globosa (Willard) (Pl. 1, figs. 24-33), Onychoplesia sp. (Pl. 2, figs. 4-6), Rostricellula sp. 1 (Pl. 2, figs. 1-3).

Conodonts (Tipnis): Taxa identified include Phragmodus *tortus* sp. 1., *Coleodus simplex*, *Appalachignathus*, *Belodella niger*, and *Phragmodus* cf. *inflexus*.

Ostracods (Copeland, 1974): "*Aparchites*" sp., "*Aparchites*" *fimbriatus* (Ulrich), *Bairdiocypris* cf. *granti* (Ulrich), *Bolbopisthia ludvigseni* Copeland, *Cryptophyllus oboloides* (Ulrich and Bassler), *Eoleperditia*? sp., *Euprimitia*? *krafti* Copeland, *Eurychilina sunbloodensis* Copeland, *Krausella minuta*? (Harris), *Leperditella* sp., *Leperditella mundula* (Ulrich), *Ludvigsenites mackenziensis* Copeland, *Schmidtella affinis* Ulrich, *Steusloffina borealis* Copeland, *Tetradella perplexa* Copeland.

Bryozoans (Ross): *Helopora* spp., *Pachydictya* sp., *Stictopora* sp., phylloporinids, trepostomes.

BATHYURUS ULU ZONE (early Blackriveran)

The interval immediately above the *Ceraurinella nahanniensis* Zone in the Sunblood Range at Sections A and P is characterized by the association of *Bathyurus ulu* n. sp. and *Ceraurinella seriata* n. sp. and is recognized as the *B. ulu* Zone. This zone is defined as spanning the interval from the first occurrence of either *B. ulu* or *C. seriata* to the first occurrence of either *Ceraurus gabrielsi* n. sp. or *Ceraurinella media* n. sp. It has not been recognized outside the Sunblood Range; the reasons for this are two-fold -- the zone is thin and its base is regressive. In the Sunblood Range at Section P, near the western outlet of the basin, the transition from the *C. nahanniensis* to the *B. ulu* Zone occurs across a sequence of strata carrying successively shallower biofacies (Text-fig. 10); that is, *Dimeropyge* Biofacies at

P 1520, Calyptaulax-Ceraurinella Biofacies at P 1575, Isotelus Biofacies at P 1585, and Bathyurus Biofacies at P 1595. Virtually the same biofacies succession is seen in the same zonal position at Section A from A 160 to A 220 (Text-fig. 11). A lowering of sea level would explain the biofacies sequence seen in this part of the study area and, also, the apparent absence of the B. ulu Zone in the interior and marginal portions of the basin. Deeper water conditions returned to the Sunblood Range before the onset of the next zone.

Parts of the trilobite fauna of the B. ulu Zone (species of Dolichoharpes, Encrinuroides, Cybeloides, Sphaerexochus, Isotelus, Nanillaenus, and Apianurus) appear identical to those of the underlying C. nahanniensis Zone. Ceraurinella seriata is a derivative of C. nahanniensis and Bathyurus ulu of B. granulosus.

No element of the trilobite fauna is directly correlatable. B. ulu is rather similar to B. extans (Hall) from the Lowville Formation of the Black River Group and Calyptaulax cf. strasburgensis is closest to C. strasburgensis (Ulrich and Delo) from the Edinburg Formation of Virginia which, in turn, is very similar to C. annulata (Raymond) from the Chazy Group and the Bromide Formation (Shaw, 1968, 1974). The trilobites suggest a Chazyan/Blackriveran age for the Bathyurus ulu Zone. It is tempting to cite the presence of species of Bathyurus as evidence for a Blackriveran assignment, but the appearance of Bathyurus at any given level within the Middle Ordovician is totally determined by biofacies and carries no age connotation, beyond that of Chazyan/Blackriveran. Tipnis assigns the conodonts from the *B. ulu* Zone to the early Blackriveran (Fauna 7 of Sweet *et al.*, 1971).

Maximum thickness: 17 m at Section A, slightly less at Section P.

Upper contact: At Section P the contact between the *B. ulu* Zone and the superjacent *C. gabrielsi* Zone falls within 12 m of strata between P 1625 and P 1665.

Assigned collections: Lower Esbataottine Formation, Sunblood Range (A 190 to A 247, P 1575 to P 1625).

Biofacies diversity: *Bathyurus* Biofacies, *Isotelus* Biofacies, *Calyptaulax-Ceraurinella* Biofacies.

Trilobites: *Amphilichas* sp., *Apianurus barbatus* Whittington (Pl. 3, figs. 3, 4), **Bathyurus platyparius* n. sp., **Bathyurus ulu* n. sp., *Calyptaulax* cf. *strasburgensis* (Ulrich and Delo), **Ceraurinella seriata* n. sp., **Cybeloides cimelia* C and L, *Dolichoharpes* aff. *reticulata* Whittington (Pl. 3, fig. 29), **Encrinuroides rarus* (Walcott), *Isotelus parvirugosus* C and L, *Nahannia humilisulcata* C and L, *Nanillaneus mackenziensis* C and L, *Remopleurides pattersoni* C and L (Pl. 3, figs. 9, 10), **Sphaerexochus arenosus* C and L.

Brachiopods: *Mimella* aff. *globosa* (Willard) (Pl. 1, figs. 24-33), *Strophomena inspeciosa* Willard (Pl. 1, figs. 34-36).

Conodonts (Tipnis): Samples with conodonts are rare from this zone. The few collections available include *Phragmodus* cf. *inflexus*, *Plectodina aculeata*, *Appalachignathus* sp., *Drepanodus subrectus*, *Scandodus* cf. *superbus*, *Coleodus simplex*, and *Belodella niger*. Tipnis assigns these to Fauna 7 of Sweet *et al.* (1971) of Blackriveran age.

Ostracods (Copeland, 1974): Eokloedenella whittakerensis Copeland, Eyrychilina sp., Leperditella mundula (Ulrich), Oepikella labrosa Copeland.

Bryozoans (Ross): Dekayia sp., Helopora sp., Pachydictya sp., Ptilodictya sp., Stictopora sp., Stictoporella? sp., Ulrichostylus sp.

CERAURUS GABRIELSI ZONE (Blackriveran)

In contrast to the zone below, the Ceraurus gabrielsi Zone is thick and is widely distributed within the study area. It occupies over half of the total thickness of the Esbataottine Formation in the Sunblood and Whittaker Ranges and is present in the upper part of the Sunblood Formation at Natla River and in the Mary Range. The zone spans the interval from the first occurrence of either Ceraurus gabrielsi n. sp. or Ceraurinella media n. sp. to the first occurrence of either Ceraurinella longispina n. sp., C. arctica n. sp., or Ceraurus hirsuitus n. sp. The definition of the base of this zone is not entirely satisfactory because C. gabrielsi is an immigrant. Its origin does not lie with any species in the underlying zones (this is the earliest occurrence of the genus in the Nahanni area), but can probably be found with "Paraceraurus" ruedemanni (Raymond) from the Chazy Group. Ceraurinella media was derived from C. kingstoni which has only been found in the C. nahanniensis Zone. It is possible that either of these species may make their first appearance at a level that would correlate with the B. ulu Zone in other areas. The only other diagnostic species that could define a zone in this interval is *Bathyurus esbataottinensis* n. sp. This taxon has the advantage of being derived from a species in the underlying zone (*B. ulu*) and, as such, its first appearance would define a level that would have more meaning than one defined by the first appearance of *Ceraurus gabrielsi* or *Ceraurinella media*. To use *B. esbataottinensis* to define the base of a zone would be to split; what is otherwise, a homogeneous zonal assemblage.

The trilobites of the *Ceraurus gabrielsi* Zone present the same correlative problems as those of the *B. ulu* Zone. Only a single species, *Encrinuroides rarus*, has been recognized outside the study area - from the Platteville Group of Wisconsin, Minnesota, and Illinois (DeMott, 1963). This species and *Cybeloides cimelia* have a total range from the *Ceraurinella nahanniensis* Zone to the *Ceraurinella longispina* Zone within the study area. *Bathyurus platyparius* n. sp. makes its first appearance high in the *B. ulu* Zone and continues through the *C. gabrielsi* Zone. This species displays some similarities with *B. superbus* Raymond from the Lowville Formation of Quebec. *Ceraurus gabrielsi* cannot be compared with any of the Chazyan or Blackriveran species of *Ceraurus* from eastern North America, aside from "*Paraceraurus*" *ruedemanni*. Species such as *Ceraurus ruidus* Cooper and *C. hudsoni* Raymond have long genal spines and forwardly placed eyes. *C. gabrielsi* was probably the ancestor to a continuous lineage of species of *Ceraurus* which appear at successive intervals in the next four zones and, as such, helps in the arrangement of the younger zones, but does not aid in the dating of the *C. gabrielsi* Zone. The occurrence of the *C. gabrielsi* Zone above the *Bathyurus ulu* Zone in the Sunblood Range supplies a lower age limit of early Blackriveran.

Copeland (1974) considered the age of the ostracods from these collections to straddle the "Porterfield-Wilderness" boundary. Tipnis suggests that the conodonts from the collections herein assigned to the *C. gabrielsi* Zone belong to Fauna 7 of Sweet *et al.* (1971); that is, of Blackriveran age.

Maximum thickness: 120 m at Section H.

Upper contact: The upper contact with the *Ceraurinella longispina* Zone is seen at Sections B and P where it falls within about 18 m of strata between B 1450 and B 1510-1520 and P 1945-1955 and P 2110.

Assigned collections: Upper Sunblood Formation at Mary Range (B 1450) and Natla River (GSC loc. 69001, D 1342, D 1375); Esbataottine Formation at Whittaker Range (H 900 to H 1300, I 780, Q 130), Sunblood Range (A 365 to A 385, P 1665-1685 to P 1945-1955).

Biofacies diversity: *Bathyurus* Biofacies, *Calyptaulax-Ceraurinella* Biofacies.

Trilobites: **Acanthoparypha evitti* C and L, *Amphilichas* sp. (Pl. 4, fig. 26), **Bathyurus esbataottinensis* n. sp., **Bathyurus platyparius* n. sp., **Bathyurus* cf. *ulu* n. sp. (Pl. 4, figs. 10-12), *Bumastoides* sp., *Calyptaulax* spp., **Ceraurinella media* n. sp., **Ceraurus blussoni* n. sp., **Ceraurus gabrielsi* n. sp., **Cybeloides cimelia* C and L,

**Encrinuroides rarus* (Walcott), *Hemiarges* sp., *Isotelus* sp., *Nanillaenus* sp., *Remopleurides* sp.

Brachiopods: *Camerella* cf. *obesa* Cooper (Pl. 2, figs. 34-36), *Doleroides* sp., *Hesperorthis* sp., *Rostricellula* sp. (Pl. 2, figs. 1-3), *Oepikina* sp.

Conodonts (Tipnis): The fauna includes *Phragmodus inflexus*, *Plectodina aculeata*, *Scandodus* cf. *superbus*, *Panderodus gracilis*, *Polyplacognathus ramosus*.

Ostracods (Copeland, 1974): *Bolbopisthia ludvigseni* Copeland, *Isochilina* cf. *gregaria* (Whitfield), *Leperditella mundula* (Ulrich), *Krausella minuta*? (Harris), *Oepikella*? sp., *Schmidtella affinis* Ulrich.

Bryozoans (Ross): *Chasmatoporella* sp., *Helopora*? sp., *Ptilodictya* sp., *Stictoporella* sp., *Stictopora* sp., phylloporinid.

CERAURINELLA LONGISPINA ZONE (late Blackriveran/Rocklandian)

The highest few meters of the Esbataottine Formation in the Sunblood Range contains a diverse and largely new trilobite fauna, assignable to the *Ceraurinella longispina* Zone, that owes its distinctiveness to actual zonal difference, but also to a pronounced biofacies shift. The effect of the latter feature is difficult to evaluate, but it may be considerable. The base of the zone is defined at the first occurence of either *Ceraurinella longispina*, *C. arctica*, or *Ceraurus hirsuitus*. Its top is marked by the onset of deposition of dolostones carrying the *Hesperorthis-Oepikina* Fauna of Ludvigsen (1975).

In some ways, the *C. longispina* Zone repeats the *Cer-*

aurinella nahanniensis Zone. On the generic level, the only new additions are Ceraurus and Anataphrus. Three species are common to both zones - Cybeloides cimelia, Encrinuroides rarus, and Dolichoharpes aff. reticulata, and another three show only slight differences with their counterparts in the older zone - Sphaerexochus atacius n. sp., Hemiarges sp., and Ceratocephala sp. That considerable time intervenes between the two zones is shown by the pronounced changes in species of Ceraurinella and Calyptaulax. The distinctiveness of the C. longispina Zone is, perhaps, more evident in the brachiopod faunas. Not a single genus is common to the two zones and, while brachiopods of the C. nahanniensis Zone are rare, those of the C. longispina Zone are highly abundant. So, the apparent biofacies duplication of the trilobite faunas is not seen in the brachiopod faunas.

In each of its collections, the C. longispina Zone occurs only in the Calyptaulax-Ceraurinella Biofacies (The assignment of G 3340 to the Bathyurus Biofacies on Text-fig. 15 is based on the presence of Ceraurus cf. hirsuitus - a species that probably belongs in the Calyptaulax-Ceraurinella Biofacies). This presents problems in correlating the zone with potentially equivalent horizons in the Bathyurus Biofacies. One collection, H 1300, from near the top of the Esbataottine Formation in the Whittaker Range contains Bathyurus platyparius and a few rhynchonellid brachiopods. This collection has been assigned to the C. gabrielsi Zone because B. platyparius is a common constituent of that zone in other areas. In this section, the C. gabrielsi Zone is uncommonly thick and it is equally possible that H 1300 represents a Bathyurus Biofacies of the C. longispina Zone. By the same token, the five-fold increase in thickness of the C. longispina Zone between the Sunblood Range and the Flood Creek area may suggest that the zone extends into older rocks in the latter section, equivalent to part of the Ceraurus gabrielsi Zone.

The diagnostic elements of the C. longispina Zone can be related to older species in the Ceraurus gabrielsi Zone. Ceraurinella longispina and C. arctica are derivatives of C. media and Ceraurus hirsuitus a derivative of C. gabrielsi (via C. blussoni). The presence of Anataphrus cf. borraeus Whittington provides a link with Trentonian faunas. Ceraurus hirsuitus is similar to "C. mifflensis" (manuscript name in DeMott, 1963) and C. plattinensis Foerste from the Platteville Group and Decorah Formation of the upper Mississippi Valley and also to C. dentatus Raymond and Barton from the lower Trenton Group. The age of the trilobites from the C. longispina Zone appears to fall within the late Blackriveran-early Rocklandian interval.

According to Copeland (1974, p. 4) the ostracods of this part of the succession belong to "a cosmopolitan Wilderness-type fauna". The brachiopods, especially Triplesia cf. subcarinatina, Skenidioides cf. anthonensis, Strophomena cf. basilica with the generic presence of Oepikina and Doleroides, suggest a "Wilderness" age and display particular affinity to the Platteville Group faunas. The conodonts from the collections herein assigned to the C. longispina Zone belong to Fauna 7 and Fauna 7/8 (Blackriveran and Rocklandian) of Sweet et al. (1971) according to Tipnis. Ross notes that the bryozoan genus, Oanduella, occurs in the lower part of the Caradocian succession of Estonia.

Maximum thickness: 60 m at Section G (12 m at Section P).

Upper contact: A satisfactory upper boundary of the C. longispina Zone has not been located. At Section B, there exists probable structural complications above the zone. At Sections A, G, and P the top of the zone is drawn at the base of the Whittaker Formation which, in these areas, comprises dolostones carrying a low diversity brachiopod fauna - the Hesperorthis-Oepikina Fauna of Ludvigsen (1975).

Assigned collections: Upper Sunblood Formation in the Mary Range (B 1510-1520), Esbataottine Formation at Flood Creek (G 3195 to G 3340), and upper Esbataottine Formation in the Sunblood Range (A 615, P 2010 to P 2050).

Biofacies diversity: Calyptaulax-Ceraurinella Biofacies, only.

Trilobites: Anataphrus cf. borraeus Whittington (Pl. 4, figs. 15, 16), Bumastoides sp., Calyptaulax sp. 2 (Pl. 4, figs. 17-19), Ceratocephala sp., *Ceraurinella arctica n. sp., *Ceraurinella longispina n. sp., *Ceraurinella media n. sp., *Ceraurus hirsuitus n. sp., *Cybeloides cimelia C and L, Dolichoharpes aff. reticulata Whittington, *Encrinuroides rarus (Walcott), Hemiarges sp., Isotelus sp., *Sphaerexochus atacius n. sp.

Brachiopods: Doleroides sp. (Pl. 2, figs. 11-15), Hesperorthis sp. (Pl. 2, figs. 23-26), Oepikina sp. (Pl. 2, figs. 18-20), *Skenidioides* cf. *anthonensis* (Sardeson) (Pl. 2, figs. 27-30), *Strophomena* cf. *basilica* Cooper (Pl. 2, figs. 16, 17), *Sowerbyella* sp. (Pl. 2, figs. 21, 22), *Triplesia* cf. *subcarinatina* Cooper (Pl. 2, figs. 31-33).

Conodonts (Tipnis): Collections belonging to both Fauna 7 and Fauna 7/8 of Sweet *et al.* (1971); that is, of Blackriveran and Rocklandian age.

Ostracods (Copeland, 1974): "*Aparchites*" cf. *fimbriatus* (Ulrich), *Bairdiocypris* cf. *granti* (Ulrich), *Bolbopisthia* cf. *lenzi* Copeland, *Eoleperditia*? sp., *Eurychilina prairiensis* Copeland.

Bryozoans (Ross): *Calopora*? sp., *Helopora*? sp., *Stictopora* spp., *Stictoporella* spp., *Oanduella*? sp., *Ptilodictya* sp., fistuliporid, two species of Arthrostylidae.

CERAURINELLA NECRA ZONE (Rocklandian/Kirkfieldian)

The *Ceraurinella necra* Zone marks the initiation of a a new series of trilobite assemblages that continue through the next two zones. These zones are more readily correlatable than any zone since the *Ceraurinella nahanniensis* Zone and form a part of a continent-wide faunal complex of Trentonian age that extends from the high Arctic (Cape Calhoun Formation, shaly beds at Silliman's Fossil Mount) to the mid-continent (lower Trenton Group, Decorah Formation, Plattin Group, Kimmswick Formation) to the south-central continent (Viola Group). These faunas follow the basal Trentonian transgression which, in the study area, is marked by a pronounced eastward shift of facies belts in the interval between the top of the *Ceraurus gabrielsi* Zone and the

Ceraurinella necra Zone (Ludvigsen, 1975, Fig. 10 - 5 and 6). The *C. necra* Zone (and the next two zones) are confined to the axial part of the Root Basin in a muddy carbonate substrate and in a fairly deep water environment. The shallower biofacies in these time intervals comprise brachiopod, coral, and mollusk faunas from which trilobites have not been collected. The correlation previously suggested of the trilobite faunas from the central part of the Root Basin (the *Strophomena*-*Ceraurus* Fauna, Ludvigsen, 1975; equals the *C. necra* to *W. planatus* Zones, herein) with the "Arctic Ordovician" fauna (*Bighornia*-*Thaerodonta* Fauna, Ludvigsen, 1975) and the *Hesperorthis*-*Oepikina* Fauna from the northern part of the Root Basin and the Redstone Arch has received support from the conodont faunas. Both the *Ceraurinella necra* and the *Ceraurus mackenziensis* Zones from the lower Whittaker Formation in the Root Basin and the *Bighornia*-*Thaerodonta* Fauna from the base of the Whittaker Formation on the western edge of the Redstone Arch at Sections D and M contain conodonts of Fauna 9 of Sweet *et al.* (1971).

The species of *Ceraurus* (*C. tuberosus*) and *Ceraurinella* (*C. necra*) from the *C. necra* Zone are intermediates between those of the underlying *C. longispina* Zone (*Ceraurinella arctica*, *Ceraurus hirsuitus*) and the *Ceraurus mackenziensis* Zone (*Ceraurinella brevispina*, *Ceraurus mackenziensis*). Similar conclusions were reached by Copeland (1974) for the ostracod collections herein assigned to the *C. necra* Zone; *Bolbopisthia lenzi* supplies a link with older fauna and *Diplopsis socialis* a link with the younger fauna.

A number of trilobites make their first appearance in this zone; among them, *Borealaspis*, *Hypodicranotus*, *Remipyga*?, "*Calyptaulax*" (of the "*C*." *lincolnensis* type), otarionids, and proetids. Most of these continue into, and are generally better represented in, the following zone. The trilobites of the *C*. *necra* Zone display a strong affinity with those of lower Trentonian age of the mid-continent. This is especially seen in such species as *Hypodicranotus* sp., *Sphaerocoryphe robustus*, and "*Calyptaulax*" cf. *lincolnensis*. The latter is very similar to such species as "*C*." *lincolnensis* (Branson), "*C*." *ottawanus* (Okulitch), and "*C*." *calderi* (Wilson) which occur widely in the pre-Shermanian part of the Trenton Group and in the Platteville Group and Decorah Formation of the mid-continent. *Hypodicranotus* appears to be restricted to the Shermanian and Kirkfieldian (Whittington, 1952). *Ceraurus tuberosus* and, probably, *Borealaspis* are present in the Cape Calhoun Formation of northern Greenland.

In weighing the combined trilobite-ostracod-conodont evidence, a Rocklandian and/or Kirkfieldian age, probably the latter, is proposed for the *Ceraurinella necra* Zone.

Maximum thickness: Not known. The *C*. *necra* Zone is recognized at a single locality each from Sections C and I.

Lower contact: At Section C, the *C*. *necra* Zone is underlain by poorly fossiliferous limestones and dolostones whose formational assignment is uncertain (possibly the Esbataottine Formation). At Section I the collection yielding the C. necra Zone occurs 150 m above one with the C. gabrielsi Zone from the Esbataottine Formation.

Upper contact: At Sections C and I the upper contact with the Ceraurus mackenziensis Zone falls within a 15-20 m interval between C 570-590 and C 640 and I 1275 and I 1350-1380.

Assigned collections: Lower Whittaker Formation at Funeral Range (C 570-590) and Whittaker Range (I 1275).

Biofacies diversity: Undifferentiated Calyptaulax-Ceraurinella-Dimeropyge Biofacies, only.

Trilobites: *Acanthoparypha? goniopyga n. sp., *Borealaspis biformis n. sp., Calyptaulax sp., "Calyptaulax" cf. lincolnensis (Branson), *Ceraurinella necra n. sp., *Ceraurus tuberosus Troedsson, Dolichoharpes sp., *Holia anacantha n. sp., Hypodicranotus sp., illaenids, isotelids, lichids, Otarion sp., proetids, Remipyga? sp. (pygidial fragments with very long paddle-shaped first spines), *Sphaerocoryphe robustus Walcott.

Conodonts (Tipnis): Panderodus gracilis, Phragmodus undatus, Plectodina furcata, Ozarkodina polita. Fauna 9 of Sweet et al. (1971).

Ostracods (Copeland, 1974): "Aparchites" cf. fimbriatus (Ulrich), Bolbopisthia lenzi Copeland, Eurychilina sp., Diplopsis socialis Levinson, Krausella inaequalis Ulrich.

Bryozoans (Ross): Escharopora sp., two species of trepostomes.

CERAURUS MACKENZIENSIS ZONE (Kirkfieldian/Shermanian)

The Ceraurus mackenziensis Zone is essentially a continuation of the Ceraurinella necra Zone, and its independent character is shown by relatively minor phylogenetic turn-over. *Ceraurus mackenziensis* n. sp. and *Ceraurinella brevispina* n. sp. are derivatives of *Ceraurus tuberosus* Troedsson and *Ceraurinella necra* n. sp., respectively. *Sphaerocoryphe robustus* Walcott, *Acanthoparypha*? *goniopyga* n. sp., and "*Calyptaulax*" cf. *lincolnensis* (Branson) continue unchanged from the *C. necra* Zone. The arguments presented for the age of the *C. necra* Zone are equally valid for the *Ceraurus mackenziensis* Zone and a Kirkfieldian/Shermanian age is suggested for the younger zone.

Remipyga serrata n. sp., one of the earliest species of the genus, may be an approximate contemporary of *R. glabra* Whittington from Silliman's Fossil Mount and *R.* "*daedalus*" Cox from the Cape Calhoun Formation (Troedsson, 1928, Pl. 17, figs. 4-9, Pl. 18, figs. 10-15, Pl. 19, figs. 2, 3). One of Troedsson's specimens (his Pl. 19, fig. 1) appears conspecific with *R. serrata*. The occurrence of *Chasmops* is the first reported from the Middle Ordovician of North America and provides a link with the Balto-Scandian area.

The *C. mackenziensis* zonal assemblage is, on the generic level, very similar to that of the deeper water biofacies of the *Ceraurinella nahanniensis* Zone of late Chazyan age (shared genera include *Ceraurinella*, *Sphaerocoryphe*, *Dimeropyge*, *Acanthoparypha*, *Calyptaulax*, *Bumastoides*, *Apianurus*, *Cybeloides*, *Dolichoharpes*, and *Sphaerexochus*). Along the same lines, the generic composition of the *C. mackenziensis* Zone is closely comparable to that of the Richmondian interval on Anticosti Island (shared genera include *Borealaspis*, *Ceraurus*, *Sphaerocoryphe*, *Remipyga*, *Chasmops*, *Calyptaulax*). These similarities between faunas of demonstrably widely-separated ages underscore the precarious basis of generic correlation and emphasize the stability of trilobite biofacies.

The *Ceraurus mackenziensis* Zone sees the full development of the ostracod fauna that Copeland (1974, p. 6, 7) equated with ostracod faunas from the Decorah Formation of Iowa and Minnesota, the Bucke Formation of Lake Timiskaming, Ontario, the lower Hull Formation at Healey Falls, Ontario, the Braeside Beds at Braeside, Ontario, and the shaly beds at Silliman's Fossil Mount, Baffin Island. Copeland cited *Ceratopsis quadrifida*, *Dicranella bicornis*, and *Tetradella*? as particularly important in these correlations and suggested a "late Wilderness-early Barneveld" age for these lower Whittaker faunas. In the stadial scheme used herein, this corresponds to Kirkfieldian-Shermanian.

Tipnis assigns the conodonts from this zone to Fauna 9 of Sweet *et al.* (1971); that is, Kirkfieldian and Shermanian. Ross notes that the genus *Escharopora*, which occurs in both the *C. necra* and *C. mackenziensis* Zones, does not range higher than the Shoreham Formation (Shermanian) in New York State.

Maximum thickness: 40 m at Section H.

Upper contact: At the Whittaker Range, the upper contact with the *Whittakerites planatus* Zone falls within a 35 m interval between Q 430 and Q 530 and within a 60 m interval between I 1410 and I 1590.

Assigned collections: Lower Whittaker Formation at Whittaker Range (H 1850 to H 1975, I 1350-1380 to I 1410, Q 430) and Funeral Range (C 640 to C 655, J 220).

Biofacies diversity: Undifferentiated *Calyptaulax-Ceraurinella-Dimeropyge* Biofacies, only.

Trilobites: **Acanthoparypha*? *goniopyga* n. sp., *Anataphrus* sp., *Apianurus* sp., **Borealaspis* cf. *biformis* n. sp., **Borealaspis whittakerensis* n. sp., *Bumastoides* sp., *Calyptaulax* sp., "*Calyptaulax*" cf. *lincolnensis* (Branson), **Ceraurinella brevispina* n. ap., * *Ceraurus mackenziensis* n. sp., *Chasmops* sp., *Cybeloides* sp., *Dimeropyge* sp., *Dolichoharpes* sp., *Hemiarges* cf. *paulianus* (Clarke), *Hemiarges* sp., *Hypodicranotus* sp., otarionid, proetid, **Remipyga serrata* n. sp., **Sphaerocoryphe robustus* Walcott, diverse lichids.

Brachiopods: *Cyclospira*? sp., *Diceromyonia* sp., *Dinorthis* sp., *Hesperorthis* sp., *Lepidocyclus* sp., *Platystrophia* sp., *Thaerodonta* sp., *Zygospira* sp.

Conodonts (Tipnis): *Belodina compressa*, *Ozarkodina polita*, *Panderodus gracilis*, *Phragmodus undatus*. Fauna 9 of Sweet *et al*. (1971).

Ostracods (Copeland, 1974): "*Aparchites*" *fimbriatus* (Ulrich), *Bairdiocypris cylindrica* (Hall), *Bolbopisthia* sp., *Ceratopsis quadrifida* (Jones), *Dicranella bicornis* Ulrich, *Diplopsis socialis* Levinson, *Eurychilina prairiensis* Copeland, ?*Krausella* cf. *acuta* (Teichert), *Krausella inaequalis* Ulrich, *Milleratia* sp., *Oepikella labrosa* Copeland, *Oepikium* sp., *Schmidtella affinis* Ulrich, *Tetradella*? sp.

Bryozoans (Ross): *Escharopora* sp., *Ptilodictya* sp., *Stictopora* sp., nematoporid.

WHITTAKERITES PLANATUS ZONE (Shermanian/Edenian)

The trilobites of the youngest zone available for study, the *Whittakerites planatus* Zone, are composed of hold-overs from the subjacent zone (*Sphaerocoryphe robustus* Walcott, *Borealaspis* cf. *biformis* n. sp., *Remipyga serrata* n. sp., *Ceraurinella brevispina* n. sp.), a new form (*Whittakerites planatus* n. sp.) whose ancestor appears to have been *Ceraurus mackenziensis* of the underlying zone, and a few immigrant species (*Ceraurus milleranus* Miller and Gurley and *Ceraurus maewestoides* n. sp.) whose affinities lie with trilobites of the Maysvillian or younger intervals of eastern North America. A strong tie with the *Ceraurus mackenziensis* Zone is indicated by four common species and the presence of *Hypodicranotus*. *Ceraurus milleranus* and *C. maewestoides* lend a younger aspect to this fauna. *C. milleranus* has previously been known only from the Maysville and Richmond Groups of Ohio and Iowa and its occurrence in the *W. planatus* Zone tends to suggest a Cincinnatian age for that unit. However, a consideration of the probable ancestors of *C. milleranus* indicates that the species could also be older; being derived from *C. globulobatus* Bradley from the Kimmswick Limestone (probably Kirkfieldian-Shermanian, Sweet *et al.*, 1971) and/or *C. mantranseris* Sinclair from the middle Trenton of Quebec. *C. maewestoides* is very similar to *C. binodosus* Cooper and Kindle from the Ashgillian of Perce. The apparent mixture of Kirkfieldian/Shermanian and Cincinnatian species in the *W. planatus* Zone implies a position near the Champlainian-Cincinnatian boundary. A Shermanian/Edenian age is suggested for this zone. The age information derived from the ostracods and conodonts is consistent with this age assignment. The sparse ostracod fauna from collections in the *W. planatus* Zone does not contain the diagnostic elements of the *Ceratopsis*-*Dicranella*-*Tetradella*? fauna seen in the subjacent zone (Copeland, 1974). A few conodont collections from the *W. planatus* Zone yielded only long-ranging forms assignable to Faunas 8-12 of Sweet *et al*., 1971 (Tipnis).

Maximum thickness: 10 m at Section R.

Upper contact: Not clear due to lack of biostratigraphic information from strata immediately above this zone. At Section Q, the *W. planatus* Zone is followed by about 300 m of Ordovician dolostone before the first definite Early Silurian graptolites appear at the base of the upper argillaceous division of the Whittaker Formation (Text-fig. 2, column 4). At Section R, the *W. planatus* Zone is followed by about 100 m of Ordovician limestones which are overlain by massive dolostones of Early Silurian age (Text-fig. 2, column 5).

Assigned collections: Lower Whittaker Formation at Whittaker Range (I 1590, Q 530) and Dusky Range (R 625 to R 655).

Biofacies diversity: Undifferentiated *Calyptaulax*-*Ceraurinella*-*Dimeropyge* Biofacies, only.

Trilobites: **Borealaspis* cf. *biformis* n. sp., *Bumastoides* sp., calymenid, **Ceraurinella brevispina* n. sp., **Ceraurus maewestoides* n. sp., **Ceraurus milleranus* Miller and Gurley, *cheirurinid gen. and sp. indet., *Cybeloides* sp., *Dimeropyge* sp., harpid, *Hypodicranotus* sp., lichids, *Otarion* sp., proetid, **Remipyga serrata* n. sp., **Sphaerocoryphe robustus* Walcott, **Whittakerites planatus* n. sp.

Conodonts (Tipnis): Belodina compressa, Drepanodus subrectus, Panderodus gracilis, Plectodina sp.

Ostracods (Copeland, 1974): Bairdiocypris cf. cylindrica (Hall), Krausella inaequalis Ulrich, ?Krausella cf. acuta (Teichert), Leperditella sp.

Bryozoans (Ross): Sceptropora, nematoporid, phylloporinid, trepostomes.

TRILOBITE BIOFACIES

Preliminary remarks

Faunas from the Middle Ordovician rocks of the South Nahanni River area are readily collectable from long, and essentially uninterrupted, stratal sequences. The faunas are largely silicified. The number of samples available is governed only by their spacing since portions of these sequences are continuously fossiliferous through hundreds of meters of strata. However, some beds are considerably more productive than others. Sampling bias introduced by selective collecting is minimized and the bias resulting from selective silicification may be estimated by comparing the composition of insoluble residues with the biota evident in slabbed hand samples and thin sections from the same collection.

The interval chosen for detailed trilobite biofacies analysis is that bounded by the Bathyurus granulosus Zone (early Chazyan) in the upper Sunblood Formation and the Ceraurinella longispina Zone (Blackriveran/Rocklandian) of the upper Esbataottine Formation. In contrast with the earlier Whiterockian and the later Rocklandian to Edenian trilobite faunas of the study area, the trilobites of this interval are now relatively well known. The total trilobite fauna from the lower Esbataottine Formation of late Chazyan age has been studied by Chatterton and Ludvigsen, ms. (see list of taxa under the Ceraurinella nahanniensis Zone in the section on Biostratigraphy; illustrations in Ludvigsen, 1975, Pl. 3) and all the bathyurid, cheirurid, and encrinurid trilobites of the Chazyan to Rocklandian interval are described in this thesis. The remainder of the trilobite fauna from the upper Esbataottine Formation has not yet been studied in detail (lichids, odontopleurids, dalmanitids, asaphids, and illaenids), but these are of types similar to those in the lower part of the formation and have been tentatively identified (see lists in the section on Biostratigraphy; Ludvigsen, 1975, Pl. 4).

The upper Sunblood/Esbataottine Formations appear to represent a single depositional episode on a broad marginal platform south of the Redstone Arch (Ludvigsen, 1975, Fig. 10-3 to 6). On the generic level, the trilobites of this interval exhibit a high degree of stability - most of the genera persist through the interval and only a few genera are added - and are largely distinct from older and younger faunas. Most of the genera that occur lower in the Sunblood Formation (including "Bathyurus", "Goniotelina", Carolinites, Cybellela?, Heliomera, Ischyrotoma, Kawina, Nileus, and Pseudomera) do not persist into Chazyan and younger rocks of the study area and the trilobite faunas from the lower Whittaker Formation contain a number of genera not present in older rocks (including Borealaspis, "Calyptaulax", Hypodicranotus, Otarion, Remipyga, Chasmops, Whittakerites, proetids, and calymenids). Since the composition of any given fauna from the studied succession must be viewed within the context of phyletic turn-over, immigration, emigration, and extinction of taxa, as well as biofacies position, the faunas of these three intervals cannot be approached as isolated units. Periodic references will be made to the relationship of taxa of the proposed biofacies scheme with those of older and younger intervals. In particular, an attempt will be made at relating the trilobite faunas of the lower Whittaker Formation (*Strophomena-Ceraurus* fauna, Ludvigsen, 1975; *Ceraurinella necra* to *Whittakerites planatus* Zones, herein) to older trilobite faunas of the Esbataottine Formation, to coeval shallow water faunas of the Whittaker Formation (*Bighornia-Thaerodonta* and *Hesperorthis-Oepikina* faunas, Ludvigsen, 1975), and to coeval deeper water faunas of the lower Road River Formation (*Cryptolithus-Anataphrus* fauna, Ludvigsen, 1975).

The taxonomic category employed in the biofacies analysis is the genus. An *a priori* assumption is that the morphological information encompassed by a generic diagnosis carries functional and ecologic meaning and that a given morphological type will persist within a single biofacies (at least, for the time period under consideration). The latter assumption is not true in every case, since it can be demonstrated that a few genera do cross biofacies boundaries through time; but it does account for the bulk of the morphological and distributional information.

In the following discussion, the term "community" has been avoided because the total fauna of this interval has not yet been studied. The trilobite biofacies must, in the future, be integrated with the brachiopod biofacies, the ostracod biofacies, the conodont biofacies, and the bryozoan biofacies before a true community synthesis can be assembled. At this stage of investigation, it is incongruous (as well as misleading) to apply the term "Calyptaulax-Ceraurinella Community" to a faunal assemblage from ~~the upper Esbataottine Formation in which brachiopods of the~~ genera Sowerbyella, Doleroides, Hesperorthis, Oepikina, and Strophomena all but flood out the still sizeable trilobite fauna assigned to the Calyptaulax-Ceraurinella Biofacies.

Procedure and Graphical Technique

The limestone blocks comprising each collection were weighed prior to etching and a slabbed hand sample was retained. After effervescence ceased in the dilute (3-5%) hydrochloric acid bath, the insoluble residue was wet sieved, carefully washed, and dried. Only the fraction retained on nylon window screening (maximum diameter of 1.8 mm) which served as a coarse sieve was used in the subsequent quantitative studies. The residue was picked and the trilobites identified. The unpaired exoskeletal elements (cranidia, pygidia, hypostomes, and rostral plates) of each species were counted and the maximum number of any one of these four elements was registered as the number of individuals of each species in a collection. A species numerical abundance was converted into generic abundance in individuals which was then expressed as relative abundance (in percent) of each genus in a collection. In this fashion, the raw trilobite abundance data of each of 41 collections from five sections (Sections A, B, G, H, and P) from the upper Sunblood and Esbataottine Formation were assembled.

A histogram of relative generic abundance was drawn up for the most diverse collection. The order of the genera on the X-axis was arranged, initially, with the high abundance ranking genera in the middle flanked, on either side, by successively less abundant genera. The procedure was repeated for the next diverse collection. The two graphs were compared and the generic order was altered, on both histograms, so that the spread of the high abundance ranking genera was minimized. This procedure was continued on successively less diverse collections until all the genera, or generic groupings, were accommodated on the X-axis. This results in a linear arrangement of the genera with Bathyurus on one end and Sphaerocoryphe on the other (Text-fig. 13).

Recurrent generic "peaks" are evident on the assembled histograms (Text-figs. 10-12). It is concluded that these "peaks" reflect groupings of naturally co-occurring genera and species.

The generic abundance data may be distilled further by recognizing that a single collection consists largely of various proportions of each of four generic "peaks";

Text-figures 10, 11, 12.

Series of diagrams showing (on the right side) relative generic abundance and (on the left side) proportion of each of four biofacies in trilobite collections from the upper Sunblood and Esbataottine Formations at Sections P, A, G, B, and H. Collection name is given in the centre column, followed by the sample size in individuals (in brackets).

Legend:

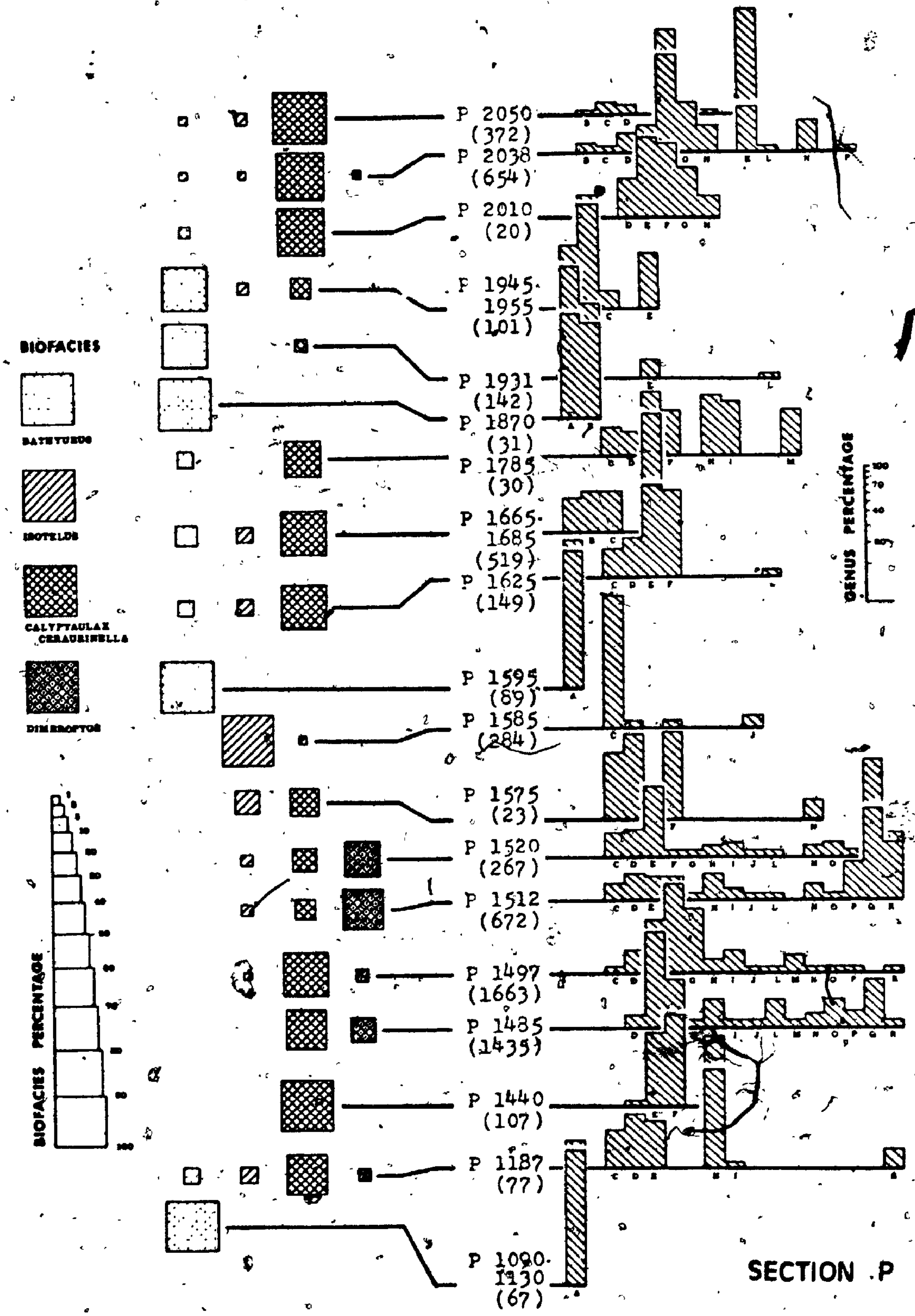
A	*Bathyurus*
B	*Ceraurus*
C	*Isotelus*
D	illaenids (*Nanillaenus* + *Failleana* + *Bumastoides*)
E	*Calyptaulax*
F	*Ceraurinella*
G	*Sphaerexochus*
H	*Cybeloides*
I	*Remopleurides*
J	*Nahannia*
K	*Anataphrus*
L	lichids (*Amphilichas* + *Hemiarges*)
M	*Encrinuroides*
N	odontopleurids (*Apianurus* + *Ceratocephala*)
O	*Carrickia*
P	*Dolichoharpes*
Q	*Dimeropyge*
R	acanthoparyphinids (*Acanthoparypha* + *Pandaspinapyga* + *Holia* + *Heliomeroides*)
S	*Sphaerocoryphe*

Bathyurus Biofacies = % *Bathyurus* + *Ceraurus*

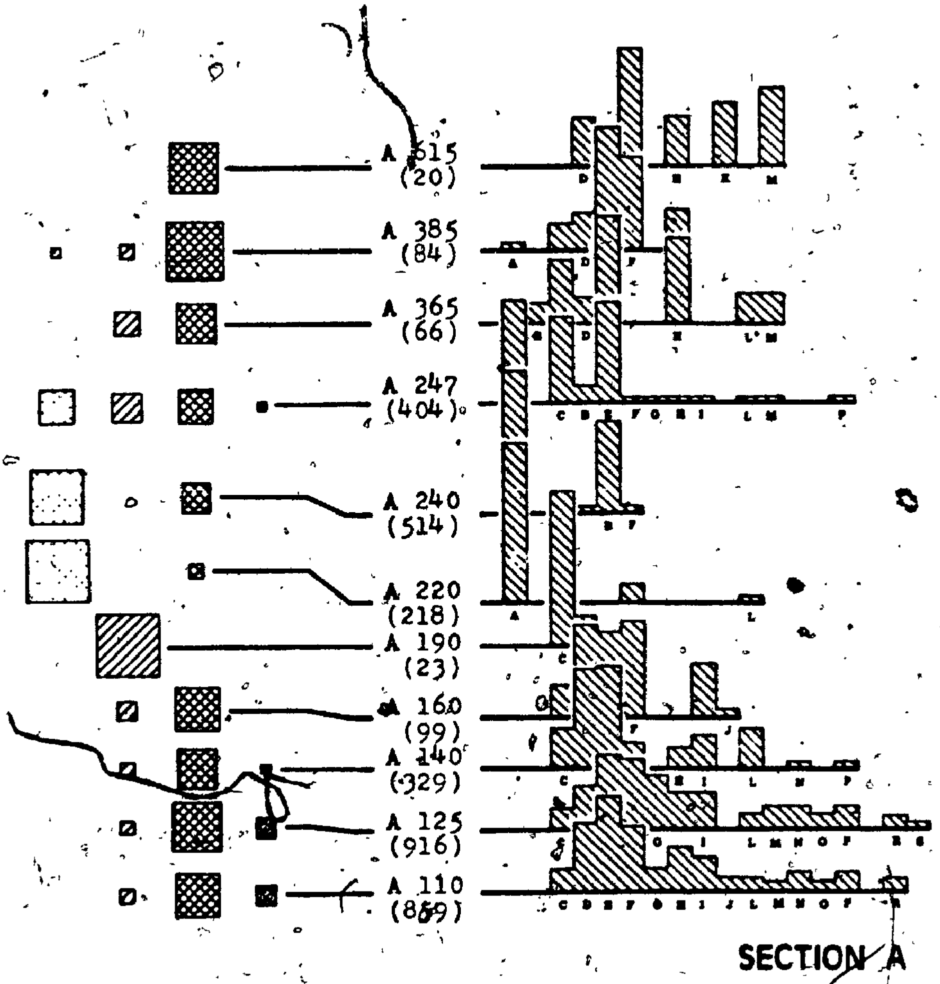
Isotelus Biofacies = % *Isotelus*

Calyptaulax-*Ceraurinella* Biofacies = % *Calyptaulax* + *Ceraurinella* + *Cybeloides* + *Sphaerexochus*

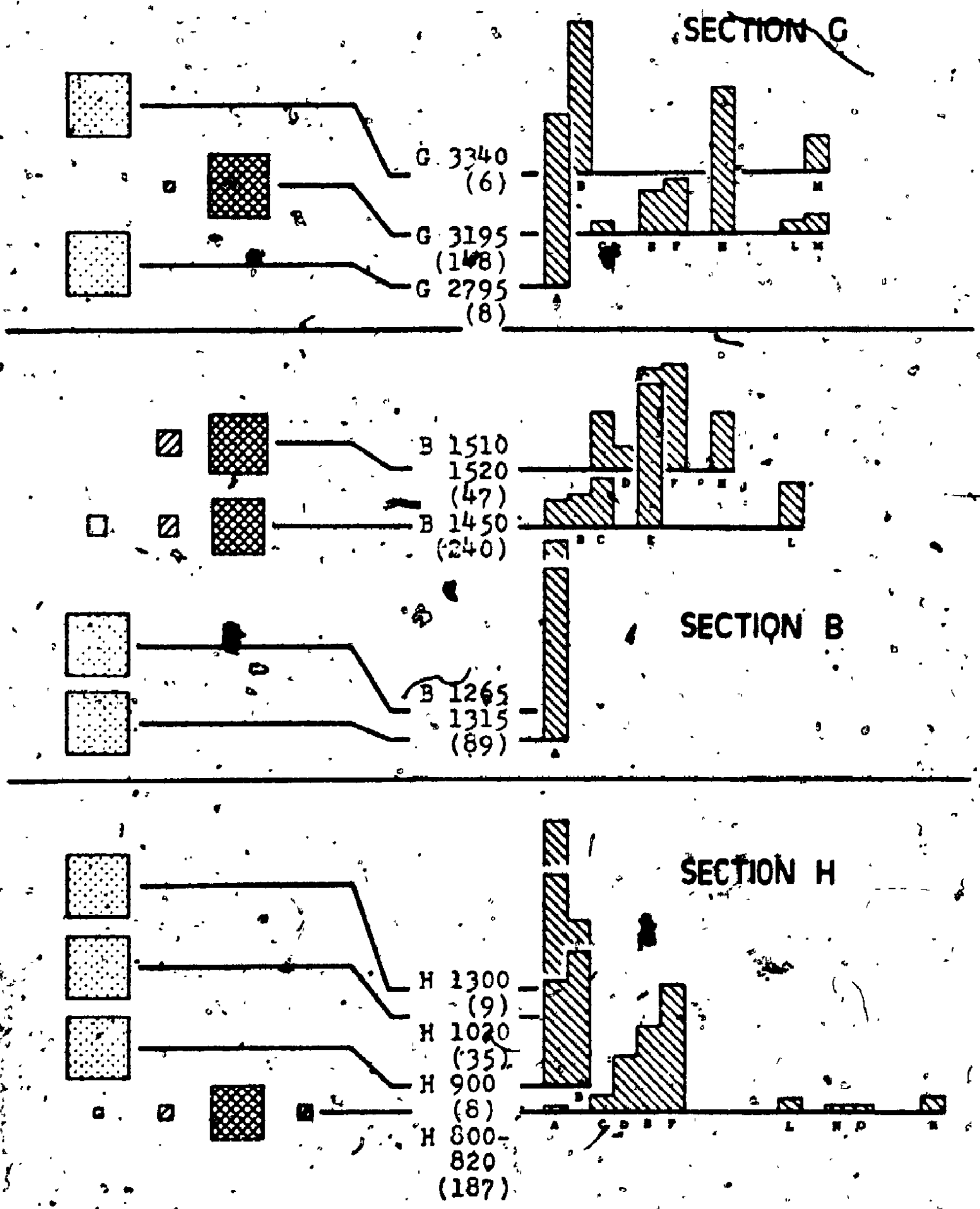
Dimeropyge Biofacies = % *Dimeropyge* + *Dolichoharpes* + acanthoparyphinids + *Carrickia*



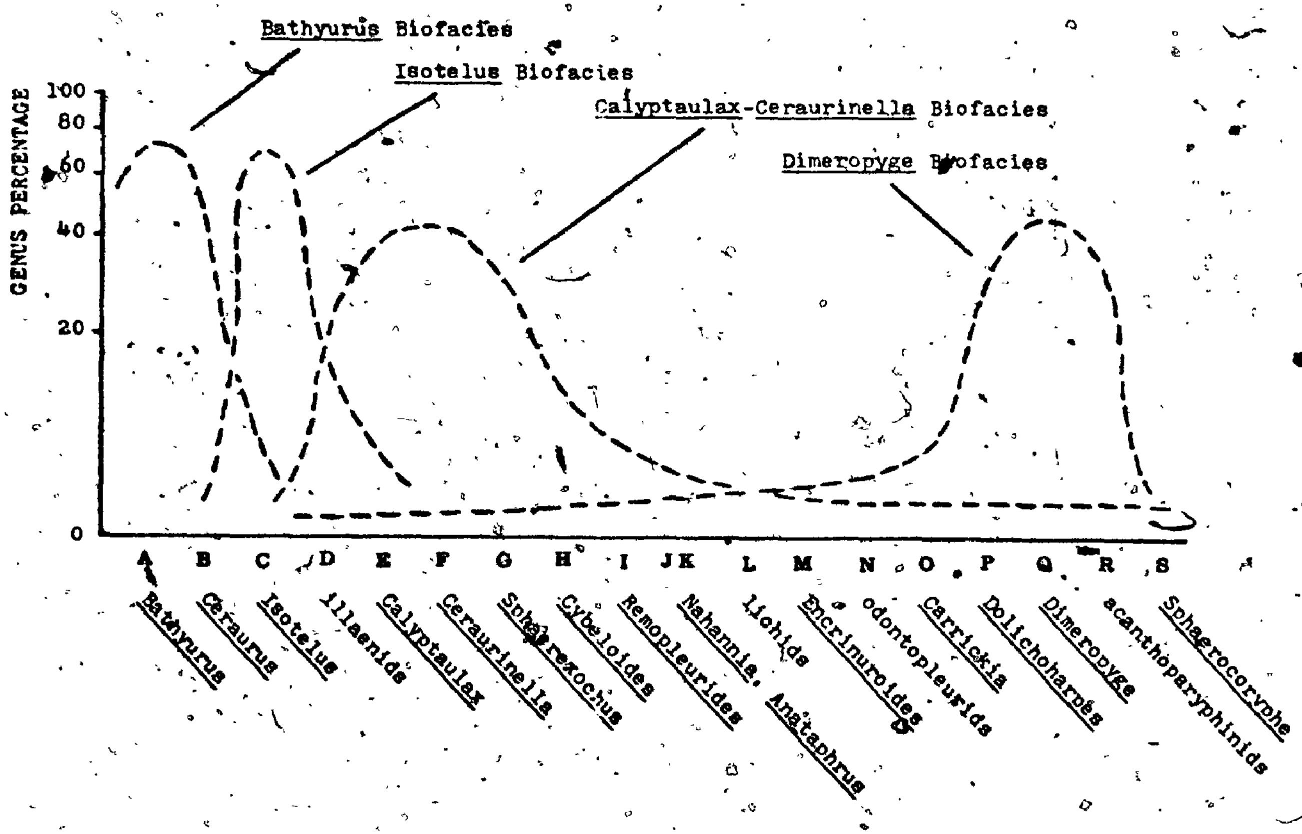
Text-figure 10.



Text-figure 11.



Text-figure 12.



Text-figure 13.

Typical abundance curves of the four trilobite biofacies recognized in the upper Sunblood and Esbataottine Formations. The generic order on the x-axis is the same as that of Text-figures 10-12.

1. *Bathyurus* and *Ceraurus*.
2. *Isotelus*.
3. *Calyptaulax*, *Ceraurinella*, *Sphaerexochus*, and *Cybeloides*.
4. *Dimeropyge*, *Dolichoharpes*, acanthoparyphinids (*Acanthoparypha*, *Holia*, *Pandaspinapyga*, *Heliomeroides*), and *Carrickia*.

These groups, named the *Bathyurus*, *Isotelus*, *Calyptaulax-Ceraurinella*, and *Dimeropyge* Biofacies, respectively, are graphically shown on the left side of Text-figures 10 to 12, opposite the histograms of generic abundance. A single biofacies dominates almost every collection, but representatives of one, two, or rarely, three of the other biofacies may be present. In sections with moderately closely spaced collections, the biofacies acme shifts gradually in successively higher collections. In particular, note the transition from P 1520 (*Dimeropyge* Biofacies-dominated) to P 1595 (*Bathyurus* Biofacies-dominated) in Section P (Text-fig. 10) and the transition from A 220 (*Bathyurus* Biofacies-dominated) to A 385 (*Calyptaulax-Ceraurinella* Biofacies-dominated) in Section A (Text-fig. 11).

Trilobite Abundance

Etching of 188 kg of limestone from 19 collections from the upper Sunblood Formation and Esbataottine Formation at Section P in the Sunblood Range (collections P 1090 to P 2050) yielded a total of 6800 trilobite individuals. The number of individuals in each collection from Section P is shown in the central column (in brackets) of Text-figure 10. The trilobite yield, which may be a measure of species density, ranges between a high of 163 individuals per kilogram of limestone to a low of 5 individuals per kilogram (Text-fig. 14).

Lithology

The upper Sunblood and Esbataottine Formations in the Sunblood Range comprise a monotonous sequence of crypto- to very finely crystalline limestones; commonly, silty and argillaceous. The bedding is regular and nodular; generally thin (3-8 cm) to medium (8-20 cm), rarely thick bedded (Ludvigsen, 1975, Appendix). Although their lithologies are closely comparable, the upper part of the resistant, light-coloured, and medium to thick bedded limestones of the Sunblood are sharply contrasted with the moderately recessive, darker coloured, and thinly bedded limestones of the Esbataottine (Ludvigsen, 1975, Figs. 5, 6).

Aside from a thin (1 m) quartzite unit marking the top of the Sunblood Formation in the Sunblood Range, sand-size components, either quartz or organically derived, are rare in the limestones of this part of the section; as are the more common biotic contributors to skeletal sands, such as pelmatozoans, heavy shelled brachiopods, algae, corals, or stromatoporoids (Anderson and Pazdersky, Chapter 4, in Ziegler et al., 1974). Biohermal or biostromal developments are not present.

Desiccation polygons are occasionally present. Other sedimentary features, including trace fossils, have not been recognized. Many beds, however, show disrupted laminae, probably caused by small burrowers.

The environment inhabited by the upper Sunblood and Esbataottine trilobites, as suggested by the lithology, is a homogeneous, probably soft bottom, carbonate mud deposited under quiet water conditions on a wide shelf ranging from the littoral to, possibly deep, sub-littoral zone. As Walker (Chapter 5, in Ziegler et al., 1974) has pointed out, this type of uniform, level-bottom environment is the primary site of parallel community development.

Bathyurus Biofacies

First ranking genera: Bathyurus and Ceraurus.

Second ranking genera: Calyptaulax and Amphilichas.

Collections assigned: A 220; A 247; B 1265-1295; B 1315; G 2795; G 3340; H 410; H 900; H 1020; H 1300; P 1090-1130; P 1595; P 1870; P 1931; P 1945-1955.

Zonal persistence: Bathyurus granulosus Zone to Ceraurus gabrielsi Zone (Chazyan to Blackriveran).

Trilobite density: 8 to 16 individuals per kilogram of limestone (average 12/kg).

Trilobite diversity: 1 or 2 species per collection, rarely 4.

The Bathyurus Biofacies is most extensively developed on the edges of the depositional basin, at Sections B and H. The occurrences of the biofacies in Sections A and P, near the western outlet of the basin, intervene between developments of the Isotelus Biofacies and/or the Calyptaulax-Ceraurinella Biofacies.

Besides the trilobites, the Bathyurus Biofacies includes abundant leperditellid ostracods of the genera Leperditella, Eokloedenella, and Schmidtella (Copeland, 1974), few brachiopods of the genera Rostricellula and Camerella, and locally abundant gastropods and bryozoans. This biofacies contains the only features indicative of periodic sub-aereal exposure (desiccation polygons) recognized in the studied interval.

Bathyurus was derived from earlier bathyurids of Whiterockian age. These bathyurids, probably had a greater ecologic tolerance than Bathyurus since they occur widely in diverse carbonate lithotopes in association with more diverse trilobite faunas (Whittington and Hughes, 1972, Table 9). The ecospace inhabited by Bathyurus in the Middle Ordovician was concisely restricted to shallow water on a carbonate mud base. This environment appears to have undergone virtual destruction as a result of the basal Trentonian transgression which, in the South Nahanni River area was accompanied by a marked eastward displacement of facies belts. Here the shallow sea floor became covered by a wide sheet of calcarenites, commonly of reefoid aspect, and populated by a newly introduced brachiopod-coral-mollusk association. In the Nahanni area (and apparently also in eastern North America), Bathyurus persists up to the level registering this eustatic event, but not above. It is concluded that the extinction and the eustatic event were related and that the demise of *Bathyurus* may be ascribed to habitat destruction of the *Bathyurus* Biofacies.

The only other common trilobite of the *Bathyurus* Biofacies underwent a different history. *Ceraurus gabrielsi* was an immigrant into the Nahanni area that became established within the *Bathyurus* Biofacies. Its origin lies with the reef dwelling "*Paraceraurus*" *ruedemanni* from the Chazy Group of eastern North America. The phylogenetic lineage initiated by *C. gabrielsi* in the Nahanni area underwent rapid diversification and successive species (*C. blussoni* and *C. hirsuitus*) started to invade the *Calyptaulax*-*Cerauriella* Biofacies in late Blackriveran to early Rocklandian interval. By Trentonian time, species of *Ceraurus* were firmly established in deeper *Calyptaulax*-*Ceraurinella*-*Dimeropyge* Biofacies within the axial part of the Root Basin and, thus, escaped the effects of the basal Trentonian eustatic event that caused the extinction of *Bathyurus*.

Isotelus Biofacies

First ranking genus: *Isotelus*.

Rare genera: *Nanillaenus*, *Bumastoides*, *Nahannia*.

Collections assigned: A 190; P 1585.

Zonal persistence: *Ceraurinella nahanniensis* Zone and *Bathyurus ulu* Zone (late Chazyan to early Blackriveran).

Trilobite density: 32 individuals per kilogram of limestone.

Trilobite diversity: Essentially, a single species.

The Isotelus Biofacies is completely developed in only a single collection each from Sections A and P. The collections are closely underlain by the Calyptaulax-Ceraurinella Biofacies and overlain by the Bathyurus Biofacies. A steady relative decrease of the Isotelus Biofacies is clearly evident above and below its acme developments in Section P (Text-fig. 10) and Section A (Text-fig. 11).

A few leperditellid and oepikellid ostracods and bryozoans also occur in these collections; as do common brachiopods of the genus Strophomena.

The Isotelus Biofacies may represent a specialized habitat along the shoreward edge of the Calyptaulax-Ceraurinella Biofacies. Very little mixing occurs with the Bathyurus Biofacies (note the Isotelus to Bathyurus Biofacies transition between A 190 and A 220 and P 1585 and P 1595. Isotelus, by itself, appears to be a minor, but integral, component of the Calyptaulax-Ceraurinella Biofacies.

Calyptaulax-Ceraurinella Biofacies

First ranking genera: Calyptaulax, Ceraurinella, Cybeloides, Sphaerexochus, and (in the highest Esbataottine Formation) Anataphrus.

Second ranking genera: Isotelus, Bumastoides, Failleana, Nanillaenus, Encrinuroides, Remopleurides.

Rare genera: Nahannia, Hemiarges, Amphilichas, Ceratocephala, Apianurus, Carrickia, Dolichoharpes, Dimeropyge, *Acanthoparypha*, *Holia*, *Pandaspinapyga*, *Heliomeroides*, *Sphaerocoryphe*, and (in the highest Esbataottine Formation) *Ceraurus*.

Collections assigned: A 110; A 125; A 140; A 160; A 365; A 385; A 615; B 1450; B 1510-1520; G 3195; H 800-820; P 1187; P 1440; P 1485 (transitional to the *Dimeropyge* Biofacies); P 1497; P 1625; P 1665-1685; P 1785; P 2010; P 2038; P 2050.

Zonal persistence: *Bathyurus granulosus* Zone to *Ceraurinella longispina* Zone (early Chazyan to Blackriveran/ Rocklandian).

Trilobite density: Considerable range of 5 to 163 individuals per kilogram of limestone (average 43/kg).

Trilobite diversity: Rarely as high as 25 species per collection; generally 10 or fewer.

The *Calyptaulax*-*Ceraurinella* Biofacies is extensively developed along the western outlet of the depositional basin. At Section P, 11 collections out of 19 and at Section A, 8 collections out of 11 belong to this biofacies. In these sections, a gradational relationship is evident with the *Dimeropyge* Biofacies on one side and with the *Isotelus* or *Bathyurus* Biofacies on the other (Text-figs. 10, 11). At Section H, located near the eastern edge of the basin, only a single collection is assignable to the *Calyptaulax*-*Ceraurinella* Biofacies (Text-fig. 12).

Besides the trilobites, the Chazyan portion of this biofacies contains locally abundant brachiopods of the genera *Mimella* and ?*Macrocoelia*. Other brachiopods of the genera *Chaulistomella*, *Rostricellula*, *Onychoplesia*, and

Glyptorthis are present, but are generally rare. In the Blackriveran/Rocklandian interval, the Calyptaulax-Ceraurinella Biofacies occurs with a different brachiopod fauna consisting of Sowerbyella, Doleroides, Skenidioides, Triplesia, Strophomena, Oepikina, and Hesperorthis. Trilobites dominate the Chazyan interval and brachiopods dominate the Blackriveran/Rocklandian interval.

Abundant ornamented and smooth ostracods occur in the Calyptaulax-Ceraurinella Biofacies (see Copeland, 1974, p. 8-12 for species lists; in particular those from A 125; P 1485; P 1497; P 2038; and P 2050), as do diverse bryozoans.

The striking characteristic of the Calyptaulax-Ceraurinella Biofacies is the high generic diversity reflected in the appearance of up to 23 genera (Text-fig. 13), of which only Isotelus and the illaenids are shared with the shallower biofacies. The inclusion of a small percentage of the Bathyurus Biofacies in the Calyptaulax-Ceraurinella Biofacies-dominated collections from the highest Esbataottine Formation (P 2010 to P 2050) is an artefact of the biofacies definition and does not reflect the presence of shallow-water components. The "Bathyurus Biofacies", here, signifies only the presence of Ceraurus which, in this part of the interval, was in the process of migrating from a shallow to a deeper habitat. The same applies to G 3340 which, in Text-figure 15, is assigned to the Bathyurus Biofacies.

Dimeropyge Biofacies

First ranking genera: *Dimeropyge*, *Dolichoharpes*, *Acanthoparypha*.

Second ranking genera: *Carrickia*, *Holia*, *Remopleurides*, *Cybeloides*, *Ceraurinella*.

Rare genera: *Encrinuroides*, *Heliomeroides*, *Amphilichas*, *Hemiarges*, *Nahannia*, *Sphaerexochus*, *Ceratocephala*, *Apianurus*, *Failleana*, *Nanillaenus*, *Bumastoides*, *Isotelus*.

Collections assigned: P 1485(transitional to the *Calyptaulax*-*Ceraurinella* Biofacies), P 1512, P 1520.

Zonal persistence: *Ceraurinella nahanniensis* Zone, only (late Chazyan).

Trilobite density: Ranges between 29 and 96 individuals per kilogram of limestone.

Trilobite diversit[illegible] 17 or 18 species per collection.

The *Dimeropyge* Biofacies has only been recognized in the Sunblood Range where it is developed in the lower part of the Esbataottine Formation. It is intimately associated with the *Calyptaulax*-*Ceraurinella* Biofacies and cannot be distinguished from that biofacies by generic composition alone - only the dominance of *Dimeropyge*, *Dolichoharpes*, and *Acanthoparypha* sets it apart (Text-fig. 13).

The *Dimeropyge* Biofacies interpreted as occupying a slightly deeper and/or softer bottom environment than the *Calyptaulax*-*Ceraurinella* Biofacies. Only rare ostracods and bryozoans occur and brachiopods are absent. The dominant trilobite taxa are either very small and spinose (*Dimeropyge*, *Carrickia*), larger and spinose (*Holia*, *Cybeloides*), or show specialized adaptations that are interpreted as measures to inhibit sinking into a soft substrate (for example, the "snowshoe adaptation" of the lower lamella of Dolichoharpes). The individuals of the Dimeropyge Biofacies are consistently of smaller size than those of the previous three biofacies. The adaptations, size, and diversity of the trilobites, and the exclusion of nearly all suspension feeders suggest a deep tranquil environment and a very soft to, possibly, fluid substrate (Walker, Chapter 5, in Ziegler et al., 1974).

Calyptaulax-Ceraurinella-Dimeropyge Biofacies

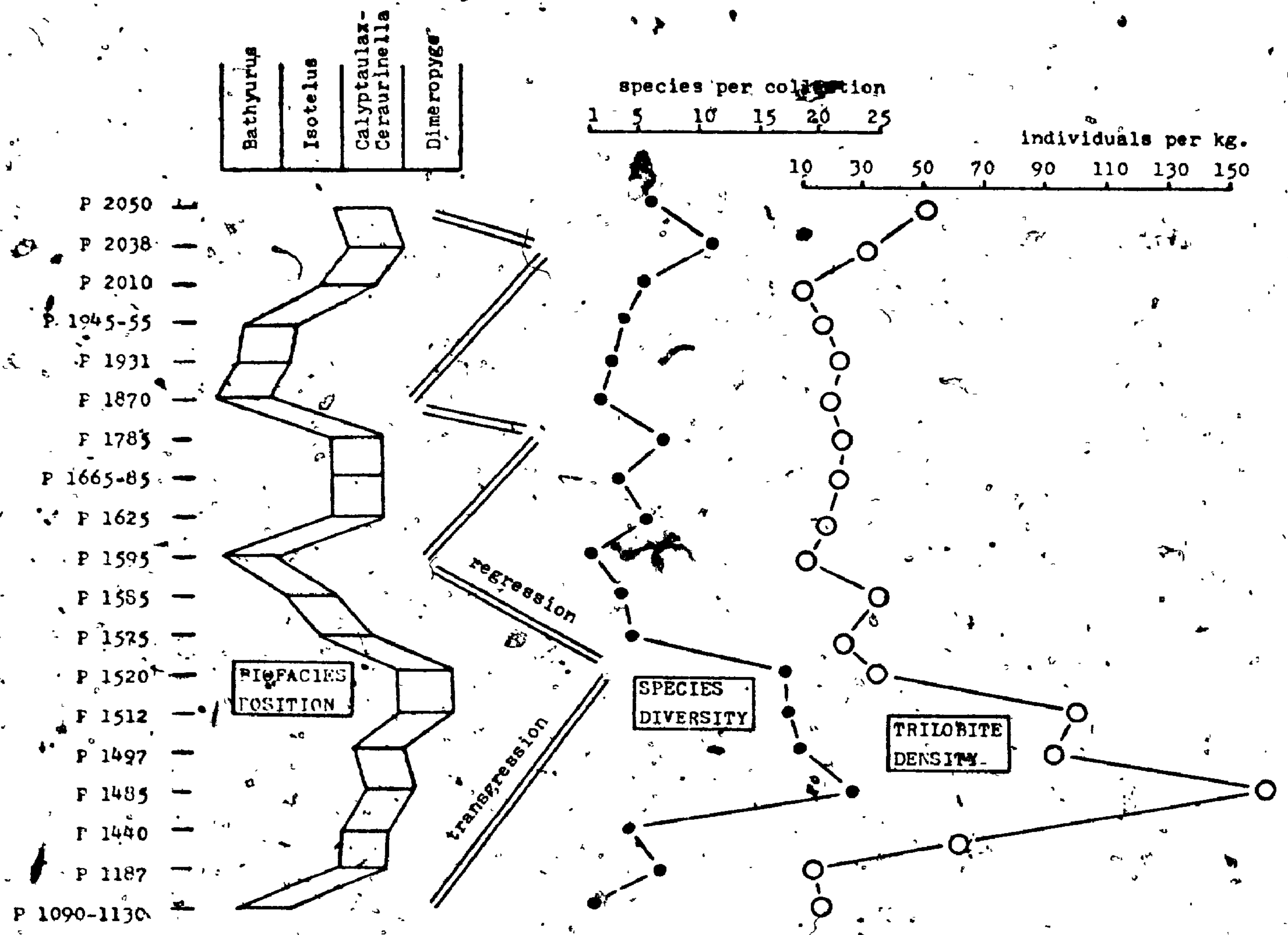
The name Calyptaulax-Ceraurinella-Dimeropyge Biofacies is tentatively applied, without supportive data of a quantitative nature, to a number of trilobite-dominated faunas from the lower part of the Whittaker Formation in the axial part of the Root Basin (Strophomena-Ceraurus fauna, in Ludvigsen, 1975). Reference to the faunal lists of the Ceraurinella necra, Ceraurus mackenziensis, and Whittakerites planatus Zones (Rocklandian to Edenian) in the section on Biostratigraphy should demonstrate the compositional similarity of this biofacies to the Calyptaulax-Ceraurinella and Dimeropyge Biofacies. The genera Calyptaulax, Ceraurinella, Cybeloides, Sphaerexochus, Ceraurus, Anataphrus, Hemiarges, and Sphaerocoryphe provide links with the Calyptaulax-Ceraurinella Biofacies and Acanthoparypha?, Holia, Apianurus, Dimeropyge, and Dolichoharpes with the Dimeropyge Biofacies.

The Calyptaulax-Ceraurinella-Dimeropyge Biofacies also contains a number of genera that are not present in the biofacies of the Esbataottine Formation (Borealaspis, "Calyptaulax" of the "C." lincolnensis type, Hypodicranotus, Otarion, Remipyga, Chasmops, Whittakerites, proetids, and calymenids) and these lend a distinctive aspect to this biofacies.

It is suggested that the Calyptaulax-Ceraurinella-Dimeropyge Biofacies represents a continuation of an undifferentiated Calyptaulax-Ceraurinella and Dimeropyge Biofacies that was displaced eastward by the pronounced transgression in the Rocklandian interval and that became established within the deeper portions of the Root Basin (Ludvigsen, 1975, Fig. 10-6). The shallow water equivalents of the Calyptaulax-Ceraurinella-Dimeropyge Biofacies are brachiopod-coral-mollusk faunas (Hesperorthis-Oepikina and Bighornia-Thaerodonta) on the fringes of the Root Basin and on the flooded Redstone Arch (Ludvigsen, 1975, Fig. 10-5 and 6).

Biofacies synthesis

The compositional information about the trilobite biofacies presented herein is largely deduced from the vertical distribution of recurring associations in a few stratigraphic sections. An attempt at extending the biofacies scheme in a lateral direction meets with problems because of the inadequate number of control points in the relatively large depositional basin. But this approach must be tried because



Text-figure 14. Relationship of biofacies position, trilobite species diversity and trilobite density of collections from the upper Sunblood Formation to the highest Esbataottine Formation at Section F. Transgression-regression curve derived from biofacies curve.

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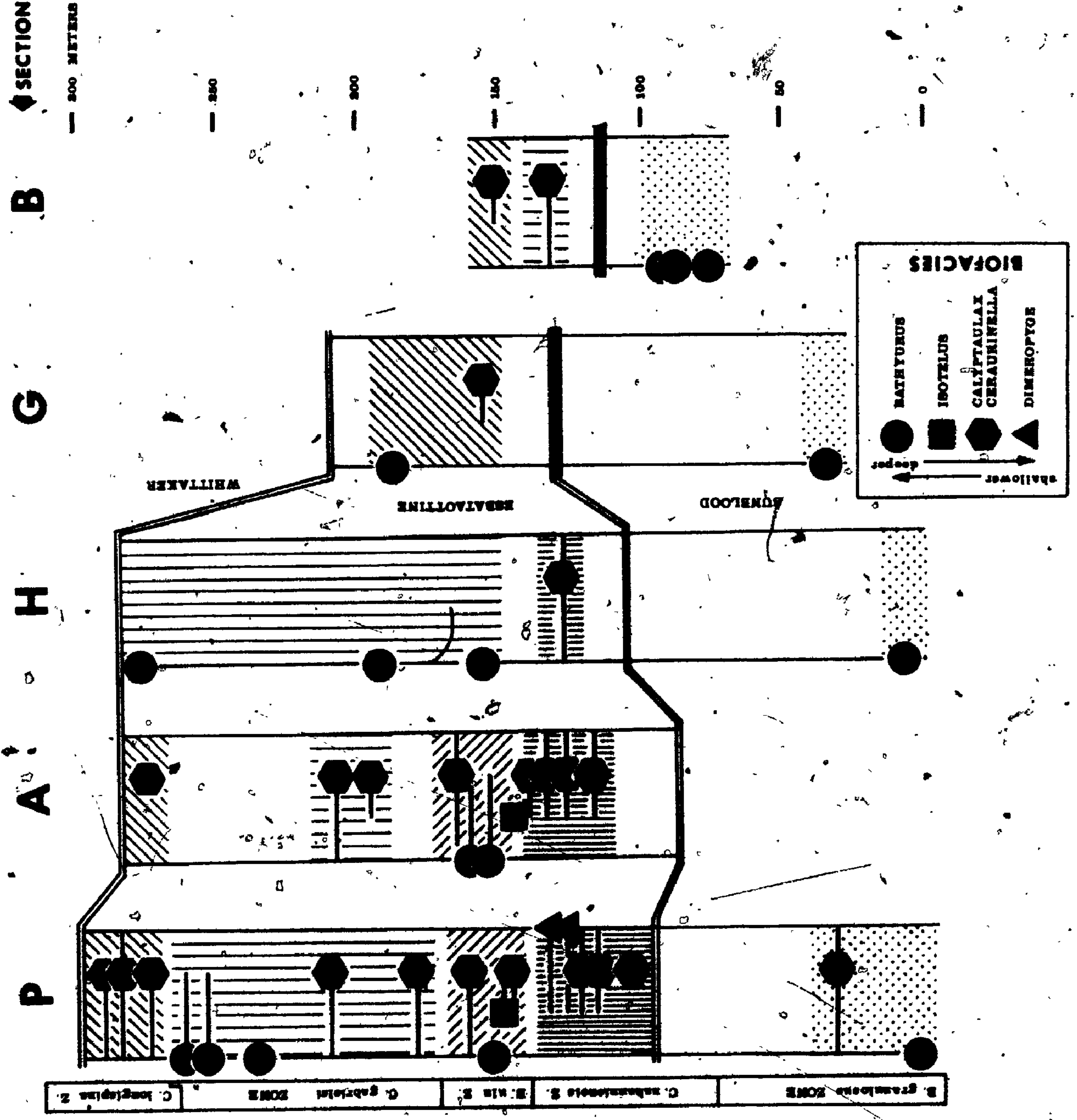


Text-figure 15.

Relationship of trilobite zonal assignment (shading) and biofacies position (symbols) of collections from the upper Sunblood and Esbataottine Formations in the Sunblood Range (Sections A and P), Whittaker Range (H), Flood Creek (G), and Mary Range (B). Horizontal line emerging from biofacies symbol signifies total biofacies range of a collection (Text-figs. 10-12). Solid black lines in Sections G and B indicate position of possible disconformity.

co-existing faunal associations can only realistically be viewed in a geographic context; that is, they should be mappable.

In Text-figure 14, I have diagrammatically depicted the biofacies position of the trilobite collections from the most extensively sampled section, Section P in the Sunblood Range. The order of the biofacies is dictated by the order of the genera arrived at by the grouping procedure outlined previously. Of these, the Bathyurus Biofacies is known from non-biologic criteria (desiccation polygons) to extend, at least in part, into a littoral environment. Analogous evidence about the other three biofacies is lacking, but it may be assumed that, at least the Calyptaulax-Ceraurinella and Dimeropyge Biofacies represent deeper water assemblages than the Bathyurus Biofacies. The biofacies positions may then be joined in a continuous ribbon that would constitute a relative depth curve. At Section P, such a curve comprises three transgression-regression couplets in the upper Sunblood and Esbataottine Formations (Text-fig. 14).

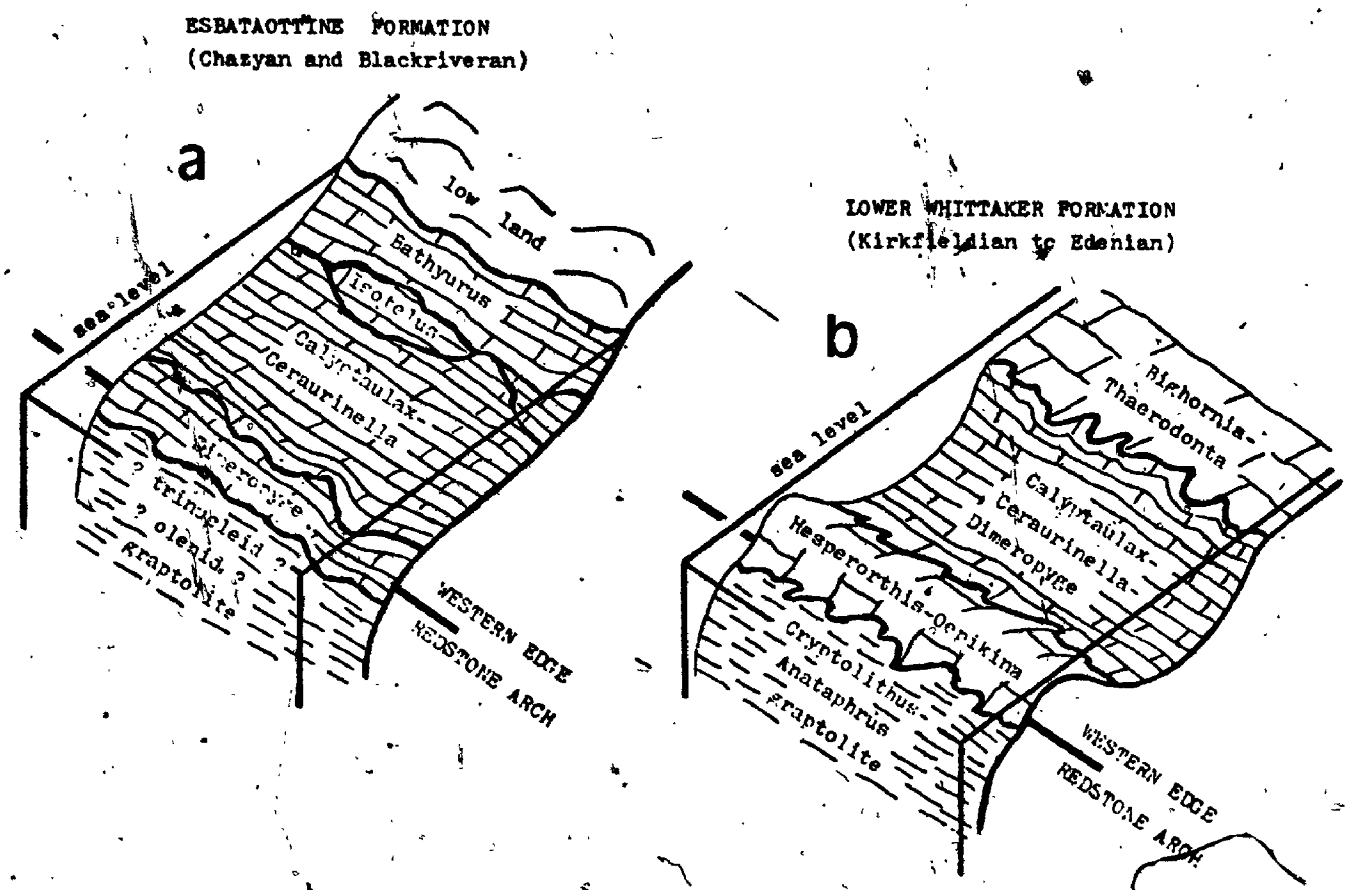
If this curve actually registers relative depth, it is to be expected that, in any given zonal interval, successively shallower biofacies should appear in sections located closer to the presumed shoreline and ultimately pinch-out against a disconformity. A test depends on the resolution capability of the zonal scheme. Text-figure 15 integrates the zonal and biofacies information from five studied sections. Sections A and P are located in the deeper portion of the basin, Section H on the eastern flank, Section G on the northern flank, and Section B on the southeastern flank (Ludvigsen, 1975, Fig. 10-4). If each zone is examined in each of the sections, the following conclusions may be drawn: The B. granulosus Zone occurs everywhere in the Bathyurus Biofacies, except in a single collection from Section P belonging to the Calyptaulax-Ceraurinella Biofacies. The C. nahanniensis Zone occurs in the Calyptaulax-Ceraurinella or Dimeropyge Biofacies in Section P, A, and H; and has not been recognized at Sections G and B. The B. ulu Zone occurs in the Calyptaulax-Ceraurinella, Isotelus, and Bathyurus Biofacies at Sections P and A and has not been recognized at Sections H, G, and B. The C. gabrielsi Zone occurs in the Calyptaulax-Ceraurinella Biofacies at Sections P, A, and B and in the Bathyurus Biofacies at Sections P and extensively at Section H; it has not been recognized at Section G. The C. longispina Zone occurs everywhere as the Calyptaulax-Ceraurinella Biofacies (the Bathyurus Biofacies in this zonal position at Section G reflects the presence of Ceraurus cf. hirsuitus which is probably not a true member of this biofacies). The extensive development of the Bathyurus Biofacies within the C. gabrielsi Zone at Section H may suggest that the zonal assignment of the highest collection is in error, and that it belongs to the C. longispina Zone.

The limited information about the geographical distribution of biofacies within the zonal scheme is consistent with a depth control of the trilobite biofacies.

In Text-figure 16a, I have diagrammatically shown the four trilobite biofacies arrayed in belts parallel to the shoreline on a broad platform supported by the southern extension of the Redstone Arch -- Bathyurus Biofacies, shallowest and Dimeropyge Biofacies, deepest. Trilobites that could be interpreted as being of deeper water origin than the Dimeropyge Biofacies have not been recognized from the Chazyan or Blackriveran interval.

An attempt at mapping the distribution of the Bathyurus, Calyptaulax-Ceraurinella, and Dimeropyge Biofacies in five intervals from the upper Sunblood and Esbataottine Formations is presented in Text-figure 17. These maps are not completely empirically derived, but should rather be viewed as models of biofacies distribution. They do, however, satisfy the limited zonal and biofacies information about the five sections summarized in Text-figure 15. Aside from aiding in the understanding of the physical determinants of these biofacies, this technique suggests a new approach to paleogeographic analysis, one that may be applied to platform areas, such as the study area, where the homogeneous nature of the strata frustrate conventional lithofacies analysis.

Although it was stated above that the distribution of the biofacies was controlled by depth, this may be a simplification because related parameters such as temperature and substrate may be equally important. The influence of the substrate may be reflected in the small size of the bulk of



ESBATAOTTINE FORMATION
(Chazyan and Blackriveran)

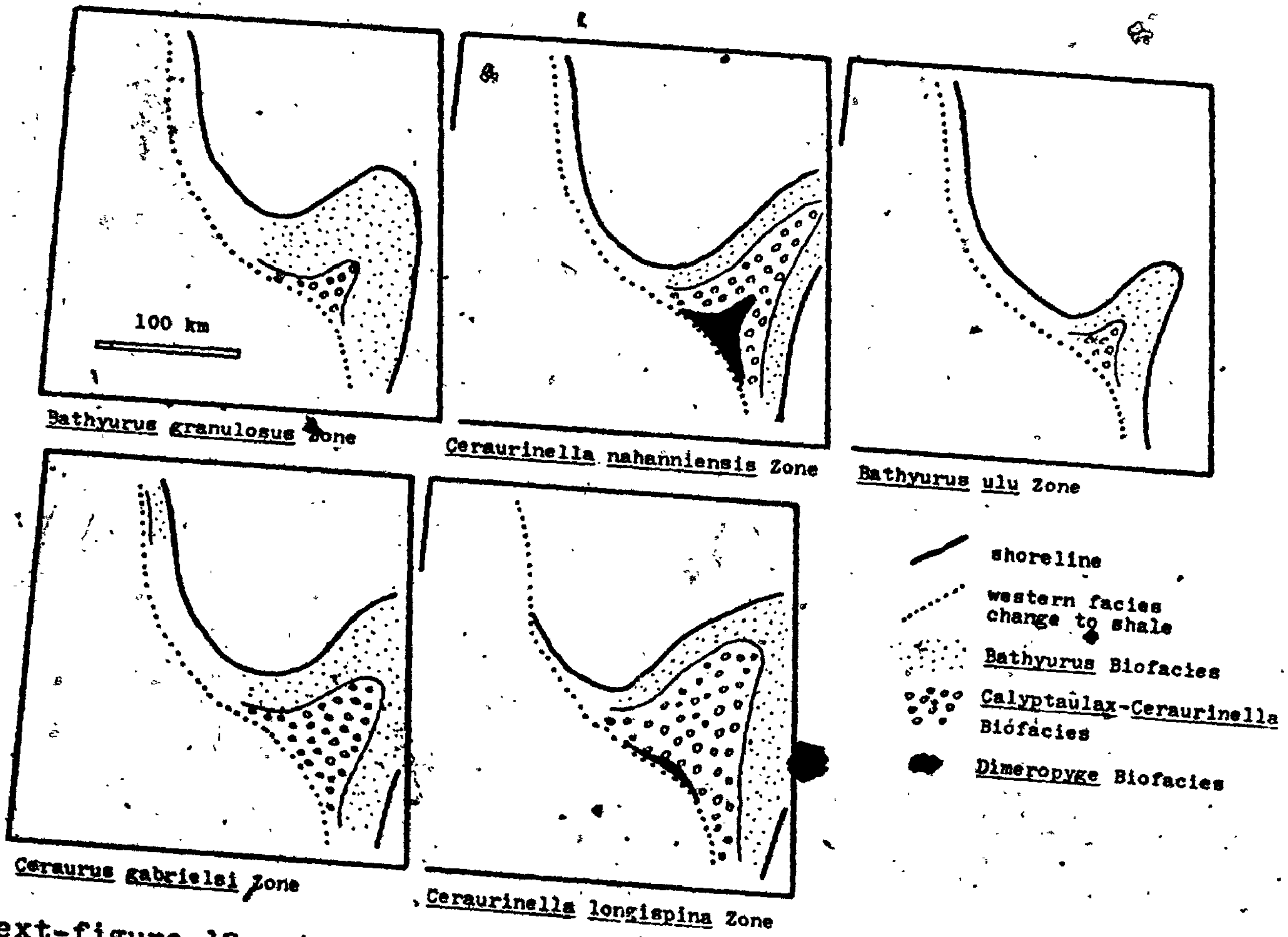
LOWER WHITTAKER FORMATION
(Kirkfieldian to Edenian)

Text-figure 16.

Schematic distribution of biofacies in the Esbataottine and lower Whittaker Formations. Rough lithologic symbols denote thin bedded limestone, heavy bedded limestone and dolostone, and shale.

the trilobites from the *Dimeropyge* Biofacies, their spinose character, or their possession of specialized adaptations that prevent sinking. A very soft to, possibly, fluid substrate and a quiet environment for the *Dimeropyge* Biofacies would also explain the virtual exclusion of definite suspension feeders, such as brachiopods, whose feeding largely depends on water movement. The same reasoning could apply to the faunas of the *Calyptaulax*-*Ceraurinella* Biofacies, but this biofacies probably existed over a more extensive and more differentiated habitat than did the *Dimeropyge* Biofacies. The *Calyptaulax*-*Ceraurinella* Biofacies contains an appreciable number of suspension feeders, including locally abundant ramose bryozoans and pedunculate and free-lying brachiopods. That a very soft substrate may have been present within this biofacies is shown by locally common ?*Macrocoelia*, a thin-shelled strophomenid brachiopod with a high surface area to volume ratio and *Onychoplesia*, a tiny and very thin-shelled triplesiid brachiopod. These brachiopods occur with a diverse trilobite fauna, but without associated brachiopods. The substrate that houses the two shoreward biofacies may have been firm to soft; sufficiently firm to support locally abundant nests of such thick-shelled pedunculate brachiopods as *Mimella* and *Camerella*.

The composition of faunas existing at the platform edge in shales of the Road River Formation in the Chazyan to Blackriveran interval is not known, but it may be surmised from the composition of deep water faunas from older and younger intervals in the same area. A fauna of Arenigian age from the lower part of the Sunblood Formation at the confluence of the Flat and Caribou Rivers, south of Sunblood Mountain, is composed of *Shumardia*, *Nileus*, ?*Ampyxina*, and graptolites (Lenz and Jackson, 1964, p. 894). Faunas of Trentonian age from the base of the Road River Formation at Sections A and G and at locality 8 (Text-fig. 1) include *Cryptolithus*, *Cryptolithoides*, *Anataphrus*, *Ampyxina*, *Triarthrus*, *Robergiella*, and graptolites (*Cryptolithus*-*Anataphrus* fauna, Ludvigsen, 1975, Pl. 5, figs. 19-32). The Arenigian and Trentonian faunas are similar to each other and it is likely that the Chazyan-Blackriveran interval of a deeper water habitat than the *Dimeropyge* Biofacies would also be dominated by a trinucleid, olenid, and graptolite association. These faunas differ considerably from their shallower counterparts higher on the platform in including a number of trilobites that either lack or have degenerate eyes. Those on the platform possess normal eyes. It is difficult to assess the significance of blind or reduced vision trilobites in terms of water depth because of the lack of knowledge about the turbidity of the water and of the light sensitivity of the trilobite eye. If the depth range of extant marine crustaceans with degenerate eyes (Clarkson, 1967) is analogous to that of blind trilobites, an order-of-magnitude depth of a few hundred meters may be suggested for the trinucleid-olenid-graptolite associations in the South Nahanni River area of Arenigian to Trentonian



Bathyurus granulosus Zone

Ceraurinella nahanniensis Zone

Bathyurus ulu Zone

Ceraurus gabrielsi Zone

Ceraurinella longispina Zone

Text-figure 17.

Possible distribution of trilobite biofacies at five successive zonal intervals from the upper Sunblood Formation and Esbataottine Formation (early Chazyan to Blackriveran/Rocklandian). Individual maps cover the same area as Text-figure 1.

age.

The basal Trentonian transgression resulted in considerable reorganization of litho- and biofacies within the study area (Ludvigsen, 1975, Fig. 10-4 to 6; this thesis, Text-fig. 16 a, b). A well-bedded dolostone facies carrying a shallow water and low diversity brachiopod-mollusk-algal-pelmatozoan association (*Hesperorthis*-*Oepikina* fauna, Ludvigsen, 1975) became established along the western edge of the southern extension of the Redstone Arch. The Redstone Arch was flooded and was colonized by a newly-introduced coral-brachiopod-mollusk association (*Bighornia*-*Thaerodonta* fauna) that, apparently, displaced the *Bathyurus* Biofacies. The deeper parts of the Root Basin supported a trilobite-strophomenid brachiopod association (*Calyptaulax*-*Ceraurinella*-*Dimeropyge* Biofacies) on a soft, carbonate mud base. This biofacies appears to be a continuation of the two deeper trilobite biofacies of the Chazyan-Blackriveran interval. The *Cryptolithus*-*Anataphrus* fauna occurs in deeper water shales and black limestones, seaward of the *Hesperorthis*-*Oepikina* fauna and gradually transgresses eastward. Based on regional stratigraphic relationships, trilobite biostratigraphy and limited conodont and graptolite information (summarized elsewhere in this thesis and in Ludvigsen, 1975); the trilobite zones comprising the *Calyptaulax*-*Ceraurinella*-*Dimeropyge* Biofacies, the *Cryptolithus*-*Anataphrus* fauna, the *Hesperorthis*-*Oepikina* fauna, and the *Bighornia*-*Thaerodonta* fauna are concluded to be, at least in part, correlative.

The species diversity curve of trilobite collections from the Bathyurus granulosus Zone to the Ceraurinella longispina Zone at Section P is roughly parallel to the biofacies curve (and to the derived depth curve, Text-fig, 14). That is, the deeper and environmentally stable biofacies are more diverse than the shallower and environmentally unstable biofacies. This is in full agreement with diversity patterns of extant marine benthos (Sanders, 1968, Fig. 6; Valentine, 1971, Fig. 1). The trilobite density curve is also approximately parallel with the biofacies curve and the species diversity curve -- an apparent point of variance with modern ecologic theory which predicts low populations in stable environments and high populations in unstable environments (Bretsky and Lorenz, 1970). However, the assumption that the number of individuals per unit of limestone is a measure of species density may be open to question because it assumes a constant depositional rate. There is evidence that some of the collections showing high "densities" were accumulated rather slowly. These collections (P 1485, P 1497, P 1512, P 2050) were etched from limestones with a high proportion of mud and these presumably reflect lower depositional rates than the less argillaceous limestones yielding many of the "less dense" collections (assuming that the supply of mud was constant!).

Previous studies of trilobite biofacies

In recent years a number of community studies of Lower Paleozoic benthos have greatly increased our understanding of the distribution and spatial relationships of these fossil faunas. With few exceptions, these studies have concentrated on the filter feeders -- the attached or free-lying epifauna (mainly brachiopods, pelmatozoans, bryozoans, and coelenterates) and shallow infauna (mainly bivalve mollusks) on a clastic base (Ziegler et al., 1968; Bretsky, 1970; Thayer, 1974; among many others). In most of these studies, the vagrant benthos (mainly deposit feeders) form a rather inconspicuous part of the biomass and is only treated as a side issue. Trilobites assume a dominant position in only a few environmental settings and these have, hitherto, escaped concise synthesis.

The few studies that have dealt with faunas which consist largely of trilobites, or that have dealt exclusively with the trilobites of diverse faunas, involve families that are poorly represented in the faunas studied herein (that is; olenids, Wilson, 1957, Henningsmoen, 1957; agnostids, Jago, 1973; trinucleids, Cisne, 1973; and proetids, Cisne, 1971) and are of limited usefulness in clarifying the present faunas.

One Lower Paleozoic type of environment in which relatively consistent associations of trilobite taxa have been noted is that of an organic reef. These trilobite faunas consist mainly of illaenids, scutelluids, cheirurids, harpids, and lichids -- commonly of very large size -- and occur in the Middle Ordovician (Whittington, 1965a; Shaw, 1968; Ross, 1972), Upper Ordovician (Warburg, 1925; Dean, 1971a), Silurian (Lane, 1972), and Devonian (Lane, 1972). Although useful taxonomic comparisons can be made with some of these faunas, notably with those of the Chazy Group (Shaw, 1968) and the Chair of Kildare Limestone (Dean, 1971a); the taxa that apparently characterize the reef habitats are, with few exceptions, minor constituents of the trilobite faunas under study; an observation consistent with the absence of reef limestone with the upper Sunblood and Esbataottine Formations. The similarity in composition between some of the biofacies outlined in this thesis and those of the off-reef beds of the Chazy Group (especially the silicified faunas from Shaw's Section PB) require comment. These collections came from dark grey-black limestone and laminated limestone (Shaw, 1968, p. 105) and contain virtually all of the genera herein considered diagnostic of the Calyptaulax-Ceraurinella and Dimeropyge Biofacies. These limestones could not have been deposited in very deep water. Pitcher (1964) suggested that the Chazy reefs developed in water depths of less than 10 meters. The Nahanni trilobite biofacies were probably appreciably deeper, in that they occur on the outer portion of a wide platform that shows no evidence of restricted circulation. This suggests that the controlling mechanism for the distribution of these faunas were substrate grain size rather than water depth.

Other lithosomes that have yielded diverse and abundant trilobites, in addition to other fauna, are those composed of thin to rubbly bedded argillaceous limestones and shales that represent soft bottom, muddy, and quiet environments. These are fairly common habitats - occurring from a probable intertidal zone to deeper platform and still deeper slope and rise environments - and are the optimum sites for parallel community development. The present biofacies scheme is the only attempt to treat the trilobites of these environments in a paleoecologic context.

Even though trilobites of level bottom communities have not been subjected to rigorous paleoecologic analysis, the constituent taxa of most of these are well known and may be compiled from faunal lists in a number of taxonomic monographs, (for example, Antelope Valley Limestone, Ross, 1967, 1970; Lincolnshire, Edinburg, Oranda; Martinsburg Formations, Whittington, 1959; Bromide Formation, Shaw, 1974; Kimmswick Limestone, Bradley, 1930; Maquoketa Formation, Slocum, 1913; Copenhagen Formation, Ross and Shaw, 1972; Saturday Mountain Formation, Churkin, 1963). In the absence of quantitative data on the occurrences of these trilobites - either of a sequential nature from measured sections or from numerous spot localities - it seems of little value to compare closely the present trilobite biofacies to other potentially identical, similar, or analagous biofacies in other parts of North America.

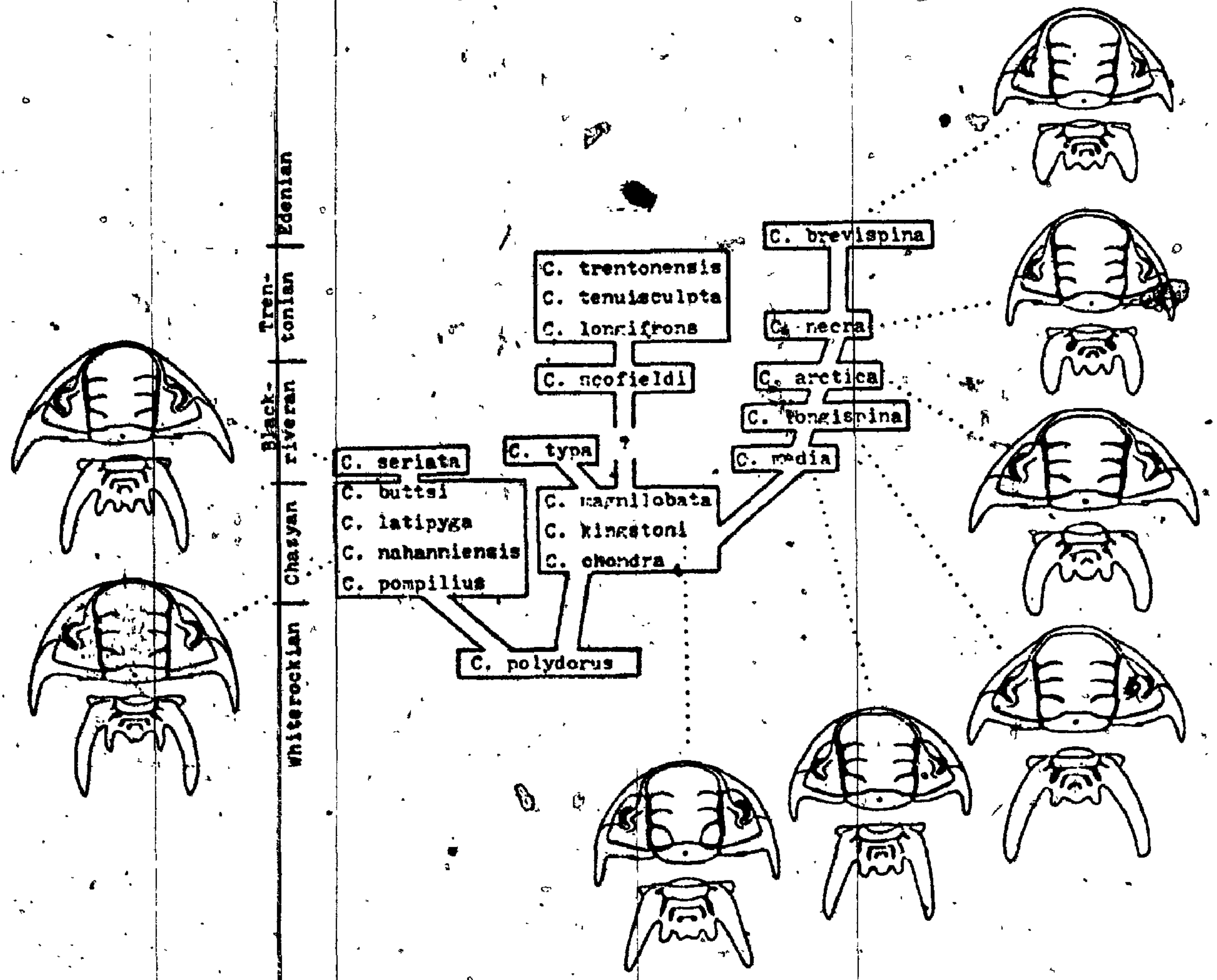
PHYLOGENY OF SELECTED GENERA

Ceraurinella

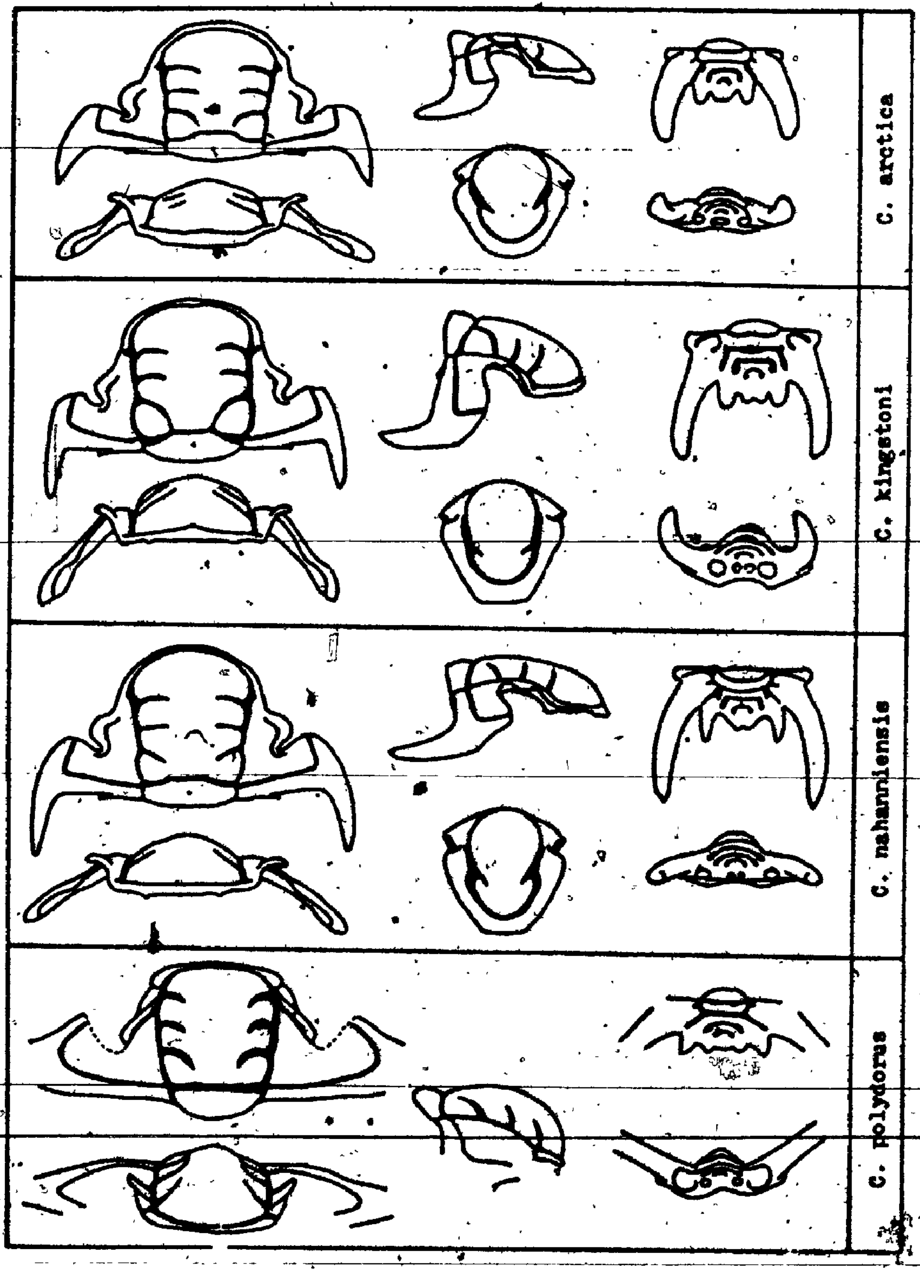
The Esbataottine to Whittaker succession contains eight species of Ceraurinella whose morphology, relative stratigraphic position, and ages are clarified in this thesis. It is now possible to suggest sequential relationship between many of these species and to relate this phylogeny to other species. Except for a few of Chazyan age (C. chondra Whittington and Evitt, C. latipyga Shaw) and Blackriveran age (C. typa Cooper) from eastern North America, species of Ceraurinella outside the study area are incompletely known and their stratigraphic position often uncertain.

Text-figure 19 compares the cranidial, pygidial, and hypostomal morphology of four representative species of Ceraurinella and Text-figure 18 shows the inferred phylogenetic relationship of North American species of Ceraurinella.

The oldest species from North America, Ceraurinella polydorus (Billings), from the Whiterockian of Newfoundland displays certain features not seen in later species (barrel-shaped glabellar outline, short anterior glabellar lobes, markedly curved and deep lateral glabellar furrows, deep and long palpebral furrows, erect and widely-divergent



Text-figure 18. Inferred phylogeny of species of Ceraurinella from North America. Outline drawings of cephala and pygidia of species occurring in the South Nahanni River area are included.



Text-figure 19.

Outline drawings of cranidia, pygidia, and hypostomes of four representative species of *Ceraurinella* from North America.

first pygidial spines, and widely separated third spines). The pygidial similarities between this species and *C. kingstoni* Chatterton and Ludvigsen from the Nahanni area are informative (compare Whittington, 1965a, Pl. 60, figs. 8-10 and this thesis, Pl. 6, figs. 13-15) and is the basis for a postulated ancestor-descendant relationship of the two species. The cranidia of these species are rather different, but this difference is one of degree and does not negate the presumed phylogenetic connection.

Ceraurinella kingstoni, *C. chondra* from Virginia, and *C. magnilobata* Tripp from Scotland (and, possibly, *Ceraurinella* sp. from Wales; Bates, 1968) belong in a species group of Chazyan age characterized by highly vaulted cephala and glabellae, isolated lp lobes, small palpebral lobes, stout and divergent first pygidial spines followed by two pairs of short and blunt spines. *C. typa* from Virginia and *C. media* n. sp. from the Nahanni area are of Blackriveran age and appear to have been derived from the Chazyan species group. *C. typa* differs by its tuberculose ornament and larger palpebral lobes and *C. media* by its slightly larger palpebral lobes, less vaulted cephalon, non-isolated lp lobes, and in possessing only five pygidial spines (the posterior pair having merged into a single median spine).

A second species group of *Ceraurinella* of Chazyan age includes *C. nahanniensis* Chatterton and Ludvigsen from the Nahanni area and three, possibly conspecific, species from the Appalachians - *C. latipyga*, *C. pompilius* (Billings), and *C. buttsi* Cooper. Also included in this group is a single species, *C. seriata* n. sp., from the Blackriveran of the Nahanni area. These species are united by their gently arched cephalon, rather faintly incised glabellar furrows, flattened genal spines, and first pygidial spines that are long, curved, gradually tapering and, basally, are aligned in the same plane as the posterior spine pairs.

The youngest group recognized in the Nahanni area comprises four successive species, *Ceraurinella longispina* n. sp., *C. arctica* n. sp., *C. necra* n. sp., and *C. brevispina* n. sp., of Blackriveran to Edenian age. This group can be related to the Chazyan group of *C. kingstoni* by a morphological and temporal intermediate, *C. media*. The younger group is united by rather flat glabellae and gently arched cephala, expanded anterior cranidial borders caused by the forward and downward migration of the rostral sutures, and pygidia with five marginal spines that are flattened in cross-section. This group can, in turn, be divided into an older group (*C. longispina*, *C. arctica*) possessing essentially parallel-sided glabellae, pre-glabellar furrows that are straight medially, large palpebral lobes, broad cheeks, and pygidia with long first spines that are diverging and markedly upturned; and a younger group (*C. necra*, *C. brevispina*) possessing slightly forwardly expanding glabellae, inflated lp lobes, evenly curved pre-glabellar furrows, small palpebral lobes, narrower cheeks, and pygidia with short first spines that diverge only slightly and are only faintly upturned. The pygidia of this group of Ceraurinella are particularly well-suited for statistical and co-ordinate analysis (Text-figs. 20 and 21). These analyses indicate that the four species are connected in a graded phylogenetic series whose components can be identified by the length and orientation of the first pygidial spine. These species possess pygidia that show a gradual decrease in the length of the first spine and a gradual co-alignment of the first spines to each other and with the posterior three spines. The earlier species have long first spines that are oriented obliquely outward and upward and the later species possess short first spines that are directed nearly straight backward. At the same time, the posterior spine of each successive species becomes narrower until, in the Edenian interval (Pl. 11, figs. 41, 43), it is the same size as the second spines. The gradualism of pygidial morphology is well seen in Text-figure 21. This diagram is based on the principles of co-ordinate transformation (Thompson, 1917) and, briefly, shows that a rectangle of width to length ratio of 3/2 superimposed on the C. longispina pygidium becomes deformed into a semi-ellipse with length of minor axis to 1/2 length of major axis ratio of 3/1.8 on the C. brevispina pygidium. The decrease in areas of the superimposed figures indicates progressively more compact pygidia; changes that are duplicated on the cephalon and shown by the narrower cheeks and shorter genal spines of the two youngest species.

1

Text-figure 20.

Scatter diagram and reduced major axes of four species of *Ceraurinella* - *C. longispina* n. sp. (●), *C. arctica* n. sp. (x), *C. necra* n. sp. (o), and *C. brevispina* n. sp. (△) - relating width of pygidium at anterior margin to maximum length of first pygidial spine. Outline drawings based on specimens oriented to display maximum spine length. Reduced major axes computed in micrometer units (10 units equals one millimeter). Statistical parameters and formulae for reduced major axes are given below:

N	sample number
$\bar{w}$, $\bar{l}$	average width, length
S_w, S_l	standard deviation
r	correlation coefficient

C. longispina $N = 95$ $\bar{w} = 25.6$ $S_w = 14.86$ $r = .9774$
$\bar{l} = 26.2$ $S_l = 15.56$

$y = 1.048x - .62$

C. arctica $N = 58$ $\bar{w} = 28.5$ $S_w = 11.88$ $r = .9700$
$\bar{l} = 24.6$ $S_l = 9.35$

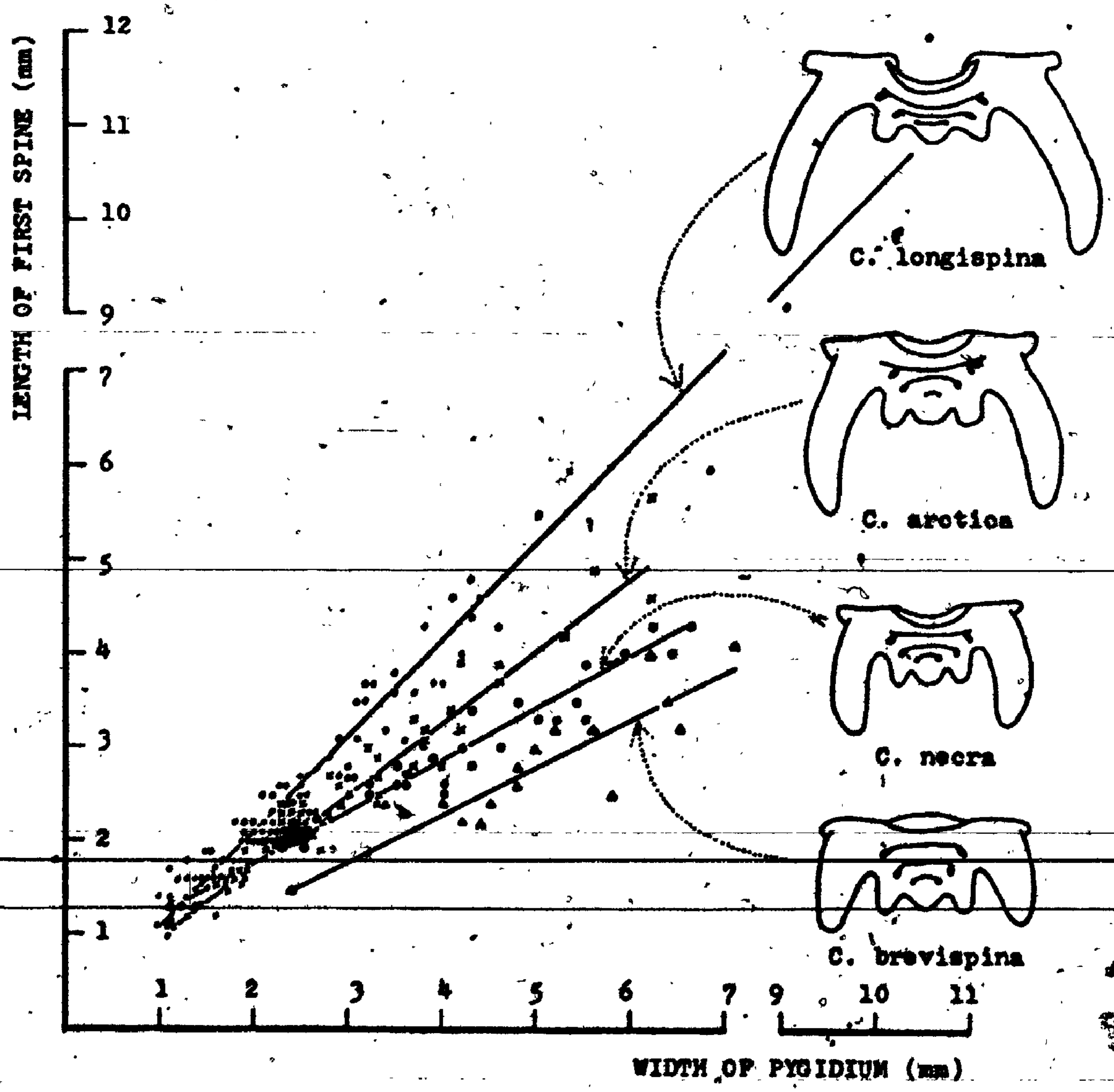
$y = .79x + 2.08$

C. necra $N = 27$ $\bar{w} = 42.6$ $S_w = 12.86$ $r = .9928$
$\bar{l} = 30.1$ $S_l = 7.19$

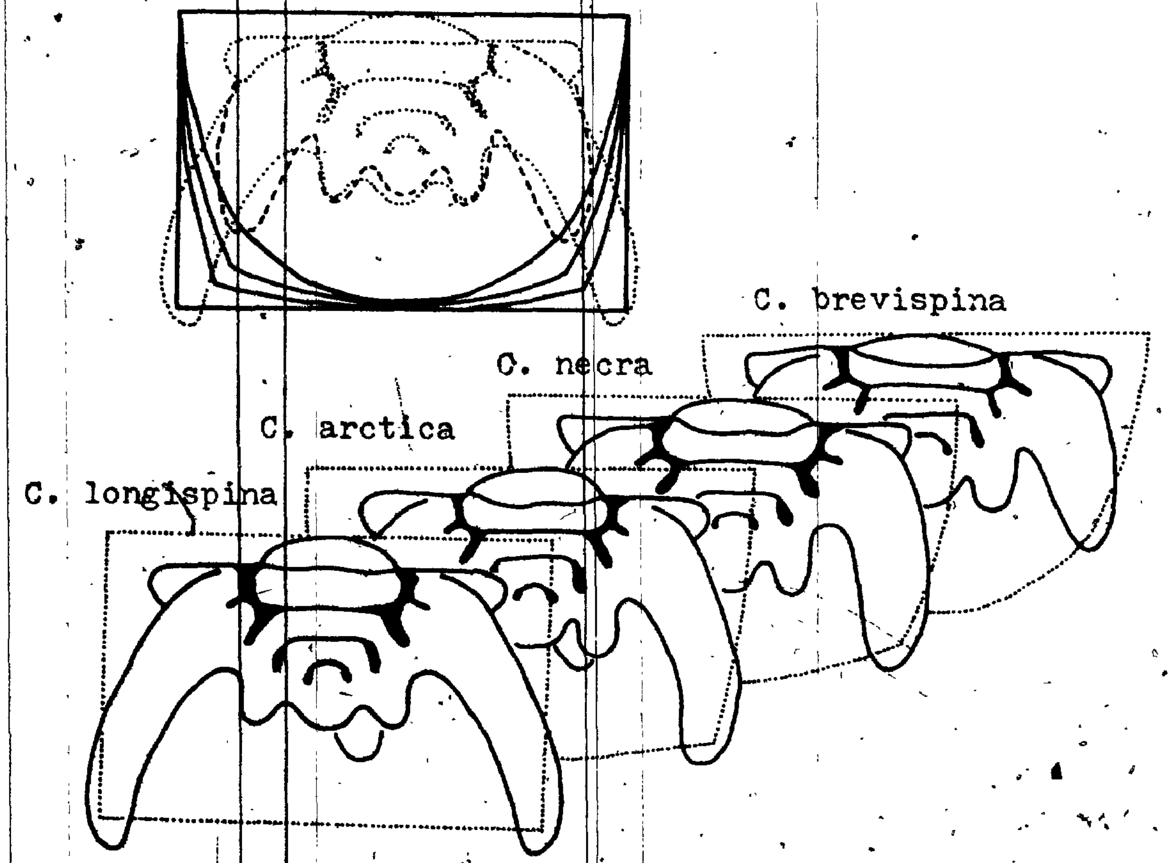
$y = .558x + 6.28$

C. brevispina $N = 17$ $\bar{w} = 49.37$ $S_w = 12.39$ $r = .9574$
$\bar{l} = 28.00$ $S_l = 6.47$

$y = .52$[illegible] $+ 2.23$



Text-figure 20.



Text-figure 21. Co-ordinate deformation of pygidia of Ceraurinella arctica n. sp., C. necra n. sp., and C. brevispina n. sp. relative to pygidium of C. longispina n. sp. Outline drawings based on specimens in true dorsal view.

The species group of *Ceraurinella* (demarcated by *C. longispina* and *C. brevispina*) is difficult to relate to a contemporaneous species group from eastern North America which includes *C. scofieldi* (Clarke) of Blackriveran age and *C. trentonensis* (Barton), *C. tenuisculpta* (Bradley), and *C. longifrons* (Troedsson) of Trentonian age. These species possess parallel-sided glabellae, deep and oblique 1s furrows, faint 2s and 3s furrows, inflated 1p lobes, and small palpebral lobes. Only the pygidium of *C. scofieldi* is known. This has a pair of long and curving first spines followed by two (?) pairs of smaller spines. These species do not recall those of the *C. longispina*/*C. brevispina* lineage, but instead appear similar to earlier Chazyan species (*C. kingstoni*, *C. magnilobata*) and may have been derived from this group.

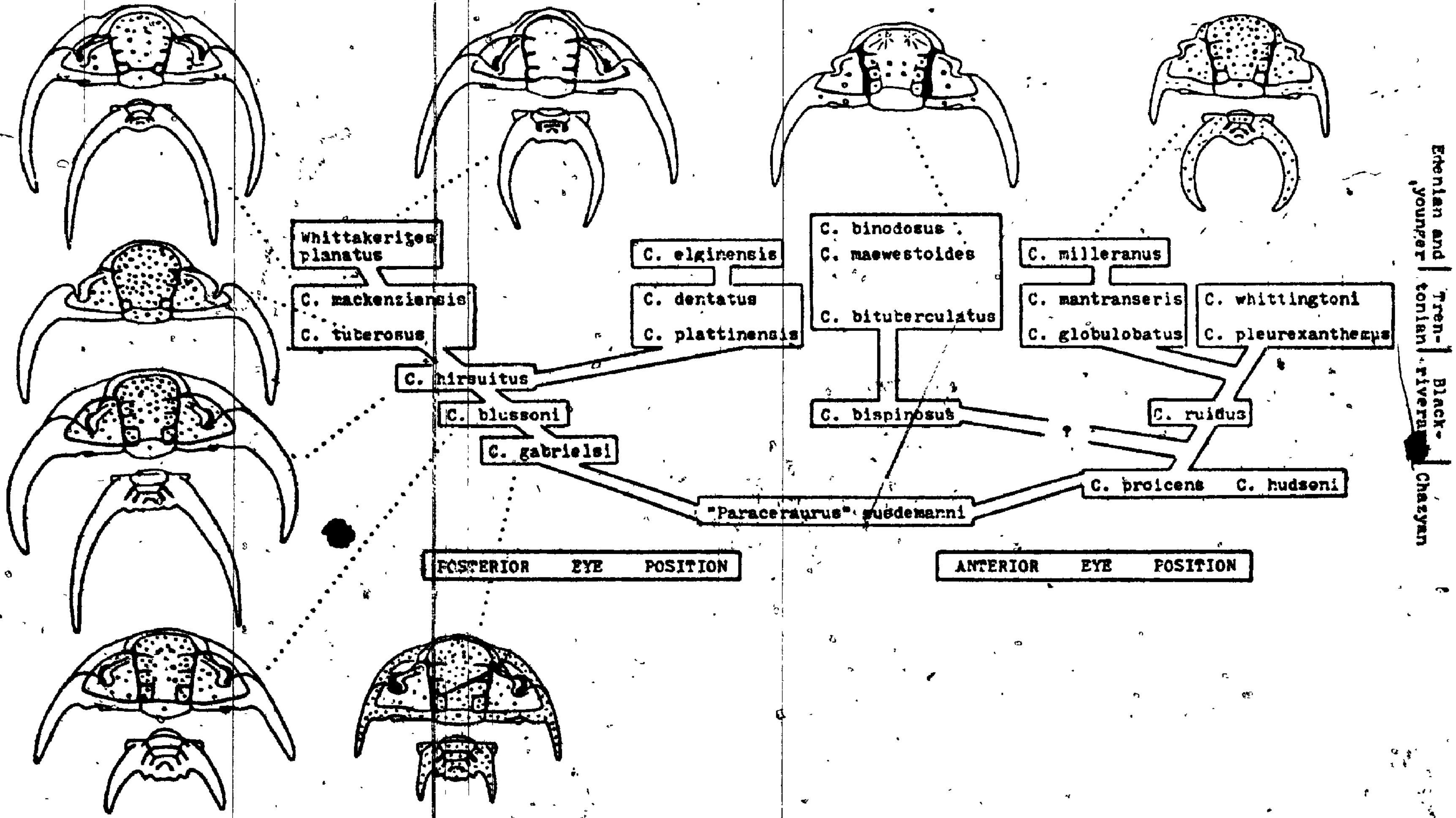
Lane (1971, p. 71-81) has succinctly treated the phylogeny of most of the known cheirurid genera. His conclusion about the phylogeny of *Ceraurinella*, however, demands revision in light of the discovery of the *C. longispina*/*C. brevispina* lineage in northern Canada. He stated (p. 77) that *Ceraurinella* shows "a progressive incorporation of the anterior border and border furrow into the frontal lobe of the glabella....and a gradual reduction and final loss of the posterier two pairs of pygidial spines". The delimitation of these trends appears to be based on Lane's choice of and members; that is, *C. ingrica* (Schmidt) and *C. polydorus* (Billings) from the late Arenigian and

Llanvirnian and *C. intermedia* (Kielan, 1955) from the Ashgillian; and not on an evaluation of the intermediate species from the Middle Ordovician. The present investigation concludes that the expansion of the frontal lobe of the glabella was completed early in the history of *Ceraurinella* (between the Whiterockian and Chazyan) and that further cranidial modification (between the Chazyan and Trentonian) includes a secondary *expansion* of the anterior border due to a forward and downward migration of the rostral suture. The acceptance of "*Ceraurus*" *intermedius* Kielan as a species of *Ceraurinella* by Lane essentially demanded that he describe the change in pygidial morphology as a reduction and loss of the posterior two pairs of spines. Reasons for the exclusion of "*C.*" *intermedius* from *Ceraurinella* will be given later and need not be repeated here. Assessment of the additional eight species described in this thesis presents a materially different picture of the phylogenetic trends within *Ceraurinella* than those suggested by Lane (1971). These trends have been outlined above and are summarized on Text-figure 18.

In the Nahanni area, and probably in other areas as well, *Ceraurinella* persisted within a moderately deep water and soft bottom environment for its total range. Species of *Ceraurinella* reached their ecologic acme within the *Calyptaulax*-*Ceraurinella* Biofacies and, generally, constitute one of the two prevalent species of this biofacies. The deeper *Dimeropyge* Biofacies contain sparse *Ceraurinella* specimens and the genus is absent from the shallow Bathyurus Biofacies. However, transitional biofacies are common and considerable mixing may occur. Within the Chazyan to Rocklandian interval, Ceraurinella often constitutes more than half of the trilobite specimens in a collection from the Calyptaulax-Ceraurinella Biofacies. Within the Kirkfieldian to Edenian interval, however, Ceraurinella is much rarer; in large collections from the undifferentiated Calyptaulax-Ceraurinella-Dimeropyge Biofacies, Ceraurinella rarely constitutes more than a tenth of the total trilobite fauna.

Ceraurus

Numerous species of Ceraurus have been described from Middle and Upper Ordovician strata of North America. These display considerable morphological variation and this variation, coupled with the incomplete knowledge about the total morphology of many of the species make phylogenetic conclusions rather difficult. Text-figure 22 is an attempt at relating about twenty of these species of Chazyan to Richmondian age in North America. A number of questions are left unanswered by this scheme, especially concerning the relationship of the eastern North American species of which I have little direct knowledge. The chart was constructed on the assumption that a single feature, that of eye position, would remain relatively constant, or show only slight change, in descendant species. A lit-



Text-figure 22. Inferred phylogeny of species of Ceraurus from North America (including "Paraceraurus" ruedemanni and Whittakerites planatus). Outline drawings of cephala and pygidia of species occurring in the South Nahanni River area are included.

erature search has indicated that this assumption is, at least, reasonable.

In the Nahanni area, the first appearance of *Ceraurus* within the zonal scheme is at the base of the *Ceraurus gabrielsi* Zone (Blackriveran). The pioneer species, *C. gabrielsi* n. sp., differs considerably from the type species, *C. pleurexanthemus* Green, in possessing pervasive ornament of spike-like tubercles, a faintly vaulted glabella, wide (tr.) lateral glabellar furrows, short (exsag.) palpebral lobes located opposite or slightly behind 2s furrows, and a wide pygidium with short and backwardly directed first spines. High in the *C. gabrielsi* Zone occurs a derivative species of *C. gabrielsi*, *C. blussoni* n. sp., in which the tubercles on the cephalic border and pygidium are supplanted by fine granules and the genal and pygidial spines are longer and flaring. Still higher in the succession, in the following zone, occurs *C. hirsuitus* n. sp., in which the granules on the cephalic borders and pygidium are replaced by fine hair-like spines and the genal and pygidial spines are very long, stout, and curving. These three species occur in the Blackriveran to Rocklandian interval in the Nahanni area and constitute a graded series. The eyes of these species are opposite or slightly behind the 2s furrow, the glabellae are sub-rectangular in outline, and the lateral glabellar furrows are broad (tr.). The replacement of coarse ornament by fine ornament on the borders of these species and the gradual lengthening of the genal and first pygidial spines is significant because it coincides with a habitat shift from the shallow *Bathyurus* Biofacies (*C. gabrielsi*) to the deeper *Calyptaulax*-*Ceraurinella* Biofacies (*C. blussoni*, *C. hirsuitus*, and all younger species of *Ceraurus* in the Nahanni area). The long genal and pygidial spines are probably an adaptation to cope with life on a soft to, possibly, fluid substrate.

Ceraurus hirsuitus is followed by two species in succession, *C. tuberosus* Troedsson and *C. mackenziensis* n. sp. of Rocklandian to Shermanian age. These species maintain the gross morphology of the parent species with a few modifications; the glabellae become strongly forwardly expanding, the glabellar furrows narrower (tr.), the palpebral lobes longer (exsag.), and the tuberculose ornament sparser. In the last species of the lineage, *Whittakerites planatus* n. sp. of Shermanian or Edenian age, the tuberculose ornament has completely disappeared, the glabella is gently vaulted and expands only slightly forwards, the glabellar furrows wider (tr.), and the eyes are shifted posteriorly to opposite 1s furrow.

The five species of *Ceraurus* and the single of *Whittakerites* from the Nahanni area are considered a graded morphologic series and their stratigraphic positions strongly suggest that it constitutes a phylogenetic series. This series sees a lengthening of genal and first pygidial spines, a shortening and complete disappearance of the posterior pygidial spine pairs, and changes in ornament from spike-like tubercles to sparser tubercles and a total effacement of tubercles. Throughout this series, the eye remains in a position opposite or posterior to 2s furrow.

If the eastern North American species of Ceraurus are considered, a slightly different picture emerges. Ceraurus makes its appearance considerably earlier here than in the Nahanni area. Already by the Chazyan, two "kinds" are present - "Paraceraurus" ruedemanni (Raymond) and Ceraurus hudsoni Raymond, both occurring in the Chazy Group. The provenance of these species within the Chazy Group is important because it provides additional evidence of a correlation between morphology and habitat preference of these and similar species. According to Shaw (1968, p. 72), "P." ruedemanni and C. hudsoni have not been collected from the same locality. The former is restricted to reef limestones of the Valcour Formation and the latter to off-reef silty limestones and calcarenites of the Crown Point and Valcour Formations. "P." ruedemanni is similar to the slightly younger C. gabrielsi from the Nahanni area from which it differs by its longitudinal glabellar furrows and its unique pygidium with elongate second spines. Both species appear to be restricted to a shallow habitat. By contrast, C. hudsoni possesses very long genal spines (the pygidium of this species has not been found, but the first pygidial spines are presumably of similar length as the genal spines, in view of the close size correspondance in other species of Ceraurus); is similar to both the younger C. hirsuitus and subsequent species from the Nahanni area and to the younger *C. ruidus* Cooper and subsequent species from eastern North America. All of these species appear to be components of biofacies that occupied deeper, and probably softer substrate, habitats than those occupied by "*P.*" *ruedemanni* and *C. gabrielsi*. This is demonstrable in the Nahanni area and is probably the case in eastern North America.

In the Nahanni area, the morphological shift evident in the *C. gabrielsi* to *C. hirsuitus* lineage corresponds to a biofacies shift of these species from the *Bathyurus* to the *Calyptaulax*-*Ceraurinella* Biofacies in the late Blackriveran to Rocklandian interval. An analogous morphological and habitat shift, predating the one from the Nahanni area, probably occurred in eastern North America during the Chazyan.

Ceraurus ruidus Cooper, *C. whittingtoni* Evitt, and *C. pleurexanthemus* Green appears in Blackriveran and Trentonian strata of eastern North America. These species are similar to each other and to *C. hudsoni* (Shaw, 1974, p. 29, 30); and also to the contemporary lineage, *C. hirsuitus* to *C. mackenziensis* of the Nahanni area. The eastern species group differs from the Nahanni species group, principally, in having the eyes located in front of 2s furrow and in possessing small palpebral lobes.

Another eastern group of Trentonian age, consisting of *Ceraurus globulobatus* Bradley and *C. mantranseris* Sinclair, and characterized by markedly forwardly expanding glabellae of moderate convexity, probably shared a common ancestry with C. pleurexanthemus and, indeed, can only be distinguished from this species with difficulty. The Edenian and younger species, C. milleranus Miller and Gurley, show particular affinity with C. mantranseris. These species maintain the eye position opposite 3p lobe or, occasionally, opposite 3s furrow.

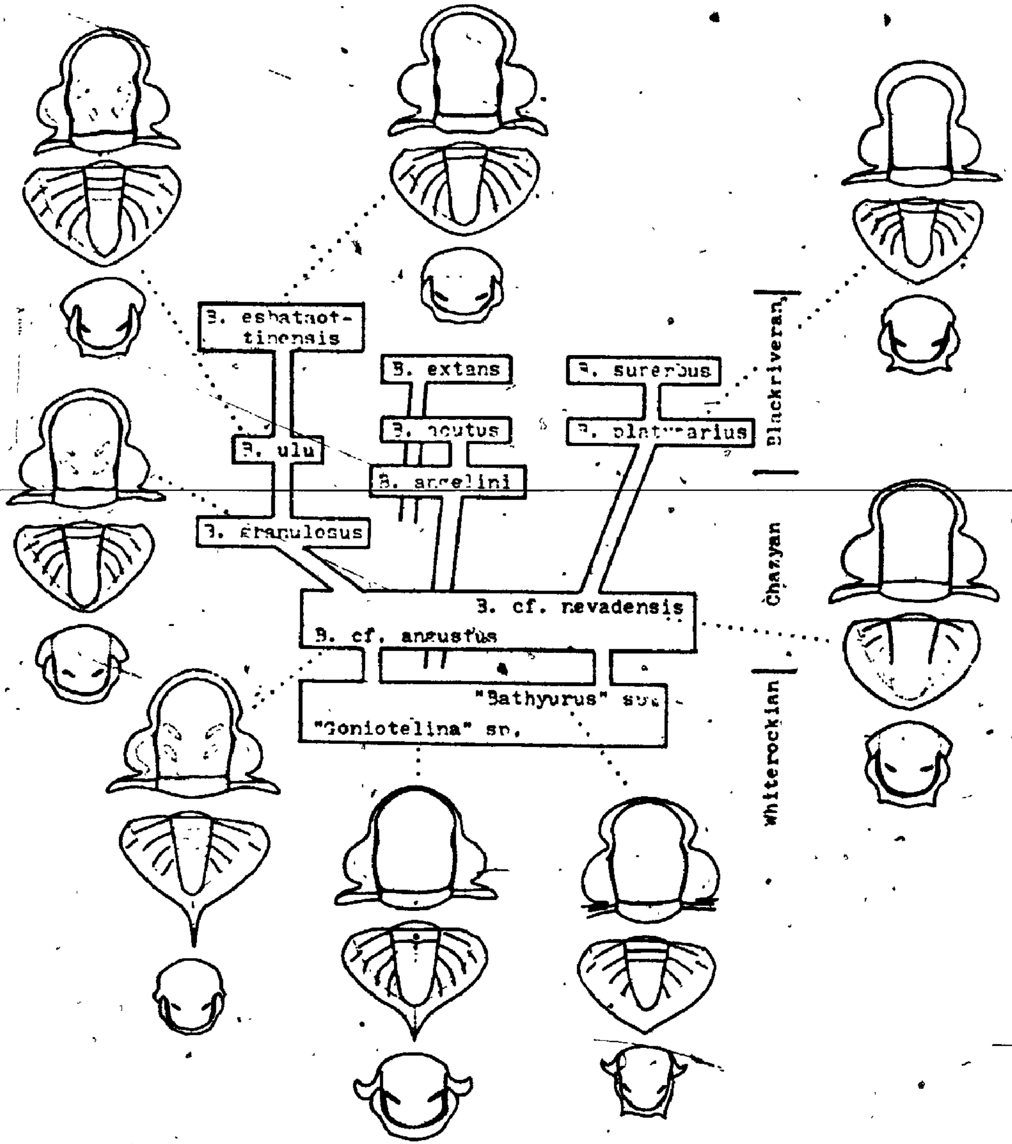
Three species, Ceraurus bispinosus Raymond and Barton, C. bituberculatus Troedsson, and C. binodosus Cooper and Kindle, each characterized by a pair of mammaliate swellings on the anterior glabellar lobe, occurs in the Blackriveran to Richmondian interval of eastern North America and Greenland. These species have eyes placed well forward, opposite 3p lobe or 3s furrow, and were probably derived from C. ruidus or a similar eastern species.

In conclusion, the bulk of Trentonian and younger species of Ceraurus (and Whittakerites) from the Nahanni area and from eastern North America are generally similar in most features, but differ consistently in the placement of the eye - the northern species group has eyes opposite or behind 2s furrow while the eastern species group has eyes opposite or in front of 3p lobe. The occurrence of "out of place" species in either area can be explained by a breakdown of isolation following the extensive Trentonian transgression. An example is the presence, in the Trenton Group and its correlatives, of Ceraurus dentatus Raymond and Barton whose eye position and other features indicate a derivation from *C. hirsuitus* from the Nahanni area. Other examples are the presence of *C. milleranus* and *C. maewestoides* n. sp. in the Edenian of the Nahanni area. The history of these two species lies with species of the eastern group.

The difference between the northern species group and the eastern species group reflects either a separate post-Chazyan evolutionary history of these two groups (as suggested on Text-fig. 22) or the presence of a single evolving species complex of *Ceraurus* during the Middle Ordovician; the extremities of which (northern Canada and eastern North America) may be reproductively isolated from each other even though they were connected by a chain of interbreeding populations. The absence of information on species from intermediate areas precludes a statement as to which isolating mechanism was operative; but in support of the first possibility, one may cite the presence of geographically extensive quartzite units of Middle Ordovician age in western United States and south-western Canada. These represent clean sand bottom habitats that must have been inimical to these trilobites.

Bathyurus

The previous lack of knowledge about the temporal relationship of species of *Bathyurus* has rendered phylogenetic considerations pointless. As a result of the present work, the range of the genus is extended downward to



Text-figure 23.

Inferred phylogeny of species of Bathyurus from North America. Outline drawings of cranidia, pygidia, and hypostomes of species occurring in the South Nahanni River area are included. Bathyurus cf. angustus, B. cf. nevadensis, "Goniotelina" sp. and "Bathyurus" sp. are based on undescribed material from the Sunblood Formation, Sunblood Range and Mary Range.

include the Chazyan, as well as the Blackriveran. Four new species of *Bathyurus* are described from the Chazyan to Blackriveran interval of the Nahanni area. These have well-defined ranges and, in one section, occur through nearly 300 m of strata. Brief consideration is also given to two additional species of *Bathyurus*, as yet undescribed, of early(?) Chazyan age that occur below those of Chazyan and Blackriveran age and to the probable root stock of the genus - the late Whiterockian "*Goniotelina*" and "*Bathyurus*".

Text-figure 23 shows an inferred phylogeny that includes most of the species of *Bathyurus* from North America and indicates a possible origin of the genus.

Bathyurid trilobites (among them, "*Bathyurus*" sp.," Ludvigsen, 1975, Pl. 1, figs. 15-17) that are very similar to *Bathyurus* are present in the *Orthidiella*-"*Goniotelina*" fauna in the Sunblood ~~Range.~~ These occur in collections that have yielded conodonts of Fauna 4 of Sweet *et al*., 1971 (Tipnis, personal communication, 1975). "*Bathyurus*" sp. differs from *Bathyurus extans* (Hall) in possessing a laterally-inflated glabella between the palpebral areas, strongly forwardly diverging anterior branches of the facial suture, and broad and flat pygidial borders. The hypostome has a pair of stout, postero-lateral spines and the anterior wings are strut-like, instead of plate-like as in species such as *B. ulu* and *B. esbataottinensis*. Aside from the hypostome, the morphology of "*Bathyurus*" sp. is not far removed from that of the type species of *Bathyurus* and it is essentially an arbitrary decision if it should be assigned to this genus.

"Goniotelina" sp. (Ludvigsen, 1975, Pl. 1, figs. 11-13) occurs at about the same level in the Sunblood Formation as "Bathyurus" sp. This species possesses glabellar ornament of small tubercles and granules of two size ranges, forwardly converging anterior branches of the facial suture, and a short posterior pygidial spine. It also has a small median occipital node and a tiny axial spine on each of the thoracic segments and on the anterior three or four axial rings of the pygidium. This species is clearly further removed morphologically from the type species of Bathyurus, but it does display similarities with species such as Bathyurus cf. angustus Ross, B. angelini Billings and B. acutus Raymond.

"Bathyurus" sp. and "Goniotelina" sp. of late Whiterockian age are considered the ancestors of Chazyan and Blackriveran species of Bathyurus. This suggestion implies a polyphyletic origin for Bathyurus.

The next interval in the Sunblood Formation contains two species of Bathyurus s.s.; that is, B. cf. angustus Ross and B. cf. nevadensis Ross. These species occur below the Bathyurus granulosus Zone with Fauna 5 conodonts of Sweet et al. (1971) that Tipnis interprets as early Chazyan in age. They are similar to B. angustus and B. nevadensis, respectively, which occur in the upper part of the Antelope Valley Limestone, Nevada and in the Kanosh and Lehman Formations, Utah. These species may be roughly the same age. The western United States occurrences were placed in the middle and upper part of the Anomalorthis Zone by Ross, 1970, p. 50 who suggested that this zone extends as high as the Blackriveran. The similarity of the Nevada/Utah species with those from the Sunblood Formation (which occur well below definite late Chazyan trilobites of the Ceraurinella nahanniensis Zone) would argue against an age younger than Chazyan for this part of the Anomalorthis Zone. The limited conodont evidence from the Anomalorthis Zone in Nevada and Utah (Sweet et al., 1971, p. 169; Hintze et al., 1972, p. 393) do not suggest ages younger than Fauna 4 or 5. Bergström et al. (1973) concluded that the upper part of the type Whiterockian is equivalent to the Chazyan, but is entirely older than the type Porterfieldian.

Bathyurus cf. angustus differs somewhat from "Goniotelina" sp. in possessing finer ornament, in lacking the tiny axial spines on the thorax and pygidium and the occipital node, in possessing faint lateral glabellar furrows, and in having a longer and more delicate posterior pygidial spine. These differences are mainly of degree as is evident in the outline drawings (Text-fig. 23).

Above Bathyurus cf. angustus, in Chazyan and Blackriveran strata, a derivative lineage is proposed that consists of B. granulosus n. sp., B. ulu n.sp., and B. esbataottinensis n. sp. The posterior pygidial spine has been lost in B. granulosus and the micro-sculpture is finely granulose - otherwise, this species is closely similar to *B*. cf. *angustus*. The differences between *B*. *granulosus*, *B*. *ulu*, and *B*. *esbataottinensis* are covered in the section on Systematic Paleontology. From a phylogenetic viewpoint, these differences are reflected in a change in micro-sculpture from granulose to scale-like, a slight forward migration of the palpebral areas, an effacement (in mature specimens) of the palpebral furrow, a change of gamma from obtuse to acute angle, and a relative increase in inflation of the glabella, especially of the anterior portion. The glabellar furrows increase in size and depth and, in the terminal species, appear to be secondarily reduced (Pl. 5, figs. 2-4). Minor changes are seen on the hypostomes and the pygidia (compare Plates 1, 2, and 3). This branch of the phylogenetic history extends from the early or middle Chazyan (*B*. *granulosus*) to late in the Blackriveran (*B*. *esbataottinensis*).

Bathyurus cf. *nevadensis* is an approximate contemporary of *B*. cf. *angustus*. It is characterized by a parallel-sided glabella that lacks any trace of glabellar furrows and which is covered by coarse and subdued granules. The palpebral furrows are not developed and gamma is ~~an~~ acute angle. The pygidium is semicircular in outline, the axis is high, axial furrows are not present, and the concave border is not crossed by furrows. The hypostome has a pair of postero-lateral spines. *B*. cf. *nevadensis* appears to have been derived from "*Bathyurus*" sp. or an allied species and gave rise to B. platyparius n. sp. which occurs in Blackriveran strata of the study area. Like B. cf. nevadensis, B. platyparius has a parallel-sided glabella, lacks glabellar furrows and palpebral furrows, and the postero-lateral corners of the hypostome bear strong spines. It is distinguished from the older species chiefly in possessing a broad and flat cephalic border and, on the pygidium, by having deeper interpleural furrows and pleural furrows that cross a broad lateral border. The microsculpture consists of fine, cuesta-like ridges.

Bathyurus platyparius is, in turn, similar to B. superbus Raymond from the Pamelia (?) of Quebec and B. cf. superbus from the Corbin Ranch Member of the Bromide Formation in Oklahoma (unpublished material collected by V. Jaanusson). These species share the following features - a faintly convex glabella that lacks glabellar furrows, absence of palpebral furrows (at least in mature specimens), broad cephalic and pygidial borders crossed by faint pleural furrows, faint and few axial ring furrows, and in possessing short (exsag.), prominent, sill-like lateral shoulders on the hypostome. The Nahanni species may be distinguished by its relatively longer glabella which is covered by fine ridges, a right-angled gamma, palpebral areas that stand as high as the highest part of the glabella, and postero-lateral spines on the hypostome. B. superbus and B. cf. superbus each possesses a glabella that is essentially smooth, palpebral areas that stand below the crest of the glabella, obtusely-angled gamma, and lack postero-lateral spines on the hypostome. Either these species shared a common ancestor, or *B. platyparius* gave rise to *B. superbus* and *B.* cf. *superbus*.

A third species group of *Bathyurus*, including *B. acutus* Raymond and *B. angelini* Billings, occur in Blackriveran and older (?) strata of Ontario and Quebec. The similarities and differences between these two species are covered in the section of Systematic Paleontology. Both possess parallel-sided glabellae, deep axial furrows, faint lateral glabellar furrows, and deep palpebral furrows. The pygidia are similar - *B. acutus* possesses a longer posterior spine and, on the mid-portion of each of the anterior few axial rings, carries a narrow (sag.), transverse, ridge-like elevation which extends between a pair of tiny spines. The hypostomes possess a narrow, convex, tube-like posterior and lateral border, isolated by deep border furrows, and a greatly inflated anterior lobe of the middle body. The posterior pygidial spine and ridge-like elevations on the pygidial axis suggest a derivation from a species of *Goniotelina* (if these elevations are analogous with axial spines). Other features of *B. acutus* and *B. angelini* are consistent with such a derivation. Both "*Goniotelina*" sp. from the Sunblood Formation and "*Goniotelina*" *moorei* Raymond from the Beauharnois Formation, Quebec are likely candidates to serve as ancestors for these two species.

The derivation of the remaining moderately well-known species, the type species, *Bathyurus extans* (Hall) from the Lowville of New York, is somewhat enigmatic. In general aspect, it resembles such species as *B. ulu* and *B. superbus*; but it is also similar to both *B. acutus* and *B. angelini* from which it differs in possessing shallower axial and palpebral furrows, a sparse pustulose micro-sculpture, and in lacking any trace of a posterior pygidial spine (Pl. 5, figs. 5-10). A feature in common with *B. acutus* is the presence of a pair of tiny spines on the central part of the anterior pygidial rings (Pl. 5, fig. 5). This unique feature strongly suggest a common origin, at least, of *B. acutus* and *B. extans*.

The phylogenetic conclusions about *Bathyurus* are not totally satisfactory. A polyphyletic origin of such generally similar Blackriveran species as *B. extans*, *B. esbataottinensis*, and *B. superbus* may be stretching the efficacy of convergent evolution. However, the evidence available at the present time suggests that the origin of *Bathyurus* lies with two bathyurid genera of late Whiterockian age. The Whiterockian bathyurids constitute a relatively diverse complex of genera, slightly reduced in diversity from the acme development of the family in the Arenigian (Whittington and Hughes, 1972). The earlier bathyurids occur in a wide variety of carbonate rock types, but by the Chazyan, the single remaining bathyurid genus appears to be restricted to shallow water habitats on a very fine carbonate mud base (with the exception of *Bathyurus acutus* and *B.*

angelini which occur in coarse calcarenites). Bathyurus appears to have had a nearly complete circum-continental distribution in the Middle Ordovician. The apparent continuity of this distribution is partly the result of grouping Bathyurus-bearing strata of different ages. If just the Blackriveran interval is considered, species of Bathyurus occur in the Nahanni area (west) and in Oklahoma, Ontario/New York, and possibly Newfoundland (east). It is unlikely that interchange occurred between the eastern and western developments - no single species is shared and unfavourable environments (sand bottom, shallow water habitats in western United States) are interposed. The restricted habitat, in what may be considered a continent-wide Bathyurus Biofacies, would severely restrict the possible adaptive strategies that Bathyurus could pursue and the Chazyan and younger evolutionary pattern would probably follow closely similar paths even though the species or species groups existed as geographic isolates. Just prior to its extinction at the base of the Trentonian, Bathyurus appears to have reached similar morphological levels in the east and in the west.

MODE OF LIFE OF BATHYURUS

Introductory Remarks

A few authors have commented, in passing, on the morphology of Bathyurus as it pertains to life habits and living position. Whittington (1953, p. 651) drew attention to the high, convex cephalon with a broad, flat or concave border and the long broad genal spines of bathyurids. He noted that this morphology, seen in such genera as Bathyurus, Raymondites, Platyantyx, and Uromystrum, is harpid in form and implied that these genera, especially those with pygidial and occipital spines, were adapted for "a swimming or drifting, rather than crawling mode of life". Walker and Laporte (1970) depicted Bathyurus as an epifaunal crawler that plowed through the top few millimeters of the sediment.

Study of a number of well-preserved species of Bathyurus from the upper Sunblood Formation and the Esbataottine Formation suggests that Bathyurus was neither a swimmer nor a crawler, but appears to have occupied a quasi-infaunal niche for most of its life. This conclusion is based on a number of pieces of, admittedly, circumstantial evidence and the interpretation of some of these may be open to question, but it does offer a more reasonable explanation for the occurrences and morphological features of the genus.

Any attempt at autecologic analysis of <u>Bathyurus</u> must take into account the following features and conditions:

1. The dorsal surface lacks prominent topographic features; the axis is wide and ornamented by distinct micro-sculpture consisting of asymmetrically developed scales, granules, or ridges that have their gentle slopes facing forward and their steep slopes facing backward; the pleural lobe is ornamented by micro-sculpture consisting of asymmetrically developed and irregular cuestas with their steep sides facing outward and backward.

2. Broad and flat or concave borders are present on both the cephalon and the pygidium and the genal spines are long and sub-parallel to the edge of the thorax.

3. The aspect of the hypostomal suture suggests that the hypostome was movable in a sagittal plane. The anterior wings are high, plate-like structures and, if the hypostome was rotated downwards and forwards, these wings would effectively enclose the mouth region of the trilobite within a box-like structure that would only be open towards the rear. The micro-sculpture of the ventral surface of the hypostome is similar to that seen on the dorsal surface of the axis, but is considerably finer and the asymmetry is developed in reverse, so that the steep slopes of the scales face forward.

4. The upper and lower edges of the cephalon (that is, the crest of the glabella and the base of the genal spine) are parallel; as are the upper and lower edges of the visual

surface of the eye. These two parallel sets, however, are positioned at an angle to each other, so that if the eye is assumed horizontal, the cephalon and, presumably, the thorax and pygidium would slope backward at an angle of about 10-20°.

5. Bathyurus is restricted to a shallow water habitat on a very fine grained carbonate mud base, in which it occurs with few other trilobites. In addition, it is persistently associated with large smooth leperditellid ostracods of the genera Leperditella and Eokloedenella in the study area. Walker and Laporte (1970) emphasized the low diversity nature of the communities with Bathyurus from the Black River Group and noted the co-occurrence with leperditiid ostracods. The same Bathyurus - smooth ostracod associations probably also occurs in Nevada (Ross, 1970) and Oklahoma (Harris, 1957).

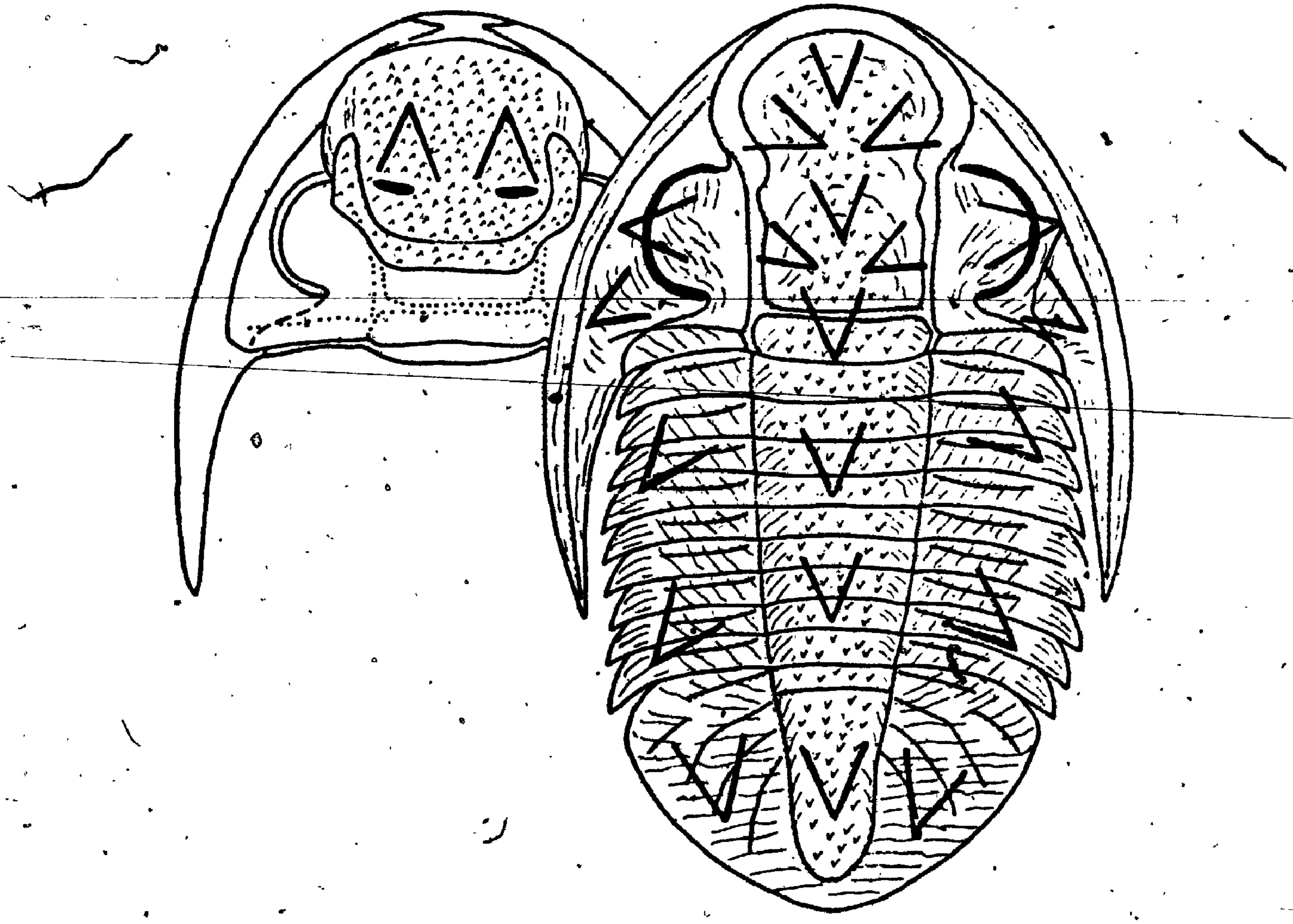
Theoretical framework

In a series of provocative papers, Seilacher (1970, 1972, 1973) emphasized that the morphology of an organism must be viewed as a compromise between three factors that he called traditional, functional, and fabricational. The traditional factor refers to the phylogenetic legacy of an organism and centers on features that are clearly traceable to its ancestors. Raup (1972) noted that the traditional factor tends to limit the potential adaptive paths available to an organism. In the case of Bathyurus, the traditional factor includes all features that label the fossil an arthropod and trilobite (growth by molting, articulated exoskeleton, etc.) and bathyurid trilobite (general relationship and size of bodily components, course of sutures, position and orientation of eye, etc.). The traditional factors are ones that are not subject to significant short term change, "because mutation rates are low or because the structure is controlled by such a large gene complex that rapid modification is unlikely *or* because the gene complex is not subject to allelism" (Raup, 1972, p. 31). The *functional factor* refers to features attributable to the process of adaptation through natural selection and, in the case of *Bathyurus*, may be considered to encompass those used to differentiate species (width, length, and convexity of cephalon and glabella, length of genal spines, width of border, depth and length of glabellar furrows, presence of axial pygidial spines, etc.). These morphological adaptations can only be expressed within the constraints imposed by the traditional factor. The *fabricational factor* produces features that have their origin in the structural limitations and characteristics of the material or derived from the mechanics of growth. Although genetic control must ultimately be responsible for the framework in which the fabricational factor can be expressed, the specific morphology of the resulting structures can be reproduced with a minimum of genetic information and their presence bears little taxonomic significance. Seilacher (1972, 1973) stated that the morphological expression of the fabricational factor may be adaptive or non-adaptive and, in adaptive cases selective processes only result in minor modifications of an established program. In the case of *Bathyurus*, the fabricational factor is judged responsible for the micro-sculpture which, in general terms, maintains a high degree of consistency in the different species, but, in detail, varies considerably within the genus.

Seilacher (1970) expressed the three factors outlined above as end members of a ternary diagram and emphasized that the placement of a given structure within this triangle gives expression to the relative importance of each end member in the formation of the structure. This technique, termed "Konstructions-Morphologie", will be employed to shed light on the life position(s) of *Bathyurus*.

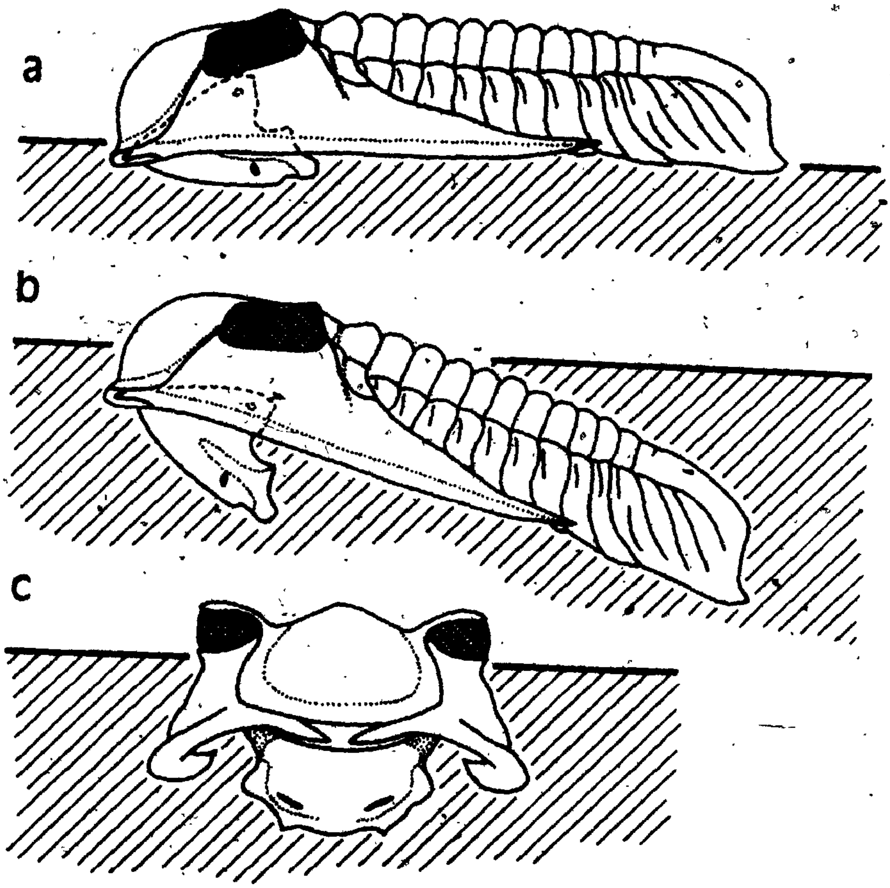
The evidence from *Bathyurus esbataottinensis*

The following discussion refers mainly to *Bathyurus esbataottinensis* n. sp. because this species supplies the best preserved material and most of the critical features are exceptionally well shown (Plates 3 and 4). The arguments, however, may equally well apply to many other species because *Bathyurus* remains a taxon that shows a minimum of variation (certainly, if compared to its contemporaries, *Ceraurinella* and *Ceraurus*) and the critical features evident in other species appear to be closely similar to those in *B. esbataottinensis*, if not in detail then in general aspect.



Text-figure 24.

Orientation of micro-sculpture and direction of asymmetry (steep edges in direction of arrows) of Bathyurus esbataottinensis.



Text-figure 25.

Inferred life positions of Bathyurus esbataottinensis n. sp.

(a) Forwardly crawling with hypostome tucked up into cephalon (epifaunal).

(b,c) Feeding position with hypostome extended (quasi-infaunal).

Sediment is shaded.

Micro-sculpture: The micro-sculpture of Bathyurus esbataottinensis has been described in the section of Systematic Paleontology and its important features are diagrammatically shown on Text-figure 24. Briefly; on the axis it consists of overlapping chevron-shaped scales whose steep slopes and apices point toward the rear; on the pleural lobes it consists of irregular cuesta-like ridges that, on the posterior part of the pygidium, are transversely directed with their steep slopes facing posteriorly and, on the thorax and cheeks, are obliquely directed with their steep slopes facing postero-laterally or laterally; and, on the ventral surface of the hypostome, consists of fine chevron-shaped scales whose apices and steep slopes face anteriorly. The micro-sculpture on the pleural lobes is of much lower relief than that found on the axis. The scale size on the axis shows a relative increase during ontogeny. A working hypothesis is that this micro-sculpture is not spurious, but that it does carry functional significance and, further, that the function is related to burrowing activity. This hypothesis can be tested by comparing the micro-sculpture of B. esbataottinensis to that of the paradigm sculpture of a burrowing bivalve (Seilacher, 1973, Fig. 1A) and by applying the requirements of the functional model (Seilacher, 1973, p. 451, 452). These requirements are cross-orientation, frictional asymmetry, perimeter smoothing, and allometric densing.

Cross-orientation: This requirement is met. On the axis, the scale rows and cuestas are arranged in forwardly curving rows and, on the pleural lobes, the cuestas are transversely and obliquely oriented (Pl. 4, figs. 1, 2, 19, 20, 23, 24).

Frictional asymmetry: This requirement is met. Both the chevron-shaped scales and the irregular cuestas have their steep slopes facing backward (Pl. 3, figs. 2, 20, 23, 24). A significant exception is the reversed asymmetry of the scales on the ventral surface of the hypostome (Pl. 4, fig. 3).

Perimeter smoothing: This requirement is met. The strongest micro-sculpture is found on the axis and the faintest on the cephalic and pygidial borders and on the thoracic spines (Pl. 4, figs. 1, 19).

Allometric densing: This requirement is partly met. The scale density does not significantly change during ontogeny (Pl. 3, figs. 16, 12, 6, 1), but the relative size of the scales increases as does the asymmetry so the functional result may be the same.

The micro-sculpture of *B. esbataottinensis* is closely analogous to the paradigm sculpture of a burrowing bivalve and constitute an important contributant to the fabricational end member of the "Konstructions-Morphologie" triangle. Before closing this section, the sculpture of the mole crab, *Emerita*, should be mentioned to show that burrowing sculpture, very similar to that observed on *B. esbataottinensis*, is also present in extant crustaceans. Seilacher (1973, p. 456-459) showed that the carapace of *Emerita* is covered by irregular ridges that satisfy the requirements of the functional model. The fact that Emerita is an observed active burrower (Seilacher, 1961) lends credence to a similar mode for the distantly related Bathyurus esbataottinensis.

Border and genal spine: The cephalic and pygidial borders and the genal spines are traditional and functional factors. These do not show obvious features that can readily be interpreted as functional in a burrowing situation. The genal spines, however, are closely aligned to the thoracic margin and streamlined so that they would not significantly hinder forward motion of the trilobite. The cephalic and pygidial borders are moderately broad and concave and are functional to the extent that they would inhibit upward and backward movement of the trilobite were it buried in the mud in a backwardly-sloping position. The borders may also have been useful in burying the trilobite by serving as sharp wedges that, directed laterally, would "slice" the trilobite into the substrate.

Hypostome: The hypostome of B. esbataottinensis is moveable in a sagittal plane, the ventral surface is covered by scales that show reversed orientation and asymmetry compared to that on the dorsal axis, and the high and plate-like anterior wings lend the appearance of a backwardly-facing scoop to the structure. The functional aspects become apparent if one visualizes the hypostome being forced open within the mud. The "inverted scoop effect" would create a sediment void in the area where the mouth is located and here the feeding activity, aided by appendages, would take place. The effect of the micro-sculpture on the hypostome would be to prevent forward motion of the trilobite while feeding and this effect would be counteracted by the opposite effect of the micro-sculpture on the dorsal surface and the cephalic and pygidial borders. The final result of the two forces acting in opposite directions on two surfaces positioned obliquely in the sediment would be to "lock" the trilobite in place while it carried on its feeding activity. This effect would be necessary because the feeding activity was probably accompanied by significant motion of the appendages which, otherwise, would have propelled the trilobite in and out of the sediment. The feeding position could easily be "unlocked" by drawing the hypostome up into the cephalic cavity, enabling the trilobite to crawl out of its feeding burrow. The outline and plan of the <u>Bathyurus</u> hypostome are traditional factors, the plate-like anterior wing is a functional factor (earlier bathyurids like <u>Goniotelina</u>, Whittington, 1953, Pl. 68, figs. 16, 17, and "<u>Bathyurus</u>", Ludvigsen, 1975, Pl. 1, fig. 17 possess strut-like anterior wings), and the micro-sculpture is a fabricational factor.

<u>Eye orientation</u>: Clarkson (1966) demonstrated that the strip-like visual surface of the eye of certain phacopid trilobites must have been horizontally oriented in order to at-

tain maximum vision in a horizontal plane. Bergström (1973) suggested that this principle could be more widely applied to other trilobites with strip-like visual fields, specifically to the illaenid, *Panderia* (Bruton, 1968). In *Panderia* the plane of the visual field is tilted forwards in relation to a plane tangent to the upper surface of the cephalon and Bergström (1973, Fig. 13) presented a diagram showing *Panderia* in a presumed life-position with the visual surfaces in a horizontal plane and located just above the sediment-water interface and the thorax proceeding obliquely downwards into the sediment. He further suggested that the similarity of gross morphology of certain illaenid, isotelid, homalonotid, and nileiid trilobites indicates common life habits -- that of burrowing in soft sediment, tail-down, in an oblique or vertical orientation. If the visual surfaces of the eyes of *B. esbataottinensis* are brought into a horizontal plane, the crest of the cephalon, thorax, and pygidium and the genal spines will slope backwards into the sediment at about 20° (Text-fig. 25). A similar relationship is evident in other species of *Bathyurus*, such as *B. granulosus*, Pl. 1, figs. 1, 45; *B. ulu*, Pl. 2, figs. 2, 47; *B. extans*, Pl. 5, fig. 7 and may be recognized in other bathyurid trilobites such as, *Raymondites longispinus* (Walcott), Whittington, 1953, Fig. 1B; *Bathyurellus nitidus* (Billings), Whittington, 1953, Fig. 4; *Bolbocephalus seelyi* (Whitfield), Whittington, 1953, Pl. 66, fig. 12; *Plantyantyx arcuata* (Billings), Whittington, 1953, Pl. 68, fig. 29.

Habitat: At the present time, the infauna is largely restricted to very shallow water whereas the epifauna has a much wider bathymetric distribution (Thorson, 1957). It is obviously simplistic to attempt a straightforward correlation of this distributional pattern to that of the Early Paleozoic, but since the physical parameters operative in a near-shore habitat would not have seen much change between the Paleozoic and the present, it is to be expected that the biota in this habitat would, in functional and ecological terms, exhibit a significant degree of stability. This is well brought out by the review of Paleozoic benthic communities by Bretsky (1969), who isolated a persistant (Ordovician to Permian), near-shore association of infaunal nuculoid bivalves and linguloid brachiopods and epifaunal bellerophontid gastropods and rhynchonellid brachiopods. This association incorporates the Lingula Community of Ziegler et al. (1968) which, alone among the five communities recognized in that study, includes a significant proportion of infaunal elements and would also accommodate the homalonotid trilobite-Plectonotus Community of Boucot et al. (1969) which is widely recognizable in Silurian and Early Devonian near-shore deposits. The latter community is particularly pertinent to the present study because it includes trilobites that are functionally similar to Bathyurus and to which a burrowing mode of life have been attributed (Bergström, 1973).

Aside from the name-bearer, the only persistently-present faunal group in the *Bathyurus* Biofacies are large, smooth leperditellid ostracods. The autecological significance of Paleozoic ostracods is difficult to decipher due to their being neglected in most paleoecologic studies. The leperditiids were singled out by Berdan (1968) as burrowers. She cited the thick smooth carapace, large muscle scars, and extensive overlap of the valves (features equally applicable to the leperditellids) and suggested that these ostracods inhabited tidal flats and burrowed just beneath the surface when the tide went out.

By analogy to other Paleozoic near-shore faunal associations, it is to be expected that the *Bathyurus* Biofacies should include a significant proportion of infaunal elements. The leperditellid ostracods contribute towards the infaunal portion, as does *Bathyurus*.

Conclusion

The previous discussion serves to demonstrate that many of the morphological features of *Bathyurus esbataottinensis* are compatible with a burrowing mode of life and, further, that this adaptation may be more widely applicable within the Bathyuridae. The presence of large, well-developed eyes in all the bathyurids clearly shows that a total-immersion type of burrowing would not be appropriate for these trilobites. A compromise solution, shown in Text-figure 25, accounts for most of the burrowing adaptations of *B. esbataottinensis* while maintaining the eyes above the sediment water interface. Implicit in this interpretation is that the burrowing micro-sculpture was not actively involved in the act of burrowing, but it served to keep the trilobite stationary within the sediment while feeding. It is suggested that B. esbataottinensis burrowed tail-first, probably by lateral shifts of the carapace, allowing the upwardly-concave cephalic and pygidial borders to slice through the relatively soft sediment. In this regard, it is important to note that in B. esbataottinensis, B. ulu, and B. extans and possibly in other species, the genal spine almost reaches the pygidium and a nearly complete wedge-shaped surface surrounds the carapace. A few sidewards wriggles would be sufficient in burying all the trilobite, except the central part of the cephalon, including the eyes, and the axial portion of a few thoracic segments. Once the trilobite was in this position, the hypostome could be rotated downwards and forwards, "locking" the trilobite in a feeding position. To move to a new feeding area, the trilobite would simply draw the hypostome back into the cephalon and crawl forward out of its burrow. Alternatively, or in addition, it is possible that Bathyurus burrowed forwardly in an oblique position.

In this chapter, I have tried to demonstrate that the micro-sculpture of B. esbataottinensis carried functional significance and that the fabricational factor was responsible for its formation. The micro-sculpture, however, is also well expressed on portions of the carapace, i.e., the central part of the cephalon, that probably were not buried under the sediment and therefore would not be functional. This may be explained by citing the origin of the fabricational factor which, by its very nature of being based on physical principles or growth systems, produces some by-products which are not necessary (Raup, 1972, p. 320). The nature of the mechanism that produced the distinctive micro-sculpture of Bathyurus is not known. Seilacher (1973, p. 458) formulated a fabricational model for similar sculpture of Emerita "in which minute fibers pull the new (unsclerotized) cuticle of the old one in the direction of molting. At every tie point the pull produces V-shaped wrinkles which link with adjacent wrinkles to form smoothly curved pull-off saddles". The constraint of this model is that it can only produce frictional asymmetry in one direction -- the direction of molting. The carapace of B. esbataottinensis (Text-fig. 24) contains micro-sculpture that shows frictional asymmetry in anterior, posterior, and left and right lateral directions and shows that this model is not directly applicable. The marked similarity between the scales and cuestas of B. esbataottinensis and the modelled pull-off structures suggests that Seilacher's model may be basically correct, but that it would require some modification to account for the additional directions of asymmetry.

SYSTEMATIC PALEONTOLOGY

Terminology and repository

The terminology and classification is basically that outlined in Moore (1959). The classification of the Cheiruridae follows Lane (1971). The terminology of articulating mechanisms follows Whittington and Evitt (1954) and Bergström (1973).

Glabella - includes the occipital ring

Palpebral area - in Bathyuridae, that area bounded by by abaxial edge of the palpebral lobe and the axial furrow

Epsilon - angle formed by facial suture at posterior end of palpebral lobe (Richter and Richter, 1949)

Gamma - angle formed by facial suture at anterior end of palpebral lobe (Richter and Richter, 1949)

GSC	Geological Survey of Canada, Ottawa
USNM	United States National Museum, Washington
UA	University of Alberta, Edmonton
UC or P	Field Museum of Natural History, Chicago
RL	Temporary numbers of illustrated specimens in author's collection

Family Bathyuridae Walcott, 1886

Genus Bathyurus Billings 1859

Type species: Asaphus? extans Hall, 1847 from the Lowville Formation, Mohawk Valley, New York State. Lectotype described and illustrated by Whittington (1953, p. 651, Pl. 65, figs. 1-3).

Discussion: Species of Bathyurus have previously been known largely from scattered occurrences in Ontario, Quebec, and New York State. The bulk of the species are represented by sparse and generally incompletely or indifferently preserved material from relatively few localities. The ventral morphology of any species of Bathyurus has not been made clear; although the rough outlines of the ventral sutures of a related genus, Raymondites Sinclair, has been sketched in by Whittington (1953); and the respective hypostomes remain incompletely known. Furthermore, in no single area can a stratigraphic sequence of Bathyurus species be demonstrated and the temporal relationship of most species, and hence phylogenetic connections, can only be surmised.

Whittington (1953, p. 653) concluded that Bathyurus is restricted to rocks of Blackriveran age. The present work demonstrates that, in excellent sequences in the Mackenzie Mountains, Bathyurus first appears at a stratigraphic interval considerably below horizons carrying definite Chazyan trilobites. And, further, that the genus is almost totally restricted to the shoreward of four trilobite biofacies.

These have decisive implications for the correlation of *Bathyurus*-bearing strata in North America. In abundance and completeness, the *Bathyurus* material from the Mackenzie Mountains is, by far, superior to any investigated to date and the total morphology of the genus can now be presented.

Many of the types of species of *Bathyurus* from eastern North America and a few from Nevada have been examined during the present study. The following comments on morphology, relationship, age, and geographic occurrence of some of these are presented; adjunctive to those of Raymond (1913), Wilson, (1947), and Whittington (1953).

Bathyurus extans (Hall, 1847): The lectotype from the Lowville Formation of the Mohawk Valley and additional material from the Lowville of Great Bend and Watertown, New York State was described and illustrated by Whittington (1953). A complete and well preserved carapace illustrated in this thesis (Pl. 5, figs. 5-10) shows, among other features previously described, as obtusely-angled gamma. The presence of this species outside of the above areas in New York State has not yet been demonstrated; it should however, be mentioned that both *B. perplexus* Billings and *B. magnus* Wilson from Newfoundland and Ontario, respectively, are possible junior synonyms of *B. extans*. Wilson (1947, p. 17) listed *B. extans* from numerous localities in Quebec and Ontario, but these occurrences should be treated with scepticism because the only two specimens illustrated by her (Wilson, 1947, Pl. 2, fig. 5, 6) differ from those illustrated by Whittington (1953) and in this thesis. The cranidium lacks glabellar furrows and the pygidium has a more rounded outline and a broader margin than the lectotype and, therefore, these specimens are probably not conspecific with the New York State material of *B. extans*.

Bathyurus superbus Raymond, 1910: This species is characterized by its wide glabella, faint axial furrows on the cephalon, wide pygidial border and a smooth surface (Raymond, 1910; Whittington, 1953). Gamma is an obtuse angle. The species has only been collected from the Pamelia(?) at Mechanicsville, Quebec (material in Geological Survey of Canada, Royal Ontario Museum, and the University of Western Ontario collections). It seems probable that the two hypostomes illustrated by Whittington (1953, Pl. 65, figs. 13, 17) from this locality and identified as *B. extans* belong to *B. superbus* because the presence of *B. extans* cranidia or pygidia has not been demonstrated at this locality. Furthermore, the two hypostomes are very similar to one associated with a cranidium of *B.* cf. *superbus* from the Corbin Ranch Member of the Bromide Formation in Oklahoma. These specimens were collected by Valdar Jaanusson and lent to the author for study.

Bathyurus perplexus Billings, 1865: The holotype pygidium (GSC 632) from Bonne Bay, western Newfoundland has been examined. As both Walcott (1896) and Raymond (1913) pointed out, this pygidium is highly similar to that of *B. extans* and may prove conspecific.

Bathyurus angelini Billings, 1859: This species is characterized by a relatively short (sag.) glabella with two pairs of broad glabellar furrows set at a high angle to the midline. Gamma is an acute angle. The palpebral areas have deep and curved palpebral furrows. The pygidium has a narrow and concave border crossed by broad interpleural furrows and the posterior margin carries a very short, thorn-like spine.. The latter feature is important because it provides a previously unnoticed link with B. acutus. The hypostome is distinguished by a greatly inflated anterior lobe of the middle body. The strata yielding the only known specimens of B. angelini at Grenville, Argenteuil County, Quebec were originally assigned to the Chazy Group by Billings (1859) and subsequently to the Beekmantown, because the strata "underlie the sandstone at the base of the Chazy" (Raymond, 1913, p. 55). However, the ostracods from these horizons described by Jones (1891) are of types unknown below the Mohawkian (M.J. Copeland, personal communication, 1975), so B. angelini may prove to be Chazyan or Blackriveran.

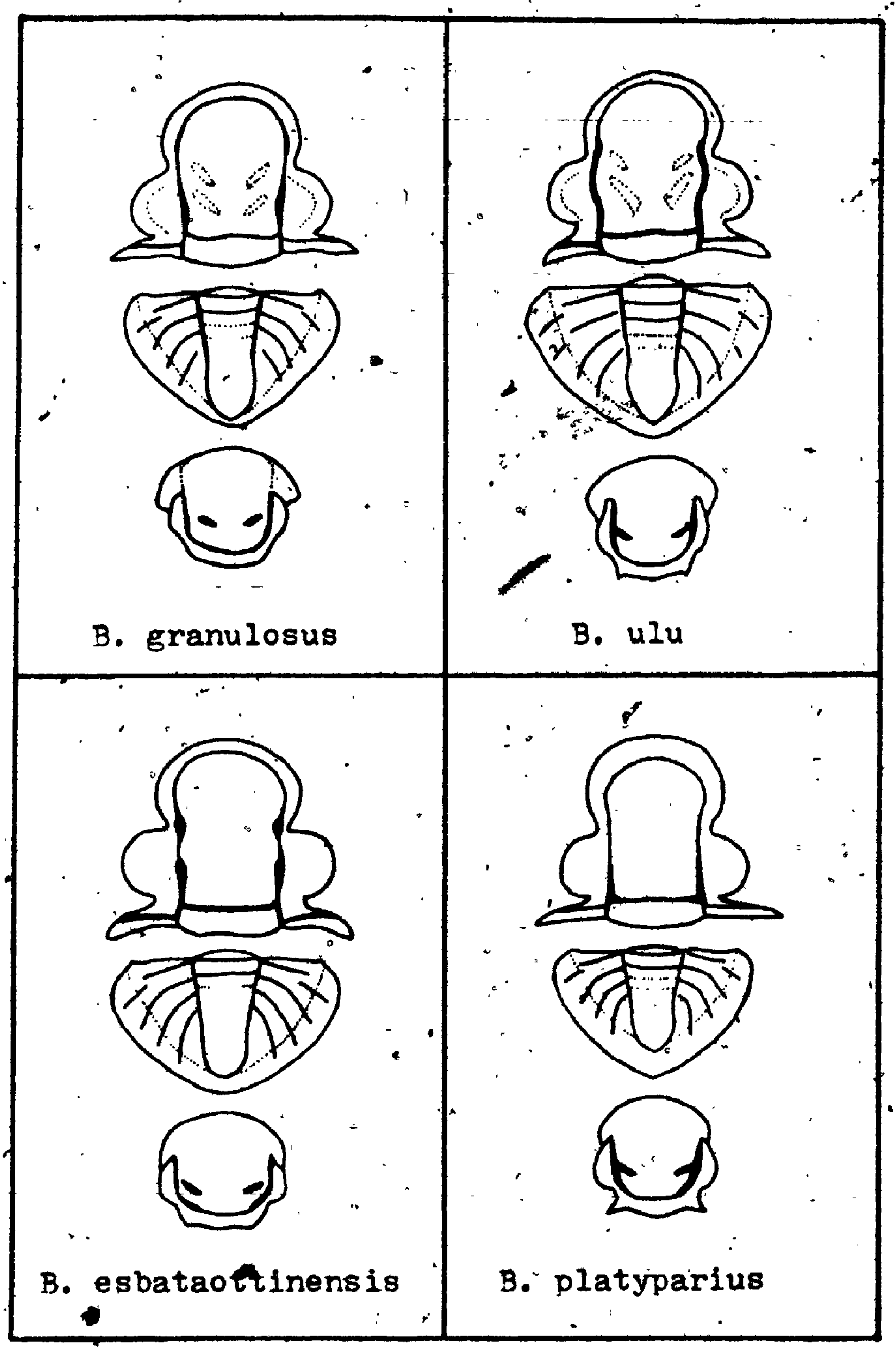
Bathyurus acutus Raymond, 1913: As noted by both Raymond (1913, p. 57) and Whittington (1953, p. 653), this species is most similar to B. angelini from which it is distinguished by possessing a trunk-like glabella that is relatively narrower (tr.), smaller palpebral areas carrying fainter palpebral furrows, an obtusely-angled gamma, and a pygidium with a stout and pointed posterior spine. The similarity of these species is well shown by the presence of an inflated anterior lobe of the middle body of the hypostomes of both

B. acutus and B. angelini. The short posterior pygidial spine of B. angelini also allies this species with B. acutus. The single locality from which B. acutus is known (the lower Pamelia at Westboro, Ontario) may not be appreciably younger than the horizon yielding B. angelini at Grenville, Quebec.

Bathyurus nevadensis Ross, 1967: This species occurs in the Lehman Formation, Utah about 35 m below the base of the Eureka Quartzite. B. nevadensis is characterized by a parallel sided glabella that expands only slightly forwardly and lacks any trace of glabellar furrows. The glabella appears to be covered by moderately coarse and subdued granules. The palpebral area does not possess a palpebral furrow. Gamma is an acute angle. The pygidium is semicircular in outline; the axis is high, broad (tr.), and tapers only slightly posteriorly; the pleural furrows do not cross the concave border, and interpleural furrows are not developed. A very similar species, for the present identified as B. cf. nevadensis, occurs in the Sunblood Formation in the Mary Range (B 1100), about 50 m below the lowest occurrence of B. granulosus n. sp.

Bathyurus cf. extans (Hall): A few cranidia and pygidia from the upper 100 m or so of the Antelope Valley Formation, Nevada and from the Kanosh Formation, Utah were illustrated by Ross (1970, Pl. 13, fig. 12, Pl. 15, figs. 16-19) under the name B. cf. extans. Reference to these specimens was made previously (Ludvigsen, 1975) and it was concluded that some of these, at least, were probably conspecific with B. granulosus n. sp. An examination of the actual specimens has revealed additional features not described by Ross, nor apparent in his published figures. The more important of these are the presence of a longitudinal row of four small spines on the anterior part of the pygidial axis, a small median occipital node, glabellar ornament consisting of small tubercles and granules of two size ranges, and a 1s furrow which is expressed laterally as a small oval depressed area devoid of tubercles and granules. None of these features are present in *B. granulosus*, confuting the affinity previously suggested by me, but they are all present in a new bathyurid genus (provisionally called "*Goniotelina*", in Ludvigsen, 1975, Pl. 1, figs. 11-13) which is found in the Sunblood Range at Section P, about 300 m below the lowest occurrence of *B. granulosus*.

The types of the following species have not been examined: "*Bathyurus*" *pogonipensis* Hall and Whitfield, 1877, p. 243, Pl. 1, figs. 33, 34; *Bathyurus johnstoni* Raymond, 1913, p. 53, Pl. 7, figs. 2, 3; *Bathyurus eskimoensis* Twenhofel, 1938, p. 72, Pl. 11, figs. 20, 21; *Bathyurus estans emaciatus* Ross, 1970, p. 85, Pl. 15, figs. 20-24; and *Bathyurus extans angustus* Ross, 1970, p. 86, Pl. 16, figs. 6-12. These appear to conclude the list of species of *Bathyurus* from North America. The large number of species described under the name *Bathyurus* by Billings (1859, 1860, 1863, 1865) and others have been divided among numerous new genera by Raymond (1913), Sinclair (1944), and Whittington (1953, 1963, 1965a).



B. granulosus

B. ulu

B. esbataottinensis

B. platyparius

Text-figure 26.

Outline drawings of cranidia, pygidia, and hypostomes of four species of Bathyurus from the upper Sunblood and Esbataottine Formations, South Nahanni River area.

Bathyurus has a nearly complete circum-North America distribution during the Middle Ordovician. It occurs in the Arctic Islands (Norford, 1966), the Nahanni area, Utah, Nevada, Oklahoma, Virginia (Butts, 1941), New York, Ontario, Quebec, and Newfoundland.

Bathyurus ulu n. sp.

Pl. 2, figs. 1-53, Pl. 5, fig. 3

Diagnosis: A species of Bathyurus with a subparallel glabella modified by a faint waisting adaxially of posterior and anterior ends of palpebral area and possessing two pairs of obliquely-disposed glabellar furrows, posterior pair longest. Anterior border of cranidium is moderately broad, slightly concave. Palpebral area is sub-semicircular, includes faintly defined and crescentic palpebral lobe. Gamma is slightly obtuse angle. Hypostome has a pair of small spines at postero-lateral corners. Pygidium is triangular to semicircular in outline, has moderately broad and concave borders; axis has 1-3 rings. Axial region of carapace crowded with small, asymmetric, chevron-shaped scales, the steep sides of which face the rear; pleurae possess fine, irregular and discontinuous ridges.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 220, A 240, A 247, P 1595, ?P 1665-1685). Bathyurus ulu Zone and (?) Ceraurus gabrielsi Zone.

Material: 925 individuals.

Holotype: A complete cranidium (RL 0201) from A 220 illustrated on Pl. 2, figs. 1-3 and Pl. 5, fig. 3.

Description: Glabella moderately vaulted (tr.) posteriorly, strongly vaulted anteriorly where front edge descends vertically to anterior border. In longitudinal profile, glabellar flanks slope outwardly from a broad and rounded keel. In lateral profile, crest of posterior 2/3rds of glabella slopes faintly backwards (using upper edge of eye as horizontal datum). Glabella essentially parallel-sided, length (sag.) slightly less than 1/2 width; anterior portion sub-circular. From occipital ring, moderately deep axial furrows converge slightly to minimum width of glabella just ahead of epsilon; then shallow markedly and bulge slightly to a second waisting which is located slightly in front of gamma. In front of this point, axial furrows flare slightly around lateral portion of glabella and then curve inwardly along sub-circular path to merge with pre-glabellar furrow. Anterior part of axial furrow defined by sharp slope change between forwardly-sloping part of fixed cheek and glabella. Pre-glabellar furrow faintly impressed medially. Pre-glabellar field moderately broad, slightly concave antero-medially, field is deflected into narrow roll which curves across anterior margin to meet rostral suture. 1s furrow consists of elongate, straight flexure which extends inwards and backwards from point just inside axial furrow at widest part of glabella at an angle of about 40° to sagittal line. Furrow becomes slightly deeper and wider (tr.) posteriorly and terminates ahead of line joining epsilon, about 1/3rd way across glabella. 2s furrow sub-parallel to 1s, but shallower and slightly shorter (tr.); extends from axial furrow at second waisting of glabella 1/3rd way across glabella. Width across palpebral area is slightly greater than sagittal length of cranidium. Palpebral area sub-semicircular in outline, length (exsag.) about 1/3 glabellar length; includes crescentic palpebral lobe which extends from gamma to epsilon and is defined adaxially by very faint palpebral furrow. Portion of palpebral area between palpebral furrow and axial furrow depressed slightly below level of palpebral lobe. In longitudinal profile, palpebral area has slight curvature and stands well below crest of glabella. Occipital furrow transverse; moderately deep with steep anterior and gentle posterior walls. Occipital ring rectangular to lenticular, 4 times as wide (tr.) as long (sag.); highly arched, but stands below level of highest portion of glabella (if upper edge of visual surface assumed horizontal). Posterior border furrow on cheek slightly deeper than occipital furrow; extends outwards and downwards with very gentle backward curvature from half-length (sag.) of occipital lobe and dies out in front of inside curvature of genal spine. Anterior branch of facial suture extends from gamma (which is slightly obtuse angle) forward in even curve, sub-parallel with glabellar margin. At a point in line with axial furrows, suture obliquely crosses anterior margin in very faint curve to meet antero-laterally curving connective suture and then proceeds adaxially in straight path, just below anterior margin, as rostral suture. Posterior branch of facial suture proceeds outwards and downwards from epsilon in sigmoidal curve, crosses posterior border furrow at low angle, and intersects posterior margin at a point halfway to lateral margin.

Rostral plate can be described in two parts. A short (tr.), gently curved (tr. and sag.), cleaver-shaped anterior portion bounded by rostral suture and strongly anteriorly divergent branches of connective suture and ~~a~~ wide (tr.), strongly flexed (sag.), strongly curved (tr.), and thin, crescent-shaped posterior portion bounded by posteriorly-diverging branches of connective sutures and posteriorly concave hypostomal suture. Considering both parts, rostral plate strongly curved (tr.) and strongly flexed (sag.) with pronounced waist formed by strongly laterally divergent connective sutures and attenuating distally to very fine, curved point. Two kinds of sutural contacts define rostral plate. The rostral and connective sutures are sharply-edged and plane surfaces set perpendicular to dorsal and ventral surface of exoskeleton. The hypostomal suture is essentially the recurved inner edge of the doublure and the portion facing the hypostome is a sagittally convex and posteriorly concave surface. The rostral and connective sutures are identical to the facial suture and their morphology would not allow motion to take place across these planes. The hypostomal suture differs from the above in being a curved surface and possessing a form that suggests the possibility of motion taking place across this contact. The area on the hypostome that receives the edge of the rostral plate is a forwardly convex and slightly sagittally concave surface and it appears highly probable that the hypostome could be moved within a sagittal plane.

Visual surface of eye strongly curved in horizontal plane and slightly (?) in vertical plane; stands on strip-like, vertically oriented and concave (tr.) eye socle. Field, below eye socle, slopes steeply to flat cephalic border which is broadest (tr.) antero-laterally. Cephalic border narrows somewhat posteriorly and becomes slightly concave, may be joined by faint continuation of posterior border furrow; continues posteriorly to tip of long, gradually tapering genal spine. In lateral view, base of genal spine straight; directed obliquely backwards at about 15-20° below horizontal (i.e., base of visual surface of eye).

On interior, occipital doublure extends about 1/3rd across occipital ring. Glabellar furrows expressed as relatively high ridges. Thin, narrow rim extends completely around lateral periphery of palpebral lobe. Genal spine encased by convex doublure as far forward as internal impress of posterior border furrow where it is notched by limiting device. Lateral parts of doublure convex, extend to inner edge of lateral border. Anteriorly, rostral plate forms part of this doublure.

Hypostome sub-trapezoidal in outline; length (sag.) slightly less than maximum width across anterior wings. Middle body slightly inflated; posterior 2/3 bounded laterally by relatively narrow lateral border furrows which are parallel-sided or slightly convergent forwardly at mid-length. Posterior border furrow follows even arc, shallowing somewhat medially; confluent with lateral border furrows. A pair of obliquely disposed maculae located on margin of middle body, slightly further than half the distance from anterior margin. Macula lenticular in outline, relatively deep with steep anterior edge and shallow posterior edge. A narrow lip on middle body may define posterior edge of macula.

Opposite maculae, lateral margins flare slightly to define distinct shoulders which, in longitudinal profile, are narrow (tr.), rounded, and horizontal ledges. From shoulder, lateral margin angles inwards and backwards to terminate at small and distinct antero-lateral spine. Posterior margin faintly bowed towards rear and posterior border slightly wider (sag.) than lateral border at shoulder. In ventral view, anterior margin of hypostome defined by broad parabolic curve between high anterior wings. On its antero-ventral edge, anterior margin carries a smooth, concave groove which is widest (sag.) medially and fades out laterally. In anterior view, anterior margin broadly U-shaped. Anterior wings high, triangular in lateral profile, nearly vertical; forward portion curves directly from middle body without interruption by furrow; rear portion defined basally by shoulder. Anterior wings divided by faint vertical furrow which runs from anterior part of shoulder to shallow pit near apex of wing. On interior, posterior doublure narrow (sag.) and convex medially;

laterally it becomes wider (exsag.), higher, and concave. In front of postero-lateral corner, doublure flexed into faint fold (which is continuation of shoulder) and inner edge of doublure elevated into thorn-like posterior wing. Broad antennal notch bounded by shoulder ventrally and anterior wings antero-dorsally. Notch directed forwardly and slightly outwardly. Except for impress of maculae, interior floor of hypostome completely smooth, lacking any trace of possible muscle insertion areas.

Number of thoracic segments unknown. Axis high, vaulted; 5 times as wide (tr.) as long (sag.); width less than 1/3rd total width of pleuron. Articulating furrow moderately deep, nearly straight, but tending to bend slightly forward near axial furrow. Pre-annulus not present. Articulating half ring extends nearly to articulating furrow of preceding segment. Axial furrows narrow (tr.), deeply incised. Inner half of pleura horizontal; outer half declines gradually to a level 45-55° below horizontal. Pleural terminus bluntly pointed with a convex anterior edge and faintly curved posterior edge. Pleural furrow V-shaped (exsag.), deepest at mid-length of pleura; sub-parallel to posterior margin; extends to about mid-length of declined portion of pleura. On interior, occipital doublure extends nearly to articulating half ring. Doublure encases slightly less than half of declined part of pleura. Dorsal edge of this doublure notched medially to form enrollment limiting device, in front of which, inner edge of doublure proceeds directly forwards and is flexed upwards slightly. This flexure extends slightly beyond anterior edge of pleura and is received by limiting device of preceding segment at maximum enrollment (Pl. 2, fig. 36). Posterior part of doublure extends inwards from limiting device in gentle curve and attenuates towards distal part of horizontal portion of pleura. Besides enrollment limiting device, articulating devices consist of small, forwardly-facing, button-like axial furrow process and corresponding backwardly-facing socket.

In fully extended state, antero-lateral part of segment covered by posterior part of preceding segment (Pl. 2, figs. 34, 35). Upon enrollment, the axial furrow process and socket remain conjoined, as do the inner horizontal parts of adjoining segments as far laterally as adaxial tip of posterior doublure; The latter point serves as a fulcrum, but it is not expressed as a structure on the margin of the segment. The relative rotation is taken up by the distal sloping part of the segment which slides underneath the segment in front until stopped by the doublural notch.

Pygidium sub-semicircular to sub-triagnular in outline; width (tr.) about 1 1/2 times length (sag.). Antero-lateral corner modified into oblique facet. Axis high and vaulted, 1/4th to rarely 1/3 as wide as pygidium; descends vertically into deep, V-shaped (tr.) axial furrows; crossed by single complete axial ring furrow and additional 1 or 2 faint furrows which only are evident on axial crest. Axial furrows converge slightly backwards for 2/3rds length of pygidium, then become parallel for short distance before fading out. In lateral profile, crest of axis declines gently; tip unbounded by furrows, defined by even sigmoidal decline to posterior border. Pleural field initially horizontal or faintly arched; outer part declines at about 50° below horizontal and flattens to form moderately broad, concave border. Pleural field crossed by 4 approximately equally-spaced interpleural furrows which, initially are nearly straight; first oriented at 75° and last at 30° to sagittal line. First pleural furrow very faint on pleural field, becomes deeper on border and extends to lateral margin. Second to fourth pleural furrows evident on border where they are broad depressions that extend nearly to margin. They cannot be recognized on pleural field. Second pleural furrow located only slightly behind distal end of second interpleural furrow. Third and fourth pleural furrows appear to be direct continuations of third and fourth interpleural furrows. Articulating devices on anterior edge of pygidium identical to those on thoracic segments. On interior, broad and flat doublure extends inward to a level halfway up declined portion of pleural field. Below axial tip doublure deflected up into broad sulcus.

M[illegible]cro-ornament of *Bathyurus ulu* is basically similar to that of *B. esbataottinensis* and because it is expressed better on the latter species it will be described later.

Discussion: *Bathyurus ulu* n. sp. is most similar to *B. esbataottinensis* n. sp. Differences with this and other species from the Sunblood and Esbataottine Formations are recorded under the respective species. Of the other North American species, *B. ulu* is only comparable to *B. extans* (Hall) from the Lowville Formation of New York State (Whittington, 1953, Pl. 65, figs. 1-9, 11, 12; this thesis, Pl. 5, figs. 5-10) from which it differs in the following points: *B. ulu* possesses deeper and narrower 1s glabellar furrows; a glabella that bulges slightly at mid-length; a narrower and higher axis on the cranidium, thoracic segments, and pygidium; a broader anterior cranidial border; micro-ornament consisting largely of chevron-shaped scales; and pygidial pleural furrows that are considered fainter than those of *B. extans*. The hypostomes are not compared because it seems probable that the two specimens assigned to *B. extans* by Whittington (1953, Pl. 65, figs. 13, 17) actually belong to *B. superbus*.

The species name is in reference to the shape of the dorsal part of the rostral plate which is identical to the outline of the Ulu - a knife used by the Innuit People.

Bathyurus granulosus n. sp.

Pl. 1, figs. 1-46, Pl. 5, fig. 2

Bathyurus sp. 1, LUDVIGSEN, 1975, Pl. 1, figs. 20-23.

Diagnosis: A species of *Bathyurus* with a lowly vaulted glabella that is essentially parallel-sided, but flares faintly between anterior parts of palpebral areas. Anterior portion of glabella slopes gradually and gently to relatively broad, concave anterior border. Two pairs of broad and faint glabellar furrows. Palpebral area is arcuate to semi-circular in outline, includes faintly to well defined and crescentic palpebral lobe. Gamma is right angle or slightly obtuse angle. Hypostome is rectangular in outline, lacks postero-lateral spines. Pygidium is triangular in outline; axis is high and long (sag.), crossed by 2 or 3 axial ring furrows, tends to expand very slightly posteriorly; border is broad and concave anteriorly, narrows posteriorly. Surface of carapace finely granulose.

Occurrence: Upper Sunblood Formation, Mary Range (B 1265, B 1295, B 1315), Sunblood Range (P 1090, P 1127, P 1187), Flood Creek (G 2795), and Whittaker Range (? H 410). Bathyurus granulosus Zone.

Material: 216 individuals.

Holotype: An incomplete cranidium (GSC 40336) from P 1090 illustrated on Pl. 1, figs. 1-3, Pl. 5, fig. 2.

Discussion: The following features distinguish Bathyurus granulosus n. sp. from B. ulu n. sp.

1. The glabella is less inflated, the axial furrows are not as deep, and the anterior portion of the glabella slopes gradually to the anterior border. This is best shown in lateral profile (compare Pl. 1, fig. 2 and Pl. 2, fig. 2).

2. The palpebral areas are situated farther to the rear. In B. granulosus, epsilon is located laterally to the occipital furrow (Pl. 1, figs. 1, 6, 9) and in B. ulu, epsilon is located slightly ahead of the occipital furrow

(Pl. 1, figs. 1, 37).

3. The glabellar furrows are much fainter; being broad and shallow depressions that are not evident on the interior (compare Pl. 1, figs. 1, 6, 9, 10, 13, 15, and Pl. 2, figs. 1, 6, 20, 37).

4. The hypostome is relatively longer (sag.) and lacks postero-lateral spines.

5. The pygidium is triangular in outline and the lateral margin is only slightly curved. The lateral border and doublure narrow posteriorly. The axial furrows terminate just behind fourth pleural furrow and, posterior to this, axis is expanded slightly.

6. The ornament consists of fine granules (compare Pl. 5, fig. 2 and Pl. 5, fig. 3).

Bathyurus platyparius n. sp.

Pl. 5, figs. 2, 11-24

Diagnosis: A species of *Bathyurus* with a moderately convex glabella which expands slightly in front of gamma. Glabellar furrows are not apparent. Palpebral areas are semi-circular in outline, lacks palpebral furrows. Anterior border and cephalic margins are very broad and flat. Hypostome has prominent shoulders and strong postero-lateral spines which are laterally deflected. Pygidium is sub-triangular in outline with bowed sides; axis is crossed by 3 faint axial ring furrows; border is broad, concave, and of even width around periphery. Cranidium and axial region of pygidium densely covered by fine, irregular ridges.

Occurrence: Upper Sunblood Formation, Mary Range (B 1450); Esbataottine Formation, Whittaker Range (H 1300) and Sunblood Range (P 1625). *Bathyurus ulu* Zone and *Ceraurus gabrielsi* Zone.

Material: 37 individuals.

Holotype: An incomplete cranidium (RL 0354) from B 1450 illustrated on Pl. 5, figs. 1, 11, 12.

Discussion: *Bathyurus platyparius* n. sp. differs from most species of *Bathyurus* in lacking glabellar furrows and palpebral furrows (except in small cranidia) and in possessing broad and flat cephalic and pygidial borders. The cephalic and pygidial doublures are very wide and, consequently, the anterior portion of the rostral plate is considerably longer (sag.) than the corresponding part of the plate of *B. ulu* or *B. esbataottinensis*.

The broad cephalic borders of *B. platyparius* and the absence of glabellar furrows and palpebral furrows indicate affinity with *B. superbus* Raymond. This affinity becomes pronounced when the free cheeks, hypostomes, and pygidia are taken into consideration. The broad cephalic border of *B. platyparius* continues to the apex of the genal spine resulting in a gradually tapering and stubby spine, very similar to that of *B. superbus* (compare Pl. 5, fig. 21 and Whittington, 1953, Pl. 69, fig. 28). The pygidium of *B. superbus* (~~Wilson, 1947, Pl. 2, fig. 10;~~ Whittington, 1953, Pl. 69, fig. 28) shows a wide border crossed by very faint pleural furrows and an axis crossed by only a single ring furrow. The pygidium of *B. platyparius* differs slightly in being sub-triangular, rather than sub-circular, in outline and in having more, but fainter, axial ring furrows. The hypostome of *B. superbus* (Whittington, 1953, Pl. 65, figs. 13, 17) is similar to that of *B. platyparius* in having a pair of prominent, rounded, sill-like lateral shoulders. The latter species has shoulders that extend farther anteriorly and is distinguished in possessing a pair of laterally-deflected postero-lateral spines. A few additional features set the Nahanni species apart from the eastern species. *B. platyparius* has a relatively longer glabella that is covered by fine, irregular, and discontinuous ridges; gamma is a right angle; and the palpebral areas stand as high as the highest part of the glabella. The glabella of *B. superbus* is largely smooth, but very faint ridges may be seen on its anterior portion; gamma is an obtuse angle; and the palpebral areas stand below the crest of the glabella.

The flat border of *B. platyparius* may indicate a link between *Bathyurus* and *Raymondites*, especially with the single species lacking an occipital and vertical pygidial spine, *R. longispinus* (Walcott; Whittington, 1953, Pl. 65, figs. 10, 14-16, 19). The origin of *Raymondites*, however, is unclear. It may have been derived from *Bathyurus* (Whittington, 1953, p. 654), but the recent discoveries of *Raymondites*-like pygidia in the Whiterockian of Nevada and Oklahoma (Ross, 1972; Shaw, 1974) would suggest that the genus had a much longer history than is indicated by its occurrences in the mid-continent and the Great Lakes region.

Bathyurus esbataottinensis n. sp.

Pl. 3, figs. 1-48, Pl. 4, figs. 1-25, Pl. 5, fig. 4

Bathyurus aff. *extans* (Hall), LUDVIGSEN, 1975, Pl. 4, figs. 20-23.

Diagnosis: A species of *Bathyurus* with a glabella of clavate outline - parallel-sided posteriorly and sub-circular anteriorly. Glabellar furrows are faint. Anterior margin is moderately broad and flat. Palpebral areas are large, semi-circular in outline; palpebral furrows absent (in large cranidia). Gamma is an acute angle. Hypostome is quadrate in outline; shoulders are moderately small; postero-lateral corners are rounded. Pygidium is sub-semi circular to sub-triangular in outline; border is moderately broad to very broad in large specimens; axial rings number 2 or 3; ring furrows are faint. Axial region of carapace covered by small asymmetric, chevron-shaped scales whose apices and steep sides face posteriorly. On glabella, scales are arranged in irregular, forwardly-curving rows.

Occurrence: Middle and upper Esbataottine Formation, Sunblood Range (P 1870, P 1931, P 1945-1955) and Whittaker Range (? H 900, H 1020, I 780); upper Sunblood Formation, Natla River (GSC loc. 69001, D 1342). *Ceraurus gabrielsi* Zone.

Material: 193 individuals.

Holotype: A nearly complete cranidium (GSC 40431) from P 1931 illustrated on Pl. 3, figs. 1-3, Pl. 4, fig. 2, Pl. 5, fig. 4.

Discussion: *Bathyurus esbataottinensis* n. sp. is represented by abundant and well-preserved specimens in the middle and upper Esbataottine Formation at Section P where it occurs above, and was undoubtedly derived from *B. ulu*. A comparison with *B. ulu* will serve to characterize the species.

Cranidium: The cranidium is parallel-sided between the palpebral areas and expands, in front of gamma, into a subcircular anterior portion. The glabellar furrows are considerably fainter and shorter. In large cranidia they are evident as very shallow, obliquely-disposed depressions that contain sparse micro-ornament. The furrows cannot be seen on the interior. Successively smaller cranidia possess more distinct glabellar furrows. Compare the progressively larger cranidia of the two species: *B. ulu*, Pl. 2, figs. 23, 22, 10, and *B. esbataottinensis*, Pl. 3, figs. 17, 16, 12, 6, 1. The palpebral areas are larger and oriented at right angles to the long axis of the glabella. In *B. esbataottinensis*, a line tangent to the curved anterior edge of the palpebral area is nearly transversely directed. The same line in *B. ulu* would be oriented at about 70-75° to the sagittal line. Palpebral furrows are absent in large cranidia, but may be seen in smaller cranidia. The palpebral areas attain the same height as the crest of the glabella (compare Pl. 3, figs. 2, 3 and

Pl. 2, figs. 2, 3). In front of the palpebral areas the facial suture diverge strongly and gamma is an acute angle. In *B. ulu*, it is obtuse (compare Pl. 3, fig. 1 and Pl. 2, fig. 1). The rostral suture is narrower.

Hypostome: Next to the cranidium, the hypostome is the most diagnostic element of *B. esbataottinensis*. It differs from that of *B. ulu* in possessing shoulders that do not extend as far anteriorly (compare Pl. 3, figs. 28, 33 and Pl. 2, fig. 24); lateral border furrows that are shallower and parallel; maculae that are more transversely oriented and situated slightly farther posteriorly; and rounded posterolateral corners that lack spines. The uniquely preserved specimen of a hypostome and an attached rostral plate shows the position of the hypostome relative to the cephalon. If the rostral suture of this rostral plate is juxtaposed with the rostral suture of the cranidium, it is apparent that the ventral surface of the hypostome will be set at an angle of about 45° to the horizontal (that is, the upper and lower edges of the visual surface of the eye). If the free cheeks are ~~then~~ attached to the cranidium to complete the cephalon, the hypostome will project a considerable distance beyond the ventral edge of the genal spines. The hypostome, in this position, would seriously impede forward motion of the trilobite were it not for its ability to be moved in a sagittal plane. In a previous section dealing with the life position of *Bathyurus*, evidence was brought forth to show that some species of *Bathyurus* could assume two viable positions --

one with the carapace positioned obliquely in the sediment and the hypostome extended beyond the ventral edge of the cephalon and another with the carapace sitting on the sediment surface and the hypostome tucked up into the cephalon so that its ventral surface would be flush with the ventral edge of the cephalon.

Pygidium: The pygidia of B. esbataottinensis and B. ûlu are very similar and can only be distinguished with difficulty. The only consistent difference appears to be the strength and width (tr.) of the axial ring furrows. In B. ulu, the anterior axial ring is convex (sag.) and outlined by deep and narrow articulating furrows and ring furrows; two additional rings are outlined by faint ring furrows, commonly only expressed medially (Pl. 2, figs. 4, 33). In B. esbataottinensis, the anterior ring is only faintly convex (sag.) and is outlined by a narrow articulating furrow and a shallow first ring furrow; two additional rings may be faintly outlined by weak axial ring furrows that shallow medially (Pl. 4, figs. 19, 20). Larger pygidia of B. esbataottinensis are semi-circular in outline (Pl. 3, fig. 20, Pl. 4, fig. 22) and develop very broad and concave borders.

Micro-sculpture: The dorsal surface of Bathyurus esbataottinensis is covered by distinct micro-sculpture whose orientation, shape, arrangement, and size changes consistently away from the axis. The micro-sculpture on the ventral surface of the hypostome is uniform. The implications of the micro-sculpture for the mode of life of some species of Bath-

yurus have been covered in a previous section. The micro-sculpture of *B. esbataottinensis* is closely matched in *B. ulu* and some of its characteristics may be recognized in *B. platyparius*, *B. angelini*, *B. acutus*, *B. extans*, and *B. superbus*.

The central part of the glabella and the axial lobe of the thoracic segments and pygidium of *B. esbataottinensis* is covered by densely distributed chevron-shaped scales whose apices point toward the rear (Pl. 4, figs. 1, 2, 20, 23, 24). In longitudinal profile these scales are asymmetric; possessing steeper posterior slopes. On the glabella the scales are connected in long, anteriorly-curving rows that, laterally, grade into long, sharp cuestas whose steep sides face postero-medially. The scale rows and cuestas follow the contours of the shell and are, largely, effaced in the lateral glabellar furrows and completely disappear adjacent to the axial furrows. The chevron-shaped scales are slightly finer on the axial lobe of the thoracic segments and the pygidium. An arrangement into forwardly-convex rows is only apparent on the flanks of the thoracic axis where fine cuestas curve downward and backward. If the micro-sculpture is observed at high magnification with light of low obliquity, additional features become apparent (Pl. 4, fig. 23). The scales are seen to be sharp posterior deflections off a series of fine cuesta-like ridges that are convex forwardly and have steep inner edges. The scales of a single row overlap those of the rows immediately behind. Only the ridges are present adjacent to the axial, arti[illegible]ating, and ring furrows and on the articulating half ring. The pleurae are ornamented by irregular, subdued, and cuesta-like ridges. On the posterior part of the pygidium, these strike perpendicular to the axis and have their steep edges facing posteriorly and on the anterior part of the pygidium, the thoracic segments and the posterior edge of the cephalon are curved forward so that the steep edges face postero-laterally. Similar ridges are found on the palpebral area and on the field below the visual surface of the eye. The cephalic borders and the thoracic spines are finely ridged parallel to the margins. The pygidial border contains fine ridges that are generally disposed perpendicular to the axis. The pygidial and cephalic doublure has fine terrace lines parallelling the margin. The ventral surface of the hypostome is densely covered by fine chevron-shaped scales. These scales are similar to those covering the dorsal axis, but are much smaller and their apices and steep edges point towards the front.

Family Cheiruridae Hawle and Corda

Subfamily Cheirurinae Hawle and Corda

Genus *Ceraurinella* Cooper, 1953

Type species: *Ceraurinella typa* Cooper, 1953 from the Edinburg Formation, Strasburg Junction, Virginia.

Diagnosis: Cheiruridae with parallel-sided or slightly forwardly-expanding glabellae. Three pairs of approximately equi-~~spaced~~ glabellar furrows; posterior pair deepest, inclined obliquely backwards, may be connected to occipital furrow. Basal glabellar lobes may be inflated. Anterior pairs of glabellar furrows shallow, directed inwards with slight curvature. Palpebral lobes located opposite 2p lobe or 2s furrow. Hypostome with broad lateral and posterior borders; moderately inflated middle body consisting of ovoid anterior lobe and crescentic posterior lobe with faint independent convexity; maculae small, but distinct. Pygidium triangular in outline; axis with three rings and a terminal piece. First ring bears pair of straight or curved, backwardly, outwardly, and upwardly-directed spines. Second pair of spines shorter, backwardly directed. Third pair may be short, distinctly separated spines; a single, broad spine with a median notch; a single, broad, flat spine; or a single spine equal in size to second spine pair. Thorax of eleven segments. Ornament of fine to medium-sized granules.

Discussion: The generic assignment of species of Middle and Late Ordovician Cheirurinae with rectangular-shaped glabellae and lacking coarsely pustulose ornamentation has long been in a state of uncertainty. Prior to 1913 such species were, for the main part, assigned to *Cheirurus* Beyrich (type species *C. insignis* Beyrich from the Wenlockian of Czechoslovakia). In that year Barton included *Cheirurus polydorus* Billings, *C. pompilius* Billings, *C. icarus* Billings, *C. scofieldi* Clarke from North America; *C. ingricus* Schmidt, *C. ornatus* Dalman, and *C. comes* Barrande from Europe; and two new species from the Trenton Group of southern Ontario in a new genus, *Ceraurinus*, with the type species of *C. marginatus* Barton. The type species was based on a single incomplete enrolled specimen from an unknown locality in Ontario. The choice of type species was rather unfortunate and the absence of an associated pygidium and the unavailability of topotypic material led Whittington and Evitt (1954, p. 63) to advocate suppression of the name *Ceraurinus*. Evidence will be presented later in support of retention of this name.

Ceraurinella Cooper, 1953 with the type species *C. typa* Cooper from the Edinburg Formation, Virginia was established for species similar to *Ceraurinus*, but with "anterior part of the fixed cheek narrow, a pygidium like that of *Ceraurus*", and a fine granular or tubercular ornamentation (Cooper, 1953, p. 28). Only one other species, *Ceraurinella buttsi* Cooper from the base of the Athens Formation, Alabama, was assigned to the new genus. Cooper referred to a species from the Tumbez Limestone, Tennessee as *Ceraurinus pompilius* (Billings) without commenting on its relationship to *Ceraurinella*.

The type species and another species, *Ceraurinella chondra* from the Lincolnshire Formation, Virginia were further elucidated and extensively illustrated by Whittington and Evitt (1954) who also demonstrated that, in spite of the statement of Cooper (1953), the pygidia of *Ceraurus* and *Ceraurinella* are only similar and that they differ consistently in the size and orientation of the first spine. *Ceraurus angustus* Raymond was also considered a species of *Ceraurinella* by Whittington and Evitt.

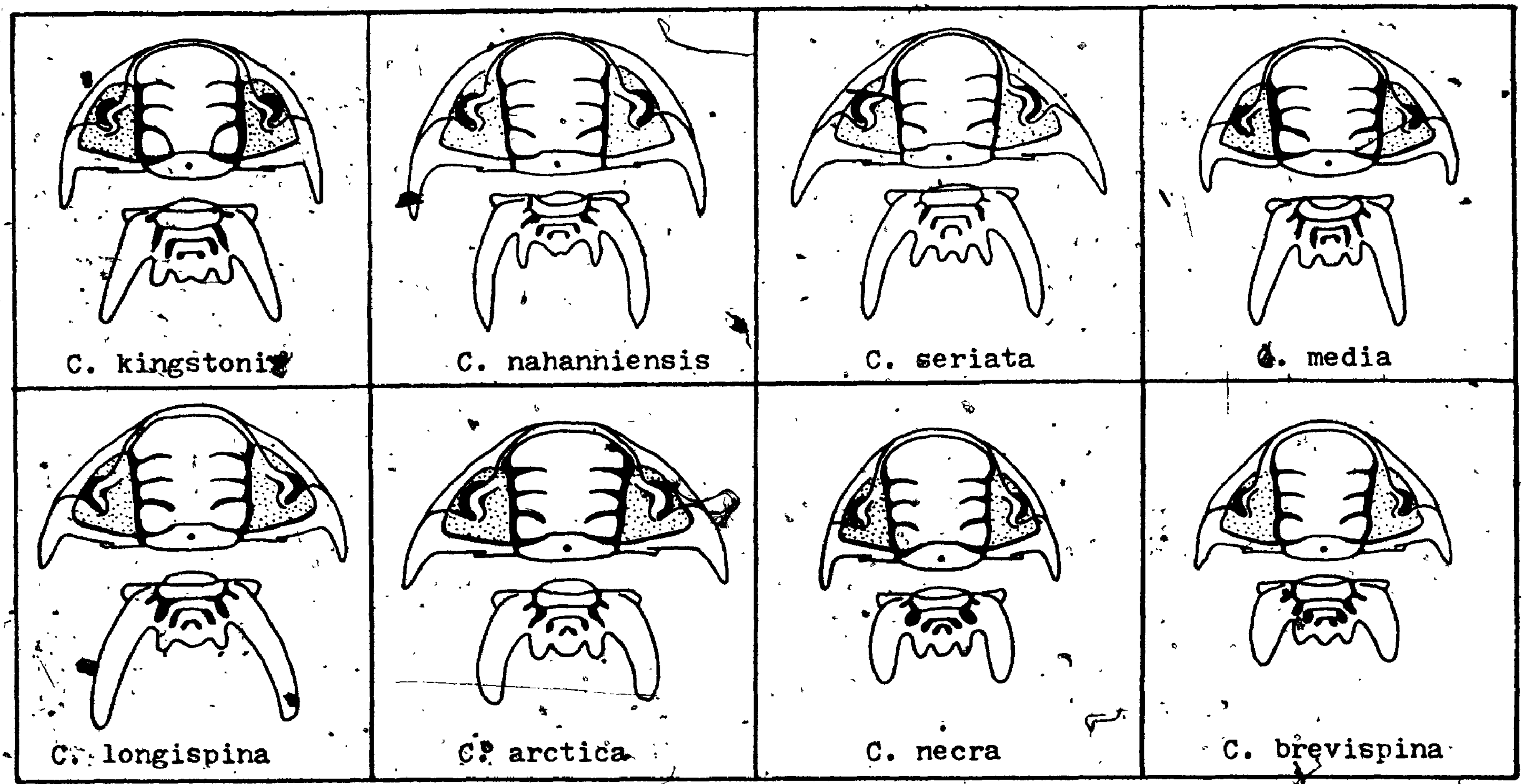
Further work on Middle Ordovician Cheiruridae added to the list of species of *Ceraurinella* at the expense of the original species group placed in *Ceraurinus* by Barton. Mannill (1958), in open nomenclature, assigned *Cheirurus ingricus*, *C. ornatus*, and *Ceraurus latifrons* Warburg from Estonia to *Ceraurinella*. Whittington (1965a) redescribed and illustrated *Cheirurus polydorus* from the Table Head Formation, western Newfoundland, and assigned that species to *Ceraurinella*. Shaw (1968) added a new species, *Ceraurinella latipyga* from the Chazy Group of New York State, and assigned *Cheirurus pompilius* to *Ceraurinella*.

Tripp (1954, 1962, 1967) described a number of Cheiruridae with rectangular-shaped glabellae from Middle Ordovician rocks of the Girvan area, Scotland under a varity of names -- *Ceraurinus craigensis* Tripp from the Craighead Mudstones, *Bartoninus dispersus* Tripp from the "Confinis" Flags, and *Ceraurinella magnilobata* Tripp from the Stinchar Limestone. Tripp (1962), in establishing *Bartoninus*, emphasized the gradational size of the three pairs of pygidial spines as the main diagnostic criterion for the genus. Lane (1971), however, maintained that a gradual decrease in spine length from the anterior to the posterior pairs is not uncommon among the Cheiruridae, apparently having developed independently in a number of lineages, and suggested that this feature is of little value as a generic character. The integrity of *Bartoninus* was further questioned by Lane in claiming that the holotype cephalon of *B. dispersus* differed from the topotypic material and should be assigned to *Ceraurinella*. Other species that Tripp (1962) assigned to *Bartoninus* were transferred by Lane into two new genera -- *Hadromeros* (type species, *Cheirurus keisleyensis* Reed from the Keisley Limestone, Westmoreland) for species with a forwardly-expanding glabella, an inflated frontal lobe and lacking an anterior border medially in front of the glabella and *Xylabion* (type species, *Ceraurinus craigensis* Tripp) for species with a parallel-sided, weakly convex glabella, a complete anterior border, and a subangular antero-lateral cephalic margin.

In 1960, Kielan following a suggestion from Whittington, reassigned her species of 1955, *Ceraurus intermedius* from the Ashgillian of Poland, to *Ceraurinella*. This generic assignment was continued by Whittington (1965b), Lane (1971), and Dean (1971a) who described conspecific material from the

Ashgillian of Britain and Eire. *Ceraurus*? *intermedius* does have a number of features in common, mainly on the cranidium and hypostome, with *Ceraurinella typa*, but the glabella differs in possessing a laterally-expanded anterior lobe and straight and transversely-directed 2s and 3s furrows. The pygidium differs notably from that of any species of *Ceraurinella* in completely lacking the second and third sets of spines. The posterior margin of the pygidium is gently curved between a pair of nearly parallel, spike-like first spines. This type of pygidial architecture, while unknown in *Ceraurinella*, is present in some species of *Ceraurus* (*C. tenuicornis* Raymond, *C. plattinensis* Foerste) and *Whittakerites* (*W. planatus*, this thesis). Furthermore, the younger species of *Ceraurinella* dealt with in this thesis (*C. arctica*, *C. necra*, *C. brevispina*) do not approach the morphology of *Ceraurus*? *intermedius* and, although this does not directly bear on the generic identity of the Ashgillian species, it does suggest that it was not a terminus of the relatively long phylogenetic lineage of species of *Ceraurinella* identified in northern Canada. A search for a phylogenetic relationship among such Balto-Scandian species as "*Paraceraurus*" *exsul* (Beyrich), "*P.*" *gladiator* (Schmidt), "*P.*" *elatifrons* (Krause), "*P.*" *latifrons* (Warburg), *Hadromeros*? *toernquisti* (Warburg), and *Ceraurus*? *intermedius* may cast light on the ancestry of *C.*? *intermedius*. For the present, this species is excluded from *Ceraurinella*.

Ceraurinella is herein suggested to constitute a rather



Text-figure 27.

Outline drawings of cephala and pygidia of eight species of <u>Ceraurinella</u> from the Esbataottine and lower Whittaker Formations, South Nahanni River area.

diverse morphological entity comprising about twenty species of Early to Late? Ordovician age. The following species are assigned and approximate ages, in terms of the North American stages, are noted:

Whiterockian: *C. polydorus* (Billings, 1865)
C.? ingrica (Schmidt, 1881)

Chazyan: *C. pompilius* (Billings, 1865)
C. buttsi Cooper, 1953
C. chondra Whittington and Evitt, 1954
C. magnilobata Tripp, 1967
C. latipyga Shaw, 1968
C. nahanniensis Chatterton and Ludvigsen, ms.
C. kingstoni Chatterton and Ludvigsen, ms.

Blackriveran: *C. typa* Cooper, 1953
C. seriata n. sp.
C. media n. sp.
C. longispina n. sp.
C. arctica n. sp.
C. scofieldi (Clarke, 1894)

Trentonian: *C. trentonensis* (Barton, 1913)
C. longifrons (Troedsson, 1928, Pl. 19, figs. 4, 5 only)
C. tenuisculpta (Bradley, 1930)
C. necra n. sp.

Edenian: *C. brevispina* n. sp.

The geographic extent of the genus shows it to be essentially a North American taxon that is widely represented in the Appalachians from Newfoundland to Alabama and in northern Canada. It is sparsely represented in the mid-continent and in the Great Lakes region. Elsewhere in North

America, records of *Ceraurinella* are few. It is present in the Great Basin (Ross and Shaw, 1971), in Oklahoma (Shaw, 1974), and in Greenland (Troedsson, 1928). Outside of North America, *Ceraurinella* occurs in Balto-Scandia (Schmidt, 1881, Mannill, 1958), in Scotland (Tripp, 1967), in Wales (Bates, 1968) and possibly on the Siberian platform (Maximova, 1955).

Ceraurinella *kingstoni* Chatterton and Ludvigsen, ms.

Pl. 6, figs. 1-40

Ceraurinella n. sp. 3, LUDVIGSEN, 1975, Pl. 2, figs. 37, 38.

Diagnosis: A species of *Ceraurinella* with a glabella that is narrowest across 2p and 3p lobes; possesses isolated and inflated 1p lobes; deep and obliquely disposed 1s furrow; and shallow and curving 2s and 3s furrows. Palpebral lobe small. First pygidial spine is straight or slightly curving; directed obliquely backwards, outwards, and upwards. Second spine is much shorter, blunt, and posteriorly directed. Third spines blunt, nearly conjoined; extend posteriorly as far as second set.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 110, A 125, A 140, A 160, P 1485). *Ceraurinella* *nahanniensis* Zone.

Material: 147 individuals.

Holotype: A complete cranidium (GSC 40382) from P 1485 illustrated on Pl. 6, figs. 1-4.

Description: Cephalon semicircular in outline;

strongly (tr.) and moderately vaulted (sag.). Glabella inflated, sub-rectangular in outline, but slightly constricted at mid-length so that maximum width (tr.) is across basal and anterior lobes. Three pairs of fairly long (exsag.) glabellar furrows; 1s initially very deep, straight, directed obliquely inwards and backwards, shallower adaxially and deflected backwards to connect with occipital furrow; 2s and 3s much shallower, sub-parallel, directed inward with slight curvature, extend about 1/3rd way across glabella. 1p lobe sub-triangular in outline, inflated, flares laterally. 2s and 3s lobes slightly shorter (exsag.) than 1p lobe, trapezoidal in outline and not inflated. Anterior lobe extends laterally as far as, and is about as long as, 1p lobe, but is not inflated. Axial furrows deep, V-shaped (tr.), deflected around inflated 1p lobe and proceed parallel with one another past 2p and 3p to deep anterior pit at 3s furrow. Pre-glabellar furrow narrow, bald; deep in front of anterior pit, become shallower and rises medially to form broad inverted V-shaped notch at midline (Pl. 6, figs. 2). Anterior border narrow (sag.), convex, widens slightly adaxially. Occipital furrow shallow and transverse, medially; deep and concave-forward, laterally. Occipital ring sub-lenticular in outline, highly arched (tr.), convex (sag.), stands about as high as highest part of glabella in front of occipital furrow, bears small median node. Cheek triangular in outline, arched (tr. and exsag.) with lateral flanks steepest; palpebral lobe occupies highest position, located fairly close to axial furrow, opposite 2p lobe. Palpebral lobe small, sub-triangular to reniform in outline, widest at mid-length, convex (tr.); bounded adaxially by narrow palpebral furrow extending in even reflexed curve from point just behind visual surface of eye to mid-length of narrow palpebral ridge of low convexity which is continuous with palpebral lobe and directed towards anterior pit. Visual surface of eye composed of numerous small lenses disposed in fine vertical files (Pl. 6, fig. 40); moderately curved in in vertical plane, strongly curved in horizontal plane through 200-220°; its base approximated by open log spiral with origin at inner edge of anterior part of eye (Pl. 6, fig. 25). Just below visual surface occurs a narrow band lacking granulation or pitting. Anterior branch of facial suture proceeds forward in straight line to point just lateral to anterior pit, then curves adaxially. In anterior view facial and rostral sutures continuous in straight line; juncture with downwardly and backwardly convergent connective sutures marked by faint V-shaped deflection. Rostral plate about as wide as occipital ring, 6 times as wide (tr.) as long (sag.), shortest sagittally, faintly convex (tr. and sag.); concave posterior side constitutes hypostomal suture. In interior view (Pl. 6, fig. 9) all four sutural edges of rostral plate sharp and bevelled inward. Posterior branch of facial suture proceeds outwards and then backwards in gentle curve. Lateral border furrow deep, V-shaped in cross-section, follows course defined by 80° arc of a circle with origin on 1p lobe; joins posterior border furrow at right angle, inside genal corner. Lateral border convex (tr.), tube-like, extended into moderately long, gradually tapering genal spine which is nearly circular in cross-section. Distal part of posterior border about as wide (exsag.) as lateral border (tr.), narrows markedly towards axial furrow. Prominent articulating flange and marginal connective device occur on posterior edge of cephalon. Entire cephalon, except furrows and most of posterior border, finely granulose. Distribution of granules varies somewhat; being dense on palpebral lobe and on lateral border and sparse on adaxial part of cheeks. In addition, entire cheek inside border furrow, except palpebral lobe, palpebral ridge, and narrow strip surrounding facial suture, possesses fine and closely spaced pitting.

On inner surface of cephalon, occipital doublure curves forward to occipital furrow. Distal part of occipital furrow extended as high tongue-shaped appendifer. 1s furrow carries high, thin, blade-like appendifer. 2s and 3s furrows appear as low, narrow, slightly curved ridges; axial furrow as a broad, massive ridge. Anterior and lateral parts of doublure fairly broad and gently convex. Facial suture crosses doublure in faint curve to postero-lateral corner of doublure. Posterior part of doublure narrower, attenuates gradually to outer edge of articulating flange.

Hypostome sub-pentagonal in outline. Length (sag.) approximately equal to maximum width (tr.) across anterior wings. Middle body ovoid with maximum width and convexity between anterior wings; composed of large, inflated, egg-shaped anterior lobe which narrows and decreases in convexity backwards to merge with small crescentic posterior lobe. Independent nature of anterior and posterior lobes only marked by slight increase in convexity at tips of latter. Very narrow unornamented middle furrow initiated in deep lateral border furrow and proceeds obliquely backwards, just in front of small oval macula located at antero-lateral tip of posterior lobe. Lateral border furrow deep, broad; opposite macula, it narrows and shallows to become evenly curved posterior furrow. Lateral border flat, tilted inwards, narrows slightly backwards from maximum width (tr.) at prominent shoulder; continuous with broad (sag.), flat posterior border. Anterior margin described by 60° arc of circle with origin just behind mid-point of posterior margin. Anterior border present laterally, but absent medially as middle body extends to anterior margin. Lateral margins nearly straight, converge backwards at 50-60°. Posterior margin slightly convex, its mid-point marked by small dorsally deflected notch. Postero-lateral corner forms angle of 110-120°; corner is sharp with slightest suggestion of a small spine. Posterior part of doublure broad, slightly concave; lateral part flexed obliquely at mid-length to form prominent shoulder which, along its inner portion, supports nearly vertical, obliquely oriented, rectangular posterior wing. In front of shoulder, doublure deflected into deep, antero-laterally directed antennal notch and, forward of this, into a high, flaring anterior wing which carries a stout, dorsally directed wing

3 OF/DE 6

process. Anterior margin to a point halfway up anterior wing formed by sharp hypostomal suture. Ventral surface of hypostome finely granulose; furrows and base of anterior wings nearly bald.

Number of thoracic segments unknown. Axis convex, approximately 1/3rd width (tr.) of entire segment. Articulating furrow broad U or W-shaped, shallowest medially. Inner portion of pleura half as wide as axis; inflated, crossed by diagonal, postero-laterally directed, deep and narrow pleural furrow. Outer portion part of pleura extended into tapering spine which curves downwards and slightly backwards. On inner surface, axial doublure extends forward to articulating furrow. Forwardly diverging, tongue-shaped appendifers arises from outer part of articulating furrow. Articulating devices as described by Whittington and Evitt (1954, p. 23, 65) consisting of prominent articulating, flange marginal connective device, ring socket and process, and axial furrow socket and process. Dense granulation on central part of axis; sparse granulation on pleural field.

Pygidium sub-triangular in outline (without spine), width (tr.) twice length (sag.). Axis short, triangular in outline, composed of an articulating half ring, three straight axial rings, and a short terminal piece separated by nearly straight articulating furrow and axial ring furrows. Axis initially high and convex, becoming faintly convex near terminal piece; outlined by very faint axial furrows. First axial ring convex (sag.), 4 times as wide (tr.) as long (sag.). Second and third segments slightly shorter (sag.) than first and progressively narrower (tr.). First and second axial ring furrows shallow at mid-line and adjacent to faintly impressed axial furrows; between these shallow zones, furrows descend into deep appendiferal pits. From distal ends of first axial ring furrow a pair of elongate and deep pits (representing interpleural furrows) extend toward posterior margin between first and second pygidial spines. Similar, but shorter (exsag.), pits extend posteriorly from distal ends of second axial ring furrows. Third axial ring furrow moderately shallow, crescentic, joins pair of fairly deep, circular pits denoting posterior end of axial lobe. Anterolateral corners, including articulating flange, triangular in outline and isolated by narrow furrow proceeding out and backwards from axial furrow. Inner portion of pleura narrow. Short and shallow pleural furrow separated from axial ring of first segment by faint axial furrow. First segment bears thick, long, and gradually tapering spine which is transversely oval in cross-section and about as long as width across anterior edge of pygidium. Spine may be straight (Pl. 6, fig. 13) or may have slight curvature (Pl. 6, fig. 17); in dorsal view directed obliquely backwards at 15 to 20° to sagittal line; in lateral view directed about 45° upwards. Second segment bears short, blunt, backwardly directed spine. Third set of spines shorter, closely spaced, nearly conjoined in some specimens; extend nearly as far posteriorly as second set. Pleural field beneath first and second spines descends vertically to right-angled margin which, below third spine set, is curved upwards into broad sulcus. Doublure flat, deflected upwards and backwards into U-shaped notch behind axis. Articulating, first, and second axial ring furrows carry small appendifers similar to those on thorax. Sparse to dense granulation on axial rings, dorsal and ventral sides of pygidial spines, and on doublure. Inner portion of pleura nearly bald.

Discussion. *Ceraurinella kingstoni* Chatterton and Ludvigsen is most similar to *C. magnilobata* Tripp, 1967 from the Stinchar Limestone of Girvan, within the limitations imposed by the preservation of the Scottish material. These two species have a common glabellar shape, share the large inflated basal glabellar lobes, and have very similar hypostomes with distinct middle furrows separating distinct posterior and anterior lobes and broad and flat posterior and lateral borders. The relative convexity of the two species cannot be compared. The finer cranidial ornamentation and a greater length to width ratio of the glabella appears to distinguish the Esbataottine species. The prominent antero-lateral corners of the pygidium of *C. magnilobata* are not seen in my material.

Ceraurinella sp. from the Garn Formation of northern Wales (Bates, 1968) is rather similar to *C. kingstoni*, but the glabellar furrows 2s and 3s appear to be slightly longer and are more curved.

From *Ceraurinella typa* Cooper, *C. kingstoni* is distinguished by its finer granulose ornamentation, smaller palpebral lobes, more inflated basal glabellar lobes, and in possessing a hypostome with deeper middle furrows and broad and flat lateral and posterior borders. The pygidia of the two species are very similar, but the Esbataottine species differ in having a high and convex axial region and straight ring furrows.

The cranidium of C. kingstoni differs slightly from that of Ceraurinella chondra Whittington and Evitt, 1954 in possessing broader (exsag.) lateral glabellar furrows, slightly broader anterior border, and more inflated and distinctly isolated basal glabellar lobes. The long curved first pygidial spines of C. chondra are distinct. And, in contrast with the Esbataottine species, the third set of spines of the Appalachian species project beyond the second set.

Ceraurinella polydorus (Billings, 1865) possesses a barrel-shaped glabella; a short (exsag.) anterior glabellar lobe; markedly curved and deep glabellar furrows; deep and long palpebral furrows; and an anterior margin which is expanded distally. The pygidium is rather similar to that of C. kingstoni; the greatest differences are the more erect first spines and the widely separated third spines (compare Pl. 6, fig. 15 and Whittington, 1965a, Pl. 60, fig. 10).

The convexity of the cephalon and the glabella, the shape of the glabella, the size of the palpebral lobes, and the inflated basal glabellar lobes of Ceraurinella kingstoni readily separate this species from C. pompilius (Billings), C. buttsi Cooper, C. latipyga Shaw, and C. nahanniensis Chatterton and Ludvigsen.

In the lower Esbataottine Formation in the Sunblood Range, Ceraurinella nahanniensis occurs in each of ten collections assigned to the C. nahanniensis Zone and is much more abundant than C. kingstoni (1102 individuals of C. nahanniensis compared to 149 individuals of C. kingstoni). The distribution of the two species is noteworthy and is not brought out in the generic compilation (Text-fig. 10). At section P, C. kingstoni is more abundant than C. nahanniensis in only a single collection (P 1485). A few meters higher in the section, in a very large collection (P 1497), C. nahanniensis occurs abundantly to the exclusion of C. kingstoni. C. nahanniensis occurs without C. kingstoni in the next four collections. Nearby, at Section A, the species co-occur in every collection, except one, assigned to the C. nahanniensis Zone; but C. nahanniensis always dominates. This indicates that an unknown controlling and isolating mechanism governs the distribution of species of Ceraurinella within the Calyptaulax-Ceraurinella Biofacies.

The species name is for D.R. Kingston, the first investigator of Ordovician rocks in the South Nahanni River area.

Ceraurinella nahanniensis Chatterton and Ludvigsen, ms.

Pl. 7, figs. 1-35, Pl. 8, figs. 1-21

Ceraurinella n. sp. 2, LUDVIGSEN, 1975, Pl. 3, figs. 16, 17.

Diagnosis: A species of Ceraurinella with a glabella that expands slightly forwards; moderately deep and obliquely-disposed ls furrows; slightly inflated lp lobe which is not isolated; and narrow, slightly curving 2s and 3s furrows. Palpebral lobe large. Eye located far out on cheek, just inside lateral border furrow. First pygidial spine long, slender, gently curved. Second spines much shorter, slender, gently curved; aligned in same plane as base of first spine. Third spines nearly conjoined in a single flat, triangular median spine with twin apices.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 110, A 125, A 140, A 160, P 1440, P 1485, P 1497, P 1512, P 1520) and Whittaker Range (H 800-820). *Ceraurinella nahanniensis* Zone.

Material: 1102 individuals.

Holotype: A complete cranidium (GSC 40399) from P 1497 illustrated on Pl. 7, fig. 1-3.

Description: Cephalon sub-semicircular in outline, sagitally and transversely gently convex. Glabella nearly straight sided, moderately vaulted, expands slightly forward to maximum width (tr.) across mid-length of anterior lobe, anterior portion evenly rounded. Three pairs of short (exsag.) lateral glabellar furrows extend almost 1/3 way across glabella 1s furrow moderately deep, directed obliquely inwards and backwards; initially straight, inner part with slight deflection towards, but does not reach, occipital furrow; 2s nearly straight, transversely directed, very faintly impressed; 3s faint abaxially, moderately incised near axial furrow, directed inwards with very slight forward curvature. Axial furrows straight, except for slight bowing around 1p lobes, terminate at anterior pit just in front of 3s furrow. 1p, 2p, and 3p lobes about same length (exsag.); anterior lobe about 1 1/2 times as long (exsag.) as either of the posterior lobes, expands slightly laterally in front of anterior pit. Pre-glabellar furrow short (sag.), bald; in anterior view nearly straight with only the slightest median rise. Anterior border narrow, convex (sag.); in anterior and dorsal view, of constant width around periphery of anterior lobe. Occipital furrow moderately deep and narrow behind 1p, swings forward slightly and proceeds in straight course across mid-portion of glabella. Occipital ring with distinct median node; longest (sag.) medially, slightly shorter (tr.) than, but with same convexity as, glabella across 1p. Palpebral lobe large, length (exsag.) 1/4 that of glabella, situated on highest part of cheek opposite 2s, 2/3rds the distance from axial furrow to border furrow. Palpebral lobe broad, crescent-shaped, sharply raised over cheek, continuous anteriorly with low, narrow palpebral ridge which swings inward and forward toward anterior pit. Sinuous palpebral furrow deepest behind mid-point of palpebral lobe. Visual surface reniform, height 1/3 width along base, moderately curved in vertical and markedly (through about 210°) in horizontal plane; consists of closest-packing array of sub-hexagonal to sub-circular lenses arranged in diagonal files. From anterior part of palpebral lobe, facial suture proceeds forwards and inwards along path following arc of circle centred on median occipital node. Juncture of facial and rostral sutures marked by slight downward cusp-shaped deflection at connective suture. From base of eye, posterior part of facial suture curves outwards and slightly forward to border furrow, then it is abruptly deflected obliquely backwards in straight line to lateral margin. Lateral border furrow narrow, moderately deep for entire length, except for effaced portion in front of palpebral ridge. Genal spine long, gradually tapering, backwards with slight curvature; flattened in cross-section in same plane as outer portion of cheek, at approximately 45° to plane of symmetry of cephalon (in anterior view).

On inner surface occipital doublure reaches occipital furrow. Tongue-shaped appendifers protrude inwardly and downwardly from outer part of occipital furrow. 1s extended as high, thin, blade-like appendifer; 2s and 3s as thin, low, ridges. Lateral and posterior portions of doublure (including rostral plate) broad, evenly curved. Posterior portion narrower (exsag.), thins gradually towards distal end of articulating flange.

Hypostome sub-oval to sub-pentagonal in outline; length (sag.) equals maximum width (tr.) across shoulders. Middle body ovoid in outline, moderately convex, narrowing slightly backwards, maximum width along line joining anterior wings. Anterior lobe nearly circular in outline, its posterior end extended to form trunk of inverted mushroom-shaped posterior lobe. Middle furrow narrow, forms postero-lateral border of anterior lobe; its posterior edge defines fairly large macula.

Lateral border furrow broad, deep, V-shaped in cross-section (tr.); continuous with narrower (sag.) and shallower posterior furrow. Lateral border slopes inwardly, rises steeply out of lateral furrow. Posterior border gently convex (sag.). Anterior border furrow very sharp and narrow; anterior border lacking, medially. Posterior margin straight; tiny spines at postero-lateral corners. Anterior margin defined by 60° arc of circle centred at mid-point of posterior margin. From shoulder, lateral margin curves gently backwards to postero-lateral corners. On inner surface, doublure behind shoulder, moderately broad, flat with its inner part curved noticeably upwards. Anterior wing high, carries distinct knob-like anterior wing process. Deep, trough-shaped lateral notch separates anterior from posterior wing. Posterior furrow expressed on interior as broad, arcuate ridge just in front of interior edge of doublure.

Number of thoracic segments unknown. Except for ornament, segments identical to those of other species.

Pygidium (without spines) triangular in outline, length (sag.) slightly less than 1/2 width (tr.). Axis short (sag.), moderately convex (tr.), narrowing and decreasing in convexity backwards; composed of articulating half ring, three axial rings, and a short, oval terminal piece separated by narrow, deep axial ring furrows. Axial furrow shallow, and narrow anteriorly; very faint posteriorly. Ring furrows terminate in deep, oval, postero-laterally disposed pits (representing interpleural furrows) which decrease in size and depth posteriorly. Broad furrow continues out of first pit to demarcate and separate inner parts of first and second pleural spines. Similar, but narrower, furrow separates second and third spines. Pleura very narrow; its anterior portion inflated, crossed by very short pleural furrow. Thin, deep interpleural furrow proceeds outwards from appendiferal pit at junction of articulating and axial furrow to isolate thin, band-like strip which contains articulating flange at its anterior edge. First segment bears long, very gradually tapering spine; curving outwards, backwards and slightly upwards, transversely oval in cross-section. Distal end of spine parallel to sagittal line; its tip carries tiny accessory spine. Length of spine slightly more than width (tr.) of anterior part of pygidium (Text-fig. 28). Second segment bears much shorter, gradually tapering spine, gently curving backwards and slightly outwards. Third spines almost completely conjoined in a broad-based, obtusely-triangular spine whose composite nature is revealed by a small median notch. Marginal spines aligned in single plane oriented at slight angle (not more than 5^{o}) to horizontal base of pygidium. Ratio of distance of first, second, and third spine tips from anterior edge of pygidium, measured in exsagittal line, is 10, 6, and 5. From beneath first and second spine pleural field descends vertically a short distance to sharp angulate margin. In posterior view, axial part of margin curves upwards in a gentle fold. Doublure narrow, triangular in outline; its inner portion curves sharply inwards and upwards. Outer parts of articulating and first ring furrows extended into small appendifers.

Ornament of very fine to fine granulation distributed as follows: Dense granulation on glabella (excepting bald glabellar furrows), anterior and lateral cephalic borders, outer parts of cephalic doublure, palpebral rim and eye ridge, hypostome (excepting furrows and doublure), central part of thoracic and pygidial axis, and dorsal and ventral sides of pygidial spines. Sparse granulation on posterior border of cephalon, pleural lobes on thorax and pygidium. Moderately sparse granulation and scattered fine pitting cover cheeks inside borders (excepting palpebral rim and eye ridge). Inner edges of cephalic, hypostomal, and pygidial doublure bald, as is outer and inner sides of thoracic spines.

Discussion: The following features distinguish Ceraurinella nahanniensis Chatterton and Ludvigsen from C. polydorus (Billings), C. typa Cooper, C. chondra Whittington and Evitt, C. magnilobata Tripp, and C. kingstoni Chatterton and Ludvigsen.

1. The eye is located far out on the cheek, immediately adjacent to the lateral border furrow.

2. 1s furrow does not connect with the occipital furrow and the 1p lobe is less inflated.

3. The genal spines are distinctly flattened.

4. The second pair of pygidial spines are relatively long and thin and the first pair of spines is aligned in the

same plane as the second and third pairs.

It is readily apparent that similarly-preserved cranidia of Ceraurinella latipyga Shaw from the Chazy Group of New York, C. pompilius (Billings) from the Mingan Formation on the Mingan Islands and the Lenoir and Tumbez Limestones of Virginia, and C. buttsi Cooper from the Athens Formation of Alabama are nearly identical (Cooper, 1953, Pl. 11, figs. 5, 6, 14; Shaw, 1968, Pl. 15, figs. 16, 22, 23). The decision of whether they are, in fact, conspecific must await discovery of well preserved pygidia. These species are probably of Chazyan age (late Pygodus serrus and P. anserinus Zones of Bergström, 1971). C. pompilius and C. buttsi are known only from incomplete cranidia. The pygidium supposedly belonging to C. pompilius illustrated by Cooper (1953, Pl. 11, fig. 7) is too fragmentary to be of any assistance in deciding on its structure. Shaw (1968) has illustrated two immature and one mature pygidium of C. latipyga. The mature pygidium, however, is rather fragmentary and appears to be pathological. C. latipyga appears to differ in the following points from C. nahanniensis:

1. The 1s furrow is complete, or nearly so, resulting in an isolated, triangular 1p lobe.

2. The eyes are located closer to the axial furrow.

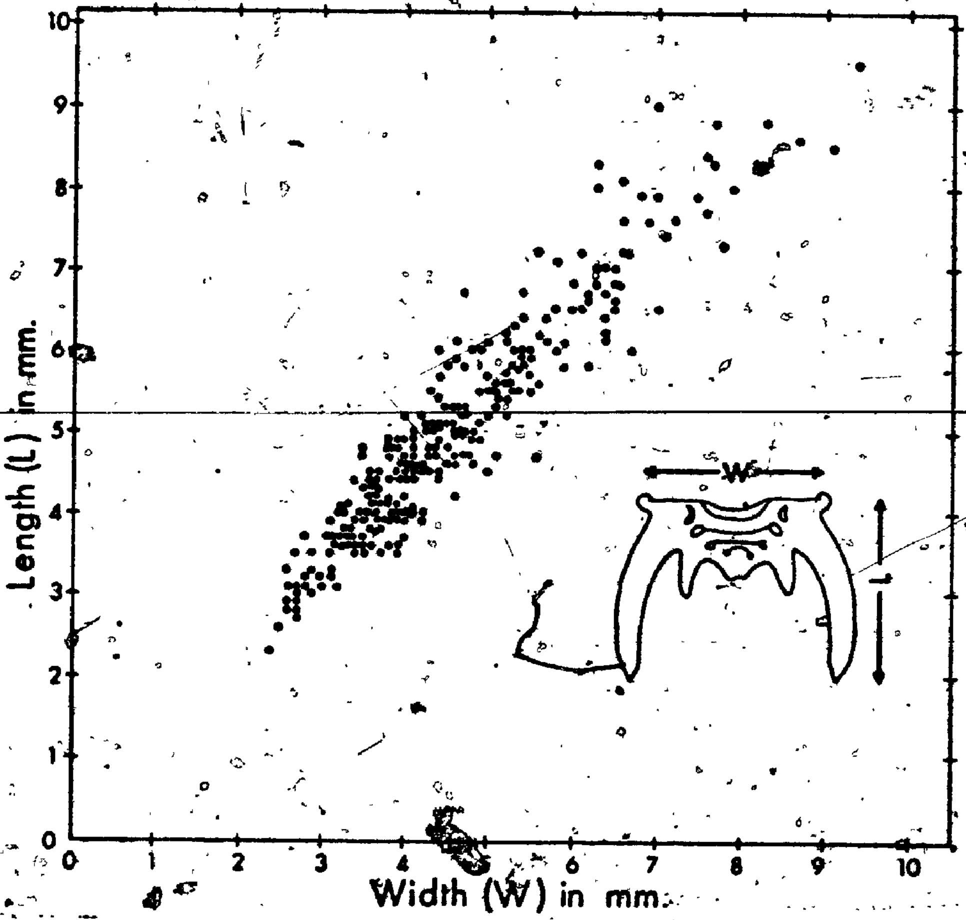
3. The hypostome possesses a pair of prominent postero-lateral spines.

4. The second pair of pygidial spines is much shorter than in C. nahanniensis and the third pair is widely separ-

ated.

Measurement of width (across anterior margin) and length (of first spines) of a large collection of holaspid pygidia of *Ceraurinella nahanniensis* from P 1497 (Text-fig. 28), shows the size increase to be isometric, but does not allow the recognition of successive instars as has been accomplished for *Trinodus elspethi* (Raymond) by Hunt (1967) and *Diacanthaspis cooperi* by Whittington (1957).

Bergström (1973, p. 25, Fig. 9) suggested that the lateral thoracic spines of *Ceraurinella typa* abut edge to edge during enrollment and thus act as the limiting devices. The only enrolled specimen of *Ceraurinella* illustrated to date is the unique silicified specimen of *C. nahanniensis* (Pl. 7, figs. 10, 34) which lacks only the posterior two(?) thoracic segments and the pygidium. Here, the lateral thoracic spines are not aligned edge to edge, but instead each spine passes over the anterior part of the spine of the succeeding segment. Since the morphology of thoracic segments of species of *Ceraurinella*, where it is known, is remarkably uniform, this style of enrollment is probably pervasive. When fully enrolled, a portion of the pygidium and all the pygidial spines of *C. nahanniensis* would probably be visible in front of the cranidium. This can be contrasted with the appearance of the enrolled specimen of *Paraceraurus aculeatus* (in Öpik, 1937, Pl. 17, figs. 1, 2). In that specimen, the tip of the pygidium is positioned below the posterior part of the hypostome and only the distal tips of the first



Text-figure 28.

Scatter diagram of 258 pygidia of *Ceraurinella nahanniensis* Chatterton and Ludvigsen, ms. from F 1497 relating length of first pygidial spine to width of pygidium across anterior margin.

pygidial spines would have been visible in front of the cephalon.

Ceraurinella seriata n. sp.

Pl. 8, figs. 22-42

Diagnosis: A species of *Ceraurinella* that differs from *C. nahanniensis* chiefly by the disposal of the third set of pygidial spines. These are closely aligned and discrete for nearly their total length.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 220, A 240, A 247, P 1575, P 1585, P 1625). *Bathyurus ulu* Zone.

Material: 80 individuals.

Discussion: *Ceraurinella seriata* n. sp. differs in a few minor, but persistent, features from the slightly older *C. nahanniensis* Chatterton and Ludvigsen. The most obvious of these is the aspect of the third set of pygidial spines. In *C. nahanniensis*, these spines are nearly conjoined in a single, broad, flat, and triangular spine whose dual composition is revealed by a small median notch. In *C. seriata* these spines are closely aligned, but discrete and separated for nearly their total length. The cephala of the two species are very similar, but *C. seriata* has a less vaulted cranidium and a glabella that is not so inflated (compare Pl. 7, fig. 3 and Pl. 8, fig. 23). In addition, the palpebral lobes of *C. seriata* are slightly larger, the anterior cephalic border narrower, and the second and third glabellar furrows are shorter (exsag.) and sharply incised (compare Pl. 7, fig. 33 and Pl. 8, fig. 42).

Ceraurinella arctica n. sp.

Pl. 10, figs. 1-34

Ceraurinella n. sp. 7, LUDVIGSEN, 1975, Pl. 4, fig. 7.

Diagnosis: A species of *Ceraurinella* with a flatly convex glabella that expands slightly forwards. 1s furrow is deep and backwardly curving, does not reach occipital furrow. 2s and 3s furrows slightly curved, subparallel. Palpebral lobe is large. Hypostome has evenly rounded postero-lateral corners. Pygidium has five spines; first long (ratio of length of spine to width of pygidium across anterior margin is 0.86), flatly oval in cross-section, directed backwards with slight outward and upward curvature; second much shorter, blunt, directed backwards; broad, tongue-shaped spine occupies median position.

Occurrence: Esbataottine Formation, Flood Creek (G 3195); Upper Esbataottine Formation, Sunblood Range (P 2038, P 2050); and upper Sunblood Formation, Mary Range (B 1510-1520). *Ceraurinella longispina* Zone.

Material: 145 individuals.

Holotype: A complete cephalon including free cheeks, rostral plate, and hypostome (RL 0001) from P 2050 illustrated on Pl. 10, figs. 1-5, 31-34.

Description: Cephalon nearly semi-circular in outline; transversely gently convex, sagitally slightly less so. Glabella moderately convex posteriorly, flatly convex anteriorly. Minimum width, across occipital ring is 5/6[illegible]s of maximum width across anterior lobe. Axial furrows deep, straight, slightly diverging as far forward as anterior pit where they are abruptly bowed slightly outwardly before turning inwardly to become pre-glabellar furrow. Three pairs of narrow, sharply incised glabellar furrows extend about 1/3 way across glabella. 1s deep, curved inwards and slightly backwards with marked backward deflection along its inner portion, which does not, however, reach occipital furrow. 2s and 3s furrows sub-parallel, slightly curved, directed inward and very slightly backward, become larger (exsag.) and deeper adjacent to axial furrow. Lateral glabellar lobes with slight independent convexity, most pronounced in 1p lobe; are sub-rectangular in outline, except for anterior lobe which is sub-triangular. Occipital furrow deep behind 1p lobe, swings gently forward and becomes narrower and shallower along median part. Deep anterior pit located just forward of juncture of 3s furrow and axial furrow. Pre-glabellar furrow narrow, sharp; in anterior view it rises faintly toward midline of glabella. Anterior border moderately wide (sag.), convex; in dorsal view, its width is constant around periphery of frontal lobe; in anterior view, it is markedly broadened in its central portion due to ventral migration of rostral suture (Pl. 10, fig. 7). Rostral suture is straight, slightly narrower (tr.) than width of glabella across occipital furrow. Cheek triangular, eye located centrally on highest point from which cheek slopes away in all directions. Palpebral lobe located opposite 2p lobe and 1s furrow; moderately large, length (exsag.) 1/4 that of glabella. Palpebral lobe delimited abaxially by short crescentic palpebral furrow; continuous anteriorly with faintly outlined palpebral ridge which curves forward to meet axial furrow at anterior pit. Visual surface curved moderately in a vertical plane and markedly (through 160°) in a horizontal plane. Anterior part of facial suture curves forward from palpebral ridge to a point opposite mid-length of anterior lobe, then turns forwards inwards in a straight path to cross anterior border and curves downward to meet rostral suture on ventral side of posterior margin. Connective suture short, straight. Rostral, hypostomal, and connective sutures (Pl. 10, fig. 33) isolate wide (tr.) and narrow (sag.) rostral plate, narrowest at midline, gently convex (sag.), area adjacent to hypostomal suture smooth. Posterior part of facial suture follows an evenly curved outward and downward course. Lateral border furrow broad, moderately shallow; interrupted by posterior facial suture (Pl. 10, fig. 34). Genal spine triangular, short, transversely oval in cross-section, directed obliquely backwards.

On inner surface, occipital doublure curves forward to occipital furrow. Outer part of occipital furrow carries downwardly and inwardly directed tongue-shaped appendifer.

1s extended as high, thin, blade-like appendifer. 2s and 3s appear as thin, slightly curving ridges. Anterior and lateral doublure gently convex, of constant width. Posterior portion much narrower, continues adaxially to distal end of articulating flange halfway between genal spine and axial furrow. Inner edge of anterior portion of doublure turned slightly upwards to receive anterior margin of hypostome. The fit is perfect. Deep pits on external side of cheek inside lateral border furrow, appear on interior as slightly raised nodes of very thin shell material. Glabellar interior smooth.

Hypostome sub-triangular to sub-trapezoidal in outline, length (sag.) slightly less than maximum width across anterior wings. Middle body moderately convex, divided into suboval anterior lobe with maximum convexity just forward of line joining anterior wings and narrow, crescentic posterior lobe with slight independent convexity. Lateral and posterior border furrows confluent, shallow and broad; anterior border furrow sharply incised, convex forwardly. Bald middle furrow initiated adaxially of shoulder, continues obliquely inwards and backwards to bound anterior side of small oval macula. Lateral border flatly convex, inwardly sloping, continuous with flatly convex posterior border; anteriorly it is deflected slightly outwardly and abruptly constricted at base of anterior wing. Anterior margin approximately described by 80° arc of circle with axis at mid-point of posterior border. Anterior border attenuates medially. Posterior margin evenly curved, its mid-point marked by minute dorsally-deflected notch. Posterior part of doublure narrow, its inner edge with distinct upward deflection. Doublure widens and rises towards rectangular, obliquely oriented posterior wing. Shoulder preminent, evident as flexure of doublure which rises to base of posterior wing. Anterior wing high, carries small node-like wing process at the apex of its dorsal side. Between anterior and posterior wings, doublure depressed into U-shaped, postero-laterally disposed antennal notch.

Thorax of eleven segments. Entire width (tr.) of first segment 4/5ths and width of eleventh segment 2/5ths that of cranidium across tip of genal spines. Axis narrows gradually backwards, width (tr.) at eleventh segment 2/3rds that at first. Axis convex, 1/3 width that of entire segment. Inner portion of each pleura inflated, crossed by short, backwardly and outwardly directed pleural furrow. Articulating flange extends along edge of pleura from axial furrow to base of spines, defined by narrow flange furrow. Outer part of pleura extended into long, gradually tapering, slightly backwardly directed spines. On inner surface outer part of articulating furrow rises to form tongue-shaped, obliquely disposed appendifer. Pleural doublure extends forward to articulating furrow and is covered by articulating half-ring of following segment.

Pygidium (without spines) sub-triangular in outline, width (tr.) twice length (sag.). Axis moderately convex at anterior margin, width (tr.) slightly less than 1/2 total width, consists of three narrow axial rings separated by axial ring furrows. Articulating stretched W-shaped, short (sag.), descends laterally into deep appendiferal pit. First axial ring convex (sag.); terminates laterally against moderately deep, narrow axial furrow. Second and third rings moderately convex, bounded laterally by very faint axial furrows. First axial ring furrow straight between axial furrows, extended postero-laterally as deep, elongate pit (representing interpleural furrow). Second axial ring furrow straight, connected laterally to pair of deep, oval, posteriorly directed pits. Third axial ring furrow small, crescent shaped. First pleural furrow short, diagonal, divides narrow inflated pleura. First segment bears long, slightly curved spine which gradually tapers to blunt point. Spine transversely oval in cross-section (about twice as wide as high); in dorsal view, directed backwards and outwards for 2/3rds length, then backwards for last 1/3rd. In lateral view, directed gently upwards with gradual increase in curvature along length of spine. Spine on second segment much shorter, blunt, directed backwards. Single, short, broad-based spine occupies central position. Width (tr.) of central spine twice that of second spine, length about the same. Doublure narrow, sharply flexed, distinct posterior U-shaped sulcus at posterior termination. Articulating and first axial ring furrows carry appendifers similar to, but smaller than, those on thorax.

Dense, even granulation covers entire exoskeleton with following exceptions which are smooth: Undersurface of genal spines and adjacent doublure, inner portion of doublure of cephalon, doublure of hypostome, under and outer surface of thoracic spines. Postero-lateral part of cephalon, just in front of spine on first thoracic segment, has scattered granules. In addition to fine granulation, cheek inside border furrows (excepting palpebral lobe and palpebral ridge) finely pitted.

Discussion: Descriptions of *Ceraurinella longispina* n. sp., *C. necra* n. sp., and *C. brevispina* n. sp., take the form of comparisons with *C. arctica* n. sp. These species are defined chiefly by the length and direction of the first pygidial spines and this information is summarized on Text-figure 20. Each of the species listed above possesses five pygidial spines and this feature renders them unique among the species of *Ceraurinella*. Indeed, only few cheirurid genera possess an uneven number of pygidial spines. *Paraceraurus* Mannill and *Cyrtometopus* Angelin have seven and *Osekaspis* Prantl and Pribyl has five. Of the Silurian and Devonian genera *Cheirurus* Beyrich and *Crotolocephalina* Pribyl and Vanek possess three pairs of pygidial spines and a short terminal mucronation which, in *Chizoon* Lane, is developed into a spine of similar size to the other pygidial spines. The uneven spine number seen in the species of *Ceraurinella* originated in a different manner than the uneven number displayed by the other genera. That is, by progressive coalescence of the third spine pair.

Ceraurinella longispina n. sp.

Pl. 9, figs. 1-31

Ceraurinella n. sp. 6, LUDVIGSEN, 1975, Pl. 4, figs. 1, 2.

Diagnosis: A species of Ceraurinella with a parallel-sided and flatly convex glabella. 1s furrow is deep, curving, does not reach occipital ring. Pygidium has five spines; first long (ratio of length of spine to width of pygidium across anterior margin is 1.03), flaring, generally with marked upward curvature; second short, blunt, backwardly directed; median spine short, broad.

Occurrence: Upper Esbataottine Formation, Sunblood Range (A 615, P 2010, P 2038). Ceraurinella longispina Zone.

Material: 256 individuals.

Holotype: A complete cranidium (RL 0011) from P 2038 illustrated on Pl. 9, figs. 1-4, 31.

Discussion: The parallel-sided and flatly convex glabella and the pygidium with five spines, of which the first pair is long, flaring, and upwardly curving, readily distinguish C. longispina n. sp. from other species. It is most similar to C. arctica n. sp. which possesses a glabella that expands slightly forwardly and shorter first pygidial spines. The granular ornament on the pygidium is coarser than in C. arctica and is more sparsely distributed. On some specimens of C. longispina the central three spines are nearly bald and the granules are confined to the tips, while other pygidia from the same sample are entirely covered by fine granules. *Ceraurinella kingstoni* Chatterton and Ludvigsen and *C. media* n. sp. from lower in the Esbataottine Formation have pygidia on which the granular ornamentation is sparsely distributed near the base of the first spines and on the central spines and *C. arctica* from the highest Esbataottine Formation have pygidia that are completely covered by fine granules. The intermediate distributional pattern of ornamentation seen in *C. longispina* appears to reflect its derivation from *C. kingstoni* (via *C. media*) and its ancestral relationship to *C. arctica* and younger species. *C. media* possesses a more inflated glabella that is slightly indented antero-medially, slightly smaller palpebral lobes that are located closer to the glabella, and a pygidium with straight and less flaring first spines.

The anterior cranidial border of *C. longispina* is slightly expanded medially resulting in an angulate antero-median cranidial margin. This effect is caused by a forward migration of the rostral suture. The same feature is evident in later species of the *C. longispina*/*C. brevispina* lineage, but in these species the sutural shift has proceeded forward and downward across the anterior edge of the cephalon.

Ceraurinella media n. sp.

Pl. 8, figs. 42-53, Pl. 9, figs. 32-37

Diagnosis: A species of Ceraurinella with an approximately parallel-sided glabella that is moderately inflated and slightly indented antero-medially. 1p lobes are moderately inflated, not isolated. Palpebral lobes are moderately small. Pygidium has five spines; first pair long, straight, directed obliquely upwards and slightly outwards; posterior three spines short, blunt, approximately equal in size.

Occurrence: Middle to upper Esbataottine Formation, Sunblood Range (A 385, P 1785, P 2038); Esbataottine Formation, Whittaker Range (Q 130). Ceraurus gabrielsi Zone and Ceraurinella longispina Zone.

Material: 46 individuals.

Holotype: An incomplete cranidium (RL 0121) from A 385 illustrated on Pl. 8, figs. 43-45.

Discussion: Ceraurinella media n. sp. displays characters which suggest an intermediate position between C. longispina n. sp. and C. kingstoni Chatterton and Ludvigsen. Its cranidium differs in a few points from that of C. longispina in possessing smaller palpebral lobes that are located slightly closer to a more inflated glabella. The anterior cranidial margin of C. media is curved and not angular as in C. longispina (although it may be slightly indented medially) and the first pygidial spines are straight. The cranidium of *C. media* is less inflated than that of *C. kingstoni*, the first glabellar furrow does not reach the occipital furrow, and the palpebral lobes are slightly larger. A point of similarity is the faint V-shaped deflection of the preglabellar furrow. The pygidium of *C. media* differs from that of *C. kingstoni* in possessing less erect first spines; other features are identical. The hypostomes of *C. media* and *C. longispina* are identical and share the faint curved furrow that joins the maculae and separates the posterior from the anterior lobe. In *C. kingstoni*, the posterior and anterior lobes are continuous between the maculae.

Ceraurinella necra n. sp.

Pl. 11, figs. 1-30

Diagnosis: A species of *Ceraurinella* with a moderately inflated glabella that expands slightly forwards; faintly inflated basal glabellar lobes that are nearly isolated; and relatively narrow (tr.) cheeks. Palpebral lobe is small. Pygidium has five spines; first pair longest (ratio of length of spine to width of pygidium across anterior margin is 0.71), oval in cross-section, directed backwards with slight outward and upward curvature; posterior three spines short, blunt.

Occurrence: Lower Whittaker Formation, Funeral Range (C 570-590) and Whittaker Range (I 1275). *Ceraurinella necra* Zone.

Material: More than 30 individuals.

Holotype: A complete pygidium (RL 0044) from C 570-590 illustrated on Pl. 11, figs. 11-13.

Discussion: *Ceraurinella mecra* n. sp. is chiefly characterized by the length and direction of the first pygidial spine which is intermediate in size and orientation between that of *C. arctica* n. sp. and *C. brevispina* n. sp. Further differences with *C. arctica* can be summarized as follows:

1. The cheeks are narrower (tr.) and the palpebral lobes smaller.

2. The glabella is slightly narrower (tr.) and the anterior glabellar lobe is longer.

3. The ornament of granules is not as densely distributed.

4. The hypostome has narrower lateral and posterior borders.

5. The glabella is perforated by minute pits which are arranged in four irregular exsagittal rows - one pair bisecting the lateral glabellar lobes and one pair located just adaxial of inner tips of the lateral glabellar furrows and scattered on the glabella, especially evident on the anterior lobe (Pl. 11, fig. 30).

The latter feature is one newly introduced to the *C. longispina*-*C. brevispina* lineage. It is definitely not a character of the two earlier species, but it appears to be present in *C. brevispina*. The function of these pits is unknown. It is unlikely that they were the loci of sensory hairs since they are not a feature of the parts of the trilobite that would be most likely to come in contact with other objects or biota. The arrangement of, at least, the larger pits in four exsagittal rows suggest that this organization may be related to the placement of the longitudinal muscles.

The species name (*nekros*, Greek for a dead body) is in reference to the type locality in the *Funeral* Range, adjacent to the *Headless* Range, and just northwest of the *Deadmen* Valley - names that serve to sustain the "Legend of the Nahanni" (Patterson, 1966).

Ceraurinella brevispina n. sp.

Pl. 11, figs. 31-57

Ceraurinella n. sp. 9, LUDVIGSEN, 1975, Pl. 5, figs. 14,15.

Diagnosis: A species of *Ceraurinella* with a glabella that expands in front of moderately inflated basal glabellar lobes. Palpebral lobe is small, located close to glabella. Pygidium has five spines; first pair longest (ratio of length of spine to width of pygidium across anterior margin is 0.57), directed backwards with faint outward and upward curvature; median three spines blunt to pointed.

Occurrence: Lower Whittaker Formation, Whittaker Range (H 1850, H 1920, H 1975, I 1350-1380, I 1410, I 1590, Q 430, Q 530); Funeral Range (C 655, ?J 220); and

Dusky Range (?R 625, R 655). *Ceraurus mackenziensis* Zone and *Whittakerites planatus* Zone.

Material: About 50 individuals.

Holotype: A complete pygidium (RL 0116) from I 1590 illustrated on Pl. 11, figs. 40, 41.

Discussion: Aside from the shorter first pygidial spines, *Ceraurinella brevispina* n. sp. differs from *C. necra* n. sp. by having more inflated basal glabellar lobes and slightly smaller palpebral lobes. The glabellar pitting is evident as faint "rosettes" in, for example, Plate 11, figure 52.

An interesting comparison can be made between the pygidium of *C. brevispina* and that of *Ktenoura retrospinosa* Lane (1971, Pl. 6, figs. 1-3, 5-12, 14, 15) from Wenlockian of Dudley, Worcestershire. The Ordovician species has five pygidial spines and the Silurian species has six; otherwise these pygidia are very similar and, if Lane's (1971, p. 77) suggestion about the derivation of *Ktenoura* is correct, these taxa are the respective products of parallel phylogenetic trends -- *Ktenoura* from an early Silurian species of *Hadromeros* by shortening of the first pygidial spines and *Ceraurinella brevispina* from *C. longispina* by the same process.

Ceraurinella brevispina occurs in both the *Ceraurus mackenziensis* and *Whittakerites planatus* Zones and is of Trentonian to Edenian age. A few poorly known and, from what can be deduced from generally inadequate illustrations, possibly conspecific species of Ceraurinella occur in the Trentonian and Blackriveran of the mid-continent and northern Greenland; that is C. scofieldi (Clarke, 1894, see Barton, 1913, unnumbered plate, fig. 4; DeMott, 1963, Pl. 10, figs. 11-19), C. trentonensis (Barton, 1913, see this thesis, Pl. 19, fig. 9), C. tenuisculpta (Bradley, 1930, see this thesis, Pl. 19, fig. 10) and C. longifrons (Troedsson, 1928, only Pl. 19, figs. 4, 5). Of these, C. scofieldi is probably of Blackriveran age (Barton, 1913; DeMott, 1963), the others are of Trentonian age. These species possess parallel-sided glabellae, deep and oblique 1s furrows, faint 2s and 3s furrows, inflated 1p lobes, and small palpebral lobes. A pygidium is known only from C. scofieldi and shows a pair of relatively long and curving first spines, followed by two (?) pairs of small spines. The cranidia of these species and the pygidium of C. scofieldi are not closely comparable to either of the two Trentonian species from northern Canada, but instead appear somewhat similar to earlier Chazyan species (C. magnilobata Tripp and C. kingstoni Chatterton and Ludvigsen).

Genus Remipyga Whittington, 1954

Type species: Remipyga glabra Whittington, 1954 from Silliman's Fossil Mount, Baffin Island.

Discussion: The rather troubled nomenclatural history of Ceraurinus has been reviewed elsewhere in this thesis. Illustrations of the type species, C. marginatus (Pl. 19, figs. 1-3) are included in an attempt to clear up some of the uncertainties surrounding its morphology and to show its diagnostic features in reference to Remipyga. Major problems in utilizing the name Ceraurinus have been the lack of a pygidium on the type specimen and the absence of precise locality data. Although serious, these deficiencies are not critical and do not influence the status of the genus. In southern Ontario C. marginatus occurs in the Edenian Cobourg Formation, generally near its top (Raymond, 1921; Wilson, 1947). The species is found in the highest Cobourg Formation near Collingwood and Craigleith on Georgian Bay and Raymond's (1921, p. 37) suggestion that this could well be the type locality for C. marginatus is probably correct. Raymond's illustrated specimen came from the lower part of the Collingwood Formation, but this information cannot be viewed as conclusive because, at this locality, about four meters of strata are exposed and the contact between the Cobourg and the overlying Collingwood is gradational over three meters (Winder and Sanford, 1972, p. 57). In any case, cranidia virtually indistinguishable from the holotype and , probably more important, a single pygidium has been collected from these beds. The pygidium is basically similar to that of *Remipyga*, but the first spines are longer and narrower (tr.) and only faintly carinate and the second and third are short and blunt. This pygidium bears a marked resemblance to that assigned to *Ceraurinus longifrons* by Troedsson, 1928, Pl. 19, fig. 6 (the cranidia of *C. longifrons* illustrated on the same plate should be assigned to *Ceraurinella*). A drawing of a complete carapace of *C. marginatus* from the Cobourg Formation near Collingwood was presented by Sproule (1936, Pl. 8, fig. 3). The tips of the first pygidial spines of this specimen are not preserved, but the remainder are in good agreement with the pygidium illustrated herein. Sproule's specimen was supposed to be housed in the Royal Ontario Museum, but according to D.H. Collins of that institution the specimen is not catalogued.

The cranidium of *Ceraurinus marginatus* differs from those of *Remipyga glabra* and *R. icarus* (Pl. 19, figs. 4, 5) in possessing first glabellar furrows that are not connected to the occipital furrow. So the important characters of *Remipyga* are the relatively short, strongly carinate, and paddle-shaped first pygidial spines and the isolated first glabellar lobe.

The differences in cranidial and pygidial morphology between *Ceraurinus* and *Remipyga* are admittedly minor, but they can be construed to constitute means whereby these genera can be distinguished. The alternatives are unsatisfactory -- that is, discontinuing use of the name *Ceraurinus* as advocated by Whittington and Evitt (1954, p. 63); suppressing *Ceraurinus* in favour of *Remipyga*; or considering *Remipyga* a junior synonym of *Ceraurinus*.

The heterogeneous collection of species assigned to *Ceraurinus* by Barton (1913) or by later authors has subsequently been divided among six cheirurid genera. *C. marginatus* resides as the type of a genus which, explicitly or implicitly, serves as a reference point for a large group of cheirurid trilobites with parallel-sided glabellae lacking tubercles.

As perceived herein, *Remipyga* has a relatively long stratigraphic range from, probably, Kirkfieldian to Richmondian. Generally, the northern occurrences of the genus (Greenland, Baffin Island, and the Nahanni area) are older than the southern and eastern occurrences (Iowa, Indiana, Gaspé, and Anticosti Island); suggesting that the genus migrated southward during the late Middle and Upper Ordovician. *Ceraurinus*, apparently, has a shorter range from Edenian to ?Richmondian and, in North America, appears to be restricted to the Great Lakes region. Elsewhere in North America, *Remipyga* or *Ceraurinus* has been recorded from the Stony Mountain Formation of Manitoba (Baillie, 1952), the upper Bighorn Formation of Wyoming (Macomber, 1970), and from carbonates on the Seward Peninsula in Alaska (R.J. Ross, personal communication, 1974).

It remains to be emphasized that *Remipyga* is not an Ashgillian genus as Lane (1971, p. 75, text-fig. 10) recently stated. Certainly, the youngest representatives of the genus are of Richmondian age and some of these (from the Whitehead Formation, Gaspé and the Vaureal Formation, Anticosti Island) are demonstrably of Ashgillian age (Riva, 1974, p. 6), but the northern species of *Remipyga*, including *R. serrata* from the Whittaker Formation and *R. glabra* from Silliman's Fossil Mount are considerably older (Ludvigsen, 1975; Copeland, 1974).

Remipyga serrata n. sp.

Pl. 20, figs. 1-32

Remipyga cf. *daedalus* (Cox), LUDVIGSEN, 1975, Pl. 5, figs. 6, 7.

?*Ceraurinus icarus* (Billings), TROEDSSON, 1928, Pl. 19, fig. 1.

Diagnosis: A species of *Remipyga* with flat, carinate, and curved (exsag.) first pygidial spines and pointed, digitate, non-carinate second and third pygidial spines whose tips fall on a gentle curve that almost reaches a line joining tips of first spines.

Occurrence: ?Cape Calhoun Formation, northern Greenland and lower Whittaker Formation, Funeral Range (C 655), Whittaker Range (H 1850, H 1920, H 1975, I 1590, Q 430, Q 530) and Dusky Range (R 625). *Ceraurus mackenziensis* Zone and *Whittakerites planatus* Zone (in Canada).

Material: About 40 individuals.

Holotype: A complete pygidium (GSC 40446) from I 1590 illustrated on Pl. 20, figs. 10, 11.

Description: Cephalon semi-circular in outline, about twice as wide (tr.) as long (sag.); moderately (tr.) and slightly (sag.) convex. Glabella flatly convex; rectangular in outline, width (tr.) 2/3rds length (sag.); faintly bowed laterally between occipital furrow and 3s furrow. Axial furrows deep, narrow; continuous with preglabellar furrow which curves around anterior lobe and becomes transverse medially. Three pairs of relatively deep glabellar furrows extend about 1/4th to 1/3rd way across glabella; 1s straight, transverse or slightly backwardly directed, deepens adaxially, inner edge connected to short longitudinal furrow which joins occipital furrow; 2s straight, transverse; 3s slightly bowed forwardly. Glabellar lobes square to trapezoidal in outline, not noticeably inflated. Anterior lobe rectangular in outline with evenly rounded antero-lateral corners, 3 1/2 times as wide (tr.) as long (sag.). Occipital ring flatly convex (sag.) and moderately convex (tr.), lenticular to rectangular in outline, tiny occipital node occupies median position; stands as high or slightly higher than glabella in front of occipital furrow which is straight medially and curves backwards and outwards behind 1p lobe. Pre-glabellar field relatively broad, slightly convex (sag.). Cheek triangular in outline, slightly convex (exsag.); lateral parts slopes downward at about 45°. Palpebral lobe ovate, about twice as long (exsag.) as wide (tr.); located opposite posterior part of 3p lobe and 2s furrow; stands slightly lower than glabella. Faint palpebral ridge proceeds inwards a short distance, but fades out before reaching axial furrow. Palpebral furrow short, sigmoid. Visual surface of eye strongly curved in horizontal plane, less so vertically. Base of eye nearly reaches lateral border furrow. Anterior branch of facial suture proceeds forwards and inwards in smooth curve; in anterior view suture descends slightly at juncture with connective suture and rises again slightly towards midline to form rostral suture. Posterior branch of facial suture nearly straight as far as lateral border furrow, then curves backwards. Posterior border furrow narrow (exsag.), moderately deep; lateral border furrow shallower, dies out anteriorly before reaching anterior branch of facial suture. Lateral border broad, flat to slightly concave; posterior border half as wide, flatly convex. Genal spines short and stout, elongate oval in cross-section, faintly carinate, flares very slightly. Entire surface of cephalon finely granulose and cheek, inside border furrows, finely pitted.

On interior, lateral doublure broad, flatly convex. Adaxial parts of 1s furrows and corresponding parts of 0s furrow extended as high appendifers. Anterior pit appears on interior just in front of 3s furrow as relatively high mound carrying a small pit on anterior side.

Hypostome shield-shaped, about as long (sag.) as wide (tr.) between shoulders; composed of oval and slightly inflated middle body with a pair of faint, obliquely-disposed maculae located inside posterior end of shoulders. Middle body completely circumscribed by relatively shallow border furrow which reaches anterior margin medially. From distinct shoulders, lateral margin converges backwards, with slight inward curvature, to obtuse and sharp postero-lateral corners. Posterior margin faintly convex posteriorly. Anterior wings flare slightly, extend laterally as far as shoulders. On interior, posterior part of doublure narrow, expands forwardly into obliquely-disposed posterior wings which extend dorsally nearly as far as anterior wings. In front of sharply defined shoulder, doublure deflected downwards into fairly broad antennal notch and then recurved up into dorso-laterally disposed anterior wing which carries short, blunt, dorsally-directed wing process.

Number of thoracic segments unknown. Axis convex; outlined by deep, forwardly-divergent axial furrows; articulating furrow stretched W-shaped. Inner portion of pleura inflated; crossed by deep, diagonal pleural furrow. Outer portion of pleura extended into broad, blunt, paddle-shaped spine which is progressively backwardly directed towards rear. On inner surface, a pair of large, blunt, tongue-shaped, ventro-medially directed appendifers arise from outer parts of articulating furrow. Articulating devices consist of relatively large axial furrow process and socket, ring socket and process, and relatively broad (exsag.) articulating flange which terminates laterally at large, open box-like marginal connective device. Base of pleural spine defined by narrow (tr.) ridge.

Pygidium, including spines, sub-rectangular in outline, flat, width (tr.) slightly more than twice length (sag.). Axis triangular; consists of three low rings that narrow posteriorly to small oval terminal piece. Rings separated by relatively shallow, slightly forwardly-curving ring furrows which terminate in deep elongate pits; first two rings defined laterally by faint axial furrows. Pleural field very narrow; crossed by single, short, faint pleural furrow opposite first axial ring. First marginal spine flat, paddle-shaped, directed outwards and backwards; carries distinct median carinae for its total length; in posterior view, first spines can be seen to slope outwardly at about 20° to horizontal. Second and third pairs shorter, pointed, non-carinate; well separated from each other and from first spine pair; their tips fall on a gentle, posteriorly convex curve which, medially, nearly reaches a line joining tips of first spines. On interior, doublure narrow, convex, broadly V-shaped. Distal parts of articulating and first and second axial ring furrows extended into small appendifers.

Discussion: *Remipyga serrata* n. sp. differs from *R. icarus* (Billings) of Richmondian age from Anticosti Island (Billings, 1860, p. 67; Foreste, 1924, Pl. 44, figs. 3a, b; Bolton, 1972, Pl. 2, fig. 4), Ohio (Meek, 1873, Pl. 14, figs. 11a-c; Barton, 1913, unnumbered plate, fig. 7), Iowa (Slocum, 1913, Pl. 17, figs. 6-9), and Gaspé(this thesis Pl. 19, figs. 4, 5) by possessing second and third pygidial spines that are non-carinate and that do not extend past the first spine pair. R. glabra Whittington (1954, Pl. 59, figs. 8-12, Pl. 60, figs. 1-4) has long and greatly expanded first pygidial spines and the eye is placed further inwards on the cheek. Ceraurinus platycanthus Bradley, 1930 from the Kimmswick Limestone probably belongs to Remipyga (as Whittington, 1954, p. 130 suggested) and not to Xylabion (as Lane, 1971, p. 41 suggested). The cranidium of R.? platycantha bears some resemblance to the large cranidium of R. serrata (Pl. 20, fig. 9), but differs in having a broader (tr.) cranidium, eyes placed far out on the cheek, and fainter glabellar and axial furrows.

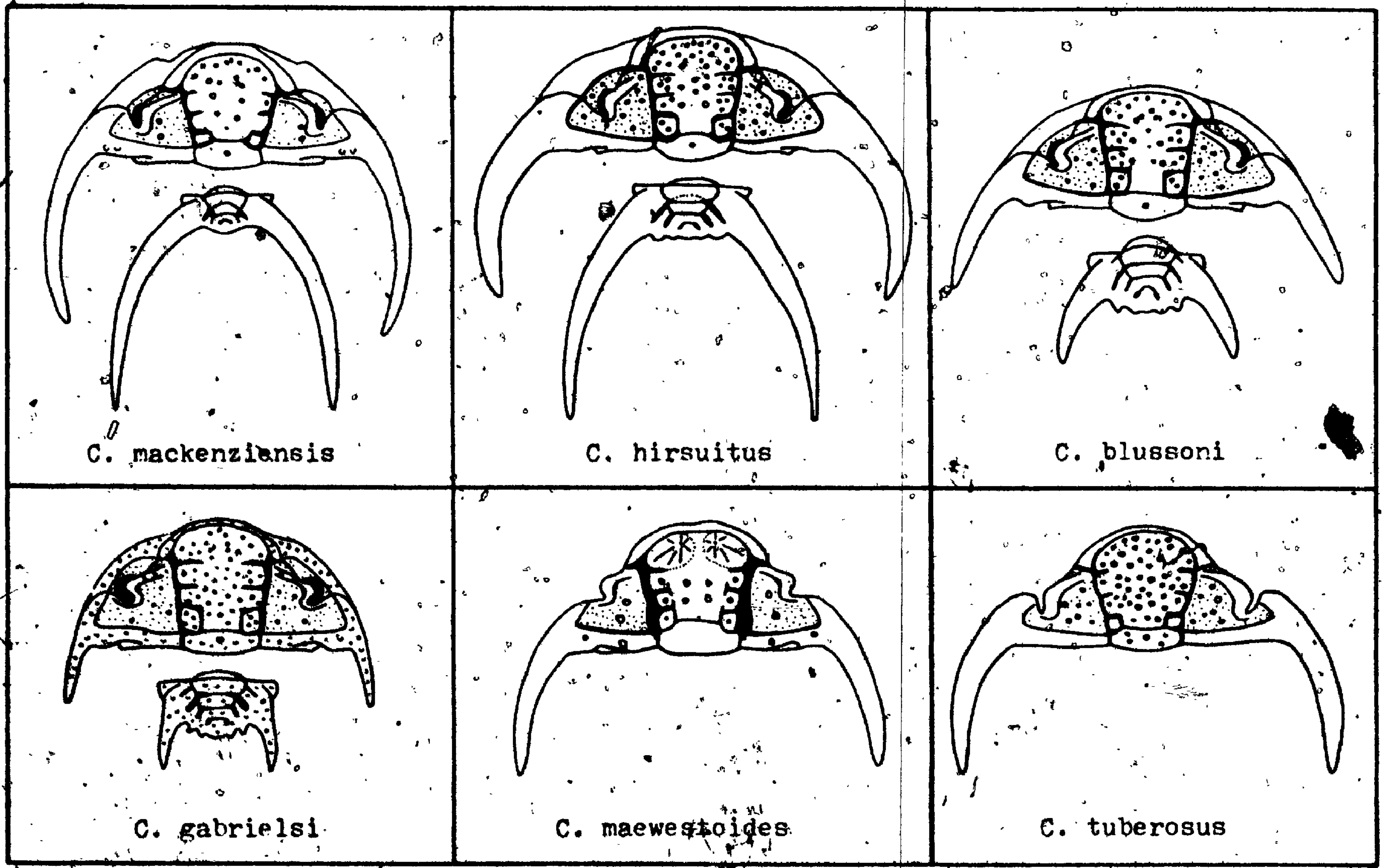
I follow Whittington's (1954, p. 130) assignment of Troedsson's (1928) illustrated material from the Cape Calhoun Formation to Remipyga (Pl. 17, figs. 4-9, Pl. 18, figs. 10a-d to 15, Pl. 19, figs. 1-3). The extreme variability of this material renders specific assignment difficult. All the pygidia illustrated show a greater affinity to R. serrata than to R. icarus in possessing short and non-carinate second and third pygidial spines. Of Troedsson's material, one pygidium (Pl. 19, fig. 1) appears identical to that of R. serrata. Whittington (1954, p. 130) suggested that the bulk of the Remipyga specimens from the Cape Calhoun should be assigned to Remipyga daedalus (Cox, 1933) which was described from Akpatok Island in Ungava Bay. Cox (1933, p. 369), however, described the R. daedalus pygidium as having carinate spines (presumably all six) whose tips lie on a very gently arc. It is difficult to accept that this description should pertain to the Cape Calhoun material (except perhaps, Troedsson, 1928, Pl. 19, figs. 2, 3).

Genus Ceraurus Green, 1832

Type species: Ceraurus pleurexanthemus Green, 1832 from the Trenton Group of New York State (described and illustrated by Evitt, 1951).

Discussion: Species of Ceraurus are common in almost any trilobite fauna of Blackriveran to Richmondian age in North America. Lane (1971, p. 19, 20) listed 26 species of Ceraurus. To this list may be added the two species assigned to Hapsiceraurus by Whittington (1954) which, in my opinion, do not differ generically from those assigned to Ceraurus and the five new species recognized from the Nahanni area. Even though some of these species are probably synonyms (Shaw, 1974), we are still left with some thirty species of Ceraurus. A possible phylogenetic relationship of twenty of these is shown on Text-figure 22.

The only definite non-North American species of Ceraurus is C. proicens Tripp, 1967 from Scotland. Other species assigned to Ceraurus have probably been misidentified. Ceraurus latifrons Warburg, 1925 from Balto-Scandia may belong to Paraceraurus. Ceraurus kassini Chugaeva, 1958 from Kazakhstan probably belongs to Hadromeros. The generic position of Ceraurus? intermedius Kielan, 1955 from northern Europe has been discussed previously. The origin of this



Text-figure 29.

Outline drawings of cephala and pygidia of six species of *Ceraurus* from the upper Sunblood, Esbataottine, and lower Whittaker Formations, South Nahanni River area.

species probably lies with either *Paraceraurus* (? or *Ceraurus* s.s.) or *Hadromeros*.

Ceraurus appears to have been derived from Balto-Scandian species of early Viruan or older age that have been assigned to *Paraceraurus* (Neben and Krueger, 1971); that is, *P. exsul* (Beyrich) and *P. neglectus* (Kummerow). The assignment of these species to *Paraceraurus* may be questioned because of the singularity of the type species, *P. aculeatus* (Eichwald; Mannill, 1958). I regard *Paraceraurus* as monotypic. The older species of *Ceraurinella*; that is, *C. polydorus* (Billings) and *C.? ingrica* (Schmidt); are highly similar to these species of "*Paraceraurus*" and suggest that *Ceraurus*, *Ceraurinella*, and *Paraceraurus* shared a common ancestor in Arenigian or Llanvirnian strata of Balto-Scandia.

Shaw (1968, p. 72) pointed out that *Paraceraurus ruedemanni* (Raymond) differs in a couple of critical features from the type species, *Paraceraurus aculeatus*. Lane (1971, p. 41) assigned *P. ruedemanni*, with query to *Xylabion*. This species, however, is considerably closer to the *Paraceraurus* and *Ceraurus* group than to the *Xylabion*, *Ceraurinus*, and *Remipyga* group and is, herein, referred to as "*Paraceraurus*" *ruedemanni*.

Ceraurus gabrielsi n. sp.

Pl. 12, figs. 1-44, Pl. 13, figs. 1-49, Pl. 14, figs. 1-8

Ceraurus n. sp. 1, LUDVIGSEN, 1975, Pl. 4, figs. 13, 14.

Ceraurus n. sp. 2, LUDVIGSEN, 1975, Pl. 4, figs. 24, 25.

Diagnosis: A species of Ceraurus with a lowly vaulted cephalon and moderately short genal spines. Glabellar furrows are wide (tr.); 1p lobe is isolated. Palpebral lobe is small, located opposite or just behind 2s furrow. Pygidium is large and bears three spine pairs and a rounded median portion; anterior spine pair longest, flares very slightly; posterior spine pairs are very short. Ornament of scattered large thorn-like tubercles and coarse granules.

Occurrence: Middle and upper Esbataottine Formation, Sunblood Range (A 365, P 1665-1685, P 1785, P 1870, P 1931, P 1945-1955) and Whittaker Range (H 900, H 1020); upper Sunblood Formation, Natla River (D 1375). Ceraurus gabrielsi Zone.

Material: 179 individuals.

Holotype: A nearly complete cranidium (RL 0216) from P 1945-1955 illustrated on Pl. 13, figs. 1-3.

Description: Cranidium semicircular in outline, half as long (sag.) as wide (tr.) across posterior margin; moderately vaulted (tr.); in lateral profile, posterior portion of glabella horizontal, slopes steeply to anterior margin. Glabella moderately inflated, sub-rectangular in outline, expands slightly to markedly forward to maximum width across anterior lobe which is 3/4th glabellar length (sag.). Faint glabellar furrow moderately deep, straight, extends slightly over 1/4th way across glabella with slight backward direction; connected to occipital furrow by slightly shallower, straight exsagittal furrow. Second and third furrows narrower (exsag.) and shallower than 1s, about the same width (tr.), nearly transversely directed with slight backward curvature, sub-parallel, extend about 1/3rd way across glabella. 1p lobe ~~isolated~~, roughly square in outline, slightly inflated; 2p and 3p lobes about the same length (exsag.) as 1p lobe, rectangular in outline, faintly inflated. Anterior lobe slightly greater than twice as wide (tr.) as long (sag.); front edge evenly rounded. Anterior border moderately narrow, curved, becomes slightly longer (exsag.) laterally. In anterior view, pre-glabellar furrow rises slightly towards mid-line in even curve. Axial furrows moderately deep, slightly flaring forwards; each terminate in small anterior pit located just ahead of 3s furrow at juncture with lateral border ~~furrow~~. Occipital ring arched, lenticular to rectangular in outline, sagittal length approximately equal to length of 1p lobe, carries small median node. Occipital furrow nearly transverse; slightly deflected posteriorly around 1p lobe. Median part of glabella, in front of occipital furrow, bears transverse inflated portion. Cheek broadly triangular in outline, moderately convex (tr. and exsag.). Palpebral lobe small, crescentic, located far out on cheek; its mid-point is opposite or just behind 2s furrow; stands slightly below crest of glabella; continuous anteriorly with long and convex (tr.) palpebral ridge which proceeds forward and inward along straight path to meet axial furrow at, or just behind, 3s furrow. Palpebral furrow S-shaped, deep and pit-like at mid-length of palpebral lobe; posteriorly it becomes narrower and curves laterally for a short distance before fading out behind visual surface of eye; anteriorly, it becomes a row of pits that defines the adaxial side of palpebral ridge. Visual surface of eye not preserved; its base is curved through about 180°. Cheek, below eye, slopes steeply to lateral border furrow which follows even arc between right-angled juncture with posterior border and anterior pit. Lateral border furrow narrow and moderately deep, V-shaped in cross-section; posterior border transverse, slightly wider than lateral border furrow. Lateral border wide, evenly convex; extended posteriorly into relatively short, gradually tapering genal spine which is directed backwards and slightly outwards. Posterior border, initially, narrower (exsag.) than lateral border; approximately transversely directed, but follows slight curve around outer edge of articulating flange; distal part flatly convex and slightly wider (exsag.), curves down to base of genal spine. Anterior branch of facial suture proceeds forwards and inwards from palpebral lobe along straight path to cross anterior part of lateral border furrow and then towards midline along anterior margin of cephalon. In anterior view, suture follows stretched W-shaped path which is approximately parallel with pre-glabellar furrow; at the ventral edge of the "W", suture is joined by strongly dorsally-divergent connective sutures. Posterior branch of facial suture follows even curve with slight forward convexity to point just past lateral border furrow, then it is sharply deflected backwards to cross lateral border in straight line.

Three pits, or groups of pits, arranged in a triangle on anterior glabellar lobe. The forward pit is located on sagittal line just behind pre-glabellar furrow (Pl. 14, fig. 4). This pit may be replaced by 2 or more pits arranged in sagittal row (Pl. 12, fig. 3), by a diffuse group of pits (Pl. 14, fig. 3), or by 3 or more pits arranged in a row along the posterior side of the pre-glabellar furrow (Pl. 12, fig. 41). Posterior pair of pits flank sagittal line in front of, and just inside, adaxial edge of 3s furrows (Pl. 12, figs. 3, 41; Pl. 14, figs. 3, 4).

Dorsal surface of cephalon covered by relatively sparsely distributed and thorn-like to rounded tubercles which are superimposed on extremely fine background granulation. On the glabella, these tubercles commonly occur in scattered clusters (especially in collections from the lower and middle Ceraurus gabrielsi Zone - Pl. 12, fig. 3, Pl. 14, fig. 5). On the lateral and anterior cephalic borders and on the palpebral lobe and palpebral ridge, the tubercles are finer, more numerous, and of more rounded profile. Cheek, inside border furrows (with exception of palpebral lobe and palpebral furrow), rather coarsely pitted. Beneath eye, the pits are finer and tend to be radially arranged.

On interior, convex lateral doublure extends to impress of lateral border furrow. Posteriorly, doublure flattens and attenuates towards distal part of articulating flange. Anterior doublure includes rostral plate and is flatly convex and slopes postero-ventrally. Adaxial part of ls and corresponding part of Os extended into high, spindle-shaped appendifers. Anterior pit expressed as high, mound-like elevation with a distinct and large pit on its anterior side.

Hypostome sub-triangular to sub-oval in outline, length (sag.) slightly less than maximum width (tr.) between anterior wings. Egg-shaped middle body narrows backwards from maximum width between anterior wings. It includes a pair of faintly expressed and oval macula located at the confluence of the lateral and posterior border furrows. Lateral border furrows deep and wide (tr.) behind shoulders; converge slightly backwards to merge with shallower posterior border furrow in even curve. Posterior border moderately narrow (sag.), merges with lateral border (a few specimens possess a tiny postero-lateral spine), which expands slightly into rounded shoulders. Anterior border eliminated medially by anterior margin which reaches middle body. Anterior border furrow, however, is complete and is expressed medially as a horizontal constriction at anterior margin (Pl. 13, fig. 33). Ventral surface of hypostome finely tuberculose, except within furrows and on posterior part of middle body. A sagittal strip on the hypostome carries tiny circular impressions of thin shelled material, which, in most specimens, appear as a broad row of pits that extend from posterior border furrow ~~to~~ anterior border furrow (Pl. 13, figs. 31, 35, 38). The functional significance of these pits is not known. Similar pits and areas of thin shell material, in other parts of the Ceraurus exoskeleton and in other genera, have been interpreted to represent muscle attachments. It is possible that here they represent attachment points of muscles that support the digestive tract. In this regard, it is important to note that the strip of pits on the hypostome is in direct line with the triangular pattern of pits on the anterior glabellar lobe. These pits may represent the dorsal and anterior attachment points of the same muscle support system. On interior, —— doublure widens and rises forwardly from its narrowest point at posterior edge into a pair of high, obliquely disposed and plate-like posterior wings that partially close off the opening into the hypostomal interior (Pl. 12, figs. 30, 33). In front of posterior wings, doublure descends abruptly into broad antero-laterally disposed antennal notch and then is recurved into a pair of triangular anterior wings. Postero-ventral face of anterior wings impressed by deep elongate slot which, on antero-dorsal face, appears as a stout, dorsally directed wing process. Anterior margin of hypostome from base of anterior wings, consists of sharp-edged sutural contact with doublure and rostral plate. Since this contact is curved in both horizontal and vertical planes, movement of the hypostome would not be allowed (if the wing processes of the hypostome remain in contact with the anterior pit of the cephalic interior).

Number of thoracic segments not known. Axis convex, slightly less than 1/3rd width of segment. Articulating furrow shallow and long (sag.) medially, becomes deeper as it swings slightly forward laterally. Axial furrows narrow (tr.) and rather shallow. Inner portion of pleura inflated; diagonally crossed by deep pleural furrow which is directed postero-laterally. Outer part of pleura extended into gradually tapering, downwardly and outwardly curving spine which, distally, is distinctly faceted into antero-lateral, lateral, and proximal facets - the juncture of each is marked by a row of tubercles (Pl. 12, figs. 28, 29; Pl. 14, fig. 2). Horizontal part of pleura bounded by anterior and posterior flanges that terminate distally in prominent marginal connective device and are defined on dorsal surfaces by deep flange furrows. Other articulating devices include axial furrow socket and process and ring socket and process. On interior, distal part of articulating furrow extended as high, tongue-shaped appendifers.

Pygidium, without spines, semicircular in outline, slightly vaulted (tr.) and nearly flat (sag.). Axis consists of articulating half ring, 3 lowly arched rings, and a transversely oval terminal piece. Anterior two rings (rarely third ring) defined laterally by narrow (tr.), shallow, and forwardly diverging axial furrows. Articulating furrow transverse, narrow, and short (sag.); first and second ring furrows somewhat longer (sag.), transverse;

shallow medially, deepest distally; third axial ring short (tr.), arched forward between a pair of small pits. Axial rings slightly convex (sag.), narrowing (tr.) and becoming shorter (sag.) posteriorly. Third axial ring and terminal piece poorly differentiated from pleural region. Pleural region moderately narrow; inflated opposite first axial ring and crossed by short diagonal pleural furrow. Flange furrow, initiated at articulating furrow; isolates very narrow anterior band which, distally, lengthens into prominent marginal connective device forming antero-lateral corner of pygidium. First and second interpleural furrows, initially deep; proceed obliquely outward and backward from distal ends of first and second axial ring furrows; become shallower toward posterior margin where they divide bases of marginal spines. Third interpleural furrow represented by deep pits at lateral ends of terminal piece. First marginal spine of variable size and orientation; generally slender, backwardly and upwardly directed with slight outward curvature, broad based and gradually tapering to fine point; length equal to, or less than, width of pygidium across anterior margin (but varies considerably, compare Pl. 12, figs. 12 and Pl. 13, fig. 14; Pl. 12, fig. 17 and Pl. 13, fig. 18). Distal parts of spines generally parallel (but again, varies considerably; some are nearly parallel for their total length - Pl. 12, fig. 43, and Pl. 13, fig. 20 while others are evenly divergent - Pl. 14, fig. 8). Second and third pairs of marginal spines very short, triangular in larger specimens, lobate in smaller specimens; directed backward (except for a few specimens in which the third pair is directed obliquely inwards - Pl. 14, fig. 8, Pl. 13, fig. 25). Third spine pair separated by median convex portion which extends as far posteriorly as third spine pair and, in rare small specimens (Pl. 13, fig. 17), appears as a tiny fourth spine pair. Marginal spines elevated above narrow rim which constitutes posterior margin of pygidium. Doublure narrow, angulate; in posterior view, arched upward medially. Tiny appendifers appear on the distal ends of articulating furrow and axial ring furrows. Dorsal surface of pygidium covered by relativley large, thorn-like tubercles and coarse granules superimposed on extremely fine background granulation (Pl. 13, fig. 24). A nearly bald and U-shaped strip traverses bases of second and third spines and terminal piece.

Discussion: Ceraurus gabrielsi n. sp. is a relatively long-ranging species which, in Section P, extends through 120 m of strata within the middle and upper Esbataottine Formation. Considerable variation is evident within this range and, initially, it was thought that two species were present (reflected in the recognition of Ceraurus n. sp. 1 and Ceraurus n. sp. 2, Ludvigsen, 1975, Pl. 4, figs. 13, 14, 24, 25). The earlier specimens of C. gabrielsi at Section P (from P 1685, Pl. 12, figs. 1-36) tend to have more forwardly-expanding glabellae, finer tuberculose ornament on the cephala, and shorter first pygidial spines than the later specimens (from P 1931 and P 1945-1955, Pl. 12, figs. 37-44, Pl. 13, figs. 1-49). In addition, the occipital rings of the earlier specimens tend to be bald. These apparent differences are diminished when the significant intra-population variation of the species is taken into account and are not thought to be grounds for specific segregation.

A few pygidia of Ceraurus gabrielsi are very similar to those of C. blussoni n. sp. (for example, Pl. 13, figs. 14-16), but they differ in possessing a coarser granulose and tuberculose ornament and less erect and less divergent first pygidial spines. Further differences with C. blussoni are covered under that species.

Aside from the species in the Nahanni area, Ceraurus gabrielsi is somewhat similar to "Paraceraurus" ruedemanni (Raymond) from the Chazy Group in New York (Shaw, 1968, p. 70-73, Pl. 15, fig. 34, Pl. 16, figs. 1-11). Detailed comparison is difficult because the material of "P." ruedemanni is significantly larger than any available of C. gabrielsi. The Chazy species, however, is clearly distinguished by its unique pygidium with elongated second pygidial spines and the presence of longitudinal glabellar furrows that join the adaxial tips of the lateral glabellar furrows. A number of features of "P." ruedemanni indicate affinity with C. gabrielsi - the slightly inflated glabella with a sub-rectangular outline and wide (tr.) lateral glabellar furrows, the relatively short genal spines, the small palpebral lobes located far out on the cheek and opposite 2p lobe, the long and convex palpebral ridges, and the large and lowly vaulted pygidium (without the marginal spines). These features also serve to distinguish "*P.*" *ruedemanni* and *C. gabrielsi* from younger species of *Ceraurus* in eastern North America.

Ceraurus gabrielsi is similar to *C. proicens* Tripp, 1967 from the Upper Stinchar Limestone, Girvan but the latter species may be distinguished by the coarser tuberculose ornament on the glabella and the markedly divergent first pygidial spines.

Finally, a similarity of *Ceraurus gabrielsi* with certain Balto-Scandian species is important because it provides some evidence of the origin of this typically North American Ordovician genus. These species are "*Paraceraurus*" *exsul* (Beyrich, Neben and Krueger, 1971, Pl. 26, figs. 20-22) from erratic boulders from the "oberen grauen Orthocerenkalk" of early Viruan age (Chazyan and slightly older, Bergström, 1971) and *Paraceraurus aculeatus* (Eichwald, Öpik, 1937, Pl. 17, figs. 1-7) from the Kukruse Stage (Chazyan and Blackriveran, Bergström, 1971). Shaw (1968) assigned *Ceraurus ruedemanni* to *Paraceraurus* and, although this generic assignment may be open to question (Lane, 1971), it does direct attention to the affinity of the Chazy species to *Paraceraurus aculeatus*. "*P.*" *exsul* has a long (sag.) parallel-sided and rather flat glabella, wide (tr.) lateral glabellar furrows, and small palpebral lobes located far out on the cheek and opposite 1s furrow. It differs from *C. gabrielsi*, chiefly, by possessing longer genal and first pygidial spines, more posteriorly placed eyes, and a lp lobe that is not isolated.

Ceraurus gabrielsi and "*Paraceraurus*" *ruedemanni* may be viewed as taxa that provide a link between contemporary and older species of *Paraceraurus* and "*Paraceraurus*" from Balto-Scandia and younger species of *Ceraurus* from North America.

The species name is for H. Gabrielse of the Geological Survey of Canada, Vancouver whose work in the northern Cordillera has contributed materially toward an understanding of the regional geology of this area.

Ceraurus blussoni n. sp.

Pl. 14, figs. 9-29

Diagnosis: A species of *Ceraurus* that differs from *C. hirsuitus* in possessing a more convex (tr.) cephalon, shorter genal and first pygidial spines, and an ornament on the cephalic borders, thoracic segments, and pygidium consisting of fine granules.

Occurrence: Upper Sunblood Formation, Mary Range (B 1450). *Ceraurus gabrielsi* Zone.

Material: 15 individuals.

Holotype: An incomplete cranidium (RL 0237) from B 1450 illustrated on Pl. 14, figs. 9-11, 29.

Discussion: *Ceraurus blussoni* n. sp. differs from *C. gabrielsi* n. sp. in having larger palpebral lobes;

longer and more divergent genal and first pygidial spines; somewhat deeper lateral glabellar furrows; a sparser glabellar ornament consisting of larger and more rounded tubercles; and cephalic borders and pygidium ornamented by fine granules. From C. hirsuitus n. sp., C. blussoni differs in having shorter genal and first pygidial spines, a pygidium of semicircular outline, a more rounded anterior facial suture/rostral suture continuum, less expanded (exsag.) distal portions of the anterior border of the cranidium, and by possessing an ornament of fine granules on the cephalic borders, thoracic segments, and pygidium.

A comparison of Plates 12, 13, 14, and 15 illustrates the similarities between Ceraurus gabrielsi, C. blussoni, and C. hirsuitus. C. blussoni is interpreted as a morphological intermediate between C. gabrielsi and C. hirsuitus. The horizon yielding C. blussoni (high in the C. gabrielsi Zone at Section B) strongly suggest that this species may be a temporal intermediate, as well.

The species name is for S.L. Blusson of the Geological Survey of Canada, Vancouver.

Ceraurus hirsuitus n. sp.

Pl. 15, figs. 1-25

Ceraurus aff. dentatus Raymond and Barton, LUDVIGSEN, 1975, Pl. 4, figs. 3, 4.

~~Diagnosis: A species of Ceraurus with a sub-rec-~~tangular and weakly inflated glabella, wide (tr.) lateral glabellar furrows, eye located opposite 2p lobe, long stout genal spines, and a relatively broad pre-glabellar field. Pygidium has a pair of very long, flaring spines followed by two small spine pairs. Glabella is coarsely tuberculose. Cephalic borders, genal spines, thoracic segments, and pygidium are non-tuberculose and covered by fine, hair-like spines.

Occurrence: Upper Esbataottine Formation, Sunblood Range (P 2010, P 2038, P 2050) and Flood Creek (?G 3340). *Ceraurinella longispina* Zone.

Material: 13 individuals.

Holotype: An incomplete cranidium (GSC 40415) from P 2038 illustrated on Pl. 15, figs. 1. 2.

Description: Cranidium crescentic in outline; three times as wide across base of genal spines as long (sag.); moderately (tr.) and gently convex (sag.). Glabella sub-rectangular in outline; expands slightly forwards to maximum width across anterior lobe which is equal to 3/4th length (sag.). Glabella rises steeply out of flanking furrows, but median portion only slightly convex. Three pairs of moderately deep, lateral glabellar furrows oriented approximately perpendicular to axial furrows. 1s deep and long (exsag.); transversely directed; extends about 1/4th way across glabella; deep exsagittal furrow runs directly back to occipital furrow from inner end of 1s furrow. 2s and 3s furrows slightly wider (tr.) and shorter (exsag.)

than 1s, transversely directed or with faint forward curvature. 1p lobe quadrate in outline, isolated, inflated; 2p and 3p lobes rectangular in outline, faintly inflated. Anterior lobe sub-rectangular in outline with evenly curved antero-lateral corners; nearly 3 times as wide (tr.) as long (sag.). Median part of glabella, adaxial of lateral furrows, has slight increased convexity; transverse portion between 1p lobes immediately in front of occipital furrow swollen. Axial furrows moderately deep; flare slightly forwardly to rather shallow anterior pit at 3s furrow. Occipital furrow broad (sag.) and deep, nearly transverse but bowed slightly around posterior portion of 1p lobe. Occipital ring elliptical in outline; stands slightly higher than rest of glabella; protrudes posteriorly in broad arc; contains tiny median node. Anterior border slightly convex; narrow (sag.) and rectilinear medially, becomes longer (exsag.) distally. Cheek semioval in outline, slightly wider (tr.) than long (exsag.), moderately (tr.) and faintly convex (exsag.). Eye occupies midpoint of cheek, opposite 2p lobe; stands nearly as high as highest part of glabella. Palpebral lobe S-shaped; posteriorly, it curves around back edge of eye and, anteriorly, it merges with faintly convex palpebral ridge which proceeds obliquely inwards in straight line to anterior pit. Visual surface of eye not seen, but its base is moderately curved in horizontal plane. Anterior branch of facial suture proceeds forwards and inwards in straight line to point just past anterior border furrow of cheek, then curves inwards sub-parallel with pre-glabellar furrow and is joined by connective suture. In dorsal view the course of the rostral suture is straight; in anterior view the suture rises slightly towards sagittal line. Rostral plate not seen, but judging by width (tr.) of rostral suture, must be as wide (tr.) as glabella across occipital furrow and probably rather narrow (sag.). From posterior edge of eye, facial suture swings outwards with forward curvature. Border furrows of cheek moderately deep and narrow, V-shaped in cross-section. Lateral border furrow evenly bowed outwards; joins nearly straight posterior border furrow at about 60°. Posterior border initially about half as wide (exsag.) as occipital ring; lateral to marginal connective device, posterior margin deflected backwards before merging with genal spines. Lateral border broad and evenly convex; extended directly into a stout, gradually tapering genal spine which, initially, curves backwards and outwards and, distally, curves slightly inwards. Genal spine oval in cross-section; extends posteriorly a distance equal to length of glabella.

Glabella, excluding occipital ring, covered by coarse, non-perforate tubercles which become somewhat denser towards front. Portion of glabella immediately in front of occipital furrow commonly non-tuberculose. Except for three pairs of tubercles arranged in two rows on mid-portion of glabella, tubercles randomly distributed. Slightly smaller tubercles occur on cheek inside border furrow, excluding palpebral lobe but including palpebral ridge. Sparse tubercles stud posterior border of cheek; including single larger tubercle located above half-width of flange furrow. Entire cheek inside border furrow, except palpebral lobe and palpebral ridge, finely pitted. In addition, entire cephalon (and thoracic segments and pygidium) covered by very fine, hair-like spines (hence trivial name). These spines also cover the outer half of cephalic doublure, but become somewhat coarser. Three or more small pits define corners of triangle located on mid-portion of anterior glabellar lobe.

On interior, anterior pit expressed as large, low, pyramid-shaped elevation with a relatively large concavity on its anterior side. Adaxial part of 1s furrow and complementary part of 0s furrow extended into high, spindle-shaped appendifers.

A fragment of a hypostome of *C. hirsuitus* shows it to be essentially identical to those of *C. blussoni* n. sp. (Pl. 14, figs. 16, 17, 19, 20).

Number of thoracic segments unknown. Axis high and arched. Articulating furrow straight medially; forwardly curving and deepest distally. Axial furrows relatively shallow, bowed outwardly. Pleura half as wide (tr.) as axis; inner 2/3rds strongly inflated, crossed by deep, diagonal pleural furrow. Outer part of pleura extended into relatively long spine which is directed downwardly, slightly outwardly, and progressively backwardly and inwardly towards posterior. Anterior edge of spine faceted. Articulating devices consist of a horizontal articulating flange that terminates distally in a prominent right-angled marginal connective device. Other articulating mechanisms consist of axial furrow socket and process, and ring socket and process. On interior, appendifers high and spindle-shaped.

Pygidium, exclusive of first spines, rectangular in outline; twice as wide (tr.) as long (sag.). Axis moderately arched; consists of 3 axial rings and rectangular terminal piece which decrease in width (tr.), length (sag.), and convexity towards rear. Axial furrow shallow and faint; obliquely disposed opposite each axial ring; converge towards rear in serrated fashion. Axial ring furrows moderately deep and straight between axial furrows; first furrow preceded by lenticular depressed portion containing a pair of transversely elongate bald spots. Deep interpleural furrows extend postero-laterally from distal ends of first and second axial furrow, shallowing markedly posteriorly. Similar interpleural furrow extends from third axial furrow and terminates in deep, circular or oval pit. Faint pleural furrow opposite first ring. Anterior pair of spines long, gradually tapering, gently outwardly and backwardly curving; in lateral view, spines directed obliquely upward at about 25°. First spines extend posteriorly a distance equal to twice width of pygidium at anterior margin. Second pair of spines very small, triangular. Third pair of spines smaller than second set; separated by broad, faintly curving median portion. On interior, doublure narrowest at postero-median margin and deflected in dorsal direction. Laterally doublure broadens and becomes convex before pinching out at antero-lateral corner. Distal end of articulating furrow and (?) first axial ring furrow extended into rather small appendifers.

Discussion: The relatively wide (tr.) and short (exsag.) lateral glabellar furrows, the sub-rectangular and weakly inflated glabella, and the pygidium with a rectangular central part and possessing two small pairs of spines behind the first pair distinguishes *Ceraurus hirsuitus* n. sp. from the type species, *C. pleurexanthemus* Green; *C. whittingtoni* Evitt, 1953; *C. tuberosus* Troedsson, 1928; *C. mackenziensis* n. sp.; *C. globulobatus* Bradley, 1930; *C. milleranus* Miller and Gurley, 1897 and *C. mantranseris* Sinclair, 1947.

From *Ceraurus ruidus* Cooper, 1953 (including *C. breviceps* Cooper, 1953; *C. convexus* Cooper, 1953; and *C. trapezoidalis* Esker, 1964; see Shaw, 1974, p. 29); *C. proiscens* Tripp, 1967; and *C. hudsoni* Raymond, 1905; *C. hirsuitus* differs by possessing a more posteriorly placed eye, a sparser tuberculose ornament, a cephalic border that lacks tubercles, a broader pre-glabellar field, less inflated glabella, and stouter genal spines.

Ceraurus hirsuitus is most similar to the species group clustered around *C. dentatus* Raymond and Barton, 1913 and including *C. plattinensis* Foerste, 1920 and "*C. mifflensis*" (a manuscript name used by DeMott, 1963). These species possess a sub-rectangular, slightly to moderately inflated glabella with relatively wide (tr.) lateral glabellar furrows, eyes located opposite 2p lobe, long stout genal spines, and cephalic borders, genal spines, and pygidium lacking tubercles. C. plattinensis and "C. mifflensis" each possess a narrow pre-glabellar field, rounded antero-lateral cranidial corners, inflated lateral glabellar lobes, and a very wide (exsag.) and deep 1s furrow and thus differ from C. hirsuitus.

Application of the name Ceraurus dentatus Raymond and Barton involves considerable difficulties. These are outlined below. The holotype (GSC 1775) was collected by Sir William Logan from an unknown stratigraphic horizon (possibly lower Trenton Group) at Vankleek Hill, east of Ottawa (Raymond, 1921). In spite of the fact that this specimen has been illustrated a number of times (Raymond and Barton, 1913; Raymond, 1921; Wilson, 1947) uncertainty exists about some of the features; for example, the extent to which it is exfoliated, the nature of the fine ornament (if any), and the exact configuration of the anterior portion of the cephalon. The type specimen has since been lost (Bolton, 1966, p. 50) and, due to the fact that the locality data are not sufficiently precise to allow a search for topotypic material and the designation of a lectotype, a problem exists about the exact diagnostic features of C. dentatus. Of the available hypotypes, GSC 1769b from the Cobourg Formation at Cobourg, Ontario (Raymond, 1921, Pl. 10, fig. 1) appears most similar to the lost holotype (if allowance is made for flattening). GSC 1769 (Raymond, 1921, Pl. 10, fig. 2) from the Verulam Formation at Belleville, Ontario was assigned to C. dentatus by Raymond (1921) and Sinclair (1964). The latter author claimed that this specimen came from Cobourg, but that appears to be in error (Bolton, 1966, p. 50). This specimen, however, differs from the lost holotype in a number of features (longer and finely tuberculose genal spines, coarsely tuberculose glabella, and shorter (tr.) lateral glabellar furrows) and, in my opinion, should not be assigned to C. dentatus. The uncertainty surrounding the exact identity of C. dentatus councils against the use of this name until a neotype can be designated.

Ceraurus hirsuitus is a very rare species which occurs in only three collections from the highest beds of the Esbataottine Formation at Section P. These strata comprise highly argillaceous micrite. The two collections combined have yielded over a thousand trilobite individuals, of which only thirteen belong to C. hirsuitus. This paucity stands in sharp contrast to the relative abundance of C. gabrielsi from lower in the Esbataottine and C. mackenziensis from the overlying Whittaker Formation. An examination of the specimens illustrated on Plate 15 will demonstrate that most of the skeletal fragments of C. hirsuitus are extensively encrusted by bryozoans. Most of the bryozoans probably grew on exuviae because commonly a single colony can be traced around sutural edges from the dorsal to the ventral side. It is quite possible, however, that the living trilobite acted as a host for some of the bryozoans.

A single cranidium (Pl. 15, figs. 16-19) displays a unique feature. The base of the right genal spine and adjacent genal corner of this specimen is deformed into a gall-like structure. On the dorsal side, this is expressed as a swelling of the area below the eye and extending to the lateral margin. This is accompanied by a slight forward displacement of the posterior branch of the facial suture and a near total effacement of the border furrow and cheek pitting at and inside the genal angle. On the ventral side, the doublure (as far inwards as the marginal connective device) is stretched forwardly and inwardly as shown by the path of the facial suture. Only the basal portion of the genal spine is preserved, but it appears that the direction and, presumably, the length of the spine was not materially altered. Likewise, the swelling terminated just below the eye and just lateral to the articulating flange indicating that neither the vision nor the articulating ability of the trilobite was seriously impaired. The gall-like structure undoubtably reflects the trilobite's response to a parasite. The infestation was localized in non-critical parts of the host's anatomy and, apparently, did not seriously hamper the vision, locomotion, or feeding of the trilobite. The parasite may have had access to the mouth of the trilobite because, on the interior, a narrow transverse furrow crosses the ridge formed by the axial furrow immediately behind the first glabellar furrow (Pl. 15, figs. 18, 19). This transverse furrow may indicate the course of some kind of conduit because it falls on a line joining the centre of the gall and the presumed position of the mouth between the first glabellar lobes.

One can only speculate on the identity of the parasite, but the morphology of the gall is very similar to the ones recently described by Warn (1974) from columns of the Late Ordovician crinoid, Heterocrinus, and attributed to myzostomid infestation. Warn (1974, p. 506) notes that,

> "Myzostomes are peculiar polychaete annelids, abundantly, and almost exclusively, parasitic on Recent crinoids. Most are ectoparasites that steal food from the ambulacra, but a few are endoparasites that form reproductive galls in crinoid arms and pinnules."

It seems quite feasible that similar worms were responsible for the gall in Ceraurus hirsuitus.

Ceraurus tuberosus Troedsson, 1928

Pl. 18, figs. 36-41

Ceraurus tuberosus TROEDSSON, 1928, p. 71. Pl. 18, figs. 1-9 (not Pl. 17, fig. 13).

Occurrence: Cape Calhoun Formation at Cape Calhoun, northern Greenland and lower Whittaker Formation, Whittaker Range (I 1275). Ceraurinella necra Zone (in Canada).

Material: 8 individuals.

Holotype: Herein designated. An incomplete cranidium (Troedsson's no. 310) from the Cape Calhoun Formation illustrated by Troedsson (1928, Pl. 18, fig. 3).

Discussion: The material from the Whittaker Formation agrees in all essential points with *Ceraurus tuberosus* from the Cape Calhoun Formation, northern Greenland. The forwardly flaring glabella, the small isolated 1p lobe, the position of the palpebral lobes opposite 2p glabellar lobe, the long genal spines, and the densely tuberculose glabella is deemed particularly important. These features also serve to distinguish this species from the other Middle and Upper Ordovician species of *Ceraurus* from eastern North America. The pygidium illustrated by Troedsson (1928, Pl. 17, fig. 13) is excluded from *C. tuberosus* because it displays marked similarity to the pygidia of *C. milleranus* from the Whittaker Formation (Pl. 16, figs. 53, 54, 56, 57). It is of interest to note that Troedsson (1928, p. 69, Pl. 17, fig. 10) described a rather poorly preserved cranidium of *Ceraurus* sp. from the Cape Calhoun and noted that it was similar to *C. milleranus*. It is here suggested that this cranidium should be associated with the above pygidium. In the discussion on the phylogeny of *Ceraurus*, I have tried to demonstrate that *C. milleranus*, *C. mantranseris*, and possibly *C. globulobatus* make up a tightly-knit species group within *Ceraurus*. The unnamed Cape Calhoun species would constitute another occurrence of this species group.

Of the other species of *Ceraurus* from the Mackenzie Mountains, *C. tuberosus* is most similar to *C. mackenziensis*; but differs by possessing coarse tubercular ornament, a shorter (sag.) pre-glabellar field, and a shorter (sag.) and more squat glabella. The anterior course of the facial suture of *C. tuberosus* runs along the front edge of the palpebral ridge, while in *C. mackenziensis* it passes well in front of it. In the Whittaker Formation, *C. tuberosus* is older than *C. mackenziensis* and could well have served as its ancestor.

Ceraurus mackenziensis n. sp.

Pl. 16, figs. 1-44

Ceraurus cf. *pleurexanthemus* Green, TROEDSSON, 1928, p. 68, Pl. 16, fig. 22 (not figs. 20, 21).

Ceraurus sp., LUDVIGSEN, 1975, Pl. 5, figs. 8, 9.

Diagnosis: A species of *Ceraurus* with a glabella that expands markedly forwards, narrow (tr.) lateral glabellar furrows, a large palpebral lobe opposite 2p lobe, very wide lateral cephalic borders, long palpebral ridge, and sparse low tubercles on glabella. Genal spines are long and upwardly curving. Pygidium has a single pair of very long, slender, and flaring spines.

Occurrence: Cape Calhoun Formation, northern Greenland, Lower Whittaker Formation, Funeral Range (C 640, C 655, J 220) and Whittaker Range (H 1850, H 1920, H 1975, I 1350-1380, I 1410, ?Q 430). *Ceraurus mackenziensis* Zone (in Canada).

Material: About 140 individuals.

Holotype: An incomplete cranidium (RL 0582) from C 655 illustrated on Pl. 16, figs. 1-3.

Description: Cephalon crescentic in outline, moderately (tr.) and faintly (sag.) vaulted. Width (tr.) across posterior margin equals 1/3rd length (sag.). Glabella inflated, expands markedly forward to maximum width (tr.) across anterior lobe which is equal to 3/4th leng~~th~~ (sag.). Three pairs of narrow (tr.) lateral glabellar furrows oriented approximately perpendicular to axial furrows; 1s deepest, widens (exsag.) slightly adaxially, extends 1/6th way across glabella; 2s about same width (tr.), but shallower; 3s slightly deeper than 2s, extends about 1/7th way across glabella. Glabellar lobes small, square or rectangular in outline, become slightly longer (exsag.) forwardly; 1p lobe isolated by faint posterior extension of 1s furrow. Anterior lobe semi-circular in outline, bounded by narrow, sharply incised pre-glabellar furrow whose semi-circular course modified by being somewhat flattened medially. Anterior border relatively long and strongly curved (sag.) across anterior margin; widens somewhat distally. Axial furrows moderately deep, nearly straight, diverge forward at about 15° to sagittal line in front of occipital furrow; terminate in small, indistinct anterior pits at 3s furrow. Occipital ring arched about as high as glabella in front of occipital furrow, flatly convex; lenticular in outline, 3 or 4 times as wide (tr.) as long (sag.). Occipital furrow narrow (sag.), deeply incised, straight or faintly concave forwardly; behind 1p lobe it swings backwards and outwards. Cheek triangular in outline, wider (tr.) than long (exsag.), moderately convex (tr. and exsag.); eye occupies highest position, opposite 2p lobe, slightly farther than half the distance out on cheek. Palpebral lobe large, oval in outline, oriented exsagittally, stands nearly as high as highest part of glabella; continuous anteriorly with narrow, convex palpebral ridge which proceeds in even curve towards anterior pit; attenuates posteriorly and curves outwards to terminate just behind visual surface of eye. Palpebral furrow very narrow and faint along its posterior course; effectively terminates in small pit adaxial of mid-length of palpebral lobe; forward of this palpebral furrow absent and palpebral ridge evident by being raised over pitted cheek. Visual surface of eye not well displayed; appears moderately curved (tr.) and strongly curved through about 180° in horizontal plane; placed on narrow and convex eye socle. Facial suture proceeds forward and inward from palpebral lobe in nearly straight line; well in front of, and at an angle to, palpebral ridge; at a level about mid-length of anterior lobe it curves slightly inwards and then across anterior margin to meet connective suture; it continues towards mid-line as horizontal rostral suture. Posterior branch of facial suture proceeds outwards in even, forwardly-convex curve. Posterior border furrow narrow (exsag.), straight, deeply incised. Lateral border furrow somewhat shallower. Lateral border very broad, flat or slightly concave in cross-section, steeply inclined; in front of eye lateral margin deflected sharply upwards and inwards so that border is drastically narrowed. In anterior view, front margin of cephalon elevated into a broad, flat-topped portal between the eyes. Lateral margin continued posteriorly as long, gradually tapering genal spines which flare slightly and possess distinct upward curvature. Posterior border convex, narrower (exsag.) than occipital ring.

Dorsal surface of cephalon finely granulose. Faint tubercles occur in a single irregular row on either side of sagittal line and scattered on front portion of anterior lobe. Three small pits in triangular pattern on anterior lobe; that is, a single pit on sagittal line behind preglabellar furrow flanked by a pair of pits just ahead of line joining 3s furrows. Cheek inside border furrow; except for palpebral lobe, palpebral ridge, and eye socle; finely pitted. In addition, a pair of tubercles located on exsagittal line adaxial to palpebral lobe. Few tubercles on posterior border of cheek. On interior, occipital doublure extends to occipital furrow. Adaxial parts of 0s and 1s produced as high, ventrally directed, spindle-shaped appendifers. Lateral part of doublure very broad and faintly convex, narrows slightly forward and medially. Posteriorly, doublure narrows rapidly towards marginal connective device at distal end of flange furrow.

Hypostome triangular in outline, considerably wider across anterior wings than long (sag.). Middle body inflated; narrows markedly backwards from maximum width just anterior of line joining anterior wings; front portion evenly rounded, extends nearly to anterior margin; pair of small oval maculae situated near lateral furrows at 2/3rds the length of hypostome. Lateral furrows initially deep, shallow posteriorly and medially. Lateral borders narrow and convex (tr.), converge backward to midline in V-shaped structure. Posterior border not distinguished. Small shoulders located just behind anterior wings. Anterior furrow narrow, continuous across hypostome. Anterior margin broadly curved; in front of shoulders deflected up to define flaring anterior wings which carry blunt, dorsally directed wing processes. On interior, doublure obliquely disposed (tr.), narrows evenly backwards from base of anterior wings to very narrow strip at posterior edge. Doublure extended into a faint posterior wing and, in front of this, depressed into a broad, antero-laterally directed antennal notch.

Pygidium, without spines, triangular or semicircular in outline. Consists of 3 axial rings; first longest (sag.) and widest (tr.), moderately arched, outlined laterally by narrow forwardly diverging axial furrows; second and third axial rings stand considerably below first and are narrower (tr.) and much shorter (sag.). First axial ring furrow deep, forwardly curving; second and third much narrower and shorter. Pleural field absent. First axial ring extended directly into very long, narrow, backwardly, outwardly and slightly upwardly curving spines which initially diverge at about 45° to sagittal line; distally they diverge ~~slightly~~ or become sub-parallel. Posterior margin between first spine pair evenly rounded without trace of spines. Beneath posterior margin and base of first spine, pygidium descends vertically to right-angled margin. Doublure narrow, convex. Distal end of articulating and first axial ring furrows carry small appendifers.

Discussion: The short glabellar furrows, the granular ~~glabellar~~ ornament with sparse tubercles arranged in two exsagittal rows, the posterior position of the eye, the broad lateral cephalic borders, the long genal spines, and the very long and flaring first pygidial spines effectively discriminate Ceraurus mackenziensis from other species of Ceraurus. The specimen from the Cape Calhoun Formation of northern Greenland illustrated by Troedsson (1928, Pl. 16, fig. 22) under the name C. cf. pleurexanthemus probably belongs to this species. This specimen differs from the other cranidium assigned to C. cf. pleurexanthemus by Troedsson (1928, Pl. 16, fig. 21) in having the palpebral lobe located opposite 2p lobe (contrary to Troedsson's statement on p. 68). Ceraurus mackenziensis is closest to C. tuberosus from lower in the Whittaker Formation in the study area and from the Cape Calhoun Formation from which it differs in having sparse and subdued tubercles on the glabella. C. tuberosus was probably the ancestor to C. mackenziensis.

The greatly expanded and strut-like lateral cephalic borders of C. mackenziensis are gradually developed during ontogeny. This feature allowed the trilobite to rest on the cephalic borders while keeping its glabella elevated and approximately horizontal. The expanded borders would pose a problem during enrollment were they not abruptly curtailed in front of the eyes. The resulting portal could then receive the bases of the long pygidial spines while the rest of the spines would project antero-laterally in front of the cephalon.

Ceraurus mackenziensis shares the distinctive triangular arrangement of three pits on the middle part of the anterior glabellar lobe with other species of *Ceraurus*, including *C. pleurexanthemus*, *C. whittingtoni*, *C. hirsuitus*, and *C. gabrielsi*, and with *Whittakerites planatus*.

Ceraurus milleranus Miller and Gurley, 1897

Pl. 16, figs. 45-57, Pl. 19, figs. 19-22

Ceraurus milleranus Miller and Gurley, RAYMOND and BARTON, 1913, p. 538, Pl. 1, figs. 6-8 (? not Pl. 2, fig. 6); SLOCUM, 1913, p. 71, Pl. 17, figs. 1-3.

?*Ceraurus tuberosus* TROEDSSON, 1928, Pl. 17, figs. 13 (not Pl. 18, figs. 1-9).

Occurrence: Maysville Group, Ohio; lower Maquoketa Shale, Iowa; ? Cape Calhoun Formation, northern Greenland; and lower Whittaker Formation, Dusky Range (R 625). *Whittakerites planatus* Zone (in Canada).

Material: 3 individuals.

Holotype: A complete carapace (UC 6062) from the Maysville Group, Ohio illustrated on Pl. 19, figs. 19-21.

Discussion: An adequate description of Ceraurus milleranus has been presented by Slocum (1913, p. 71-73). The material from the Whittaker Formation differs in only a few minor characters from the type specimen - the posterior part of the glabella is narrower and the palpebral lobe is located opposite 3p lobe rather than 2s furrow. The short genal spines of the holotype flare more widely than on the Whittaker cranidium. This may be ascribed to a slight flattening of the carapace, which is preserved on a shale chip - as Evitt (1953, p. 36) convincingly argued for similarly preserved specimens of C. pleurexanthemus. The overall similarity of the Whittaker material to the holotype of C. milleranus is striking and, for the first time, permits recognition of this species outside the mid-continent area. C. mantranseris Sinclair, 1947 (this thesis, Pl. 19, figs. 7, 8) from the middle Trenton Group of Quebec and C. globulobatus Bradley, 1930 (this thesis, Pl. 19, figs. 11-15) from the Kimmswick Formation of Missouri are similar to C. milleranus, but possess longer genal spines and paired tubercles on the glabella. In addition, the posterior pygidial margin ~~of~~ C. globulobatus is extended as a broad, apron-like field bearing faint traces of spines between the bases of the first spines (Pl. 19, fig. 11). This may indicate a common ancestry with C. pleurexanthemus because Evitt (1953, Pl. 8, figs. 8-16) illustrated pygidia of C. pleurexanthemus var. montyensis showing the same characteristic.

The hypostome of Ceraurus milleranus is illustrated for the first time. It is similar to the hypostomes of C. whittingtoni and related species illustrated by Evitt (1953, Pl. 7), but it has a more triangular outline and a less inflated middle body. The anterior wings are not so high and are less flarig and the anterior margin is more strongly curved (tr.). On the interior, the posterior wings extend to the inner edge of the posterior doublure and inwardly to restrict the opening between the lateral doublure to a narrow triangular gap.

Among the species of Ceraurus from the South Nahanni River area, C. milleranus is unique in possessing eyes that are located far forwards, at the lateral border furrow of the cheek. Only C. maewestoides n. sp. has similarly placed eyes. It has been argued before that the following species, C. gabrielsi, C. blussoni, C. hirsuitus, C. tuberosus, C. mackenziensis, and Whittakerites planatus are connected in a graded phylogenetic series. For the duration of this series, the eye remains in a position opposite or behind 2p glabellar lobe. The sudden appearance of C. milleranus, which has its eye located opposite 3p lobe, suggests that the previous history of this species lies, not with species of the C. gabrielsi/W. planatus lineage, but with the C. pleurexanthemus and C. whittingtoni group of eastern North America. The slight morphological gap can be bridged by C. mantranseris and C.

globulobatus (Text-fig. 22).

Ceraurus maewestoides n. sp.

Pl. 14, figs. 30-33

Diagnosis: A species of Ceraurus with a forwardly expanding and smooth glabella possessing a pair of large mammaliate swellings on the anterior lobe and, behind these, four tubercles arranged in a square. Palpebral lobes are located far out on the cheek and opposite 3p lobes. Genal spines are long and flaring.

Occurrence: Lower Whittaker Formation, Dusky Range (R 625). Whittakerites planatus Zone.

Material: A single cranidium.

Holotype: An incomplete cranidium (RL 0581) from R 625 illustrated on Pl. 14, figs. 30-33.

Description: Cranidium crescentic in outline, 2 1/2 times as wide across base of genal spines as long (sag.), gently convex (tr.). Glabella moderately vaulted, widens forward to maximum width across anterior lobe. Axial furrows deep. Three pairs of short (tr.) glabellar furrows oriented approximately transversely; their adaxial tips connected by faint longitudinal furrow. Glabellar lobes small, oval in outline, inflated; only 1p lobe distinctly isolated; 2p, and 2p lobes nearly isolated. Anterior lobe almost totally occupied by pair of large mammaliate swellings separated by narrow "cleavage". Lateral parts of swellings occupy entire area between 3s furrows and pre-glabellar furrow; medially they rise steeply from glabellar floor. Pre-glabellar field narrow, ribbon-like. Occipital ring broad, moderately vaulted (tr.), flatly convex (sag.). Occipital furrow shallow and transverse medially; laterally it curves backwards around 1p lobe. In addition to large anterior swellings, glabella has 4 large tubercles arranged in square between 2p and 3p lobes; single smaller tubercle occupies mid-point of each glabellar lobe. Fixed cheek triangular, moderately vaulted (tr.) and slightly convex (exsag.). Palpebral lobe oval in outline, occupies highest part, far out on cheek, opposite 3p lobe; low convex palpebral ridge continues to axial furrow. Anterior branch of facial suture runs along outer edge of palpebral ridge; posterior branch proceeds outwards and backwards in even curve. Posterior border furrow narrow, transverse. Genal spines apparently long, moderately stout, gradually tapering, flare widely. Cheeks inside border furrows (except palpebral lobe and palpebral ridge) rather coarsely pitted. Three large tubercles located on approximately exsagittal line between palpebral lobe and axial furrow. A few smaller tubercles located on posterior border and base of genal spine. Entire cranidium smooth, lacking granules.

Hypostome, thoracic segments, and pygidium unknown.

Discussion: The presence of a pair of prominent anterior swellings on the glabella effectively limits comparison with three species. *Ceraurus maewestoides* n. sp. is very similar to *C. binodosus* Cooper and Kindle, 1936, p. 369, Pl. 53, fig. 20 from the Whitehead Formation at Percé from which it differs by lacking scattered tubercles on the cranidium (other than four prominent and regularly arranged tubercles on the glabella and three on the fixed cheek). The Gaspé species possesses markedly oblique 3s furrows, a large occipital tubercle, and the anterior swellings seem to be smaller than the ones on the Whittaker species. *C. bituberculatus* Troedsson, 1928, p. 69, Pl. 17, fig. 12 (not fig. 11 which is probably a species of *Borealaspis*) from the Cape Calhoun Formation of northern Greenland has a wider (tr.) glabella that does not expand noticeably towards the front, widely spaced anterior swellings, more slender and less flaring genal spines, and less inflated lateral glabellar lobes. *C. bispinosus* Raymond and Barton, 1913, p. 536, Pl. 1, figs. 3, 4 from the Black River Group near Tetreauville, Québec also has a pair of swellings on the anterior lobe, but differs markedly from *C. maewestoides* in possessing densely distributed tuberculose ornament on the cranidium, widely-set eyes, deep occipital furrow, and a pre-glabellar furrow that curves around the front edge of the anterior swellings.

The species name is meant to be descriptive.

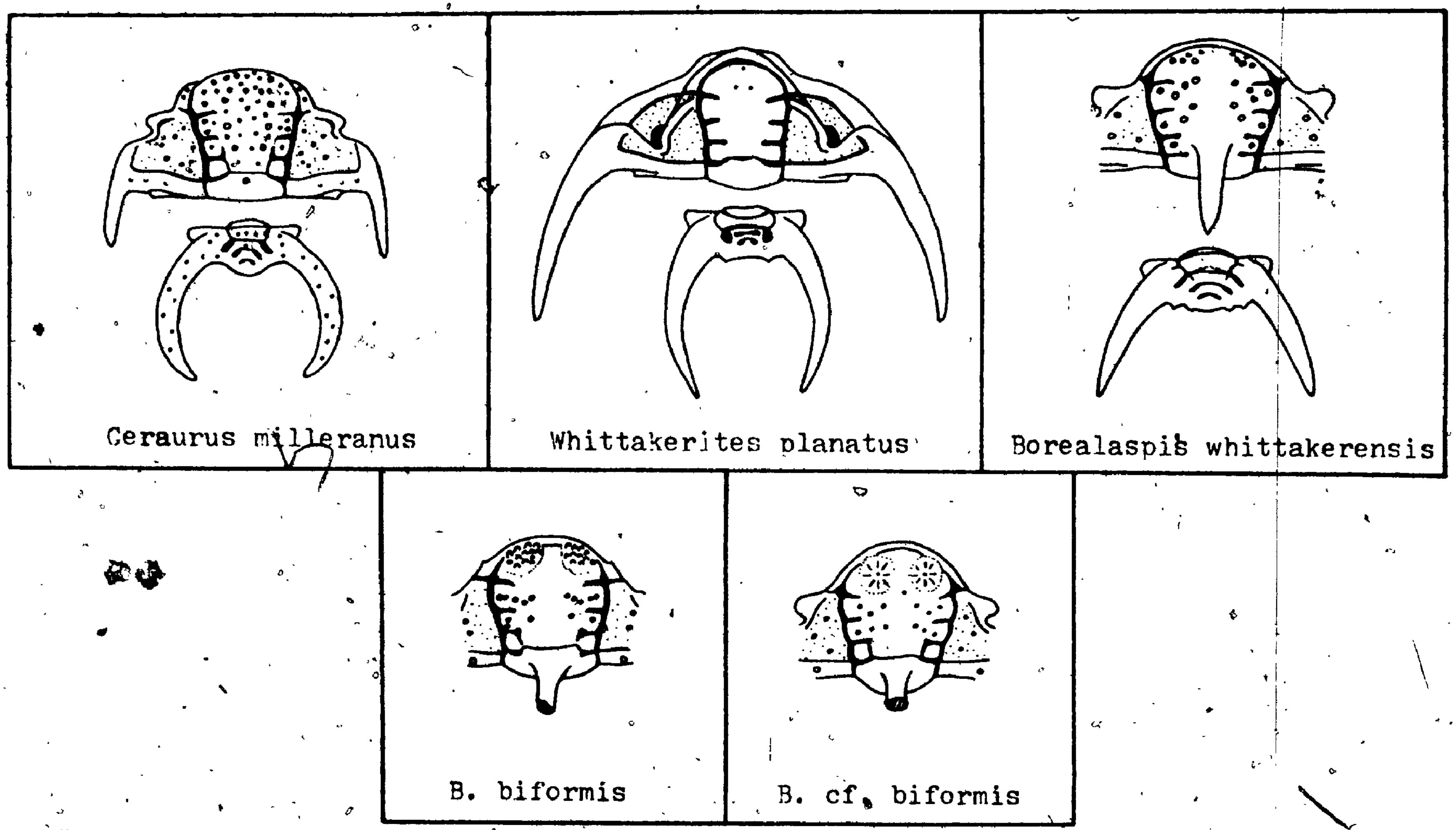
Genus *Whittakerites* n. gen.

Type species: *Whittakerites planatus* n. sp., Lower Whittaker Formation, Whittaker Range and Dusky Range, District of Mackenzie.

Diagnosis: A genus of Cheirurinae possessing a long (sag.) and weakly convex glabella which expands only slightly forward. Three pairs of relatively wide (tr.) and equally spaced glabellar furrows are approximately transversely directed. The glabella is finely granulose; lacking tubercles. The eye is located opposite 1s furrow; palpebral ridge is very long. Pre-glabellar field is flat and broad and arcuate towards the front. Genal spines are long and flaring. The anterior pair of pygidial spines are stout and long and the posterior margin between these spines is nearly straight, but possesses a single pair of tiny spines.

Discussion: The general aspect of the cranidium and, especially, the pygidium and hypostome of *Whittakerites planatus* n. sp. recalls some species of *Ceraurus*. *Whittakerites*, however, is clearly distinguished from *Ceraurus* by the weakly convex glabella with nearly parallel sides, the relatively wide (tr.) glabellar furrows, and the absence of tuberculation on the glabella. The pygidium and hypostome, considered apart from the cranidium, could easily be accepted as belonging to a species of *Ceraurus*. An additional feature of *Whittakerites*; that is, the three pits arranged in a triangle on the anterior glabellar lobe provides clear testament to its origin from Ceraurus. This feature is seen in species such as *Ceraurus mackenziensis* n. sp., *C. gabrielsi* n. sp., *C. blussoni* n. sp., *C. hirsuitus* n. sp., as well as *C. pleurexanthemus* Green (Evitt, 1953, Fig. 1A), but has not been noted in other cheirurinid genera. It is perhaps precarious to use this feature to trace phylogenetic lineages because similar, or analogus, pits and markings are known in diverse cheirurinid and phacopinid genera (Öpik, 1937; Evitt, 1951; Eldredge, 1971). The position of the three pits in many species of *Ceraurus* and in *Whittakerites* is, however, so consistent that it appears improbable that their appearance in these two genera could have any meaning other than phylogenetic. In this regard it is elucidating to cite the resemblance between *W. planatus* and the older *Ceraurus mackenziensis*. In the latter species, the tubercular ornament characteristic of *Ceraurus* has largely been effaced, the eyes are located far back on the cheek, and the palpebral ridge is long and curving. These features, plus a general similarity in the genal spines and in pygidial and hypostomal architecture, places *C. mackenziensis* as a prime candidate for the ancestor of *Whittakerites*.

The nearly parallel-sided glabella, the absence of glabellar tuberculation, and the wide (tr.) and transverse glabellar furrows of *Whittakerites* brings to mind such genera as *Ceraurinus*, *Ceraurinella*, *Remipyga*, *Xylabion*, and *Osekaspis*. The posterior position of the eyes, the flat and forwardly-curving pre-glabellar field, the long genal spines,



Text-figure 30.

Outline drawings of cephala and pygidia of one species of Ceraurus, one of Whittakerites, and three of Borealaspis from the lower Whittaker Formation, South Nahanni River area.

and the hypostome and pygidium readily distinguish Whittakerites.

The pygidium of Ceraurus tenuioornis from the middle part of the Athens Formation, Tennessee (Raymond, 1925, p. 141, Pl. 8, fig. 23) appears rather similar to that of W. planatus. Further comment cannot be made at the present time. If the stratigraphic data is correct, C. tenuicornis is considerably older than W. planatus.

Whittakerites planatus n. sp.

Pl. 17, figs. 1-47

Diagnosis: As for genus.

Occurrence: Lower Whittaker Formation, Whittaker Range (I 1590, Q 530) and Dusky Range (R 625). Whittakerites planatus Zone.

Material: About 60 individuals.

Holotype: An incomplete cranidium (RL 0909) from Q 530 illustrated on Pl. 17, figs. 4, 5.

Description: Cephalon, excluding genal spines, broadly triangular in outline; front portion protrudant; 2 1/2 times as wide across posterior margin as long (sag.); gently arched (tr. and sag.). Glabella faintly (sag.) and moderately convex (tr.), expands slightly forward to 3p lobe; maximum width 2/3rds length (sag.). Axial furrows faintly incised and narrow (tr.) or only marked by slight inflation of glabella over cheek. Three pairs of approximately equally-spaced glabellar furrows of equal width (tr.) extend about 1/4 to 1/5th way across glabella. Furrows nearly transversely directed, but 1s typically directed slightly backwards and 2s slightly forwards; 1s wider (exsag.) than 2s or 3s and becomes deeper adaxially. Glabellar lobes roughly square in outline, faintly inflated; except for 1p lobe which is shorter (exsag.) and more inflated than 2p or 3p. Anterior lobe sharply raised over pre-glabellar field; front edge defined by arc of circle with origin on sagittal line just behind line joining 3s furrows. Occipital furrow deep and forwardly curving behind 1p lobe; narrower (sag.) and nearly straight and transverse medially. Occipital ring more convex (tr.) than rest of glabella, but stands slightly lower; 3 times as wide (tr.) as long (sag.); flatly convex (sag.); posterior edge projects backwards in broad arc. Pre-glabellar furrow, like axial furrow, essentially seen because glabella rises steeply from flat or faintly convex (sag.) anterior border which is long (exsag.) and slightly expanded medially. Cheek approximately defined by quarter circle, moderately (exsag.) and faintly (tr.) convex; eye situated at midwidth near posterior border furrow. Palpebral lobe elliptical, exsagittally directed; mid-point located opposite 1s furrow and posterior part of 2p lobe; poorly differentiated from palpebral ridge which proceeds in broad inward curve across cheek to intercept axial furrow just behind 3s furrow. Palpebral ridge narrow (tr.), slightly raised over cheek. Palpebral furrow very faint. Visual surface of eye not seen.

but its base appears to be moderately curved. Anterior branch of facial suture proceeds forwards and inwards along a nearly straight path; initially runs along front edge of palpebral furrow; near mid-line suture curves inwards to be joined by connective ~~suture.~~ Rostral plate not seen, but judging from position of front edge of free cheek, must be rather narrow (tr.) and short (sag.). Posterior branch of facial suture proceeds outwards with slight forward curvature. Lateral border furrow shallow and broad, V-shaped in cross-section; curves forwards and inwards to meet axial furrow at righ angle; adaxial part deep. Posterior border furrow narrower and deeper, nearly straight. Lateral and posterior borders moderately broad, evenly curved in cross-section, stand slightly higher than cheek inside border furrows. Genal spine long, tapers gradually, flares slightly, extends posteriorly for distance equal to length (sag.) of glabella.

Entire dorsal surface of cranidium rather coarsely granulose. Three pits arranged in triangular pattern on anterior glabellar lobe. Cheek inside border furrows, except palpebral lobe and palpebral ridge, finely pitted.

On interior broad, doublure extends forward to occipital furrow. Cranidial furrows expressed as low ridges. 2s and 3s furrows appear as moderately high ridges. Anterior pit expressed as low, thorn-shaped elevation. Adaxial part [illegible] 1s furrow and part of 0s furrow inside axial furrow extended as rather high appendifers. Posterior edge of cranidium carries flange furrow and small marginal connective device.

Hypostome shield-shaped in outline. Length (sag.) approximately equal to width between anterior wings. Middle body moderately inflated; carries pair of small maculae near lateral furrows about 2/3rds distance back. Immediately in front of macula occurs very faint and short middle furrow, obliquely directed. Lateral furrows shaped like a stretched letter S and Z; deepest and widest (tr.) at midlength. Anterior furrows narrow (sag.and exsag.), follows arc of circle between base of anterior wings. Anterior border very narrow medially, widens and curves upwards to form anterior wings distally. Lateral margin directed obliquely inward with very slight curvature from prominent shoulders. Lateral and posterior borders confluent, convex in cross-section. On interior doublure very narrow posteriorly, widens and becomes outwardly sloping as it proceeds forwards. In front of shoulders, doublure flexed into moderately narrow antennal notch and then recurved upwards and backwards into a triangular anterior wing carrying a blunt, node-like, dorsolaterally directed wing process. Ventral surface of hypostome appears granulose.

Number of thoracic segments unknown. Axis weakly convex, about 3 times as wide (tr.) as long (sag.); divided by articulating furrow which is narrow (sag.) with slight forward curvature medially and which distally descends into deep, forwardly-diverging slot-like pits. Axial furrows very faint. Inner part of pleura inflated, narrower (tr.) than axial lobe; crossed diagonally by rather faint, backwardly-directed pleural furrow. Outer part of pleura extended into stout spine which curves outwards, downwards, and slightly backwards. Spine encased by doublure and tapers to rather blunt point. Pleura defined anteriorly and posteriorly by narrow flange furrows which, distally, curve around prominent marginal connective device. Other articulating devices consist of articulating flange and small axial furrow socket and process. On interior distal ends of articulating furrow support large, plate-like, forwardly diverging appendifers.

Pygidium, without first spines, broadly rectangular in outline; about 2 1/2 times as wide (tr.) as long (sag.). Axis consists of prominent, relatively long and wide, and moderately convex (tr.) first ring and two subdued posterior rings which are much narrower (sag.) and shorter (tr.). Faint, laterally bowed axial furrows bound first axial ring. First ring furrow forwardly curved; terminates distally in deep, triangular pits which delimit lateral extent of second and third rings. Second ring furrow consists of a pair of transversely elongate slots which almost reach deep, triangular pit. Third ring furrow narrow, forwardly curved or inverted V-shaped; terminates in small pits located well in front of posterior margin. Pleural field narrow; only made evident by presence of extremely faint and short pleural furrow opposite first ring. Anterior spines long, laterally bowed or laterally flaring, basally stout, tapers gradually to fine point; extend posteriorly a distance equal to 1 1/2 to 2 times width of pygidium at anterior margin. In lateral view, spines directed obliquely upwards at 20 to 35°. Posterior margin between spines nearly straight; very short, triangular second spines visible immediately inside first spines. Doublure strongly curved; medially deflected dorsally into narrow fold. Distal ends of articulating and (?) first axial ring furrow extended into appendifers. Second and third axial rings flanked by large triangular elevations which extend ventrally to inner edge of doublure.

Discussion: Since *Whittakerites* is monotypic, *W. planatus* cannot be compared with other species, aside from the ones discussed under the generic heading.

Genus *Borealaspis* n. gen.

Type species: *Borealaspis whittakerensis* n. sp. Lower Whittaker Formation, Funeral Range, District of Mackenzie.

Other species assigned: *Cheirurus numitor* Billings, 1866; *Borealaspis biformis* n. sp.; "*Ceraurus bituberculatus*" Troedsson, 1928, Pl. 17, fig. 11, only.

Diagnosis: A genus of Cheirurinae possessing an evenly inflated bulb-shaped glabella. Maximum width of glabella is across 3p lobe. It may possess a pair of swellings or spines on the anterior lobe and a single median occipital or pre-occipital spine. Presence/absence of median spine may reflect sexual dimorphism. Occipital ring stands lower than glabella in front of occipital furrow. Palpebral lobes are small and located opposite 3p lobe or 3s furrow. In front of eye, facial suture descends vertically.

Discussion: The above aggregation of features distinguishes *Borealaspis* from other Cheirurinae. The median spine, in particular, places the genus in a unique position within the subfamily, but this must be used with caution because both *B. biformis* and *B.* cf. *biformis* include individuals without median spines. The presence of a pre-occipital spine prompted Billings (1866, p. 28) to consider *B. numitor* allied to *Nieszkowskia cephaloceras* (Nieszkowski) and, apparently, influenced Lane (1971, p. 66) in his assignment of *B. numitor* to *Nieszkowskia*. Raymond and Barton (1913, p. 540), however, correctly concluded that the glabellar features of *B. numitor* ally it to *Ceraurus* rather than to *Nieszkowskia* or *Youngia*. The illustration of the neotype of *B. numitor* (Pl. 17, figs. 16-18) should settle the subfamilial assignment of this species. The pygidium and hypostome of *B. whittakerensis* and *B. biformis*, respectively, are very similar to those of *Ceraurus* and clearly demonstrate that *Borealaspis* is a cheirurinid and not an acanthoparyphinid.

A probable occurrence of *Borealaspis* in northern Greenland is indicated by the poorly preserved glabella illustrated by Troedsson (1928, Pl. 17, fig. 11, not fig. 12) as *Ceraurus bituberculatus*. The glabellar outline of this specimen cannot be determined, but the presence of a pair of large spines on the anterior lobe and a broad-based occipital spine suggests an assignment to *Borealaspis* and, in particular, an affinity with *B.* cf. *biformis* (Pl. 18, fig. 29). This generic assignment was anticipated by Troedsson (1928, p. 71) in pointing out the resemblance of this specimen to *Borealaspis numitor*.

Borealaspis biformis occurs in the *Ceraurinella necra* Zone and the *Ceraurus mackenziensis* Zone. *B. whittakerensis* occurs in the *Ceraurus mackenziensis* Zone. *B.* cf. *biformis* also occurs in the *C. mackenziensis* Zone and a few poorly preserved specimens from the *Whittakerites planatus* Zone suggests it persists into younger rocks. These occurrences in the Whittaker Formation are of Trentonian to ?Edenian age (Copeland, 1974; Ludvigsen, 1975). *B. numitor* from the Vaureal Formation is of Richmondian age (Sinclair, 1956;

Bolton, 1972).

Borealaspis whittakerensis n. sp.

Pl. 18, figs. 1-12

"Ceraurus" cf. numitor (Billings), LUDVIGSEN, 1975, Pl. 5, fig. 11.

Diagnosis: A species of Borealaspis with an inflated and bulb-shaped glabella, short and slightly curving glabellar furrows, an erect or posteriorly directed median pre-occipital spine, palpebral lobes located opposite 3p lobes, and sparse tubercular ornament on glabella. Pygidium is rectangular, the first spine pair is long and curving, the second and third pairs are very short.

Occurrence: Lower Whittaker Formation, Funeral Range (C 655) Ceraurus mackenziensis Zone.

Material: 13 individuals.

Holotype: An incomplete cranidium (GSC 40450) from C 655 illustrated on Pl. 18, figs. 1-5.

Description: Glabella inflated, bulb-shaped in outline; expands from minimum width (tr.) across occipital ring to maximum width across 3p lobe. Three pairs of fairly shallow and narrow (exsag.) lateral glabellar furrows of equal length (tr.); 1s transversely directed, extends about 1/5th way across glabella, terminates adaxially in small apodemal pit; 2s and 3s slightly narrower than 1s, subparallel, proceed inward with slight curvature about 1/7th way across glabella. Occipital furrow reduced to a pair of lateral glabellar furrows, about the size as 1s furrow; terminate in small appendiferal pits. 1p lobe rectangular in outline, slightly wider (tr.) than long, not inflated. 2p and 3p lobes sub-trapezoidal in outline, 1 1/2 times as long (exsag.) as 1p lobe, slightly inflated. Anterior lobe crescentic, longer (sag.) than 2p or 3p lobes, slopes steeply to pre-glabellar furrow. Axial and pre-glabellar furrows aligned in single evenly curved arc; juncture of moderately deep axial furrow and narrow, straight (in anterior view) pre-glabellar furrow marked by small, inwardly and downwardly directed anterior pit at 3s furrow. Pre-glabellar field narrow and convex medially, widens slightly laterally. Occipital ring arched (tr.); does not stand above any part of glabella in front of 0s furrow. In lateral view, glabella curves steeply to pre-glabellar furrow and faintly to posterior margin from maximum height between eyes. Long, stout spine occupies median position between 1p lobes; spine tapers gradually to sharp point. In one specimen spine directed obliquely upwards and backwards; in another directed nearly straight backwards. Inner portion of fixed cheek gently arched (tr. and exsag.), approximately triangular in outline. Short (exsag.), oval, apron-like palpebral lobe located opposite 3p lobe; bounded by straight, forwardly convergent palpebral furrow which does not extend past adaxial end of palpebral lobe. From palpebral lobe, facial suture proceeds inwards and sharply downwards to point lateral to anterior pit, then in an even curve towards midline. In anterior view, suture parallels pre-glabellar furrow, but is faintly scalloped because it descends along broad inverted V-shaped path to meet connective sutures. On interior, occipital doublure extends forward to posterior side of median spine. Anterior pits appear as stout swellings. Adaxial parts of Os and 1s furrows extended into moderately high, ventrally directed appendifers. Dorsal surface of cranidium sparsely granulose. In addition, glabella bears large, prominent, sparsely distributed, and commonly perforated tubercles grouped in a pair of triangular patterns on anterior lobe and two pairs of irregular and diagonal rows proceeding backward and outward from median part of glabella to mid-portion of 3p and 2p lobes. Single small tubercle occurs on midpoint of 1p lobe. Portion of fixed cheek inside posterior border furrow finely pitted and carries two tubercles posterior to palpebral lobe.

Outer portion of fixed cheek, free cheek, hypostome and thoracic segments unknown.

Pygidium known from a single, incomplete holaspid and a few incomplete meraspid specimens. Outline of pygidium (without first spines) sub-rectangular, twice as wide (tr.) as long (sag.). Axis low, consists of three posteriorly narrowing (sag.) rings and faint terminal piece; outlined by faint axial furrows. Rings divided by straight to slightly forwardly convex ring furrows. Pleural field narrow, crossed by single short pleural furrow opposite first axial ring. Anterior pygidial spines apparently moderately long, directed outwards and backwards in even curve. Second and third spines very short, blunt; separated by faintly convex median piece. Pygidium sparsely granulate.

Discussion: The differences between Borealaspis whittakerensis and other species of Borealaspis are evident in the discussion under the respective species.

Borealaspis numitor (Billings, 1866)

Pl. 19, Figs. 16-18

Cheirurus numitor BILLINGS, 1866, p. 27, 28, Fig. 11.

Ceraurus numitor (Billings), RAYMOND and BARTON, 1913, 1913, p. 540, Pl. 1, fig. 5; BARTON, 1916, p. 137.

non Ceraurus numitor (Billings), TWENHOFEL, 1927, p. 333.

Nieszkowskia numitor (Billings), LANE, 1971, p. 66.

Neotype: Herein designated according to Art. 75 of the International Code of Zoological Nomenclature. An incomplete cranidium (GSC 2199) collected by T.C. Weston from the English Head Formation, Makasti Bay, Anticosti Island. This location is within the upper Vaureal Formation (Richmondian) according to Bolton (1961, 1972). The only specimen in the type series (Billings, 1866, Fig. 11) has apparently been lost (Bolton, 1966). This specimen was collected at English Head by James Richardson. The specimen illustrated by Raymond and Barton (1913, Pl. 1, fig. 5) was collected by the Shaler Expedition from English Head and cannot be considered part of the type series.

Discussion: Borealaspis numitor is most similar to B. whittakerensis; but differs in possessing deeper and more curved glabellar furrows, a more inflated glabella, palpebral lobes that are situated farther out on the cheek and opposite 2s furrow, distinct palpebral ridge, and a denser tubercular ornament which is distributed without apparent pattern on the anterior two-thirds of the glabella.

The neotype (GSC 2199), illustrated herein for the first time, agrees quite well with the original description and illustration (possibly somewhat diagrammatic) of the lost holotype by Billings (1866, p. 27, 28, Fig. 11). That specimen appears to have an anterior glabellar margin that is less convex than that on the neotype and palpebral lobes that are located opposite 3p lobe. Billings, however, states (p. 28) that, "the eyes are small and about opposite or a little in advance of the second pair of furrows". The median glabellar spine of B. numitor, of which only the base is retained on the neotype, is very similar to that seen on a larger cranidium of B. whittakerensis (Pl. 18, figs. 6, 7), judging by Billings' description and illustration.

The specimen of B. numitor illustrated by Raymond and Barton (1913, Pl. 1, fig. 5) is much larger than the neotype and, because the left side is incomplete, it is difficult to judge the outline of the glabella. The features that can be seen, however, are in total accord with those of the neotype. The maximum width of the glabella appears to be across 3p lobes, the occipital furrow is reduced to a pair of lateral furrows between which stands the base of a very stout median spine, and the anterior two-thirds of the glabella possesses scattered coarse tubercles.

Twenhofel (1927) did not illustrate *B. numitor*, ~~but~~ did present a fairly detailed description ostensibly based on the specimen herein designated the neotype and additional specimens in the Twenhofel collection at Peabody Museum from a number of localities on the north-west coast of Anticosti Island. Twenhofel's description is rather enigmatic because some of the features described are definitely not present on GSC 2199. He writes (p. 333),

> "The neck furrow extends to the genal spines, is shallow and narrow on the cheeks, but deep and wide over the axis. The occipital segment is prominent, particularly over the axis....The axial portion (of the occipital segment) is high and prominent with three tubercles or short stout spines on the apex, with the middle spine a little in advance of the other two."

Particularly revealing is the reference to the occipital furrow being deep and wide over the axis and the presence of three tubercles on the prominent occipital ring. It is clear that this description does not pertain to the neotype of *B. numitor*. Examination of three collections from the Peabody Museum labelled "*Ceraurus numitor* (Twenhofel, Ordovician, English Head; Locs. 808, 809, 822)" brought to light a few cranidia that do, however, fit Twenhofel's description. Aside from a general "cerauríd" aspect, these specimens bear little resemblance to *B. numitor*. The glabella expands slightly forwards to a maximum width across the anterior lobe, the occipital furrow is deep and wide (sag.), the glabellar furrows are short (tr.), the occipital ring is high and ponderous and projects posteriorly in a broad arc, and the glabella is covered by coarse, composite tubercles including three tubercles on the median part of the occipital ring. These specimens are very similar to *Ceraurus hispidus* (Whittington, 1954) from Silliman's Fossil Mount on Baffin Island and are here assigned to *C.* cf. *hispidus* (the retention of a discrete generic name, *Hapsiceraurus* Whittington, 1954, for two species *C. hispidus* and *C. horridus*, that are patently of the *Ceraurus* type cannot be justified). The three Twenhofel collections from English Head did not contain a single specimen that could be assigned to *B. numitor*; all of the specimens are probably referrable to *Ceraurus* cf. *hispidus*.

Borealaspis biformis n. sp.

Pl. 18, figs. 13-27

Diagnosis: A species of *Borealaspis* with a moderately inflated glabella, a prominent and curved occipital spine or small median occipital node, and paired swellings on anterior lobe covered by tubercles.

Occurrence: Lower Whittaker Formation, Funeral Range (C 570-590) and Whittaker Range (H 1850, ?I 1275). *Ceraurinella necra* Zone and *Ceraurus mackenziensis* Zone.

Material: About 20 individuals.

Holotype: An incomplete cranidium (RL 0617) from C 570-590 illustrated on Pl. 18, fig. 13-16.

Description: The description of the cranidium of *B. biformis* takes the form of a comparison with the cranidium of B. whittakerensis (see "Discussion"). The hypostome is described below.

Hypostome shield-shaped. Length (sag.) equal to maximum width across anterior wings. Middle body moderately inflated; greatest width anteriorly, narrows gradually posteriorly. A pair of small, oval, obliquely disposed maculae located just inside lateral furrows, 2/3rds distance from anterior edge. Lateral furrows deep and wide, becoming narrower as they converge posteriorly. Lateral border narrow and convex (tr.); in front of maculae lateral margin deflected outward to form small shoulders. Anterior furrow much narrower and shallower than lateral furrow, curves forward in even arc at base of anterior wings; medially it is hidden by anterior portion of middle body. Anterior wing triangular in ventral view; posterior edge of wing deflected straight up and spindle-shaped wing process protrudes dorso-laterally from anterior face. On interior, doublure very narrow at posterior edge, widens and becomes obliquely disposed forwardly into broad forwardly-diverging antennal notch, and then vertically to form anterior wings. Ventral surface finely and coarsely granulate and anterior third of middle body covered by fine hair-like, anteriorly directed spines. Lateral portions of anterior part of middle body contain tiny rimmed perforations which appear on the interior as rather coarse pits.

Discussion: B. biformis differs from B. whittakerensis in the following points:

4 OF/DE 6

1. The glabella is not as inflated and does not widen as markedly forward.

2. The occipital furrow is continuous across the glabella. Across the axial part it is narrow, faintly incised, and transversely disposed; behind 1p lobe it swings backwards and outwards to the axial furrows.

3. The anterior lobe is longer (sag.) and topographically differentiated into a pair of faint swellings, covered by coarse tubercles, and divided by a broad longitudinal valley.

4. The glabellar tubercles are distributed differently. The pattern can best be seen on smaller cranidia (Pl. 18, figs. 19, 28), but is also present on larger cranidia (Pl. 18, figs. 13, 17) and consists of crowded tubercles grouped in three separate circular pairs arranged in longitudinal rows. The largest pair is located on the swellings on the anterior lobe; a medium pair located just inside and between 3s and 2s furrows; and the smallest pair just posteriorly of the 2s furrows. In addition, crowded tubercles occur on the mid-portion of 2p and 3p lobes. On the larger cranidia, the two posterior tubercle sets are reduced in size to a single tubercle each.

5. The median spine of B. <u>biformis</u> is occipital rather than pre-occipital as in the type species. The spine is stout, long, and directed upwards and backwards with pronounced curvature.

6. On one specimen (Pl. 18, fig. 17) the occipital spine is replaced by a tiny occipital node. This specimen

is about the same size as the one with a prominent occipital spine (Pl. 18, fig. 13) and, in all other features, appear identical. This demonstrates that the spine is not a feature that can be attributed to ontogenetic development. It is the writer's opinion that the presence/absence of the occipital spine reflects sexual dimorphism. The scarcity of material, however, precludes definite statements to that effect.

7. The interior opening of the hollow occipital spine is completely covered by the occipital doublure.

Borealaspis cf. *biformis* n. sp.

Pl. 18, figs. 29-35

Occurrence: Lower Whittaker Formation, Whittaker Range (H 1920, Q 430); Funeral Range (J 220); and Dusky Range (R 625). *Ceraurus mackenziensis* Zone and *Whittakerites planatus* Zone.

Material: About 8 fragmentary individuals.

Discussion: *Borealaspis* cf. *biformis* n. sp. differs from *B. biformis* in possessing a pair of dorsally directed spines in place of the swellings on the anterior lobe. These spines are high and prominent, but it should be mentioned that, on the larger specimen illustrated (Pl. 18, figs. 29-33), their height is somewhat exaggerated by secondary overgrowth of silica on their apices. The absence of an occipital spine on the smaller specimen (Pl. 18, fig. 34, 35) demonstrates that the dimorphism evident in

B. biformis is not a local aberration, and suggests that it could be a pervasive feature within the genus. It is not clear if the presence of anterior glabellar spines, in place of swellings, should be considered of sufficient importance to warrant the establishment of a discrete species, but the available material is sparse, rather poorly preserved, and fragmentary and a decision must await discovery of more abundant and complete specimens.

Cheirurinid indet. n. gen. and n. sp.

Pl. 17, figs. 48-51

Occurrence: Lower Whittaker Formation, Dusky Range (R 625). Whittakerites planatus Zone.

Material: 2 pygidia.

Description: Pygidium, without first spines, broadly triangular. Antero-lateral corners acute in front of first spines. Axis short (sag.), consists of two moderately convex (tr.) rings separated by narrow axial ring furrows that terminate laterally in deep pits. Position of a possible third axial ring furrow is indicated by a small pit located at mid-point of central pygidial spine. Axis outlined opposite first ring by faint axial furrows; pleural field not present. Stout, sausage-shaped first pygidial spine arises directly from distal end of first ring; spine directed obliquely backwards and outwards with slight curvature and upwards at about 40°; length of spine slightly greater than 1/2 width of pygidium across anterior margin.

Central three spines blunt and rounded, directed backwards and slightly upwards; much shorter and narrower than first, & median spine wider (tr.) than flanking spines. Beneath spines, pygidial field descends vertically and is recurved into convex doublure. Fine tubercles on dorsal surface become sparser towards axial furrows and denser on ventral side of pygidial spines and on doublure.

Discussion: The pygidia at hand were found in a single collection from the Whittaker Formation. A search for associated cranidia proved unsuccessful. These pygidia bear some resemblance to those of Ceraurinella necra and C. brevispina in possessing a longer first spine pair followed by three shorter spines, but this resemblance is merely superficial. They differ from those of Ceraurinella in having only two axial rings and in possessing five pygidial spines that are all directed obliquely upwards. In Ceraurinella only the first spine pair is set at an oblique angle. This material undoubtably belongs to a new genus, but its establishment must await discovery of associated cranidia.

MIDDLE ORDOVICIAN TRILOBITES,
SOUTH NAHANNI RIVER AREA,
DISTRICT OF MACKENZIE

by

Rolf Ludvigsen

Department of Geology

1

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Subfamily Acanthoparyphinae Whittington and Evitt, 1954

Genera assigned: Those listed by Lane (1971, p. 66) plus Heliomera Raymond, 1905 and Heliomeroides Evitt, 1951.

Diagnosis: See Lane (1971, p. 66).

Discussion: The composition of this subfamily is revised from that of its latest assessment (Lane, 1971) to include Heliomeroides and Heliomera. These two genera were originally placed in a separate subfamily, Heliomerinae by Evitt (1951) who emphasized the dominating glabella and the radial arrangement of the glabellar furrows. Whittington's (1965, p. 411) assignment of Heliomera (including Heliomeroides) to the subfamily Sphaerexochinae Öpik, 1937 has generally been followed by later authors (Lane, 1971; Dean, 1971), with the exception of Shaw (1968) who retained the Heliomerinae. It is here maintained that Heliomeroides can better be placed in the Acanthoparyphinae. The evidence for subfamily assignment of Heliomera is somewhat equivocal, but the unanimity of opinion on the close morphological connections of these two genera demands the same suprageneric classification. The evidence for placing Heliomeroides in this subfamily is summarized below:

1. The pygidium of Heliomeroides teres Evitt, 1951 has two pairs of spines. The number of pygidial spines for members of the Acanthoparyphinae appears fixed at four. Material of Youngia sp. recently discovered by Perry (1974) from the Wenlockian or Ludlovian part of the Delorme Formation,

District of Mackenzie, establishes that the pygidium has two pairs of spines and is essentially like that of *Acanthoparypha*. The pygidium of *Ainoa* Mannil, 1958 is unknown. All of the members of the Sphaerexochinae, whose pygidia are known, bear three pairs of pygidial spines (in *Pompeckia* Warburg, 1925, a central spine has been added). Uncertainty exists about the taxonomic placement of the six-spined "heliomerinid pygidium" illustrated by Whittington (1965, Pl. 25, fig. 3) so this specimen does not elucidate the present problem.

2. The cranidium of *Heliomeroides teres* lacks anterior pits. In this respect it is similar to members of the Acanthoparyphinae. *Acanthoparypha echinoderma* Chatterton and Ludvigsen (this thesis, Pl. 23, figs. 8, 9) lacks anterior pits. *Acanthoparypha evitti* Chatterton and Ludvigsen, *A. perforata* Whittington and Evitt, and *A. chiropyga* Whittington and Evitt (this thesis, Pl. 21, figs. 41, 5; Whittington and Evitt, 1954, Pl. 14, figs. 1, 4, Pl. 29, figs. 4, 2) each possesses a faint elongate anterior pit which appears on the interior as a low rounded elevation. *Holia secristi* Whittington and Evitt and *H. cimelia* Whittington and Evitt each possesses a large shallow anterior pit which is expressed on the interior as a slight rise (this thesis, Pl. 22, figs. 9, 10; Whittington and Evitt, 1954, Pl. 18, figs. 1, 4). *Sphaerexochus*, by contrast, has a small and relatively deep anterior pit which emerges on the interior as a small thorn-like cone (this thesis, Pl. 25, fig. 21; Whittington and Evitt, 1954, Pl. 32, fig. 24).

3. The thoracic segments of *H. teres* are basically like those of *Acanthoparypha* in possessing tubular, unfaceted spines and narrow axial furrows which are expressed on the interior as high ridges. The unfaceted spines indicate that the spine tips were probably not in contact during enrollment. This situation can be contrasted with the devices in *Sphaerexochus* which allowed contact between adjoining thoracic segments and the anterior thoracic segments with the cranidium during enrollment -- a smooth band along the anterior side of the pleural lobes and the pygidium permits partial overlap of segments (Pl. 25, fig. 25), faceted thoracic spines allow "nesting" of the spine tips, and the notch in the posterior part of the lateral margin of the cephalon accommodates the spine tips of one of the anterior segments during enrollment (see Whittington and Evitt, 1954, figs. 25, 27 and Bergstrom, 1971, p. 25). None of these features are seen in any genus of the Acanthoparyphinae. In discussing the subfamily affinities of *Heliomeroides teres* Evitt (1951, p. 591) states that "the articulation is strongly suggestive of that in a new subgenus of *Nieszkowskia* represented in the same material and to be described in a subsequent paper". The reference is undoubtably to *Acanthoparypha* (Whittington, 1959, p. 384).

4. Most members of the Sphaerexochinae either lack fixigenal spines in large holaspids or possess them in a very reduced state. The Acanthoparyphinae typically possess prominent genal spines. *Heliomeroides* has short triangular fixigenal spines and the ones of *Heliomera* are long and

spike-like.

A totally satisfactory grouping of the genera herein assigned to the Acanthoparyphinae and Sphaerexochinae cannot be made at the present time. It is recognized that many of the arguments presented above could equally well be directed towards genera like *Kawina* Barton and *Cydonocephalus* Whittington which, although placed in the Sphaerexochinae, share a number of features with *Acanthoparypha* and allied genera. This becomes understandable when the phylogeny of the two subfamilies are examined. Lane (1971, text-fig. 13) suggested that "*Kawina*" *sexapugia* Ross (1951, Pl. 35, figs. 6, 7, 11-17, 1-21 - see also Hintze, 1953, Pl. 21, fig. 18) from Zone J (late Canadian) of Utah served as the ancestor to the rest of the Sphaerexochinae. Lane (1971, p. 79) commented on the apparent intermediate position of this species between the Pilekiinae and the Sphaerexochinae. He avoided consideration of the origin of the Acanthoparyphinae. We suggest that "*K.*" *sexapugia* could equally well have served as an ancestor to the Acanthoparyphinae. The cranidium, hypostome, and thoracic segments are similar to those of *Acanthoparypha*; as is the pygidium (with the elimination of the anterior pair of spines). Particularly noteworthy is the presence of a double row of rimmed pits on the pleural lobe of the thoracic segment (Ross, 1951, p. 128, Pl. 35, fig. 21) and paired rimmed pits on the axial rings of the pygidium and a single (?) row along the pygidial spines (Hintze, 1953, Pl. 21, fig. 18). Aside from the fact that it is a double row, rather than a single row, on the thoracic segment; the distribution, size and general aspect of these pits are remarkably similar to those seen in *Acanthoparypha evitti* (Pl. 21, fig. 15), especially; but also in *Acanthoparypha echinoderma* (Pl. 23, fig. 18), *Acanthoparypha chiropyga* and *A. perforata* (see Whittington and Evitt, 1954, Pl. 30, fig. 28, Pl. 13, fig. 6). The appearance of this unique feature must surely attest to a phylogenetic connection between "*K.*" *sexapugia*, or a related species, and the Acanthoparyphinae. Thus, the Sphaerexochinae and the Acanthoparyphinae probably shared a common ancestor in the late Canadian and the similarities which tend to subvert attempts at suprageneric classification of some of these early Middle Ordovician cheirurids become understandable. I suggest that prime importance be placed on the number of pygidial spines when distinguishing between these two subfamilies.

Genus *Acanthoparypha* Whittington and Evitt, 1954

Type species: *Acanthoparypha perforata* Whittington and Evitt, 1954 from the Edinburg Formation, Virginia.

Acanthoparypha evitti Chatterton and Ludvigsen, ms.

Pl. 21, figs. 1-41

Acanthoparypha n. sp. 1, LUDVIGSEN, 1975, Pl. 3, figs. 20, 21.

Diagnosis: A species of *Acanthoparypha* possessing a large inflated glabella covered by fine granules and low, commonly perforated, tubercles. Cheek is narrow (tr.), genal spine short. Posterior branch of facial suture proceeds outwards in even curve. Pygidium has two axial rings and four relatively short, equally spaced, and pointed spines which are directed backwards and slightly upwards.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 110, A 125, A 140, P 1485, P 1497, P 1512) and Whittaker Range (?H 800-820, ?Q 130). Ceraurinella nahanniensis Zone and (?) Ceraurus gabrielsi Zone.

Material: 59 individuals.

Holotype: An incomplete cranidium (GSC 40403) from P 1497 illustrated on Pl. 21, figs. 1-4.

Description: Cranidium semi-circular in outline, moderately convex (sag.) and strongly convex (tr.). Ratio of length to width (between bases of genal spines) varies from 2:3 in large cranidia to 1:2 in small cranidia. Convex glabella oval (almost circular) in outline, narrowing slightly forward; maximum width, across 1p and 2p lobes, slightly less than length (sag.). In smaller specimens glabella sub-rectangular in outline (Pl. 21, figs. 10, 11). Glabella partly overhangs narrow and moderately deep axial and pre-glabellar furrows. Three pairs of glabellar furrows partly define sub-triangular to sub-rectangular glabellar lobes. 1s furrow longest and deepest, runs diagonally inwards and backwards, curves slightly backwards medially, terminates well in front of occipital furrow. 2s and 3s furrows parallel, gently curving, not as deep as 1s furrow. In dorsal view, 1s furrow 1/3rd, 2s 1/4th, and

3s 1/5th width of glabella at their junction with axial furrow. 1p lobe longest (exsag.), sub-triangular, slightly swollen over axial and occipital furrows; 2p and 3p lobes progressively shorter, sub-trapezoidal in dorsal view, very slightly inflated; anterior lobe shortest, triangular, not inflated. Portion of glabella inside adaxial termination of furrows has slight increased convexity (Pl. 21, fig. 4). Axial and pre-glabellar furrows continuous; their juncture marked by shallow, elongate oval anterior pit at or just in front of 3s furrow (Pl. 21, figs. 5, 9). Pre-glabellar furrow moderately deep, evenly concave (sag.) in lateral view incised posteriorly(Pl. 21, fig. 9); isolated narrow, convex (sag.), anteriorly-facing anterior border. Occipital ring arched, 4/5ths as wide (tr.) as maximum width of glabella, slightly longer (sag.) medially than distally, does not stand as high as glabella in front of occipital furrow. Cheek sub-triangular, steeply inclined. Palpebral lobe occupies highest position on cheek, very close to axial furrow, slightly behind halfway point between anterior and posterior border furrows and opposite 1s furrow and 2p lobe. Palpebral lobe narrow (tr.), slightly arched in lateral view, lenticular in outline, bald; outlined adaxially by faint palpebral furrow which is sub-parallel with axial furrow anteriorly, curves parallel with facial suture posteriorly, and fades out just behind eye. Eye surface convex (hor. and tr.), oval in outline, composed of a few hundred dome-like facets stacked in irregular vertical files (Pl. 21, figs. 32, 40).

Cheek below eye surface descends nearly vertically to roll-like lateral border; contact of cheek with border accentuated by relatively broad trough-shaped lateral furrow. Lateral margin curves evenly to a point opposite anterior pit on cranidium where it is flexed into a shallow antennal notch. Facial suture proceeds forward from upper edge of eye in a curve parallel with axial furrow and, between anterior pit and antennal notch, crosses anterior border to meet rostral and connective sutures. In anterior view, rostral suture straight, parallel to pre-glabellar furrow; nearly as wide (tr.) as width of glabella at occipital furrow. From behind eye, facial suture directed outwards and slightly forward; near lateral border its course curves backwards to cross lateral border at low angle. Facial suture occupies faint, but sharp, sutural ridge - particularly evident on crossing lateral border furrow. Width (tr.) of lateral border maintained from antennal notch to base of short, rapidly tapering, backwardly and outwardly directed genal spine. Lateral border possesses blunt, thorn-like anterior lateral spine immediately behind facial suture. Posterior border widens gradually (exsag.) from axial furrow to base of genal spine.

Entire cephalon (except palpebral lobe and thin strip below eye surface, glabellar furrows and immediately adjacent areas, inner portion of posterior border, and doublure) covered by densely distributed granules. Additional ornamentation on glabella consists of rather widely spaced, circular low, rounded tubercles ranging in size from 1/20 to 1/3 mm; larger tubercles possess minute central perforation. Cheek, inside lateral and posterior borders, contain minute, widely spaced pits and few small tubercles which, occasionally, are perforated. Genal spine, from base to tip, densely covered by fine, irregularly spaced, perforated, and unperforated tubercles.

On inner surface occipital doublure does not reach occipital furrow. On flanks, convex doublure almost reaches lateral border furrow. Posterior doublure consists of narrow recurved portion of exoskeleton which, abaxially, broadens to encase inner side of genal spine. As a rostral plate has not been recognized, the anterior doublure not certainly known. The rostral plate, however, must be wide (tr.) gently curved and, probably, narrow (sag.). Axial, pre-glabellar, glabellar, occipital, and border furrows expressed on interior as relatively high, narrow, rounded ridges. Appendifers not present.

Hypostome sub-trapezoidal in outline. Ratio of length to maximum width across anterior wings, 2:3. Anterior margin forms gentle convex curve; lateral margins straight, convergent posteriorly; posterior margin gently curved, modified medially by faint posterior and dorsal projection. Middle body slightly inflated; outlined by straight, moderately deep lateral border furrows which merge with broader, shallower, and gently curved posterior border furrow. Anterior border furrow curved, narrow, and deep, medially it almost reaches anterior margin. Lateral and posterior borders broad, gently inclined inwards, modified anteriorly into small shoulders which do not project laterally as far as anterior wings. Middle body partitioned into sub-triangular anterior lobe and crescentic posterior lobe with very faint independent convexities by short, narrow middle furrow which is initiated just inside lateral border furrow opposite shoulders from where it curves backwards and inwards. Near its adaxial termination middle furrow defines posterior side of small oval macula. Lateral parts of doublure broad, slightly concave, attenuates to narrowest portion at mid-point of posterior margin. An angular juncture at shoulder marks descent of doublure into antennal notch. In front of notch, doublure flares dorsally and laterally into anterior wing which, distally, carries small, node-like, wing process. Sutural contact with rostral plate evenly curved and sharp-edged. Wing processes project well in front of this suture.

Entire hypostome, except middle furrows, maculae, and doublure (including anterior wings), ornamented by granules and tubercles in same manner as glabella. However, tubercles smaller, not commonly perforated, and, for the main part, restricted to anterior lobe. Small oval area in front of maculae bears irregularly disposed pits (Pl. 21, fig. 31).

Number of thoracic segments unknown. An incomplete articulated specimen (Pl. 21, fig. 18) preserves seven segments in front of pygidium. Anterior segments consist of broad convex axis occupying between 1/3 and 1/2 total width;

Pleura narrow (tr.) than axis, curves noticably downward and terminates as short, tapering, postero-ventrally directed spine. Pleurae become narrow (tr.) towards rear and pleural spines become relatively longer and increasingly posteriorly directed. Posterior segment has very narrow inner portion of pleura and long pleural spines, oriented parallel to axis (Pl. 21, figs. 18, 36). On inner surface at anterior side of axial furrow, a small forwardly-directed knob fits into a socket at posterior side of next segment. From the axial furrow knob, a thin ribbon-like flange follows a gentle curve along the anterior side of inner portion of pleura (Pl. 21, fig. 35) and terminates at forwardly-projecting protuberance at base of pleural spine. Posterior side of pleural spine base is not modified into a socket to receive this protuberance; instead, the doublure persists as a very thin roll-like continuation from base of spine towards axial furrow (Pl. 21, figs. 33, 34). This process at base of pleural spine is the marginal connective device of Bergstrom (1973). Appendifers and pleural furrows not present. Doublure extends 2/3rds across axis. Entire dorsal surface of small to medium-sized segments covered by fine granules and common small tubercles; the latter especially noticable on posterior side of axial lobe. Single row of widely spaced pits bisect inner portion of pleurae. On larger segments, axis bald and granules restricted to inner portion of pleurae. (Pl. 21, fig. 37). In addition, a single row of pits cross posterior side of axis.

Pygidium, including marginal spines, rectangular to square in outline. Axis semi-circular, composed of two segments and short oval or angular terminal piece. Anterior segment broadly trapezoidal, outlined anteriorly and posteriorly by straight,narrow, and moderately deep articulating and axial ring furrows; and laterally by forwardly-diverging axial furrows. Moderately deep pits mark juncture of articulating and first axial ring furrows with axial furrows. Second segment bounded posteniorly by short (tr.) and slightly shallower axial ring furrow which joins a pair of moderately deep pits located in front of mid-point of posterior set of spines. This furrow may be straight, forwardly curving, or straight-sided and obtusely angled medially. Axial furrow terminates in elongate pit which bounds antero-lateral part of second segment. Pleural portions of segments produced directly in two pairs of posteriorly and slightly dorsally directed spines which are closely aligned and sub-parallel. Spines 2 1/2 to 4 times as long as wide, oval in cross-section, gradually tapering to blunt point. Anterior set of spines initiated close to axial furrow, carries faint carina on abaxial edge for 1/2 total length. Posterior set of spines with combined width (tr.) equal to that of second axial ring. In small specimens, a line joining tips of pygidial spines is a slight curve, forwardly convex; in larger specimens this line is straight or forwardly concave. On inner surface, spine bases lodged in curved, raised inner portion of doublure. This curved portion is longest (exsag.) below axial furrows, narrows laterally to form marginal connective device, and is deflected posteriorly into broad fold. Axial ring and ring furrows expressed on interior as moderately thin (sag.) ridges. Apendifers not present. Ornament of pygidia, including doublure, consists of fine granulation. On larger specimens, granulation restricted to antero-medial portion of dorsal surface of spines, lateral portions of second axial segment, and ventral surface (including doublure). Remaining exoskeletal parts of larger specimens bald (Pl. 21, figs. 12, 15, 30). Distinct pattern of small rimmed pits observed on larger pygidia. These pits appear to be derivatives of rather closely spaced, and more numerous, tubercles evident on axial segments and spines of smaller pygidia (Pl. 21, figs. 17, 38). These tubercles can be traced to less closely spaced perforated tubercles on larger pygidia (Pl. 21, fig. 19) and to widely spaced, and fewer, pits on the largest pygidia (Pl. 21, figs. 12, 15) distributed as follows - pair of pits on each of first and second axial segments, single pit at mid-point of terminal piece, and single pit located at mid-point of each pygidial spine.

Discussion: *Acanthoparypha evitti* from the Esbataottine Formation is extremely similar to *A. chiropyga* Whittington and Evitt (1954) from the Lincolnshire Limestone of Virginia, and most of the obvious differences can be attributed to the generally larger size of the Canadian material. Small cranidia and pygidia of comparable size of

se two species are virtually indistinguishable (compare
ttington and Evitt, 1954, Pl. 28, fig. 43 and Pl. 30,
. 23 with Pl. 21, fig. 11 and Pl. 10, fig. 21 of this
sis). The large fragmentary cranidium of *A. chiropyga*
ustrated by Whittington and Evitt (1954, Pl. 29, figs. 7-
compares favorably in general proportions and ornament
similar sized cranidia of *A. evitti* (Pl. 21, figs. 1-4,
9). Hypostomes of the Esbataottine species differ slight-
from the Virginia species in having the middle furrow at
reater angle to the sagittal line. The only persistent
ference between these two species is the course of the
ial suture. This is most readily displayed by the out-
e of the free cheeks (compare Whittington and Evitt,
4, Pl. 29, figs. 15, 18, with Pl. 21, figs. 32, 40 of
s thesis). In *A. evitti*, the facial suture follows an
nly curved course from ~~just be~~hind the eye to the lateral
gin of the cephalon. In *A. chiropyga*, the suture follows
traight line from behind the eye to the border furrow and
n is sharply deflected backwards to cross the lateral
gin in nearly a straight line.

Acanthoparypha perforata Whittington and Evitt, 1954,
easily distinguished from *A. evitti* in possessing a
nounced forwardly-narrowing glabella, much longer genal
nes, and ornament composed of coarse granules and tub-
les. The material of *Acanthoparypha* sp. from the Chazy
up of New York illustrated by Shaw (1968, Pl. 15, figs. 1-
is not sufficient to permit comparison.

Acanthoparypha sp. (Tripp, 1967, p. 63, Pl. 2, fig. 49) from the Stinchar Limestone of Girvan is assignable to Pandaspinapyga. This generic assignment was anticipated by Tripp when he suggested close affinity of the Scottish species to Acanthoparypha stubblefieldi (Bancroft) from the Caradocian of Shropshire. The latter species was subsequently assigned to Pandaspinapyga by Lane (1971).

The pygidium and associated seven thoracic segments (Pl. 21, fig. 18) gives a fair indication about the overall shape of the exoskeleton of Acanthoparypha evitti. Assuming twelve thoracic segments, this trilobite would be oval in outline and about twice as long as wide. The genal spine would probably be poorly differentiated from the thoracic spines, as are the pygidial spines. The latter point suggests that in the reconstruction of A. projecta Whittington and Evitt (1954, Fig. 18) the pygidium is too large in relation to the thoracic segments and the cranidium.

The species name is for W.R. Evitt of Stanford University who, singly and with H.B. Whittington, published the first descriptions of silicified trilobites of Chazyan age.

Acanthoparypha echinoderma Chatterton and Ludvigsen, ms.

Pl. 23, figs. 1-15, 20-25

Diagnosis: A species of *Acanthoparypha* with a nearly circular glabella. Pygidium with two axial rings and small terminal piece and four short, blunt spines. Entire exoskeleton covered by closely-spaced and fine, spike-like granules.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 115, A 125, P 1512, P 1520). *Ceraurinella nahanniensis* Zone.

Material: 58 individuals.

Holotype: A nearly complete cephalon lacking the left free cheek (RL 0263) from A 125 illustrated on Pl. 23, figs. 5-9.

Discussion: The proper assignment of exuviae of *Acanthoparypha evitti* Chatterton and Ludvigsen, *Acanthoparypha echinoderma* Chatterton and Ludvigsen, and *Pandaspinapyga dactyla* Chatterton and Ludvigsen in collections from the lower Esbataottine Formation presents some vexing problems. Association of pygidia and cranidia of *Acanthoparypha* in the collections under study is based on distinctive ornament and co-occurrence in different collections. Of the two species of *Acanthoparypha*, *A. evitti* (Pl. 21) possesses a generally smooth pygidium and a glabella covered with very fine granules and low rounded tubercles. *A. echinoderma*, on the other hand, possesses a pygidium and cranidium covered by fine spike-like granules. Small pygidia of either species are readily identifiable (compare *A. evitti*, Pl. 21, fig. 17 and *A. echinoderma*, Pl. 23, fig. 14), but small cranidia of both species are rather coarsely granulose and tuberculose and proper specific assignment presents problems. I have assigned the small cranidia with a quadrate glabella and ornament of coarse granules to *A. evitti* (Pl. 21, fig. 11) and those with a circular glabella and ornament of small, thorn-like tubercles to *A. echinoderma* (Pl. 23, fig. 15). Only one, but somewhat variable, type of *Acanthoparypha* hypostome has been found in these collections (Pl. 21, figs. 22-28, 31). These have provisionally been assigned to *A. evitti*, but if the characteristic ornamentation on the dorsal surface of *A. echinoderma* is, at least partially, duplicated on the ventral surface then the hypostome illustrated on Pl. 21, fig. 22 may belong to this species.

Finally, the presence of two large pygidia of *Pandaspinapyga dactyla* in one collection each from Sections A and P raises the question of whether the pygidia assigned to *Acanthoparypha echinoderma* are actually those of small *Pandaspinapyga dactyla*. This possibility is suggested by the disparity in sizes. The largest *A. echinoderma* pygidium is 2.5 mm in breadth while the smallest *P. dactyla* pygidium measures 8.5 mm. It also finds support in the similarity of the cranidia of *Acanthoparypha echinoderma* and *Acanthoparypha salsa* Esker, 1964 (Shaw, 1974, Pl. 8, figs. 3-5, 7, 9, 10). Both of these species apparently possess the same ornament of fine spike-like granules and small tubercles on the cranidia, but *P. salsa* may be distinguished by its relatively greater basal glabellar breadth, more inflated 1p lobes, and by its swollen cheeks (inside the border furrows). It is difficult to assess these slight cranidial differences because *Pandaspinapyga* stands as a genus that can only be identified by its pygidium (as pointed out by Lane, 1971, p. 68 and Shaw, 1974, p. 30); its cranidium and hypostome cannot be differentiated from those of *Acanthoparypha*. I have avoided assigning specimens, other than the two large pygidia, to *Pandaspinapyga dactyla* for the following reasons. Firstly, it has not been possible to establish close co-occurrence of the cranidia and pygidia of *A. echinoderma* and pygidia of *P. dactyla*. Both species of *Acanthoparypha* and *P. dactyla* are present, but rare, in A 125; *A. evitti* and *P. dactyla* are rare in P 1485; and *A. echinoderma* and *A. evitti* are relatively common in P 1512. The absence of *Pandaspinapyga dactyla* pygidia in the last collection with common *Acanthoparypha echinoderma* is noteworthy. Secondly, a credible match in ornament of *A. echinoderma* pygidia and cranidia can be established. The ornament of the *P. dactyla* pygidium, however, consists of fine granules and scattered perforated tubercles and it is difficult, although not impossible, to accept the development of the large and generally smooth pygidium from a much smaller, but probably still holaspid, and coarsely granulose pygidium. Thirdly, and probably most important, an ontogenetic derivation of the P. dactyla pygidium from the A. echinoderma pygidium would involve the addition of an axial ring while the number of pygidial spines remained constant at four. The addition of segments to the pygidium during the late meraspid and holaspid periods is, in itself, not unique and has been shown to occur in such genera as Shumardia (Stubblefield, 1926), Dalmanitina, and Dionide (Whittington, 1957, p. 442). But in all genera of Cheiruridae where fairly complete developmental series are known (Ceraurus, Ceraurinella, Sphaerexochus, Acanthoparypha, Holia), the opposite appears to be the case. That is, segments are shed from the transitory pygidium throughout the meraspid period (Whittington and Evitt, 1954, p. 72; Whittington, 1957, p. 444). It seems highly unlikely that two very similar genera, such as Acanthoparypha and Pandaspinapyga, should have radically different developmental series. For these reasons I will treat Acanthoparypha echinoderma and Pandaspinapyga dactyla as discrete taxa.

The cephalon of Acanthoparypha echinoderma differs from that of A. evitti and A. chiropyga Whittington and Evitt, 1954 in possessing ornament consisting of spike-like granules and tubercles. In most respects the cephala are very similar. The genal spines of A. echinoderma show considerable variation from slender and delicate (Pl. 23, fig. 10) to broad and triangular (Pl. 23, fig. 12). The main differences between the two species reside in the pygidia. Aside from the differences in ornament and shape of the pygidial spines already mentioned, A. echinoderma possesses a tiny circular terminal piece which is circumscribed by furrows extending postero-medially from the second axial ring furrow. In A. evitti, the second axial ring furrow terminates in small pits and the terminal piece is not limited by furrows. A. perforata Whittington and Evitt, 1954, has much longer genal spines and a forwardly-narrowing glabella.

A single cephalon of A. echinoderma (Pl.23 , fig. 9) retains a small fragment of the rostral plate and helps to explain why this element has not been found associated with similarly-preserved species of Acanthoparypha. The rostral plate is very wide and extremely short - about 15 times as wide (tr.) as long (exsag.). It is gently curved (tr.) and appears particularly fragile. It is directed inwardly and downwardly and the connective sutures diverge forwardly. Judging from this fragment it appears that the reconstructed rostral plate of A. perforata Whittington and Evitt (1954, Fig. 19) is basically correct, but probably too long (sag.).

Acanthoparypha? goniopyga n. sp.

Pl. 24, figs. 1-18

Acanthoparypha sp., LUDVIGSEN, 1975, Pl. 5, fig. 10.

Diagnosis: A species of Acanthoparypha? with a weakly inflated, forwardly narrowing glabella and strongly divergent genal spines. Pygidium with a nearly vertical anterior portion lacking axial rings or furrows, but possessing a pair of slot-like pits; and four pointed spines that are square in cross-section..

Occurrence: Lower Whittaker Formation, Whittaker Range (H 1850, I 1275, I 1350-1380, I 1410) and Funeral Range (C 655). Ceraurinella necra Zone and Ceraurus mackenziensis Zone.

Material: About 25 individuals.

Holotype: A complete pygidium (RL 0253) from I 1275 illustrated on Pl. 24, figs. 7-9.

Discussion: The cranidium of Acanthoparypha? goniopyga n. sp. is essentially like those of other species of Acanthoparypha. The flatly convex glabella, the strongly divergent genal spines, and the sigmoidal first lateral glabellar furrows appears diagnostic. The latter feature indicates an affinity with A. subcircularis (Bradley, 1930) from the Kimmswick Formation of Illinois. The pygidium of A.? goniopyga differs from any previously described pygidium of Acanthoparypha in lacking axial furrows, axial rings, or axial ring furrows. The anterior part of the pygidium is sharply flexed from the base of the genal spines into a near-vertical position below an articulating furrow that extends two-thirds the distance across the anterior margin. The upturned portion of the pygidium is scored by a pair of dorsally-convergent slot-like pits which, by their position and orientation, appear to represent the second axial ring furrow as seen in Acanthoparypha evitti Chatterton and Ludvigsen (compare Pl. 24, figs. 7, 8 and Pl. 21, fig. 15). The pygidium of A.? goniopyga is also unique in possessing four spines which are square in cross-section.

From the material at hand it appears certain that Acanthoparypha? goniopyga was derived from a species of Acanthoparypha (probably A. evitti or A. chiropyga), but it is not clear whether the singularity of the pygidium demands a separate generic home for this species. The post-Chazyan/early Blackriveran history of Acanthoparypha is vague at the present time. Only two other species of the genus are known from this interval in North America, A. trentonensis (Clarke) and A. subcircularis (Bradley); both of which are known only from incomplete cranidia.

The recent work of Lane (1971) clearly demonstrates that the exclusively Silurian genus, Youngia Lindström, is an acanthoparyphinid. The discovery of a pygidium of Youngia sp. from the Wenlockian or Ludlovian part of the Delorme Formation of the Mackenzie Mountains (Perry, 1974) corroborates the subfamily assignment. This pygidium possesses four short pointed spines which appear to be quadrate in cross-section. The anterior part of the pygidium curves gradually upwards and, apparently, lacks furrows. The last point cannot be stated with certainty because the dorsal side of the pygidium is covered by coarse pustules. The resemblance of this pygidium to the Acanthoparypha? goniopyga pygidium suggests that Youngia was derived from Acanthoparypha, specifically A.? goniopyga of Rocklandian to Shermanian age. Lane (1971, p. 81) suggested that the gap between the last Ordovician acanthoparyphinid and the first appearance of Youngia was bridged by "Sphaerexochus" canadensis Billings from Anticosti Island. This suggestion, however, was based on a misconception about the age of "S". canadensis. This species occurs in the Chicotte Formation of late Llandoverian or early Wenlockian age (Bolton, 1972, p. 17); that is, probably slightly younger than the age of the type species of Youngia from Girvan, Y. trispinosus (Young).

Genus *Pandaspinapyga* Esker and Levin, 1964

Type species: *Acanthoparypha projecta* Esker, 1961 from the Kimmswick Limestone, Missouri.

Pandaspinapyga cf. *stubblefieldi* (Bancroft)

Pl. 24, figs. 30-32

Acanthoparypha stubblefieldi (Bancroft), DEAN, 1961, p. 314, Pl. 49, figs. 1, 3-6, 11.

Pandaspinapyga stubblefieldi (Bancroft), LANE, 1971, p. 68, Pl. 15, figs. 3-6.

Occurrence: Upper Sunblood Formation, Sunblood Range (P1187), *Bathyurus granulosus* Zone.

Material: 3 individuals.

Discussion: From the slightly younger *Pandaspinapyga dactyla* Chatterton and Ludvigsen, *P*. cf. *stubblefieldi* (Bancroft) differs in possessing shorter and less flaring pygidial spines, shorter (sag.) and more convex (sag.) axial rings, shallower and narrower (sag.) axial ring furrows, angular antero-lateral pygidial corners, and in lacking axial furrows opposite the second ring. The furrows which extend posteriorly from the second axial ring furrow have different courses in the two species. In *P*. *dactyla* these furrows converge posteriorly to partially enclose a shield-shaped area which includes the terminal piece. In *P*. cf. *stubblefieldi* these furrows curve outward and backward from the faint ring furrow, but do not converge. *P*. cf. *stubblefieldi* lacks pits on the pygidial spines and possesses high, unperforated tubercles on the first two axial rings.

The pygidium of P. cf. stubblefieldi from the Sunblood Formation differs in a few minor points from that of P. stubblefieldi from the Caradocian of Shropshire. The Sunblood species has shallower pygidial furrows and slightly longer spines. The British species appears to possess a short pleural furrow opposite the first axial ring instead of a row of small pits as seen in P. cf. stubblefieldi, but this could equally well be a result of imperfect preservation. The incomplete cranidial fragment of P. cf. stubblefieldi shows the course of the posterior branch of the facial suture, the moderately long and slightly curving genal spine, and a trace of an uninflated first glabellar lobe. The latter feature further allies the species to P. stubblefieldi and serves to differentiate it from P. projecta and P. salsa.

Pandaspinapyga dactyla Chatterton and Ludvigsen, ms.

Pl. 23, figs. 16-19

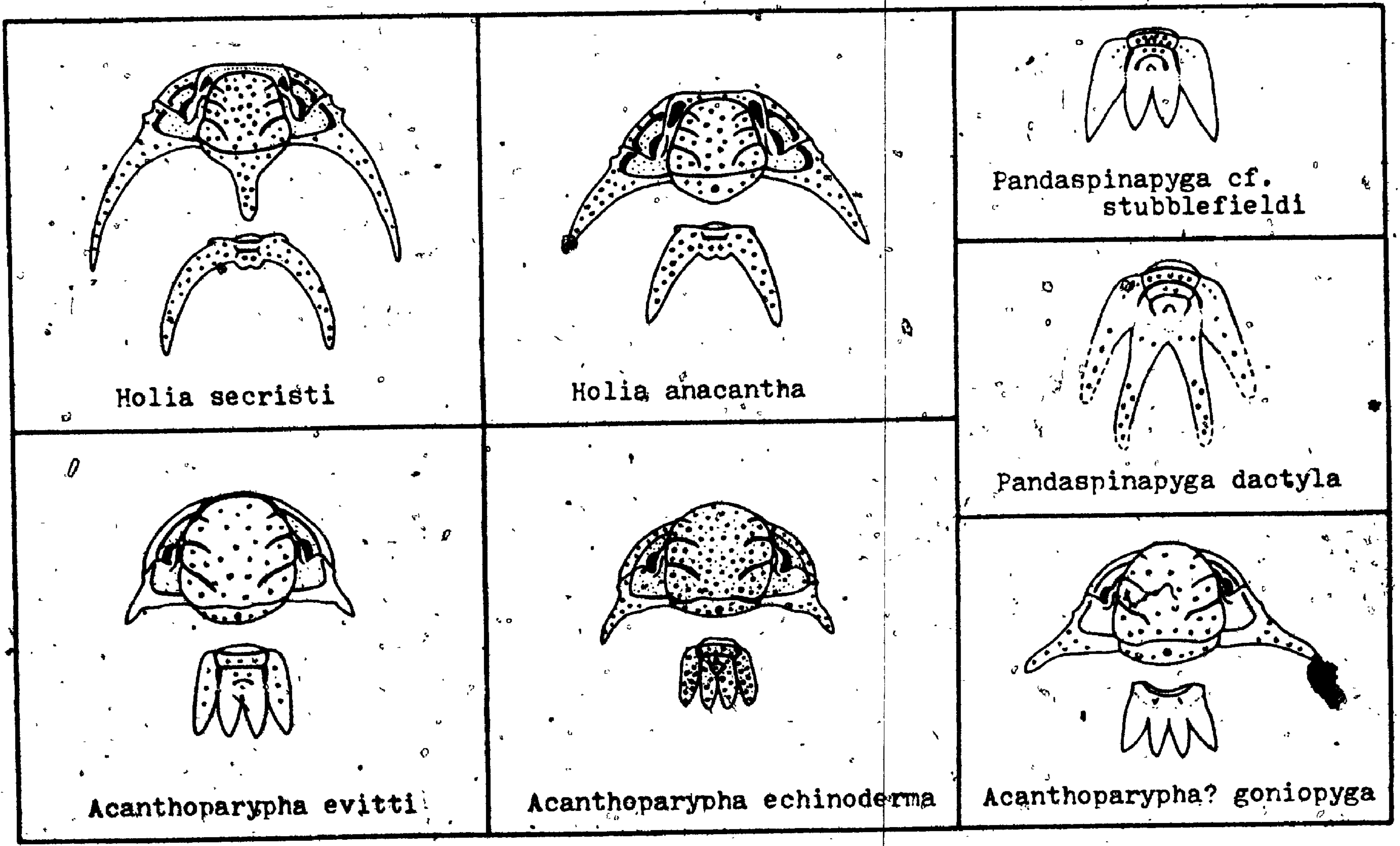
Pandaspinapyga sp., LUDVIGSEN, 1975, Pl. 3, fig. 24.

Diagnosis: A species of Pandaspinapyga possessing long, digitate pygidial spines.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 125, P 1485), Ceraurinella nahanniensis Zone.

Material: 2 pygidia.

Description: Pygidium, excluding spines, transversely oval in outline. Axis triangular, moderately convex; narrows posteriorly to wedge-shaped tip halfway between terminal piece and posterior margin; consists of 3 flatly convex (sag.) axial rings and small circular terminal piece; rings approximately of equal length (sag.); narrowing (tr.) posteriorly. First two axial ring furrows slightly convex forwardly; narrow and shallow medially, deeper laterally. Third furrow faint and shallow, strongly bowed forwardly; descends distally into two small pits flanking terminal piece. Axial furrows shallow, but distinct. Pleural field relatively broad; flat to slightly concave; merges with bases of marginal spines; crossed by row of 3 pits opposite first axial ring and, opposite first ring furrow, by moderately deep, outwardly and backwardly curving furrow which continues to posterior margin as faint depression. Moderately deep furrow extends from distal end of second ring furrow along path of axial furrow to a point opposite terminal piece. Total length of pygidial spines not known; second pair is at least as long as pygidium is wide (tr.) across second axial ring. Spines are digitate, diverge from each other at about 40°; slightly tapering; flatly oval in cross-section. In lateral view, second pair curves slightly upwards. Ventral side of pygidium, including spines, nearly flat. Anterior part of doublure flexed into narrow rim; portion under axis deflected backwards in broad fold. Inner edge of doublure curves outwards and slightly forwards to prominent marginal connective device located opposite first axial ring. On interior,



Text-figure 31.

Outline drawings of cephala and cranidia of two species of *Holia*, two of *Pandaspinapyga*, and three of *Acanthoparypha* from the upper Sunblood, Esbataottine, and lower Whittaker Formations, South Nahanni River area.

rows expressed as low ridges; appendifers not present. sal and ventral surface of pygidium finely granulose. In-ition, few rimmed pits on axial rings and along mid-por-n of spines. The pits on the spines decrease in size ward and each occurs immediately in front of a single, y, spindle-shaped spine.

Discussion: *Pandaspinapyga dactyla* Chatterton and vigsen differs from *P. projecta* Esker, *P. salsa* Esker, *P. stubblefieldi* (Bancroft) by possessing long, digitate idial spines that are well separated for their total gth.

Genus *Holia* Bradley, 1930

Type species: *Holia magnaspina* Bradley, 1930 m the Kimmswick Limestone of Missouri and Illinois.

Holia secristi Whittington and Evitt, 1954
Pl. 22, figs. 1-42

ia secristi WHITTINGTON and EVITT, 1954, p. 81, Pl. 30, figs. 29-42, Pl. 31, figs. 1-43, Pl. 32, figs. 1-5.

ia cf. *secristi* Whittington and Evitt, LUDVIGSEN, 1975, Pl. 3, figs. 7, 8.

Occurrence: Lincolnshire Formation, Tumbling Run, enandoah County, Virginia and lower Esbataottine Formation, ablood Range (A 110, A 125, P 1485, P 1497, P 1512, P 1520). *raurinella nahanniensis* Zone (in Canada).

Material: 62 individuals.

Holotype: An incomplete cranidium (USNM 116549) from the Lincolnshire Formation illustrated by Whittington and Evitt, 1954, Pl. 31, figs. 1-6.

Discussion: The Esbataottine material is extremely similar to the type material from the Lincolnshire Limestone of Virginia, and the minor differences do not seem to warrant specific segregation. Aside from these differences which are enumerated below, the description of the Virginia Holia secristi given by Whittington and Evitt (1954) is equally valid for the present material.

1. The palpebral lobes of the Esbataottine form are located slightly closer to the axial furrows.

2. In equivalent-sized cranidia, the Esbataottine form has smaller lateral spines than the Lincolnshire form (compare Pl. 22, fig. 11 and Whittington and Evitt, 1954, Pl. 31, fig. 1).

3. The first pygidial spines of the Esbataottine form do not possess the initial strong upward curvature evident in the Lincolnshire form and, as a consequence, the spine-tips are not elevated as high (compare Pl. 22, fig. 24 and Whittington and Evitt, 1954, Pl. 31, fig. 43, Pl. 32, fig. 3).

Whittington and Evitt (1954, p. 86) noted that the occipital spine of Holia secristi becomes longer (relative to the rest of the cephalon) during ontogeny. This is also well expressed in the Esbataottine material. In a small specimen (Pl. 22, fig. 15) the ratio of the length of the occipital spine, measured from the occipital furrow, to the length of the glabella from the pre-glabellar furrow to the occipital furrow is 4/10. In successively larger cranidia this ratio shows the following change: 6.8/10 (Pl. 22, fig. 14), 7.7/10 (Pl. 22, fig. 17), 8/10 (Pl. 22, fig. 1), and 10/10 (Pl. 22, fig. 9). The relative size increase of the occipital spine appears to be duplicated by the genal spines. The ratio of glabellar length (as measured above) to length of the genal spines, measured from the corner formed by the posterior and lateral border furrows of the cheek shows the following change (from small cranidia to large) -- 10/14 (Pl. 22, fig. 15), 10/10 (Pl. 22, fig. 16), and 10/21 (Pl. 22, fig. 11). An allometric relationship between the length of the genal spines and the size of the remaining cephalon would be necessary if these spines served the function of supporting the trilobite on a soft substrate. A life position of *Holia secristi* would be with the genal spines stretched out in nearly horizontal direction and the pleural spines stacked behind it in about the same orientation. Such an orientation would bring the ventral surface of the genal and pleural spines flush with the substrate. In this position, the anterior part of the cephalon would be elevated off the sea bottom and the upper edge of the central part of the glabella and the occipital spine would be brought into nearly a horizontal plane. This suggested reconstruction differs from that presented for *H. secristi* by Whittington and Evitt (1954, figs. 21, 22) who rotated the cephalon forward so that the posterior margin of the occipital ring was vertical. In this position, the genal and occipital spines project obliquely backwards and upwards at an angle of about 45° and the antero-ventral margin of the cephalon is in close proximity to the sea floor. That both of these reconstructions are viable is suggested with reference to the functionally comparable Silurian odontopleurid trilobite, Leonaspis deflexa (Lake). In a study of this species, Clarkson (1969) suggested that L. deflexa was capable of two life positions -- a "resting" position in which the trilobite was supported by the outstretched genal and pleural spines and the posterior portion of the glabella and the occipital ring were nearly horizontal, and an "active" position in which the cephalon was rotated forward, bringing the anterior margin close to the sea floor and elevating the genal spines. These life positions are closely comparable to those suggested for Holia secristi -- the reconstruction in Whittington and Evitt (1954, fig. 22) can be viewed as the "active" position and the one suggested herein with the glabella and the outstretched genal spines nearly horizontal as the "resting" position.

Holia anacantha n. sp.

Pl. 24, figs. 20-29

Diagnosis: A species of Holia lacking an occipital spine and possessing stout and straight first pygidial spines.

Occurrence: Lower Whittaker Formation, Funeral Range (C 570-590). *Ceraurinella necra* Zone.

Material: 10 individuals.

Holotype: An incomplete pygidium (RL 0348) from C 570-590, illustrated on Pl. 24, figs. 27-29.

Discussion: Although the available material is sparse and rather poorly preserved, this species is obviously distinct from any of the three previously described species of *Holia*. *H. cimelia* Whittington and Evitt, 1954, from the Edinburg Formation and *H. secristi* from the Lincolnshire and Esbataottine Formations each possesses a distinct and long median occipital spine and first pygidial spines which curve outward and backward. The type species, *H. magnaspina* Bradley, 1930, from the Kimmswick Limestone is known from only two incomplete cranidia. The distinctive features are the broad, flat, and triangular occipital spine and the swellings at the distal ends of the occipital ring.

The outline and ornament of the cranidium of *H. anacantha* are very similar to those of *H. secristi*. Aside from the absence of an occipital spine, the only differences seem to be a slightly longer 3s furrow and a more elongate (exsag.) anterior pit. The moderately large, but crushed, cranidium of *H. anacantha* (Pl. 24, fig. 22) displays a long (sag.) and flat occipital ring with the slightest trace of a median node. The latter feature is better shown on the smaller cranidium (Pl. 24, fig. 21). The pygidium of *H. anacantha* possesses first spines which diverge at about 30° to the sagittal line and, in lateral view, are directed upwards at about 40°. The spines are, basally, much stouter than the ones of *H. cimelia* of *H. secristi* and are straight for their total length. The ornament on the pygidium is considerably coarser than that seen on the other species of *Holia*.

H. anacantha is morphologically closer to the older *H. secristi* than to its near-contemporary from the mid-continent, *H. magnaspina*, and could well have been derived from *H. secristi* by paedomorphosis. In meraspid cranidia of *H. secristi* and *H. cimelia*, the occipital spine is reduced in size to a short triangular spike and its absence in *H. anacantha* may be ascribed to neoteny.

Genus *Heliomeroides* Evitt, 1951

Type species: *Heliomeroides teres* Evitt, 1951 from the Lincolnshire Formation, Virginia.

Discussion: *Heliomeroides* was relegated to a subgenus of *Heliomera* Raymond by Whittington (1965a, p. 417) and was considered a junior synonym of *Heliomera* by Tripp (1967, p. 67) and Lane (1971, p. 56). Its generic status was maintained by Shaw (1968, p. 69). The discussion has centrered mainly on the taxonomic value of the pair of longitudinal furrows which join the inner ends of the lateral glabellar furrow. In the type species of *Heliomera*, *H. sol* (Billings), a slight change in slope outlines the adaxial tips of the lateral glabellar furrows (Whittington, 1965a, p. 417). In *Heliomera alacer* (Whittington) this feature is accentuated by the inflated lateral lobes, resulting in a pair of shallow depressions along the inner tips of the lateral furrows (Whittington, 1963, Pl. 25, fig. 6). These depressions are similar to the longitudinal glabellar furrows seen in Heliomeroides teres Evitt, but are distinct from the lateral furrows in being both wider and shallower. In H. teres the longitudinal glabellar furrows are about the same depth and width as the lateral furrows and do not owe their origin to inflation of the lateral lobes. Whittington's (1965a, Pl. 63, fig. 3) preparation of the lectotype of Heliomera sol illustrates yet other differences between the type species of Heliomera and Heliomeroides. The fixed cheek of H. sol is wide (about one-third the maximum width of the glabella), the genal spine is long and spike-like, and the palpebral lobe is situated opposite the anterior end of 2p lobe and 2s furrow. The fixed cheek of H. teres is narrow (about one-tenth the maximum width of the glabella), the genal spine is short and stubby, and the palpebral lobe is situated opposite the posterior end of 2p lobe and 1s furrow (Evitt, 1951, Pl. 85, fig. 1; this thesis, Pl. 23, fig. 26). These differences, in my opinion, warrant generic segregation of Heliomera sol and Heliomeroides teres. The absence of exoskeletal elements, other than cranidia or cephala, of any species of Heliomera cautions against attempts at synonymy of Heliomera and the considerably better known Heliomeroides. The six-spined "heliomerinid pygidium" from the boulder at Lower Head, western Newfoundland (Whittington, 1965a, Pl. 25, fig. 3) neatly illustrates the problem. This pygidium was, without query, associated with a *Heliomera* cranidium by Lane (1971, text-fig. 13). If it can be demonstrated that this is actually the *Heliomera* pygidium, it would be strong evidence in favour of an assignment of this genus to the subfamily Sphaerexochinae. The *Heliomeroides teres* pygidium possesses four digitate spines and this forms part of the evidence that suggests an assignment to the subfamily Acanthoparyphinae.

Heliomeroides teres Evitt, 1951
Pl. 23, figs. 26-43

Heliomeroides teres EVITT, 1951, p. 594, Pl. 85, figs. 1-5, Pl. 86, figs. 1-18, Pl. 87, figs. 1-4.

Heliomera chipperfieldi TRIPP, 1967, p. 66, Pl. 4, figs. 14-17.

Heliomeroides akocephala SHAW, 1968, p. 69, Pl. 4, figs. 14, 15, 22, 23, 28.

Heliomeroides teres Evitt, LUDVIGSEN, 1975, Pl. 3, figs. 5, 6.

Occurrence: Lincolnshire Formation, Tumbling Run, Shenandoah County, Virginia; Chazy Group, Lake Champlain, New York State; upper Stinchar Limestone, Stinchar Valley, Girvan, Scotland; and lower Esbataottine Formation, Sunblood Range (A 110, P 1485, P 1497). *Ceraurinella nahanniensis* Zone (in Canada).

Material: 9 individuals.

Holotype: An incomplete cranidium (USNM 116294) from the Lincolnshire Formation illustrated by Evitt, 1951, Pl. 85, figs. 1-5.

Discussion: The material from the Esbataottine Formation conforms in every respect to Evitt's (1951) material of <u>Heliomeroides</u> <u>teres</u> Evitt from the Lincolnshire Limestone of Virginia and little can be added to his exhaustive description.

The meraspid cranidium of <u>H</u>. <u>teres</u> (Pl. 23, fig. 43) displays a circular glabella, faintly developed lateral and longitudinal glabellar furrows, a narrow (tr.) occipital ring studded with four spines, long slender fixigenal spines, and a broad flat pre-glabellar field whose anterior margin is spinose. The palpebral lobe appears to be opposite 2s furrow. The antero-median depression of the central glabellar lobe is developed as a relatively broad longitudinal sulcus which separates a pair of small swellings outlined laterally by the 3s furrows. The fixigenal spines are considerably shorter than the ones on the smallest cranidia of <u>Heliomera</u> <u>alacer</u> and <u>H</u>. <u>albata</u> illustrated by Whittington, 1963, Pl. 24, figs. 15, 9; consonant with their respective sizes in holaspid cranidia.

The surface ornament consists of small elevated granules which may be produced into hair-like spines. Larger elevations composed of crowded fine spines occur sparingly on one thoracic segment (Pl. 23, fig. 35) and on one pygidium

(Pl. 23, fig. 32). Some of these elevations are perforated.

Heliomeroides has a wide geographic distribution. It occurs in rocks of Chazyan age in New York State (Shaw, 1968), Virginia (Evitt, 1951), Scotland (Tripp, 1967), and the South Nahanni area; of Trentonian age in Illinois (Bradley, 1930; Evitt, 1951); and of Ashgillian age in Eire (Dean, 1971a). Within the lower Esbataottine Formation, *H. teres* is extremely rare; seven individuals (mostly immature) out of a total trilobite population of 1435 from P 1485, a single individual out of 1663 from P 1497, and a single out of 859 from A 110 belong to this species. The rarity is apparently not unique to the Esbataottine populations and this makes it difficult to decide upon allowable intraspecific variation. However, it is here suggested that *Heliomera chipperfieldi* Tripp, 1967 from the Stinchar Limestone of Girvan and *Heliomeroides akocephala* Shaw, 1968 from the Chazy Group of New York are junior synonyms of *H. teres*. Following Evitt (1951), Tripp and Shaw emphasized the absence and presence, respectively, of an antero-median depression within the central glabellar lobe of their two species as diagnostic. In the Esbataottine material of *H. teres*, this feature is evident as a faint longitudinal concavity, but it seems slender evidence on which to base a species, especially since only one of the two glabellae of *H. akocephala* illustrated by Shaw (1968, Pl. 4, figs. 22, 23) clearly shows the furrow. Apparently, this is a function of the difficulty of photographing such a minute feature since its presence was noted in both specimens by

Shaw (1968, p. 70). The furrow, or alternatively a small area devoid of ornament, is not evident in all the six cranidia of H. teres illustrated by Evitt (1951, Pl. 86, figs. 1-6). A feature that cannot consistently be reproduced photographically is a poor choice as diagnostic. The convexity of the glabellar lobes has also been cited as diagnostic. This must also be treated with caution because increased convexity may be a function of ontogenetic change and the preservation of cranidia as internal molds tends to emphasize the glabellar furrows and thus accentuate the convexity of the central and lateral glabellar lobes.

Heliomeroides raymondi (Bradley, 1930) from the Kimmswick Limestone of Illinois is rather similar to H. teres. The high and convex occipital ring isolated by a broad V-shaped (in lateral view) occipital furrow and the flattening of the antero-median part of the central glabellar lobe (Evitt, 1951, p. 603) appears to characterize this species. The rectangular outline of the central glabellar lobe of H. treta Evitt, 1951 from the Athens Formation of Virginia, caused by the only slightly divergent 3s furrows, sets this species apart. The youngest species, H. novissima Dean 1971a from the Chair of Kildare Limestone, Eire, is characterized by nearly parallel 3s furrows, straight 2s furrows, and long divergent fixigenal spines.

Genus Heliomera Raymond, 1905

Type species: Cheirurus sol Billings, 1865 from the Table Head Formation, Newfoundland. Lectotype described and illustrated by Evitt, 1951, p. 603, Pl. 85, figs. 24-29 and Whittington, 1965a, p. 417, Pl. 63, figs. 1-6, 8, 12.

Heliomera cf. sol (Billings, 1865)
Pl. 24, figs. 33-35

Heliomera sol (Billings), EVITT, 1951, p. 603, Pl. 85, figs. 24-29; WHITTINGTON, 1965a, p. 417, Pl. 63, figs. 1-6, 8, 12.

Heliomera cf. sol (Billings), LUDVIGSEN, 1975, Pl. 1, fig. 18.

Occurrence: Sunblood Formation, Mary Range (B 145). Orthidiella-"Goniotelina" Fauna. 50 m below a collection yielding conodonts of Fauna 4 (late Whiterockian) of Sweet et al. (1971).

Material: A single incomplete cranidium.

Discussion: Whittington (1963, p. 88; 1965a, p. 418) summarized the diagnostic features of Heliomera sol (Billings), H. albata Whittington, and H. alacer (Whittington). The outline and inflation of the single available glabella and the evenly curved path of the 2s glabellar furrow (in lateral view) suggest that the Sunblood material is closest to H. sol. Whittington (1965a, p. 418) pointed out that H. sol is very similar to H. alacer; the glabellar differences being the more inflated lateral lobes and the antero-median row of pits on the latter species. The present material shows slightly less inflated lateral glabellar lobes than does H. alacer and the row of pits on the front part of the median lobe does not appear to be present.

The reassessment of the two similar genera, Heliomera and Heliomeroides (see discussion of Heliomeroides), suggests that Heliomera is confined to strata of Whiterockian age - presently known from the middle Table Head Formation and the enormous limestone boulder at Lower Head, western Newfoundland (Whittington, 1963, 1965a); the bioherm in the Antelope Valley Limestone at Meiklejohn Peak in Nevada (Ross, 1972); and the Sunblood Formation, Mackenzie Mountains. Heliomeroides has a considerably longer range - from Chazyan to Ashgillian.

Subfamily Sphaerexochinae Öpik, 1937

Diagnosis: See Whittington, 1965a, p. 411.

Genera assigned: Sphaerexochus Beyrich, Cydonocephalus Whittington, Kawina Barton, Pompeckia Warburg, Xystocrania Whittington, "Kawina" sexapugia Ross (see discussion under subfamily Acanthoparyphinae).

Genus Sphaerexochus Beyrich, 1845

Type species: Sphaerexochus mirus Beyrich from the Wenlockian of Bohemia.

Sphaerexochus arenosus Chatterton and Ludvigsen, ms.
Pl. 25, figs. 1-48

Sphaerexochus n. sp. 1, LUDVIGSEN, 1975, Pl. 3, figs. 1, 2.

Diagnosis: A species of Sphaerexochus with strongly curved 1s glabellar furrows that either do not reach occipital furrow or become moderately shallow posteriorly. Pygidium has two axial rings and a triangular terminal piece; three pairs of distinctly separated and clavate pygidial spines, each containing a narrow granulose band.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 110, A 125, A 247, P 1485, P 1497, P 1512, P 1520). Ceraurinella nahanniensis Zone and Bathyurus ulu Zone.

Material: 538 individuals.

Holotype: A small incomplete cephalon lacking the left cheek (UA 1388) from A 125 illustrated on Pl. 25, figs. 10-

<u>Description</u>: Cephalon semicircular in outline,
ngly convex (sag. and tr.), length (sag.) to width (be-
n genal spines) ratio 2:3. Glabella (excluding occipital
) nearly circular in outline in dorsal view (Pl. 15,
1), elongate oval in outline if cephalon tilted to show
mum view of glabella (Pl. 25, fig. 3); strongly inflated,
to 3/4ths as high as long (sag.), overhangs anterior bor-
and axial furrows. Axial and pre-glabellar furrows deep,
cted inwards and downwards; form continuous curve; their
ture marked by slight flare at oval anterior pit, just in
t of 3s furrow. Occipital furrow broad (sag.), straight,
ens laterally. Three pairs of approximately equi-spaced
ellar furrows; 1s furrow deepest, widest (exsag.), in
al view strongly curved inwards and backwards, does not
n occipital furrow (but faint concave extension of adax-
termination of furrow may extend to occipital furrow), ex-
s 1/4th way across glabella at line joining palpebral
s; sigmoid in lateral view. 2s and 3s furrows narrow
ag.), faintly incised, sub-parallel and with very slight
ward curvature. 2s furrow longest; reaches 1/4th way
ss mid-point of glabella. Anterior two pairs of glabel-
lobes rhombic in lateral outline, not inflated. 1p lobe
in outline, very slightly inflated. Occipital ring
ed (tr.), convex (sag.) and directed upwards and back-
s; possesses tiny median tubercle. Occipital furrow
d (sag.), moderate in depth at mid-line, deepens behind

lp lobe; outlined laterally by narrow, faint axial furrow. Anterior border short (sag.), convex, faces forward and slightly downward. Cheeks triangular, slightly convex, steeply inclined. In anterior view, front edge of cheeks form angle of 120-130° with anterior margin below pre-glabellar furrow (Pl. 25, fig. 13). Eye located close to axial furrow, opposite and below 2p lobe and ls furrow. Visual surface convex (tr. and hor.), sub-oval in outline, lower edge straight; composed of 100-130 hexagonal and pentagonal facets. Upper edge of eye stands slightly higher than curved (exsag.) and narrow (tr.) palpebral lobe which parallels suture for a short distance above and behind eye. Palpebral furrow narrow, deep; in anterior view it is straight, obliquely disposed; in lateral view highly arched. From anterior edge of eye, facial suture follows somewhat sinuous course, sub-parallel to axial furrow; turns inward just in front of anterior pit (Pl. 25, fig. 48) to cross below front part of glabella and become rostral suture at junction with ventrally convergent connective suture. Faint antennal notch located just lateral to connective suture. Rostral plate (Pl. 25, fig. 10) broadly wedge-shaped, sharp edge directed obliquely downwards and inwards, slightly curved (tr.). In anterior view, facial and rostral sutures straight between anterior pits (Pl. 25, fig. 8). From base of eye, facial suture follows very gentle curve to lateral furrow, then curves sharply backwards to cross margin just in front of short blunt genal spine. Facial suture situated on convex granulated sutural ridge on crossing bald border furrows. Thus, relatively deep, trough-shaped, slightly curved lateral border furrow isolated from both posterior border furrow and anterior pit (Pl. 25, fig. 7). Posterior border furrow continuous with, and initially as wide as, occipital furrow; widens slightly distally and curves forward to abut sutural ridge. Ignoring sutural ridges, posterior and lateral border furrows form V- or U-shaped continuum with terminations at distal end of occipital ring and at anterior pit. Lateral border convex, tube-like (tr.); in front of posterior branch of facial suture, diagonally crossed by sharp V-shaped furrow which curves around margin and terminates on inner edge of doublure immediately in front of genal spine (Pl. 25, figs. 6, 7). Postero-lateral margin, between V-shaped furrow and facial suture, deflected into a rounded nub-like bulge, which, in large holaspid cephala is considerably larger than reduced fixigenal spine. Posterior margin similar in width to lateral margin. Smaller specimens possess relatively long, tapering outwardly and downwardly directed, spike-like fixigenal spines located just inside facial suture. Fixigenal spine progressively reduced in larger specimens to slight bulge (Pl. 25, fig. 27).

Central portion of glabella, except glabellar furrows, covered by very fine granulation of two sizes (Pl. 25, figs. 45, 48) -- larger granules, evenly spaced at approximately 40/mm^2 and intervening smaller granules. Only finer granulation evident on glabellar flanks ~~and~~ cheeks, except posterior and lateral border furrows. In addition, portion of cheek outlined by lateral border furrow and facial suture possesses irregularly-disposed pits (Pl. 25, fig. 46).

On inner surface of cephalon, axial, pre-glabellar, and occipital furrows expressed as moderately high, rounded ridges; in slightly tilted view (Pl. 25, figs. 10, 21) these form nearly perfect circle. Anterior pit appears as small thorn-like elevation. Doublure extends inwards to faintly elevated lateral border furrow. At genal corners doublure widened (tr.) and diagonally crossed by sharp V-shaped furrow which isolates crescent-shaped "pseudo-librigenal spine" in front of blunt fixigenal spine (Pl. 25, fig. 6). Glabellar furrows appear as thin ridges. Appendifers not present, but distal parts of occipital furrow elevated into elongate knobs (Pl. 25, fig. 21). In posterior view, posterior part of cephalon exactly mirrors posterior part of thoracic segments (compare Pl. 25~~, figs~~. 5 and 40).

Hypostome rectangular to trapezoidal in outline; ratio of width between shoulders to maximum length (exsag.) 3:2. Anterior margin straight to faintly convex forward, extended laterally into long, dorsally-divergent anterior wings which carry small antero-dorsally directed wing processes. From narrow antennal notch at base of anterior wings, lateral margin flares slightly into shoulders and then narrows slightly backwards before curving inwards and forwards to form bilobate posterior margin. Ovate middle body extends to anterior margin medially; bounded laterally and antero-laterally by narrow border furrows which converge slightly backwards and then curve inward to form shallower posterior border furrow. Middle body slightly raised over broad and flat lateral and posterior margins. Middle furrow initiated at anterior edge of lateral border furrow, extends 1/3rd way across middle body, converges adaxially at about 60° to sagittal line. Macula not obvious, but may be represented by small bald, oval area in front of adaxial termination of middle furrow of some specimens. Abaxial part of anterior margin deflected ventrally nearly perpendicular to rest of hypostome (Pl. 25, fig. 32). Anterior sutural margin flat-edged, with sharp rims. Posterior part of hypostomal doublure flat, extends inward to lateral and posterior border furrows. Anteriorly, it is deflected slightly dorsally into moderately prominent shoulder and then ventrally into steeply sloping antero-laterally directed antennal notch. Furrows appear as faint or strong rounded ridges on interior. A pair of elongate depressions are located immediately adjacent to anterior margin, in front of juncture of lateral border furrow and middle furrow. Anterior 2/3rd of middle body and lateral borders ornamented by closely-spaced granules of same size range as coarse set on mid-areas of glabella. Posterior 1/3rd of middle body, posterior border, and doublure bald.

Number of thoracic segments unknown. Axis high, convex, slightly wider (tr.) than 1/3rd total width of thorax, outlined by narrow, moderately impressed axial furrows. Pleura slopes slightly outwards, anterior 1/3rd contrasted with posterior portion in being unornamented and bevelled forward to fit under posterior portion of adjacent pleura. Outer portion of pleura extended outwards and downwards into long, blunt, tubular, club-shaped spine whose inner posterior edge is modified into high, triangular facet to accomodate inner anterior edge of next pleural spine. Articulating furrow moderately shallow, descends laterally into moderately deep pit which includes the ring socket. Faintly outlined pre-annulus present in some segments. From the ring socket, forwardly-facing anterior flange curves along lower edge and turns outward to terminate at marginal connective device at base of pleural spine (Pl. 25, fig. 34). Tiny, button-like axial process situated slightly laterally to rather indistinct ring socket located at change in slope between axis and pleural region. Articulating devices duplicated on posterior side of pleura -- ring process accomodates the ring socket and axial socket the axial process (Whittington and Evitt, 1954, fig. 27; Bergström, 1971, fig. 7); however, marginal ~~connective~~ device not evident in posterior view since it is tucked under pleura (Pl. 25, fig. 40). On inner surface, axial doublure projects forward to near impress of articulating furrow. Appendifers not present. Entire pleura, except doublure and anterior 1/3rd of pleural field, but including median part of articulating furrow and posterior half of articulating half ring, ornamented by granulation of same size range as fine set on glabella. Median portion of axial ring also bears relatively few scattered coarse granules.

Pygidium, including spines, lenticular in outline; about 1/2 as long (sag. and exsag.) as wide (tr.). Axis triangular, convexity decreases gradually posteriorly, tapers to sharp point just in front of posterior margin; composed of two moderately convex rings and a long triangular terminal piece separated by narrow, straight ring furrows and outlined laterally by broad, weakly concave axial furrows. Position of incipient third ring furrow indicated by pair of lateral notches at mid-length of terminal piece (Pl. 25, figs. 30, 31). Articulating furrow straight, descends distally into pit which includes ring socket and, slightly laterally, axial process. Three pairs of short, blunt, digitate marginal spines; first pair directed obliquely backwards and downwards, second and third pairs directed progressively horizontally and backwards. Spines about as long as wide; distinctly separated; and near tip flare slightly before terminating in rounded point. Tips of pygidial spines and posterior few thoracic spines defined by arc of circle with axis at midline of 8th? thoracic segment (second from rear). Pygidial ornament concisely restricted to certain areas. Fine, closely-spaced granulation covers axial rings, terminal piece, and posterior half of articulating half-ring; axial ring furrows and articulating furrow have less dense granulation; broad axial furrows bald. Slightly raised bands with closely-spaced granulation run down inner portion of pleurae and median parts of pygidial spines; posteriorly these bands expand to cover entire tip of blunt spines. Band on first set of spines nearly reaches axial ring; band on second and third spines initiated lateral to broad axial furrow. Remaining parts of dorsal surface of spines and intervening thoracic field bald. On inner surface doublure broad, increasingly convex posteriorly. Doublure in front of third set of spines deflected upwards, leaving a broad sulcus below axis. Axial and axial ring furrows faintly impressed. Posterior part of doublure and ventral side of third spines densely granulated. This granulation becomes sparser anteriorly, and ventral side of first spines nearly bald.

Discussion: The cranidium of Sphaerexochus arenosus Chatterton and Ludvigsen differs from those of most of the species of Sphaerexochus listed by Lane (1971, p. 53) in possessing an incomplete 1s furrow which does not extend to the occipital furrow or one that becomes markedly shallow along its posterior portion. The pygidium with its short (sag.), narrow, and triangular terminal piece and clavate and distinctly separated spines which contain a narrow granulated band; is readily distinguishable from all previously described Middle Ordovician species. S. filius Tripp, 1967, S. eurys Tripp, 1962, and S. parvus Billings (Shaw, 1968) possess compact pygidia with blunt or square-tipped spines which are closely aligned for most of their length. S. costabilis Dean, 1971b has a long swollen terminal piece and short third spines. Such species as S. balclatchiensis Reed (Lane, 1971), S. pulcher Whittington and Evitt, 1954, and

S. hapsidotus Whittington and Evitt, 1954, like S. arenosus, possess clavate pygidial spines. The material of S. balclatchiensis (Lane, 1971, Pl. 11, figs. 1-8) from Girvan is badly distorted, but appears very similar to the Esbataottine species. It can be distinguished by the deep, complete 3s furrows. Detailed comparison is further hampered by the much larger size of the Scottish species. S. pulcher from the Edinburg Limestone of Virginia has a less inflated glabella than S. arenosus and possesses a pygidium whose entire dorsal surface is granulose. S. hapsidotus from the Lincolnshire Limestone of Virginia is closest to S. arenosus. This is especially evident if the pygidia are compared. These are highly similar and only the broader granulated bands along the pygidial spines identifies the Virginia species. S. hapsidotus can further be distinguished by its narrow (tr.) and nearly vertically disposed cheeks.

Lane (1971, p. 53) commented on the change within species of Sphaerexochus throughout their range from the Middle Ordovician to the Middle Silurian and suggested that Silurian species, if compared to Middle Ordovician species, have weaker 2s and 3s glabellar furrows, genal spines reduced to small swellings, fused terminal piece and third axial ring of the pygidium, and reduced pygidial spines. The first three of the suggested changes can effectively be nullified by pointing to their presence in S. arenosus which is one of the earliest known species of Sphaerexochus.

The species name (areno, Latin for sand) is in reference to the sandpaper-like ornament on the dorsal surface of this species.

Sphaerexochus atacius n. sp.

Pl. 24, figs. 36-58

Sphaerexochus n. sp. 2, LUDVIGSEN, 1975, Pl. 4, figs. 8, 9.

Diagnosis: A species of Sphaerexochus possessing deep, S-shaped first glabellar furrows that terminate well in front of occipital furrow; slightly inflated basal glabellar lobes; and very faint second and third glabellar furrows. Pygidium has three pairs of short, square-tipped spines that are nearly conjoined and are accentuated by broad granulated band.

Occurrence: Upper Esbataottine Formation, Sunblood Range (P 2110, P 2038). Ceraurinella longispina Zone.

Material: 100 individuals.

Holotype: A complete cranidium (GSC 40420) from P 2038 illustrated on Pl. 24, figs. 36-38, 58.

Discussion: According to Lane's (1971, p. 53) recent diagnosis of Sphaerexochus, S. atacius n. sp. does not belong to this genus because the first glabellar furrows are definitely incomplete and the basal glabellar lobes are not isolated. However, in all other respects, S. atacius is a typical member of the genus. The incomplete furrows may be viewed as an extreme condition of the variably developed 1s furrow seen in *S. arenosus* from lower in the Esbataottine Formation which changes from shallow or deep to complete or nearly effaced medially. The fact that, at least, some of the cranidia of *S. parvus* Billings illustrated by Shaw (1968, Pl. 14, figs. 9, 16) show an incomplete 1s furrow demonstrates that the diagnosis of *Sphaerexochus* should be modified to allow reception of these species.

Sphaerexochus atacius differs from *S. arenosus* in the following points:

1. The first glabellar furrows are deep and generally narrower and do not extend to the occipital furrow. The basal glabellar lobes are longer (exsag.) and slightly more inflated.

2. The granulose ornament is considerably finer (compare Pl. 24, fig. 58 and Pl. 25, fig. 45).

3. The anterior branch of the facial suture is deflected around a relatively large anterior pit and the anterior cranidial margin is only faintly bowed towards the front. In *S. arenosus* the facial suture passes closer to the anterior pit and the anterior cranidial margin is strongly bowed towards the front (compare Pl. 24, fig. 56 and Pl. 25, fig. 21).

4. The pleurae of the segments slope outwards at about the same orientation as the distal parts of the axis and the axial furrows are very faint. In *S. arenosus* the inner parts of the pleurae are nearly horizontal and the position of the axial furrow is emphasized by a distinct slope change

(compare Pl. 24, fig. 52 and Pl. 25, fig. 40).

5. The lateral margins of the hypostome are more convergent posteriorly, the lateral and posterior borders and doublure are narrower, and the anterior wings are higher and more flaring (compare Pl. 24, figs. 47, 48 and Pl. 25, figs. 32, 33).

6. The pygidial spines are shorter, broader, and closely aligned. The spines are square-tipped and each spine carries a broad granulose band. The pygidial spines of S. arenosus are clavate, distinctly separated with rounded terminations, and each carries a narrow granulate band (compare Pl. 24, figs. 43, 44 and Pl. 25, figs. 30, 31).

The non-isolated basal glabellar lobes of this species, atypical for Sphaerexochus, suggests its name (atacio, Greek for "out of order").

Genus Kawina Barton, 1916

Type species: Cheirurus vulcanus Billings, 1865 from Cow Head, Newfoundland (redescribed by Whittington, 1963, p. 91).

Kawina sp.

Pl. 28, figs. 49, 50

Kawina sp., LUDVIGSEN, 1975, Pl. 1, fig. 19.

Occurrence: Sunblood Formation, Sunblood Range (P 55). Collection occurs between two samples yielding

Fauna 4 (late Whiterockian) conodonts of Sweet et al. (1971).

Material: 2 individuals.

Discussion: The single pygidium at hand differs from most species of Kawina in possessing three axial rings, but no terminal piece. In this respect it is similar to ~~the~~ Kawina sp. from the upper Antelope Valley Limestone, Nevada illustrated by Ross (1970, Pl. 18, figs. 16-18) and the Kawina sp. from the Oil Creek Formation, Oklahoma illustrated by Shaw (1974, Pl. 7, fig. 20). The absence of a terminal piece may suggest an assignment of Xystocrania Whittington, 1965a; but Kawina sp. differs from both species of which pygidia are known, X. unicornica (Hintze, 1953) and X. cf. perforator (Billings, see Ross, 1970) in that the spines are fused for nearly half their length.

Subfamily Deiphoninae Raymond

Diagnosis: A diagnosis for this subfamily has been presented by Lane (1971, p. 58). This must be revised, in part, to read, "Glabella, in front of 1p lobe *or 2p lobe*, subspherically swollen, unfurrowed; 1p lobe nodular or transversely elongate; *2p lobe obsolescent, its position indicated by pit-like 1s and 2s furrows seen on interior*..." and "...Pygidium with four *or more* rings on the axis and two pairs of spines" to accommodate *Onycopyge* and new information on *Sphaerocoryphe robustus* (Revised parts italicized).

Genera assigned: See Holloway and Campbell (1974).

Genus *Sphaerocoryphe* Angelin, 1854

Type species: *Sphaerocoryphe dentata* Angelin, 1854 from the Late Ordovician of Sweden.

Sphaerocoryphe robustus Walcott, 1875

Pl. 20, figs. 33-53

Sphaerocoryphe robustus WALCOTT, 1875, p. 273, figs. 18a, b; WILSON, 1947, p. 52, Pl. 10, Figs. 1, 2a, b; SHAW, 1968, Pl. 14, fig. 1.

Sphaerocoryphe sp., LUDVIGSEN, 1975, Pl. 5, figs. 12, 13.

Occurrence: Trenton Group, Trenton Falls, New York State and Hull, Quebec; lower Whittaker Formation, Funeral Range (C 655, J 220), Whittaker Range (H 1920, I 1275,

350-1380), and Dusky Range (R 625). *Ceraurinella necra*
e, *Ceraurus mackenziensis* Zone, and *Whittakerites planatus*
es (in the Nahanni area).

Material: About 35 individuals.

Holotype: A complete carapace (MCZ 7567) from the
nton Group at Trenton Falls, New York illustrated by Shaw
68, Pl. 14, fig. 1).

Description: Cranidium, without swollen part of
bella and genal spines, crescentic in outline, 3 times as
as long (sag.); slightly vaulted (tr.) and strongly con-
(sag.). In lateral view, anterior margin descends nearly
tically from palpebral lobe and curves underneath poster-
portion of swollen part of glabella. Occipital ring
ed, short (sag.); stands well above posterior portion of
bella. Occipital furrow transverse, deepest distally.
ion of glabella behind swollen portion, sub-rectangular
utline, moderately arched; defined laterally by very shal-
and broad axial furrows which curve around slightly in-
ed 1p lobes of triangular outline. That part of glabella
een inflated 1p lobes is flat to slightly concave. Hol-
y and Campbell (1974, p. 419) employed the term "pre-
pital depression" (not to be confused with "post-coital
s") for this feature and emphasized that it consists of
occipital furrow and part of the median glabellar lobe.
ront of 1s furrow, axial furrows diverge and become deep
ows that undercut swollen part of glabella and then des-

cend to ~~become~~ deep inwardly and upwardly directed pre-glabellar furrow. 2p lobe obsolescent; its position shown by 1s and 2s apodemal pits on interior (Pl. 20, fig. 37). Glabella dominated by swollen anterior portion which is spherical, unfurrowed; occupies 2/3rds total glabellar length (sag.) and is 1 1/2 times as wide (tr.) as occipital ring. In lateral profile, swollen portion stands higher than occipital ring and extends below level of base of genal spines; its "centre of gravity" is located slightly below level of eyes. It is isolated from posterior portion of glabella by relatively long (exsag.) furrows that shallow adaxially and that, apparently, represent combined 1s and 2s furrows. Posterior portion of fixed cheek nearly horizontal; anterior portion nearly vertical in front of eyes. Palpebral lobe small, lenticular in outline, sharply raised over floor of cheek; located opposite combined 1s and 2s furrow; stands lower than crest of posterior portion of glabella; defined adaxially by narrow palpebral furrow which, posteriorly, is continuous with faint furrow bounding sutural ridge and, anteriorly, curves steeply down and terminates in front of visual surface of eye. Anterior branch of facial suture descends vertically in front of palpebral lobe and curves underneath posterior portion of swollen part of glabella along path sub-parallel with pre-glabellar furrow. A forwardly deflected anterior border is thus isolated. Posterior branch of facial suture positioned on short (exsag.) sutural ridge; curves outwards and downwards with faint forward curvature. Cheek, adaxially of palpebral lobe, slopes steeply towards deep axial furrow. Deep posterior border furrow of cheek is lateral continuation of occipital furrow; terminates abruptly at base of genal spine; bounds narrow and convex (exsag.) posterior border. Only posterior part of lateral border furrow seen; appears to be deep and wide (tr.), interrupted by narrow sutural ridge. Lateral border convex, slightly wider (tr.) than length (exsag.) of posterior border. A pair of small, nub-like lateral cephalic spines located on ventro-lateral part of lateral border, between posterior branch of facial suture and base of genal spine (Pl. 20, fig. 37). On smaller cranidia (Pl. 20, fig. 43), these spines are relatively longer and laterally curving. Distinct, rounded (exsag.) ridge proceeds transversely across fixed cheek, halfway between eye and posterior margin. This ridge is bounded by the posterior border furrow and by the depressed area surrounding eye and continues part way down genal spine; so that the base of the genal spine is faintly carinate. Genal spine stout, curving, gradually tapering; extends posteriorly as far as 1/2 length (sag.) of cranidium. On interior, 0s, 1s, and 2s apodemal pits appear as rounded knobs along forwardly-flaring axial furrows. Occipital doublure extends to faint ridge representing occipital furrow. Doublure encases genal spine and, adaxially, thins towards tiny marginal connective device. Swollen portion of glabella is rather coarsely granulose; remainder of dorsal surface of cranidium (except furrows) is finely granulose.

Free cheek, rostral plate, and thoracic segment have not been recognized in these collections.

Hypostome trapezoidal in outline with straight and parallel anterior and posterior margins; lateral margins converge posteriorly from maximum width (tr.) at faintly defined shoulders to obtusely-angled postero-lateral corners. Middle body ovoid in outline, arched (tr.); bracketed by deep, outwardly-bowed lateral border furrows, posteriorly by narrow (tr.) and short (sag.) posterior border furrow, and anteriorly by faint anterior border furrow that deepens laterally. A very faint macula (or middle furrow) proceeds obliquely inwards and backwards from juncture of lateral and anterior border furrows. Lateral and posterior borders convex, tube-like. In posterior view, the posterior border thickened medially. Anterior border narrow, deflected upwards at nearly right angle to rest of hypostome. Anterior margin straight medially where it forms the sutural contact with the rostral plate; in front of maculae, it is notched to form sutural contact with doublure of free cheek and continues laterally into small dorso-laterally-directed anterior wing. Faint antennal notch separates anterior wing from shoulder. On interior, doublure nearly reaches high rounded ridge forming interior impress of lateral border furrow. Macula (or middle furrow) expressed as relatively high ridge that separates distal portions of anterior and posterior lobes of middle body. Ventral surface of hypostome sparsely granulose.

Pygidium (without second marginal spines) crescentic in outline, 3 times as wide (tr.) as long (sag.); composed of anterior segment which, apparently, duplicates morphology of the thoracic segments; followed by 3 segments. First axial ring short (sag.), highly arched, bounded by narrow (tr.) axial furrows, outlined by short (sag.) articulating furrow, relatively long (sag.) first axial ring furrow which is continuous laterally with deep interpleural furrow. Pleural field, opposite first axial ring, composed of a transverse and convex (exsag.) band which, distally, is produced into pair of short, stout, square-tipped, ventrally-directed spines. Second axial ring stands well below first axial ring and is only faintly outlined by the axial furrows; extended posteriorly into pair of long, stout, curved, gradually tapering spines which proceed outward and backward; and, distally, converge to form tong-shaped continuum. Spines carry distinct carinae that appear to be extensions of the faintly arched second axial ring. Third and fourth axial rings very short (sag.) and narrow (tr.); confined to lenticular depression outlined, anteriorly, by second axial ring furrow and, posteriorly, by approximately transverse furrow joining elongate slots at posterior ends of second, third, and fourth axial ring furrows (Pl. 20, fig. 53). Posterior border of pygidium between bases of great spines, formed by short and convex (sag.) band which curves slightly posteriorly. Doublure narrow, convex; forms stretched U-shaped curve between bases of second marginal spines and, beneath posterior border, is extended into a pair of triangular, transversely-oriented spines which are ventrally produced (Pl. 20, figs. 45, 51).

Discussion: The material from the Whittaker Formation is assigned to Sphaerocoryphe robustus Walcott despite a few differences. The holotype from Trenton Falls, New York (Shaw, 1968, Pl. 14, fig. 1) shows a more inflated fixed cheek inside the border furrows and a slightly longer posterior glabellar portion (behind the swollen anterior glabellar portion) than the Whittaker material and the palpebral lobes appear to be located farther out on the cheek. It is difficult to evaluate these points in light of the considerable differences that, apparently, distinguish the twenty or so named species of Sphaerocoryphe (Shaw, 1968; Lane, 1971; Webby, 1974). These differences, however, appear on specimens of various preservational states and of considerable size range. Sphaerocoryphe undergoes extensive morphological change during its ontogeny (more critical in this genus than in most other cheirurid genera because of its small size) and it is difficult to ascertain the diagnostic value of many of these features. Only in exceptionally-preserved specimens may features such as the small, antero-ventrally directed lateral cephalic spines and the triangular and ventrally directed posterior pygidial spines of S. robustus be seen.

It is clear from the aspect of the hypostomal suture on the hypostome and the downwardly-deflected anterior cranidial margin of Sphaerocoryphe robustus that the hypostome would be positioned at a high angle to the remaining exoskeleton. Holloway and Campbell (1974, p. 420, 421) suggested that the hypostomes of the Deiphoninae were moveable and cited, as evidence, the well-developed articulating devices of Deiphon, the "embayments in the anterior border of the cephalon on either side of the hypostomal suture that received the posterior spines of the pygidium", and the "deep furrow across the anterior half of the hypostome (that) probably also fitted into the doublure of the pygidium". The presence of articulating devices do not, necessarily, require the ability of total enrollment and the "embayments" may be viewed as antennal notches rather than receptors of the posterior pygidial spines. The variably developed anterior border furrow of the hypostome and the variety of morphologies of the doublure of the pygidium (including stout, ventrally-directed spines) argue against a close connection of these features. Furthermore, the sharp-edged and laterally indented hypostomal suture suggests that rotation of the hypostome of S. robustus would not be allowed. In fact, none of the cheirurids investigated during the present study possesses hypostomal sutures that display a morphology suggesting that was a surface of rotation.

Sphaerocoryphe cf. pemphis Lane, 1971

Pl. 29, figs. 44-46 .

Sphaerocoryphe pemphis LANE, 1971, p. 62, Pl. 14, figs. 1-8.

Occurrence: Lower Esbataottine Formation, Sunblood Range (A 125). Ceraurinella nahanniensis Zone.

Material: 1 individual.

Discussion: A single cranidium of Sphaerocoryphe cf. pemphis shows a glabella that is swollen and circular in outline in front of pit-like 1s furrows. The shape of the swollen part of the glabella is that of a partially deflated sphere which drapes over the anterior margin. The left fixed cheek is somewhat crushed, but appears to be arched (exsag. and tr.). The genal spine is moderately long and has distinct upward curvature. The lateral margin in front of the genal spine bears two, short, outwardly and downwardly directed marginal spines. The hypostome is rectangular in outline with straight lateral and anterior margins and a concave posterior margin. The anterior wings extend slightly beyond the small triangular shoulders. The middle body is rectangular in outline and completely circumscribed by moderately deep border furrows. The middle furrows are deep next to the border furrows and shallow towards the mid-line.

The presence of two marginal spines in front of the genal spine in the Esbataottine species effectively limits comparison with Sphaerocoryphe pemphis Lane, 1971 from the

Caradocian of Girvan and S. thomsoni Reed, 1906 from the Ashgillian of Girvan. S. cf. pemphis differs from both of these species in possessing a longer (sag.) glabellar portion behind the swollen portion, a higher occipital ring, and a hypostome with a concave posterior border and deep middle furrows.

Sphaerocoryphe cf. pemphis is readily distinguishable from S. robustus from the lower Whittaker Formation in possessing slender and curved genal spines, an anterior cranidial margin that descends obliquely in front of the eye (in lateral view), a higher occipital ring, a partially "deflated" anterior glabellar portion, and two relatively long lateral cephalic spines (compare Pl. 29, fig. 44 and Pl. 20, fig. 36). The hypostomes differ considerably (compare Pl. 29, fig. 46 and Pl. 20, fig. 47).

Family Encrinuridae Angelin, 1854

Subfamily Encrinurinae Angelin, 1854

Genus *Encrinuroides* Reed, 1931

Type species: *Cybele sexacostata* Salter, 1848 from the Ashgillian of Wales. Redescribed and illustrated by Whittington (1950).

Encrinuroides rarus (Walcott, 1877)

Pl. 19, fig. 6, Pl. 28, figs. 42-48, Pl. 29, figs. 1-43

Ceraurus rarus WALCOTT, 1877, p. 68.

Encrinurus raricostatus WALCOTT, 1877, p. 69.

Encrinurus vannulus CLARKE, 1894, p. 739, text figs. 56, 57.

Encrinurus rarus (Walcott), RAYMOND and BARTON, 1913, p. 541,
Pl. 2, fig. 3.

non *Encrinurus rarus* (Walcott), TROEDSSON, 1928, p. 59,
Pl. 16, figs. 4-9.

Encrinuroides rarus (Walcott), DeMOTT, 1963, p. 168, Pl. 11,
figs. 13-25.

Encrinuroides cf. *rarus* (Walcott), LUDVIGSEN, 1975, Pl. 3,
figs. 22, 23.

Diagnosis: A species of *Encrinuroides* with a mushroom-shaped glabella bounded by deep, forwardly flaring axial furrows. Three pairs of short glabellar furrows are oriented perpendicular to axial furrow. Glabellar ornament consists of coarse tubercles, largely restricted to anterior lobe. Pygidium has 17-19 axial rings and 7 pleural ribs.

Occurrence: Platteville Group, Wisconsin and Esbataottine Formation, Sunblood Range (A 110, A 125, A 247, A 365, A 615, P 1485, P 1497, P 1785), Flood Creek (G 3195, G 3340). *Ceraurinella nahanniensis* Zone, *Bathyurus ulu* Zone, *Ceraurus gabrielsi* Zone, and *Ceraurinella longispina* Zone (in Canada).

Material: 131 individuals.

Holotype: An incomplete cranidium (UC 12322) from the Platteville Group, Beloit, Wisconsin illustrated on Pl. 19, fig. 6.

Description: Cephalon roughly triangular in outline, moderately vaulted (tr.); length (sag.) slightly less than 1/2 maximum width (tr.) between base of genal spines; in lateral view, ventral and dorsal edges of cephalon parallel, dorsal crest curves gradually down into vertical preglabellar field (Pl. 29, fig. 3); in anterior view, lower edge of cephalon defines broad obtuse angle (Pl. 29, fig. 4). Forwardly expanding glabella moderately convex (tr.); minimum width across basal lobes about 1/4th maximum width of cephalon between base of genal spines; expands to 1 1/3rd minimum width across 3s furrows; maximum width of glabella at anterior pits 1 2/3 times minimum width. Axial furrows deep, outwardly flaring. 3 pairs of moderately deep lateral glabellar furrows oriented perpendicular to axial furrows; approximately of equal length (tr.); 1s directed transversely, extends 1/4th way across glabella; 3s runs inward and forward, extends less than 1/4th way across glabella. Lateral glabellar lobes short (exsag.), rectangular; increase slightly in length (exsag.) forward. Anterior lobe bulbous, expanded laterally; about as long (sag.) as combined length of posterior 3 lobes. Anterior margin reaches and protrudes slightly beyond pre-glabellar furrow; notched on sagittal line by nearly vertical longitudinal furrow which is slightly shorter (in dorsal view) than lateral glabellar furrows. Glabella rises steeply out of deep axial furrows which diverge forward in even curve and descend to join lateral border furrow on cheek (Pl. 29, fig. 7). Pre-glabellar furrow narrow, sub-horizontally disposed; joins axial furrow halfway between 3s furrow and anterior border furrow; juncture marked by small inwardly and downwardly directed anterior pit. Occipital furrow moderately short (sag.) and deep, with slight median forward flexure. Occipital ring arched, evenly convex (sag.), stands slightly higher than and is appreciably wider (tr.) than glabella immediately in front of occipital furrow. Pre-glabellar field vertical, high (sag.), narrows slightly adaxially; very faint and broad anterior border furrow proceeds inward from juncture of axial and lateral border furrows, dies out before reaching sagittal line. Cheek inside palpebral lobe; moderately arched, stands lower than glabella; antero-lateral and lateral flanks of cheek curve steeply down to lateral border furrow. Palpebral lobe located far out on cheek, opposite 2p lobe and 2s furrow; triangular in outline, moderately curved (tr. and exsag.); outlined adaxially by deep, straight palpebral furrow which continues for a short distance around posterior and anterior side of visual surface. Palpebral lobe bald; perforated by single minute pit near abaxial termination (Pl. 29, fig. 2). Cheek in front of eye descends nearly vertically; behind eye it curves steeply. Visual surface of eye protrudes from cheek in bulbous fashion, moderately curved (tr. and hor.), very finely and evenly granular, individual lenses not visible. Base of eye not clearly defined; essentially marked by change in slope and ornamentation, but coarse pitting on cheek persists into lower part of visual surface (Pl. 29, fig. 11). Poorly defined palpebral ridge is outlined on each side by single row of pits; proceeds forwards and inwards to anterior glabellar lobe from front edge of palpebral lobe. Anterior branch of facial suture curves inwards and downwards immediately in front of and parallel with palpebral ridge; intersects axial furrow just below anterior pit, then swings forwards and inwards across anterior border, below and parallel with pre-glabellar furrow. Nearly at sagittal line, facial suture joined by vertical connective suture which outlines high, narrow, forwardly-facing rostral plate. Posterior branch of facial suture proceeds outwards and downwards in even curve from posterior edge of visual surface and intersects lateral margin just in front of genal spine; occupies narrow, steep-sided sutural ridge (Pl. 29, fig. 11). Posterior border furrow as long (exsag.) as occipital furrow; in lateral view, directed perpendicular to both glabellar crest and to lateral border furrow (Pl. 29, fig. 3); fades out just prior to reaching course of posterior branch of facial suture at genal angle. Posterior border evenly convex (exsag.), as wide as occipital ring; at genal angle, a short delicate genal spine (in large cranidia) curves obliquely backwards. Lateral border furrow deep, sharply incised; initiated just in front of genal angle, proceeds in straight line to join axial furrow (Pl. 29, fig. 7). Lateral border fairly flat, nearly vertical; narrows towards sagittal line; anteriorly it is separated from pre-glabellar field by faint anterior border furrow.

Ornament on anterior glabellar lobe consists of numerous, large, round, and perforated tubercles; these tubercles become progressively sparser and smaller, posteriorly; opposite posterior glabellar lobes ornament consists of a few tiny rimmed pits arranged in irregular transverse rows. Areas flanking axial and glabellar furrows and pre-glabellar field above anterior border furrow possess smaller tubercles, commonly unperforated. Cheeks inside border furrows (except palpebral lobe and palpebral ridge) perforated by relatively large pits; in addition, cheek (except palpebral lobe) contains scattered large tubercles. Occipital ring bare except for single pair of tiny pits (Pl. 29, fig. 1). Posterior border smooth. Small tubercles scattered on surface of genal spines of smaller cranidia. Lateral border, from smooth posterior sutural ridge to rostral

, contains irregular horizontal rows of small tub-
s, rarely perforated. Faint vincular furrow finely
late; distinct row of granules mark abaxial edge of
w (Pl. 29, fig. 11). Posterior border furrows smooth,
osterior side of furrow contains single row of gran-
similar granule rows flank lateral border furrow (Pl.
ig. 2).

On interior of cephalon occipital doublure short (sag.),
ds nearly to occipital furrow. Posterior pleural doub-
short (exsag.), expands at genal angle and turns for-
to become faintly convex lateral doublure. Ventral
of lateral doublure flat to slightly concave in the
of a faint vincular furrow. Antero-median part of
ure slightly narrower to accommodate evenly curved and
edged hypostomal suture. Axial furrow expressed as
, high, evenly convex ridge; projecting off adaxial
of this ridge are high, prong-like, vertically direct-
pendifers; 1s largest, 0s and 2s slightly smaller, 3s
est, barely visible; this ridge also contains moder-
large, inwardly and downwardly-directed projection
is impress of anterior pit (Pl. 29, fig. 8). Oc-
al, pre-glabellar, longitudinal, lateral and posterior
r furrows appear as low, rounded ridges.

Hypostome oval in outline; ratio of length (sag.) to
across shoulders 3:2. Anterior 3/4th occupied by
y conv[illegible](tr. and sag.) middle body, approximately
lar in outline, which rises steeply from planar lat-

eral and posterior borders. Postero-lateral edge of middle body partially undercut by deep furrow (probably representing middle furrow and maculae?) which dies out just in front of shoulders; furrow shallows posteriorly leaving narrow, faintly convex (tr,) apron curving up from median part of posterior border. Antero-median part of middle body contains inflated hump, delimited laterally by sharp, forwardly converging furrows which merge with anterior border furrow (Pl. 29, fig. 10). Anterior margin follows bell-curve between flaring anterior wings; it is slightly raised over middle body and anterior border furrow. From base of anterior wings, lateral margin deflected into small antennal notch; then curves laterally to define almost indistinct shoulder before curving towards midline. Lateral and posterior borders confluent, crescent-shaped, widest sagittally, narrow anteriorly and pinch out at base of antennal notch; posterior border has faint dorsal curvature, lateral border tilted slightly inwards. On inner surface narrow convex anterior doublure flares laterally into large, plate-like, forwardly facing anterior wings which, along their mid-portion, carry blunt and slightly divergent wing processes. Behind wing process, anterior wing consists of high thin dorsally produced plate which has short recurved portion at apex and which stands above wing process. From mid-portion of posterior edge of anterior wing, doublure descends slightly into faint antennal notch and is then produced into thin, prong-like, postero-medially directed posterior wings. Lateral and posterior doublure narrow, except for anteriorly produced, sagittal prong which is elevated above hypostomal floor. Middle furrow (?) appears as low rounded ridges between deep middle body and flat lateral and posterior borders.

Number of thoracic segments unknown. Axis moderately high and convex, approximately 1/3rd width of segment; outlined by narrow (tr.) and deeply impressed axial furrows; articulating furrow nearly straight with slight forward curvature distally; articulating half ring short (sag.), more convex (tr.) than axis. Pleura short (exsag.), slopes gradually with increasing curvature to terminate as pointed, downwardly and outwardly directed spine. Anterior side of pleura bears short (exsag.) pleural furrow which divides pleura into convex (exsag.) pleural band and very short (exsag.) and depressed anterior pleural band. Anterior band curves down to limiting device at base of pleural spine. Articulating devices consist of short, forwardly-facing anterior flange which bears node-like axial process below axial furrow. Posterior flange, very short, outlined dorsally by faint flange furrow which, below axial furrow, is notched to form axial socket. Dorsal surface of segments bald, except for few scattered granules on steep anterior and posterior flanks and in articulating furrow. On interior a pair of short, downwardly and inwardly directed appendifers arise from distal ends of articulating furrow.

Pygidium roughly triangular in outline; width (tr.)

slightly greater than length (sag.); highly vaulted (tr.); in lateral view pygidial crest descends gradually from nearly horizontal at anterior margin to nearly vertical at posterior margin. Axis conical, twice as long (sag.) as wide (tr.) at anterior margin; moderately convex at anteriorly, slightly wider than 1/3rd total width (tr.) of pygidium; consists of 17-19 convex (sag.) rings which become narrower (tr.) posteriorly; rings separated by short and deeply incised ring furrows which are complete anteriorly and become progressively shallower medially towards rear. Axial furrows straight, convergent posteriorly; initially deep, become shallower towards axial tip. 7 pairs of pleural ribs separated by deep, concave interpleural furrows; first 4 pairs curve outwards and downwards to terminate as progressively shorter, blunt free spines; next 2 pairs shorter, sub-parallel with sagittal line, conjoined distally into blunt, posterior thickening; 7th pair very short, V-shaped, does not extend to posterior margin, bounds very small, triangular post-axial piece. Dorsal surface essentially smooth; anterior axial rings and pleural furrows contain a few scattered granules; tips of pleural spines and doublure finely and densely granulated; minute pits, often paired, occur on axial rings. Pygidial doublure V-shaped, convex (exsag.). Dorsal topography impressed on interior; single pair of small appendifers occur at distal ends of articulating furrow.

Discussion: The mushroom-shaped glabella of Encrin-

uroides rarus (Walcott),outlined laterally by deep and forwardly flaring axial furrows, and possessing tubercular ornament mainly on the anterior lobe appears unique. The type species, *E. sexacostata* (Salter) described by Whittington (1950) and four species from the Middle Ordovician of the Girvan area (*E. autochthon* Tripp, 1962; *E. obesus* Tripp, 1965; *E. polypleura* Tripp, 1967; and *E. periops* Tripp, 1967) possess evenly tuberculose glabellae which are bounded by straight or slightly flaring axial furrows. The eyes of most of these species stand higher than those of *E. rarus* and are commonly basally constricted. *E. insularis* Shaw, 1968 from the Chazy Group of New York has very high pustulose palpebral lobes and a high inflated glabella. *E. capitonis* Frederickson, 1964 (Shaw, 1974) from the Bromide Group of Oklahoma is rather similar to *E. insularis*, but has lower palpebral lobes. It differs from the Esbataottine *E. rarus* in possessing a posteriorly attenuate hypostome, evenly tuberculose glabella, and shorter glabellar furrows. *E. waigatschensis* Burskyi, 1966 has a very broad pygidium with 9 or 10 pleural ribs. *Encrinuroides zhenxiongensis* Sheng, 1964 has four pairs of glabellar furrows and should be assigned to *Encrinuraspis* Webby, Moors and McLean (Webby, 1974).

The holotype cranidium of *Encrinuroides rarus* (Pl. 19, fig. 6) from the Platteville Group of Wisconsin differs slightly from the Nahanni River material in possessing an anterior glabellar lobe that is slightly longer. Two additional cranidia of *E. rarus* from the Platteville Group, illustrated by DeMott (1963, Pl. 11, figs. 13-19) appear identical to the present material.

The Platteville Group of Wisconsin is probably late Blackriveran to, possibly, Rocklandian in age (DeMott, 1963; Sweet <u>et al</u>, 1971, p. 176). Within the study area, <u>E. rarus</u> has a considerably longer, and largely older, range of late Chazyan to (?) Rocklandian.

Subfamily Cybelinae Holliday, 1942

Genus *Cybeloides* Slocum, 1913

Type species: *Cybeloides iowensis* Slocum, 1913 from the Maquoketa Group of Iowa.

Cybeloides cimelia Chatterton and Ludvigsen, ms.

Pl. 27, figs. 1-43, Pl. 28, fig. 1-41

Cybeloides sp., NORFORD, 1962, Pl. 4, fig. 2.

Cybeloides cf. *prima* (Raymond), LUDVIGSEN, 1975, Pl. 3, figs. 18, 19, Pl. 4, figs. 5, 6.

Diagnosis: A species of *Cybeloides* with a subcircular glabella modified anteriorly by a triangular extension which terminates at a pair of tubercles on anterior margin, relatively deep and forwardly-flaring longitudinal glabellar furrows, and swollen lateral tricomposite lobes that lack tubercles. Glabellar tubercles largely restricted to six pairs on median lobe.

Occurrence: Esbataottine Formation, Sunblood Range (A 110, A 125, A 140, A 147, A 365, A 385, P 1440, P 1485, P 1497, P 1512, P 1785, P 2010, P 2038, P 2050, GSC loc. 32936) and Flood Creek (G 3195); upper Sunblood Formation, Mary Range (B 1510-1520). *Ceraurinella nahanniensis* Zone, *Bathyurus ulu* Zone, *Ceraurus gabrielsi* Zone, and *Ceraurinella longispina* Zone.

Material: 605 individuals.

Holotype: An incomplete cranidium (UA 1358) from A 125, illustrated on Pl. 27, figs. 7-10.

Description: Cephalon, excluding genal spines, crescentic, moderately vaulted (tr. and sag.). Anterior margin indented medially in anterior view. Glabella sub-circular in outline; modified anteriorly by triangular extension terminating at twin tubercles on anterior margin; slightly longer (sag.) than wide (tr.); defined laterally by deep, outwardly convex axial furrows which terminate abruptly against palpebral ridge; and composed of three lobes separated by two curved, sub-longitudinal, forwardly-diverging furrows, each connecting four apodemal pits (0s, 1s, 2s, 3s). Pre-glabellar furrow not present. Central lobe moderately convex, narrowest between 2s pits; flares slightly posteriorly and markedly anteriorly to maximum width just in front of anterior pits. Longitudinal furrow shallow between 0s and 1s pits, deepest between 2s and 3s, and terminates abruptly in 3s. Lateral tricomposite lobe swollen, composed of confluent lateral glabellar lobes; not as high as central lobe; ovate in outline, twice as long (exsag.) as wide and half as wide as minimum width of central lobe. Axial furrow flares widely out of 0s pit, deepens and becomes parallel with sagittal line opposite 2s; and would continue to deep anterior pit were it not interrupted by palpebral ridge. Occipital ring lenticular in outline, moderately convex; outlined anteriorly by faint, forwardly-convex occipital furrow. Occipital ring slightly narrower (tr.) than maximum width of glabella, projects posteriorly over part of first thoracic segment. Long, slender, upwardly and backwardly curved spine occupies central position. Cheek triangular in outline; cone-shaped with high, stalk-like eye defining apex; antero-lateral and adaxial flanks steeply inclined, postero-lateral and posterior flanks moderately inclined. Palpebral lobe twice as high as long (exsag.), ribbon-like, narrow and slightly convex inwardly (in horizontal plane), vertically oriented behind visual surface; near apex it forms nearly horizontal apron which covers upper edge of visual surface. highest portion of palpebral lobe stands considerably higher than glabella, at about same level as tip of occipital spine (Pl. 27, fig. 7). From base of palpebral lobe, a narrow, convex palpebral ridge proceeds downwards and diagonally inwards to join glabella in front of 3s pit. Eye perched on cylindrical stalk whose base is defined by gradual change in slope from vertical to steeply inclined cheek. Holochroal visual surface slightly curved (tr.) and strongly curved through about 240° in horizontal plane. Base of visual surface not marked by topographic change, but made evident by change in thickness of test and change in surface granulation (Pl. 27, fig. 15). From base of eye, facial suture proceeds diagonally [illegible]ards and forwards, outside of and sub-parallel with palpebral ridge, to a point just lateral to anterior pit from where it curves upwards and then inwards to form rostral suture which bisects a pair of prominent tubercles (Pl. 27, fig. 11). Rostral plate not located, but must be tetragonal in outline with sub-parallel, dorsal and ventral sides (dorsal edge carrying remainder of bisected tubercle pair of cranidium); lateral sides formed by connective suture, straight, ventrally convergent. Posterior branch of facial suture gently curved outwards and backwards, crosses lateral border furrow immediately in front of its connection with posterior border furrow; continues obliquely across lateral border and intersects lateral margin just behind lateral marginal spine. In dorsal view anterior and posterior branches of facial suture approximately defined by straight line terminating at twin tubercles at anterior margin of glabella and oriented at 60° to sagittal line. Lateral and anterior borders continuous, tubular, of constant width from front of glabella to base of genal spines; anteriorly it is confluent with front part of glabella; laterally and antero-laterally it is defined by being sharply raised over internal portion of cheek at lateral border furrow. Posterior part of lateral margin carries short, tapering, slightly curved, downwardly and backwardly directed lateral marginal spine. Posterior margin convex, short (exsag.) and horizontal from axial furrow to area immediately behind eye, then it widens gradually and slopes down to merge with base of genal spine. Posterior border furrow narrow (exsag.), directed perpendicular to sagittal line in dorsal view. Genal spines long (twice length of glabella excluding occipital spine), tapering, slightly flaring with distinct upward curvature (Pl. 27, fig. 5).

Ornament on cephalon consists of ubiquitous fine, even granulation and, for the main part, regularly arranged coarse tubercles, ranging up to 1/3 mm in diameter and crowded with fine granules. A persistent arrangement of five pairs of tubercles stud the central glabellar lobe; first pair smallest, located just in front of occipital furrow; second pair located just forward of 2s pits; third and fourth pair largest, located on either side of line joining anterior pits; fifth pair located on anterior glabellar margin, antero-dorsally directed. One (rarely 2) pair of tubercles flanks central spine on occipital ring and 3 (rarely 2) pairs of tubercles are aligned along antero-lateral margin of glabella. In addition, small unpaired tubercles are scattered on central lobe. Lateral tricomposite lobes lack tubercles. Distinct pit located on sagittal line between third and fourth pair of tubercles. On cheek, an irregular group of widely spaced tubercles surrounds base of eye. In addition to fine granulation, cheek inside border furrow (except palpebral ridge) marked by closely-spaced pits causing fine reticulate to anastomosing pattern. Along a strip defining lateral border furrow and around base of eye, pits are elongate and aligned radially (separating ridges that represent genal caecae?). Lateral, anterior, and distal part of posterior border studded with single row of tubercles.

On interior, occipital doublure extends forward to back of occipital furrow. Lateral and distal parts of posterior pleural doublure faintly convex, reach border furrows. Axial furrows expressed as moderately high, rounded ridges. Apodemal pits appear on interior as high, thin, ventrally-directed spikes and anterior pit as blunt, thorn-like, ventro-medially directed protuberance. Median pit between third and fourth tubercle pair appears as low rounded elevation. Relatively deep pits mark location of tubercles on dorsal surface.

Hypostome tongue-like in outline, length (sag.) slightly less than maximum width (tr.) across anterior wings. Composed of convex, shield-shaped middle body, sharply raised over flat lateral and posterior borders, possessing pair of rather large, but indistinct, maculae. Middle furrow very faint to imperceptible. Lateral border furrows are slight linear depressions at break in slope between margin and middle body. Anterior border furrow shallow, convex forward, deflected around slight median swelling of middle body. Anterior margin convex forward to sub-angular medially, between anterior wings. From broad antennal notch behind anterior wings, lateral margin flares in even curve to point opposite maculae; then curves inwards along path defined by 90° arc of circle. Posterior margin studded by 7 tiny spines (one median spine flanked by 3 pairs). Anterior border oriented at obtuse angle to lateral border, projected distally into anterior wings whose posterior face contains deep pit or slot which, on the anterior face, appears as relatively large, antero-laterally directed, thorn-like wing process. Behind anterior wings, lateral margin folded inwardly into concave, postero-laterally directed antennal notch. Posterior part of doublure of antennal notch drawn out into long, thin posterior wing that extends obliquely backwards and inwards. Posterior part of doublure very narrow; on sagittal line, in front of median spine, small prong extends forward. Antero-median part of middle body and lateral and posterior border of hypostome finely granulate.

Number of thoracic segments unknown (possibly 12 as in _Cybeloides_ _iowensis_ and _C_. _girvanensis_). Anterior segments gently arched, posterior segments progressively narrower (tr.) and more convex. Axis outlined by faint axial furrows, convex; deflected posteriorly in gentle curve so that a straight line approximately defines anterior edge of pleural lobes and articulating half ring, and posterior edge of axis projects beyond posterior edge of pleural lobes over articulating half ring of following segment. Articulating furrow shallow and broad (sag.) with a preannulus medially, narrows and deepens distally into pair of forwardly-diverging slot-like pits located near anterior edge, well inside axial furrows. Pleura divided by moderately deep transverse pleural furrow into two sub-equal and slightly convex (tr.) bands. Posterior pleural band extends distally into tapering, downwardly and slightly backwardly projecting spine. Anterior pleural band extends distally into vertically oriented, forwardly projecting plate which includes a short, thorn-like spine. This plate is, apparently, an accentuated facet that acts as a limiting device. Anteriorly, the posterior pleural spine dominates and the anterior plate and accessory pleural spine is short (tr., in lateral view). Posteriorly, the anterior pleural plate attains about the same length (tr., in lateral view) as the posterior pleural spine, due largely to reduction of posterior pleural spine. On sixth (?) segment (macropleura), pleural furrow does not extend adaxially to axial furrow, and posterior pleural spine greatly lengthened into gradually tapering spine which projects posteriorly a distance equal to, at least, 3 times the width (tr.) of entire segment across axis. Articulating mechanism composed of forwardly-facing anterior flange which extends from inside axial furrow to upper part of vertical plate on anterior band. Tiny, button-like axial process located on this flange below axial furrow. Similar flange, outlined by narrow flange furrow, located on posterior edge of segment. Below axial furrow, this flange is notched to form axial socket. Axial lobe and inner parts of pleurae finely granulose; in addition, a pair (rarely 2) of tubercles flanks sagittal line on axis and 2 or 3 pairs of smaller tubercles located on posterior pleural band. On interior, doublure extends forward to articulating furrow. From base of posterior pleural spine, doublure deflected forward and outward to form lower part of anterior pleural plate.

Pygidium triangular to shield-shaped in outline, length (sag.) slightly greater than maximum width (tr.) at anterior margin; highly convex, height at anterior margin slightly less than length (sag.). Axis moderately convex (tr.)

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slightly wider than 1/3rd width of pygidium at anterior margin, narrows gradually to blunt point at 2/3rd length of pygidium; a faint ridge continues from tip of axis to posterior margin. In lateral view axial crest slopes at about 45°, has slight median sag; post-axial portion slightly steeper. Axial furrows narrow and sharp behind first axial ring which is continuous across axis. Ring furrows numerous (generally 18, rarely as many as 26); evident as narrow (exsag.) notches which extend 1/4th to 1/3rd way across axis. Median part of axis unfurrowed, flanked by 4 or 5 pairs of small tubercles. Four pairs of pleurae. First widest (tr.); divided by moderately deep pleural furrow which separates vertical facet forming antero-lateral margin of pygidium and convex posterior pleural band which curves laterally and posteriorly to terminate as posteriorly-directed, short, tapering free spine. Posterior 4 segments divided by pleural furrows into flat, depressed, and finely pitted anterior pleural bands and higher, rib-like posterior pleural bands. Second posterior pleural band initiated at juncture of first pleural furrow and axial furrow, curves back with slight outward flare (in posterior view), terminates as short, free spine. Third and fourth posterior pleural bands initiated just behind second pair, become progressively narrower and sub-parallel with axial furrows; terminate as very short free spines at posterior margin. Single prominent tubercle, occasionally perforated, located on mid- to upper portion of each posterior pleural band. Entire dorsal surface finely granulated. On interior, narrow (sag.), flat doublure similar in width from front to back.

Discussion: Cybeloides cimelia Chatterton and Ludvigsen is most similar to C. prima (Raymond) from the Chazy Group of New York State (Shaw, 1968, p. 66, Pl. 9, figs. 9-21, Pl. 10, figs. 1-8) from which it differs in lacking tubercles on the lateral tricomposite glabellar lobes and, in general, possessing fewer tubercles on the cephalon; and in possessing longitudinal glabellar furrows that only become slightly shallower between 2s and 3s pits, a longer and more slender occipital spine, and more swollen lateral tricomposite lobes. The pygidia and hypostomes of the two species are extremely similar. C. virginiensis Cooper (1953, p. 31, Pl. 13, figs. 1-14, 18-20) from the Edinburg Limestone of Virginia is even more coarsely tuberculate than C. prima and, apparently, lacks the prominent pair of tubercles on the antero-median glabellar margin that is present in both C. prima and C. cimelia. The type species, C. iowensis Slocum (1913, p. 64, Pl. 16, figs. 1-4; see Whittington, 1965b, Text-fig. 3 for reconstruction of cephalon) from the Maquoketa Formation of Iowa has unstalked eyes placed well forward on cheeks, fairly shallow longitudinal glabellar furrows, and a short blunt occipital spine. C. spinifera Tripp (1954, p. 679, Pl. 4, figs. 6-11) from the Craighead Mudstone of Girvan, Scotland is similar to C. cimelia in possessing deep longitudinal glabellar furrows, swollen tricomposite glabellar lobes, high stalked eyes, and a long tapering occipital spine. It differs from the Nahanni species in possessing an evenly curved anterior glabellar margin and coarsely tuberculose tricomposite lobes. C. terrigena Tripp (1962, p. 25, Pl. 3, figs. 28-34) from the "Confinis" Flags of Girvan lacks an occipital spine and has shallow longitudinal glabellar furrows. C. ella (Raymond and Narraway) from the Trenton Group possesses a wide median glabellar lobe and narrow tricomposite lobes. C. girvanensis (Reed) and C. loveni (Linnarsson) from the Ashgillian of Britain and Sweden differ markedly from C. cimelia in possessing faint longitudinal glabellar furrows and slot-like glabellar pits, in lacking a long occipital spine, and in possessing long free pygidial spines (Ingham, 1968).

Cybeloides anna n. sp.

Pl. 26, figs. 15-36

Diagnosis: A species of Cybeloides with a parallel-sided glabella of pentagonal outline, obliquely-disposed and slot-like apodemal pits, and moderately inflated lateral tricomposite lobes whose long axes are aligned exsagittally. Glabellar tubercles are large and paired. Median pit on anterior glabellar lobe forms apex of triangle that apparently represents an area of muscle insertion. Lateral cephalic border is broad; lateral marginal spine is short and stout.

Occurrence: Upper Sunblood Formation, Sunblood Range (P 1187), Bathyurus granulosus Zone.

Material: 37 individuals.

Holotype: An incomplete cranidium (RL 0446) from P 1187 illustrated on Pl. 26, figs. 15, 16, 28.

Discussion: From *Cybeloides prima* Raymond, *C. virginiensis* Cooper, and *C. spinifera* Tripp; *C. anna* n. sp. differs in possessing a parallel-sided glabella with exsagittally-oriented lateral tricomposite lobes that lack tubercles and sparser and, for the main part, paired tubercles on the median glabellar lobe. Differences with *C. iowensis* Slocum, *C. terrigena* Tripp, *C. ella* (Raymond and Narraway), *C. girvanensis* (Reed), and *C. loveni* (Linnarsson) are covered in the discussion of *C. cimelia*. *Cybeloides anna* is most similar to *C. cimelia* from which it differs in a few persistent characters. The axial furrows of *C. anna* flare only slightly from the distal end of the occipital furrow and the glabella is parallel-sided and pentagonal in shape. The longitudinal glabellar furrows are very shallow between 2s and 3s pits and the lateral tricomposite lobes are moderately inflated and exsagittally directed. The pit on the median part of the anterior glabellar lobe is located just behind a line joining the anterior tubercle pair. The lateral marginal spine is short and stout. In *C. cimelia*, the axial furrows flare widely from the distal end of the occipital furrow resulting in a sub-circular glabella. The longitudinal furrows are deep and the lateral tricomposite lobes are swollen and their long axes diverge slightly forward. The pit on the anterior part of the median glabellar lobe is located at the intersection of lines joining the anterior two tubercle pairs. The lateral marginal spine is relatively long and gently curving.

The prominent pit located on the mid-point of the anterior lobe of most species of Cybeloides has been judged to be a point of muscle attachment (Tripp, 1954, p. 681). This interpretation receives support from additional features associated with the anterior pit in C. anna (Pl. 26, fig. 28). In this species the pit forms the right-angled apex of an equilateral triangle whose base is approximately defined by two widely-spaced tubercles located on the anterior margin. These tubercles are shared with the rostral plate (Pl. 26, fig. 30) and, thus, they define the width of the rostral suture. The equal sides of the triangle are faintly excavated into the fine granulose ornament as very narrow and bald furrows. The area enclosed by the triangle possesses fine, elongate pits. This pitting is better expressed on the interior (Pl. 26, fig. 36) where it appears as a triangular cluster of small shallow depressions. Analogous muscle insertion patterns are seen in many genera of the Phacopina (Eldredge, 1971), in Ceraurus (Evitt, 1953), and in Ceraurus and Whittakerites (this thesis). In the latter genera the outline of the pattern is an anteriorly-pointing triangle, while in Cybeloides (and in the Phacopina) the triangle points towards the posterior. If these patterns reflect attachment of muscles that support the anterior portion of the digestive tract (Eldredge, 1971) then a change in the outline of the muscle insertion patterns should signify a change in the visceral organization and, presumably, different feeding habits.

The species is affectionately dedicated to my mother, Anna Ludvigsen.

Genus *Cybellela* Reed, 1928

Type species: *Zethus rex* Nieszkowski, 1857 from the Middle Ordovician of Estonia.

Discussion: Whittington (1965b) upheld the validity of *Cybellela* - a taxon which Öpik (1937) regarded as a subgenus of *Cybele* Loven and Henningsmoen (in Moore, 1959) considered a junior synonym of *Atractopyge* Hawle and Corda. Recently, Dean (1971a) redescribed the type species of *Atractopyge*, *A. verrucosa* (Dalman), and suggested that some of the species assigned to *Cybellela* by Whittington (1965b), including *C. dentata* (Esmark) and *C. aspera* (Linnarsson), should probably be assigned to *Atractopyge*. A decision on the validity of *Cybellela* must be postponed until the type species is redescribed.

Cybellela? *thor* n. sp.

Pl. 26, figs. 1-14

?*Paracybeloides* sp., NORFORD, in Gabrielse *et al*., 1973, p. 57.

Diagnosis: A species of *Cybellela*? with parallel-sided glabella of pentagonal outline, three pairs of deep, slit-like lateral glabellar furrows which do not reach axial furrow, and faint pre-glabellar furrow. Lateral glabellar lobes short (exsag.), faintly inflated. Palpebral lobes high; palpebral ridge distinct. Occipital ring carries short, asymmetrical, hammer-shaped spine. Pygidium high, short (sag.); includes four pairs of pleurae axis traversed by only one ring.

Occurrence: An unknown horizon within the Sunblood Formation about 10 km southwest of Section P. GSC loc. 58678 (61° 41' N, 126° 04' W). Associated with *C.*? *thor* in this collection is a species of *Calyptaulax* that is similar to *C. incepta* Whittington from the lower Table Head Formation of Newfoundland. The occurrence of *C.*? *thor* in the Sunblood Formation in this area indicates a Chazyan or earlier age; the co-occurrence with *C.* cf. *incepta* suggests a probable Whiterockian age.

Material: 11 individuals.

Holotype: An incomplete cranidium (RL 0374) from GSC loc. 58678 illustrated on Pl. 26, figs. 1-3.

Description: Cranidium crescentic in outline, about 2 1/2 times as wide as long (sag.); moderately vaulted (tr.); front margin defined by very narrow evenly curved pre-glabellar furrow. Pre-glabellar field very narrow on lateral flanks, slightly wider medially where it is composed of a row of 3 large tubercles. Lateral furrows deep slits; 1s furrow approximately transverse, 2s and 3s increasingly obliquely disposed. Furrows terminate slightly adaxially to axial furrow; a thin (tr.), faintly inflated "incipient lateral tricomposite lobe" defined by abaxial tips of glabellar furrows and shallow axial furrow. Lateral glabellar lobes short (exsag.), rectangular to rhomboid in outline; confluent with "tricomposite lobe"; stand lower than inflated median glabellar lobe. Anterior lobe long (sag.), diamond-shaped; includes a prominent pit at midpoint. Occipital ring lenticular in outline, arched, as wide (tr.) as glabella in front of occipital furrow; midportion extended dorsally [illegible] stout, broad-based, slightly curving spine which, distally, flares into a pair of knoblike terminations which may be unequally developed (Pl. 26, fig. 8) or may comprise 3 knobs (Pl. 26, fig. 6). Occipital furrow moderately shallow and forwardly curving behind median glabellar lobe; descends distally into deep, transversely disposed pits behind lp lobe. Fixed cheek moderately vaulted (tr.), but convexity appears greater due to highly elevated palpebral lobe located opposite 2s furrow. Palpebral lobe oval in outline, slopes inwardly; stands considerably higher than glabella. Narrow palpebral ridge descends palpebral lobe and runs obliquely forward to join glabella just in front of 3s furrow immediately behind shallow anterior pit. Anterior branch of facial suture parallels course of palpebral ridge, passes front edge of anterior pit, and parallels lateral part of faint pre-glabellar furrow. In dorsal view, entire path of suture from palpebral lobe to juncture with connective suture defined by straight line. Posterior branch of facial suture swings outwards with gentle forward curvature. Posterior border furrow narrow, transversely directed outwards from distal end of occipital furrow. Nature of genal angle not known. Free cheek similar to that described from Cybeloides cimelia with the exception that the lateral marginal spine is shorter and the tubercles on the lateral and anterior border are more numerous.

Ornament consists of pervasive, fine, even granulation. In addition, scattered tubercles, which rarely are perforated, occur on anterior glabellar lobe and on median lobe as 3 or 4 tubercle pairs. Irregular group of 7-8 tubercles surround eye. Three distinct tubercles occur on median part of strip-like pre-glabellar field.

On interior, lateral glabellar furrows and corresponding part of occipital furrow expressed as moderately high, plate-like apodemes. Anterior pit on its anterior face. Occipital doublure extends nearly to occipital furrow.

Pygidium shield-shaped in outline, height about equal to width (tr.) and 1 1/2 times length (sag.). Axis slightly convex, about 1/3rd width of pygidium; narrows very gradually to blunt termination at about 2/3rds pygidial length. In lateral view crest of axis slopes at 45°, post-axial field descends nearly vertically to margin. Axis outlined by shallow axial furrows and is composed of single, short (sag.), band-like axial ring followed by about 13 ring furrows which are evident as closely-spaced notches on lateral flanks of axis. Each of 4 pleura divided by a pleural furrow into a depressed anterior and pitted pleural band carrying a faint accessory rib and into a convex, rib-like posterior pleural band which curves downwards and backwards to terminate as sharp, hollow, backwardly-directed free spines immediately above margin. Entire pygidium finely granulose. 4 or 5 pairs of small tubercles flank sagittal line on axis. Larger and often perforated tubercles occur on posterior pleural bands generally a single tubercle located on upper part of each band.

Discussion: *Cybellela*? *thor* n. sp. is herein viewed as a taxon that spans the morphological gulf between *Atractopyge* and *Cybellela* on one hand and *Cybeloides* on the the other. With *Atractopyge* and *Cybellela* it shares a common glabellar, cranidial, and pygidial outline, but many morphological deviations from these two genera points to close affinity with *Cybeloides*. The following features distinguish *C.*? *thor* from the *Atractopyge*/*Cybellela* group of species and, at the same time, ally it to *Cybeloides*:

1. The pre-glabellar furrow is very faint. The pre-glabellar field is narrow (tr.) and short (sag.) and is only obvious medially where it is occupied by three tubercles. *Atractopyge* and *Cybellela* have complete pre-glabellar furrows and relatively long (sag.) pre-glabellar field. *Cybeloides* has neither. A progression involving the tubercle number at the antero-median cranidial margin presents itself. *Atractopyge*/*Cybellela* have many spine-like tuber-

cles on the anterior margin; C.? thor has three; Cybeloides anna has three or two; Cybeloides cimelia, C. prima, and C. iowensis have two; and C. girvanensis and C. loveni have one. Whether this sequence is phylogenetically based remains to be proven. Fewer tubercles on the anterior margin seem to denote successively younger species.

2. The lateral glabellar furrows terminate before reaching the axial furrow isolating an "incipient lateral tricomposite lobe". In species of the Atractopyge/Cybellela group, the lateral glabellar furrows typically reach the axial furrow. In Cybeloides the lateral glabellar furrows are reduced to apodemal pits and the lateral tricomposite lobe is isolated and swollen.

3. The tubercular ornament is sparser than that seen on most species of Atractopyge and, on the median lobe, is reduced to three or four tubercle pairs. The arrangement of paired tubercles is similar to that seen on many species of Cybeloides and Cybellela.

4. A prominent pit is present at the mid-point of the anterior lobe. A similar pit is seen on most species of Cybeloides, but it has not been noted in the Atractopyge/Cybellela group of species.

5. The occipital ring carries a moderately high and stout spine. To my knowledge an occipital spine is not present in any species of the Atractopyge/Cybellela group, but is common in many species of Cybeloides in the Middle Ordovician. It appears to be secondarily reduced in such

Late Ordovician species as C. iowensis, C. girvanensis, and C. loveni.

6. The pygidium is similar to both of the generic groups being compared, but differs from the Atractopyge/Cybellela group in that the axis is traversed by only a single ring - a feature that it shares with all described species of Cybeloides.

In northern Europe, species of the Atractopyge/Cybellela group range from strata of Llanvirnian to Ashgillian age (Whittington, 1965b; Dean, 1971a), but a pygidium from the Glaukonitkalk (Arenigian) has also been assigned to Atractopyge (Neben and Krueger, 1971). With the exception of A. condylosa Dean, 1971b from Newfoundland, species of this group have not been previously described from North America. Species of Cybeloides have an age range of Chazyan to Richmondian in North America and late Caradocian to Ashgillian in Britain (Ingham, 1968); if one disregards the occurrences in the Girvan area (Tripp, 1954, 1962) which must be considered part of the Ordovician "North America".

Unfortunately, the age of Cybellela? thor is not exactly known. It is definitely of Chazyan or earlier age and probably of Whiterockian age. In other words, the species is an approximate contemporary of the earliest species of the Atractopyge/Cybellela group and older than any species of Cybeloides. It is here suggested that C.? thor was derived from, or shared a common ancestor with, the Atractopyge/Cybellela group and that it served as an ancestor to Cybeloides.

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Plate 1

Figs. 1-46	Bathyurus granulosus n. sp. Upper Sunblood Formation, Mary Range and Sunblood Range.
1-3	Dorsal, lateral, and anterior views of incomplete cranidium, Holotype, GSC 40336, X 3.8, P 1090.
4	Dorsal view of incomplete cranidium, RL 0287, X 3.8, P 1090.
5,6	Lateral and dorsal views of large incomplete cranidium, RL 1018, X 2.4, P 1090.
7,8	Lateral and dorsal views of incomplete cranidium, RL 1011, X 4, B 1315.
9	Dorsal view of incomplete cranidium, GSC 40339, X 3, B 1315.
10	Ventral view of cranidium, RL 1013, X 4.3, B 1315.
11	Dorsal view of small cranidium, RL 1022, X 6.6, P 1090.
12,14	Anterior and dorsal views of cranidium, RL 0398, X 3.6, B 1315.
13	Dorsal view of cranidium, RL 1014, X 5.5, B 1315.
15	Ventral view of cranidium, RL 0294, X 3, B 1265.
16,17	Anterior and dorsal views of cranidium, RL 0293, X 3, B 1265.
18,24	Detail of axial region and dorsal view of pygidium, RL 0401, X 8 and 2, B 1315.
19,20	Dorsal and lateral views of large pygidium, RL 1012, X 3.5, B 1315.
21	Dorsal view of pygidium, RL 1019, X 5.6, P 1090.
22,23	Dorsal and lateral views of pygidium, GSC 40338, X 3.6, P 1090.
25	Ventral view of pygidium, RL 0402, X 3, B 1315.
26	Ventral view of pygidium, RL 1016, X 4.1, B 1315.
27	Dorsal view of pygidium, RL 0299, X 4, P 1127.
28	Ventral view of pygidium, RL 0289, X 3.5, P 1090.
29	Ventral view of pygidium, RL 1021, X 5, P 1090.
30,31	Dorsal and lateral views of pygidium, RL 0298, X 4, P 1127.
32	Ventral view of pygidium, RL 0300, X 4, P 1127.
33	Dorsal view of pygidium, RL 0295, X 3, B 1265.
34	Ventral view of pygidium, RL 0296, X 3, B 1265.
35	Ventral view of hypostome, RL 0404, X 3.3, B 1315.
36	Ventral view of hypostome, RL 0301, X 4, P 1127.
37	Ventral view of hypostome, specimen broken after photography (inadvertently assigned type number GSC 40337, Ludvigsen, 1975), X 4, P 1090.

38 Ventral view of hypostome, RL 0403, X 3.1, B 1315.
39 Ventral view of hypostome, RL 1017, X 4.3, B 1315.
40 Ventral view of hypostome, RL 0290, X 3.8, P 1090.
41 Dorsal view of free cheek, RL 0405, X 2, B 1315.
42 Interior view of free cheek, RL 1015, X 3.6, B 1315.
43 Interior view of free cheek, RL 0291, X 3.7, P 1090.
44 Lateral view of free cheek, RL 1024, X 5.2, P 1090.
45,46 Lateral and dorsal views of free cheek, RL 0292, X 3.7, P 1090.

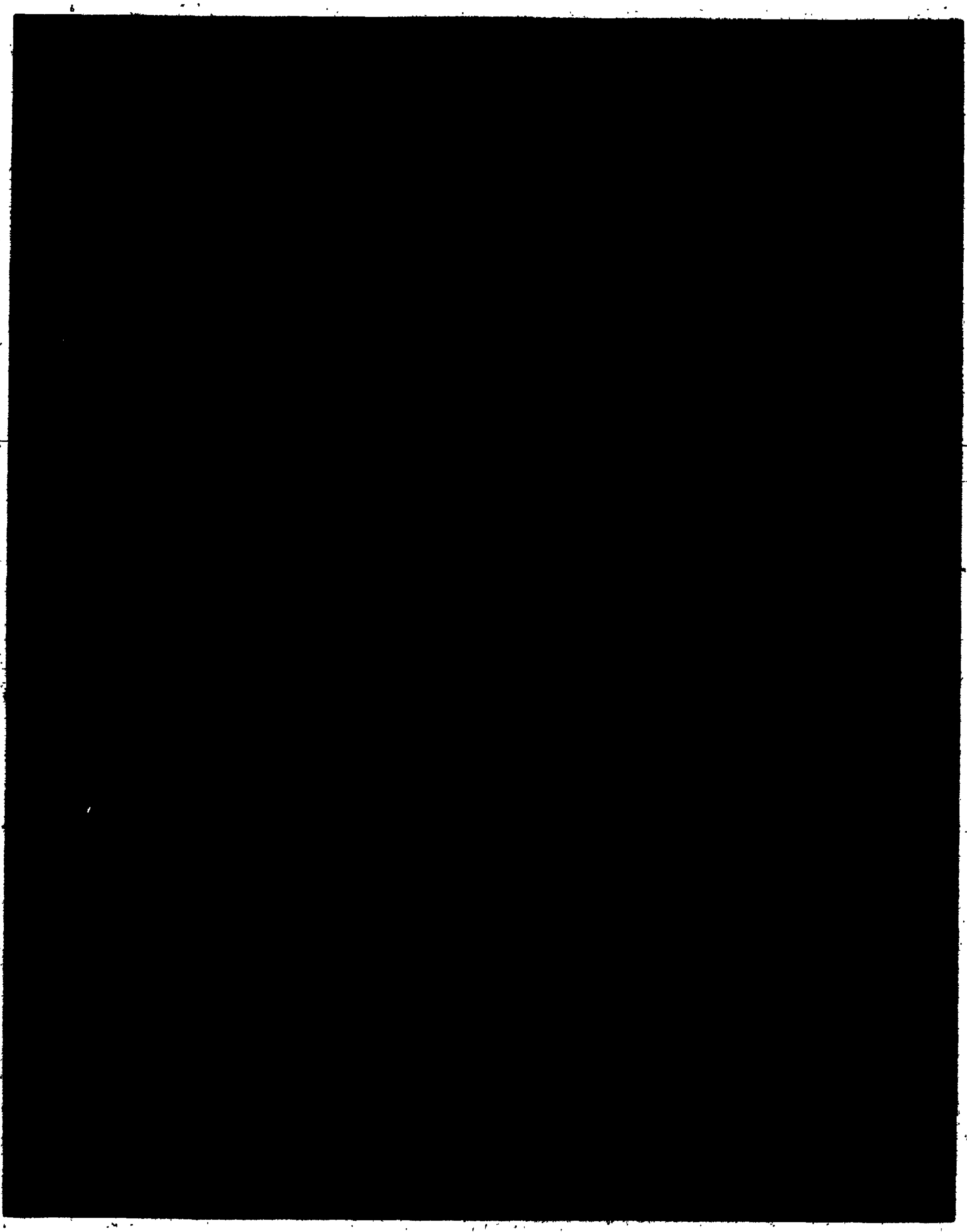

Plate 1

Plate 2

Figs. 1-53	<u>Bathyurus</u> <u>ulu</u> n. sp. Lower Esbataottine Formation, Sunblood Range. Figs. 37-45 from P 1595; the remainder from A 220.
1-3	Dorsal, lateral, and anterior views of cranidium, Holotype, RL 0201, X 3.2.
4,5	Dorsal and lateral views of pygidium, RL 0988, X 3.
6	Ventral view of cranidium, RL 0202, X 3.2.
7-9,33	Dorsal, lateral, and posterior views of pygidium, RL 0205, X 3.3, and 6.8.
10,11	Dorsal and anterior views of small cranidium, RL 0203, X 5.
12,13	Ventral and anterior view of rostral plate, RL 0212, X 4.
14	Dorsal view of cranidium, RL 0987, X 4.1.
15	Dorsal view of rostral plate, RL 0213, X 4.
16	Dorsal view of pygidium, RL 0208, X 4.
17	Dorsal view of small (meraspid?) pygidium, RL 0209, X 5.
18	Ventral view of pygidium, RL 0990, X 3.6.
19	Ventral view of pygidium, RL 0207, X 2.5.
20,21	Oblique anterior and dorsal views of cranidium, RL 0986, X 4.1.
22	Dorsal view of small cranidium, RL 0204, X 5.
23	Dorsal view of small cranidium, RL 0206, X 5.
24-26	Lateral, posterior, and ventral views of hypostome, RL 0210, X 4.4.
27	Ventral view of hypostome, RL 0991, X 5.7.
28-30	Dorsal, anterior, and oblique lateral views of hypostome, RL 0211, X 4.4.
31	Ventral view of hypostome, RL 0993, X 6.6.
32	Ventral view of small hypostome, RL 0994, X 6.6.
34	Dorsal view of two thoracic segments, RL 0995, X 5.7.
35,36	Ventral view of two thoracic segments, RL 0555, X 3.5, and 7.
37	Dorsal view of incomplete cranidium, RL 0381, X 4.
38	Dorsal view of incomplete cranidium, RL 1030, X 3.7.
39	Dorsal view of pygidium, RL 1031, X 3.7.
40	Dorsal view of pygidium, RL 0382, X 4.
41	Dorsal view of free cheek, RL 0384, X 4.
42	Interior view of free cheek, RL 1033, X 2.6.
43	Ventral view of rostral plate, RL 1034, X 3.7.
44	Ventral view of hypostome, RL 1032, X 3.7.
45	Ventral view of hypostome, RL 0383, X 4.
46,52	Lateral and dorsal views of free cheek, RL 0989, X 3.3.
47,50,51	Lateral, dorsal, and anterior views of free cheek, RL 0215, X 2.8.

48 Interior view of free cheek, RL 0992, X 4.1.
49 Interior view of free cheek, RL 0214, X 3.
53 Dorsal view of thoracic segment, RL 0556, X 5.7.

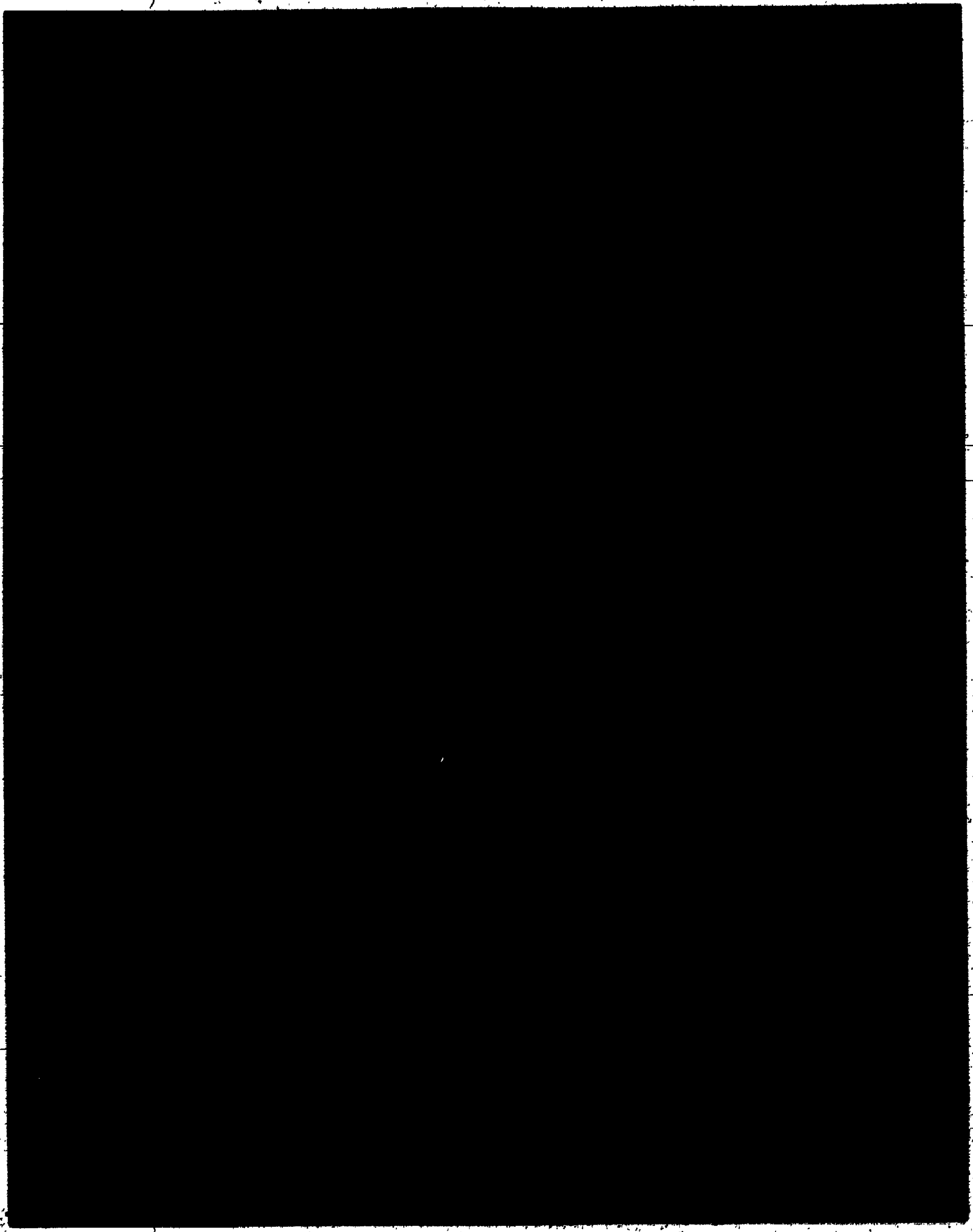

Plate 2

Plate 5

Figs. 1-48	Bathyurus esbataottinensis n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 1931.
1-3	Dorsal, anterior, and lateral views of cranidium, Holotype, GSC 40431, X 3.1.
4,5	Ventral view of cranidium, RL 0158, X 3.1, and 6.2.
6	Dorsal view of cranidium, RL 0973, X 3.6.
7	Dorsal view of cranidium, RL 0972, X 3.4.
8	Ventral view of pygidium, RL 0163, X 2.7.
9	Dorsal view of pygidium, RL 0976, X 3.4.
10,11	Lateral and dorsal views of pygidium and seven attached thoracic segments, RL 0165, X 2.7.
12	Dorsal view of cranidium, RL 0159, X 3.8.
13-15	Dorsal, lateral and posterior views of pygidium, GSC 40432, X 2.5.
16	Dorsal view of small cranidium, RL 0160, X 3.8.
17	Dorsal view of small cranidium, RL 0161. X 4.
18	Dorsal view of small pygidium, RL 0163a, X 3.1.
19	Dorsal view of small pygidium, RL 0164, X 3.1.
20	Dorsal view of large incomplete pygidium, RL 0162a, X 1.3.
21	Ventral view of cranidium, RL 0974, X 3.6.
22	Dorsal view of rostral plate, RL 0167, X 2.6.
23-26	Anterior and ventral views of rostral plate, RL 0166, X 2.6, and 6.5.
27,28	Ventral and lateral views of hypostome, RL 0975, X 3.6.
29,30	Ventral and lateral views of hypostome, RL 0169, X 2.8.
31-35	Oblique lateral, ventral, lateral, dorsal, and anterior views of hypostome with attached rostral plate, GSC 40434, X 4.7.
36-39	Oblique lateral, dorsal, anterior, and posterior views of hypostome, RL 0168, X 4.5.
40	Interior view of free cheek, RL 0171, X 2.5.
41,42	Dorsal and lateral views of free cheek with preserved visual surfaces of eye, RL 0977, X 5.5.
43,44	Dorsal and lateral views of free cheek, GSC 40433, X 3.
45,46	Ventral and posterior views of thoracic segment, RL 0173, X 3.4.
47,48	Dorsal and anterior views of thoracic segment, RL 0172, X 4.

Plate 3

Plate 4

Figs. 1-26 <u>Bathyurus esbataottinensis</u> n. sp. Upper Esbataottine Formation, Sunblood Range and Whittaker Range and Sunblood Formation, Natla River.

1 Dorsal view of pygidium and seven attached thoracic segments, RL 0165, X 6.3, P 1931 (same specimen as Pl. 3, figs. 10, 11).

2 Dorsal view of cranidium, Holotype, GSC 40431, X 5.3, P 1931. (same specimen as Pl. 3, figs. 1-3).

3 Oblique lateral view of hypostome with attached rostral plate, GSC 40434, X 9.5, P 1931. (same specimen as Pl. 3, figs. 31-35).

4 Dorsal view of cranidium, RL 0366, X 3.6, I 780.

5 Dorsal view of hypostome, RL 0371, X 4.8, I 780.

6 Dorsal view of pygidium, RL 0368, X 4.8, I 780.

7 Dorsal view of cranidium, RL 0367, X 3.6, I 780.

8 Interior view of free cheek, RL 0373, X 4, I 780.

9 Ventral view of hypostome, RL 0370, X 4.8, I 780.

10 Dorsal view of free cheek, RL 0372, X 3.2, I 780.

11 Dorsal view of pygidium, RL 0407, X 4, P 1870.

12 Dorsal view of cranidium, RL 0406, X 3.3, P 1870.

13 Dorsal view of free cheek, RL 0410, X 3.2, P 1870.

14 Ventral view of hypostome, RL 0408, X 3.2, P 1870.

15 Dorsal view of small cranidium, RL 0409, X 4.3, P 1870.

16 Ventral view of pygidium, RL 0369, X 4.8, I 780.

17 Dorsal view of cranidium, RL 0389, X 3.3, P 1945-1955.

18,20 Dorsal view of pygidium and detail to show micro-ornament, RL 0390, X 2.2, and 8.6, P 1945-1955.

19 Dorsal view of pygidium, GSC 40432, X 6.2, P 1931. (same specimen as Pl. 3, figs. 13-15).

21-25 Lateral and dorsal views of pygidium and four thoracic segments, RL 0385, X 1.6, and details to show micro-ornament, X 8, Upper Sunblood Formation, Natla River, GSC loc. 69001.

26 Dorsal view of pygidium, RL 0386, X 1.6, Upper Sunblood Formation, Natla River, GSC loc. 69001.

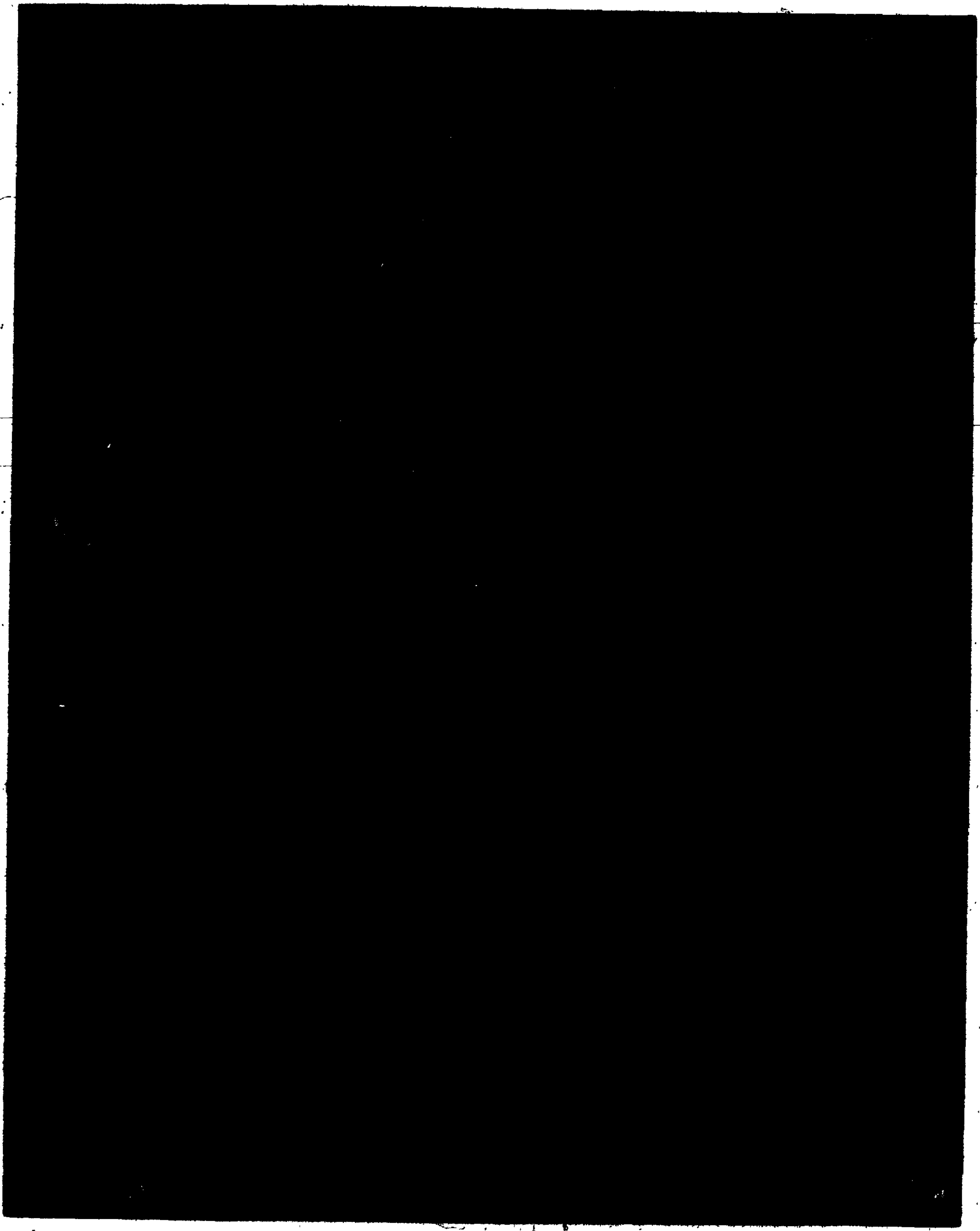

Plate 4

Plate 5

Figs. 1-4 Comparison of cranidial micro-ornament and shape of palpebral areas of four species of *Bathyurus*. Sunblood and Esbataottine Formations.

1 *Bathyurus platyparius* n. sp., Holotype, RL 0354, X 7.8, B 1450 (same specimen on this plate, figs. 11, 12).

2 *Bathyurus granulosus* n. sp., Holotype, GSC 40336, X 9.5, P 1090 (same specimen as Pl. 1, figs. 1-3).

3 *Bathyurus ulu* n. sp., Holotype, RL 0201, X 6.4, A 220 (same specimen as Pl. 2, figs. 1-3).

4 *Bathyurus esbataottinensis* n. sp., Holotype, GSC 40431, X 6.2 (same specimen as Pl. 3, figs. 1-3; Pl. 4, fig. 2).

Figs. 5-10 *Bathyurus extans* (Hall), USNM 306, Lowville Formation, Great Bend, N. Y. Same specimen illustrated by Whittington, 1953, Pl. 65, figs. 6-8, 12.

5-8 Maximum extended dorsal, true dorsal, lateral, and posterior views of complete carapace, X 1.9.

9,10 Oblique lateral and dorsal views of cephalon, X 4.

Figs. 11-24 *Bathyurus platyparius* n. sp. Upper Sunblood Formation, Mary Range and lower Esbataottine Formation, Sunblood Range.

11-12 Anterior and dorsal views of cranidium, Holotype, RL 0354, X 5.3, B 1450.

13 Ventral view of pygidium, RL 0355, X 5.3, B 1450.

14 Ventral view of incomplete cranidium, RL 1025, X 3.5, B 1450.

15 Dorsal view of small cranidium, RL 1027, X 6.3, B 1450.

16,17 Lateral and dorsal views of pygidium, RL 0356, X 4, B 1450.

18 Dorsal view of pygidium, RL 1026, X 3.5, B 1450.

19,20 Anterior and dorsal views of free cheek, RL 0358, X 3.5, B 1450.

21 Dorsal view of free cheek, RL 0659, X 2.5, P 1625.

22 Ventral view of rostral plate, RL 0662, X 5.7, P 1625.

23 Ventral view of hypostome, RL 1028, X 4, B 1450.

24 Ventral view of hypostome, RL 0357, X 4.7, B 1450.

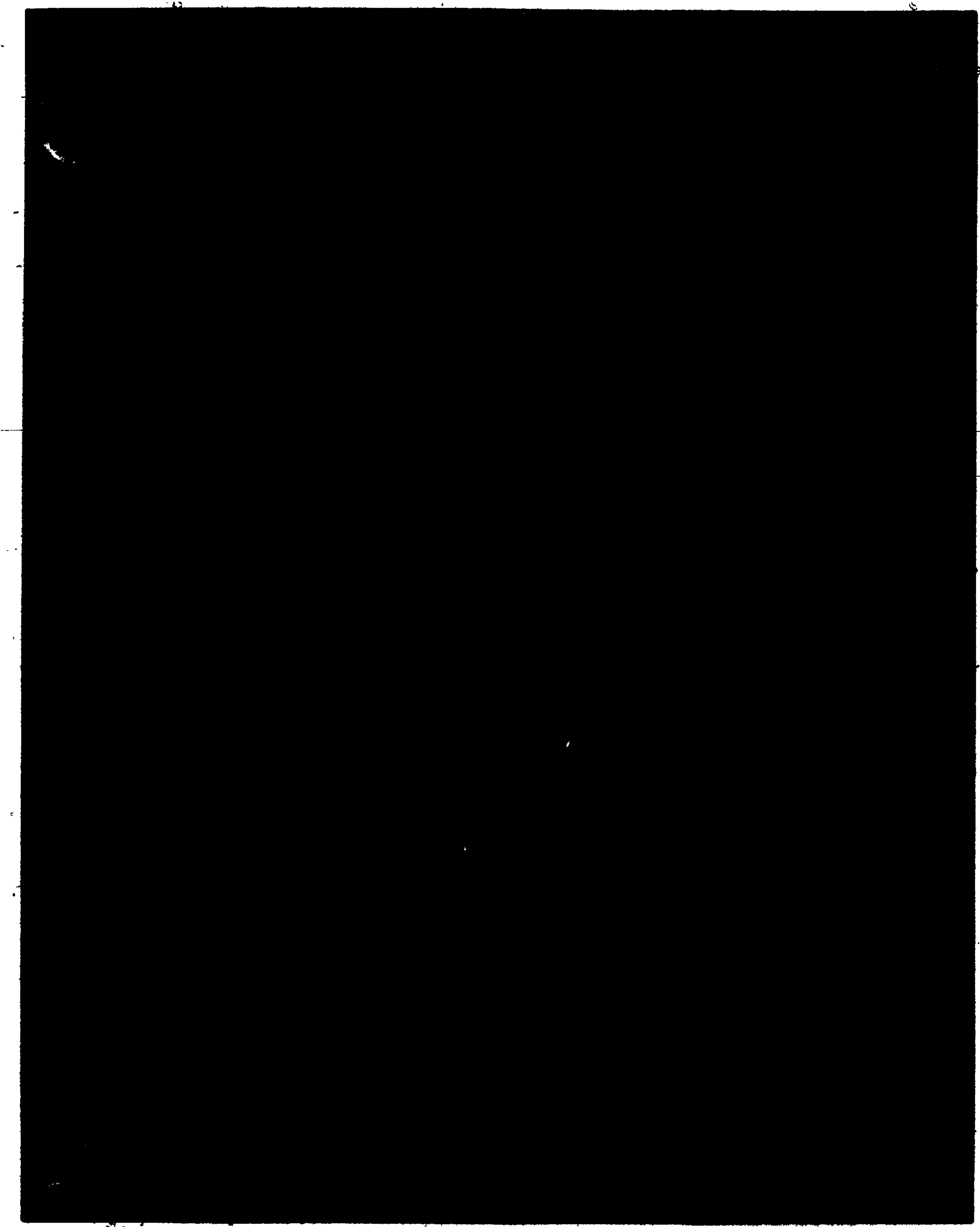

Plate 5

Plate 6

Figs. 1-40	Ceraurinella kingstoni Chatterton and Ludvigsen, ms. Lower Esb[illegible]aottine Formation, Sunblood Range.
1-4	Dorsal, anterior, posterior, and lateral views of cranidium, Holotype, GSC 40382, X 3.1, P 1485.
5	Dorsal view of cranidium, UA 1319, X 5.5, A 115.
6,7	Ventral and oblique ventral views of cranidium, RL 0070, X 3.1, P 1485.
8	Ventral view of rostral plate, RL 0851, X 7.7, P 1485.
9	Dorsal view of rostral plate, RL 0853, X 7.7, P 1485.
10,11	Dorsal and ventral views of cranidium, UA 1320, X 2.4, A 125.
12	Dorsal view of incomplete cephalon, UA 1321, X 5.5, A 115.
13-15	Dorsal, lateral, and posterior views of pygidium, GSC 40383, X 4.5, P 1485.
16,17	Posterior and dorsal views of pygidium, RD 0071, X 4.5, P 1485.
18	Ventral view of pygidium, RL 0073, X 5.4, P 1485.
19	Dorsal view of pygidium, UA 1322, X 5.5, A 115.
20	Dorsal view of pygidium, UA 1323, X 5.5, A 125.
21	Lateral view of pygidium, UA 1324, X 5.5, A 115.
22,23	Posterior and dorsal views of small pygidium, RL 0075, X 5.2, P 1485.
24	Interior view of free cheek, RL 0078, X 3, P 1485.
25	Dorsal view of free cheek, RL 0077, X 3, P 1485.
26,27	Dorsal and oblique interior views of hypostome, RL 0081, X 4.4, P 1485.
28	Ventral view of hypostome, UA 1325, X 5.5, A 115.
29	Dorsal view of thoracic segment, RL 0852, X 6, P 1485.
30	Dorsal view of thoracic segment, RL 0083, X 4, P 1485.
31,32	Ventral and posterior views of hypostome, RL 0080, X 4.3, P 1485.
33,34	Ventral and posterior views of thoracic segment, RL 0084, X 5, P 1485.
35,36	Anterior and dorsal views of thoracic segment, RL 0854, X 4, P 1485.
37,38	Lateral and ventral views of hypostome, RL 0849, X 4, P 1485.
39	Dorsal view of pygidium, UA 1326, X 5.5, A 115.
40	Oblique view of free cheek, UA 1327, X 5.5, A 115.

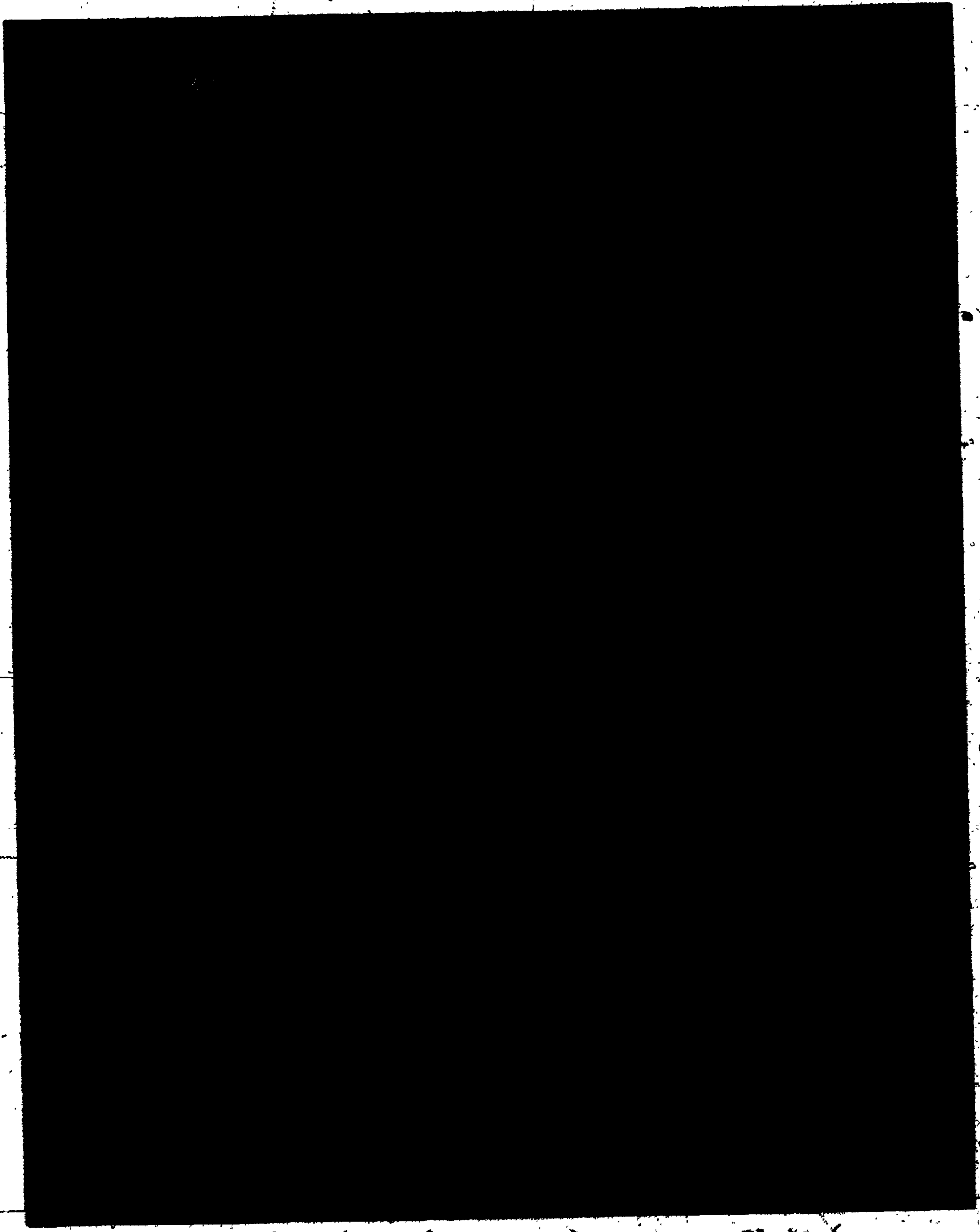

Plate 6

Plate 7

Figs. 1-35 Ceraurinella nahanniensis Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.

1-3 Dorsal, lateral, and anterior views of cranidium, Holotype, GSC 40399, X 4.5, P 1497.
4 Dorsal view of incomplete cephalon and one thoracic segment, UA 1304, X 5.5, A 115.
5 Ventral view of cranidium, RL 0087, X 7.5, P 1497.
6 Dorsal view of incomplete cephalon, UA 1305, X 5.5, A 115.
7 Dorsal view of incomplete cranidium, UA 1306, X 5.5, A 125.
8 Dorsal view of cranidium, UA 1307, X 5.5, A 115.
9 Dorsal view of cranidium, UA 1308, X 5.5, A 115.
10,34 Dorsal and ventral views of enrolled individual lacking pygidium and two (?) thoracic segments. Note displaced free cheeks, UA 1309, X 5.5, and X 7, A 115.
11 Dorsal view of pygidium, GSC 40402, X 7.5, P 1497.
12 Ventral view of pygidium, RL 0092, X 7.5, P 1497.
13,14 Dorsal and posterior views of pygidium, RL 0751, X 7, P 1497.
15 Dorsal view of pygidium, RL 0139, X 4.3, A 125.
16 Oblique dorsal view of hypostome, UA 1311, X 5.5, A 115.
17 Dorsal view of pygidium, UA 1310, X 5.5, A 125.
18 Posterior view of pygidium, UA 1312, X 5.5, A 125.
19 Dorsal view of pygidium, RL 0750, X 7, P 1497.
20 Ventral view of hypostome, UA 1318, X 5.5, A 125.
21 Interior view of free cheek, RL 0099, X 7, P 1497.
22 Ventral view of hypostome, RL 0748, X 7, P 1497.
23,24 Dorsal and oblique views of free cheek, RL 0098, X 4.6, and X 7.3, P 1497.
25 Dorsal view of small cranidium, RL 0090, X 5.2, P 1497.
26 Ventral view of rostral plate, UA 1313, X 7, A 125.
27 Dorsal view of thoracic segment, RL 0100, X 9, P 1497.

28 Ventral view of thoracic segment, RL 0101, X 9, P 1497.

29 Ventral view of thoracic segment, UA 1314, X 5.5, A 115.

30 Dorsal view of thoracic segment, UA 1315, X 5.5, A 115.

31,32 Dorsal and oblique lateral views of hypostome, RL 0749, X 7, P 1497.

33 Dorsal view of incomplete cranidium, UA 1316, X 5.5, A 115.

35 Dorsal view of hypostome, UA 1317, X 5.5, A 115.

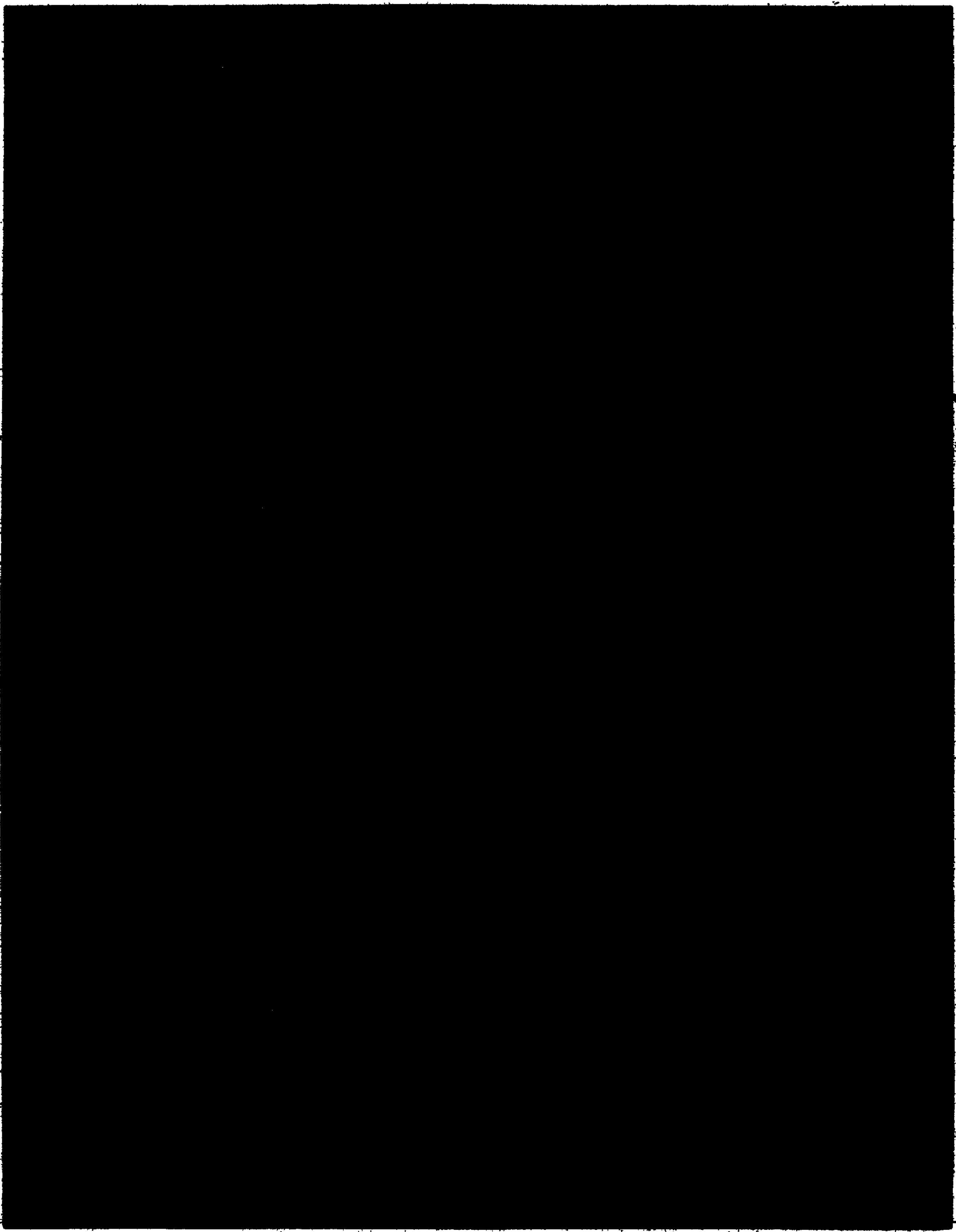

Plate 7

Plate 8

Figs. 1-21	Ceraurinella nahanniensis Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range, all from P 1440.
1-3,19	Dorsal, anterior, and lateral views of incomplete cranidium, RL 0028, X 4 and 8.2.
4,5	Dorsal and oblique anterior views of incomplete cranidium, RL 0029, X 4.2.
6,7	Ventral and oblique anterior views of incomplete cranidium, RL 0030, X 5.
8-10	Dorsal, posterior, and oblique lateral views of pygidium, RL 0032, X 5.
11	Ventral view of incomplete pygidium, RL 0033, X 4.5.
12,13	Dorsal and oblique lateral views of incomplete pygidium, RL 0031, X 5.
14,15	Dorsal and oblique lateral views of hypostome, RL 0035, X 4.7.
16,18	Ventral, lateral, and posterior views of hypostome, RL 0034, X 5.2.
20	Interior view of free cheek, RL 0036, X 3.8.
21	Dorsal view of free cheek, RL 0037, X 4.5.
Figs. 22-42	Ceraurinella seriata n. sp. Lower Esbataottine Formation, Sunblood Range, all from P 1625.
22-24	Dorsal, anterior, and lateral views of incomplete cranidium, RL 0056, X 4.
25	Dorsal view of small incomplete cranidium, RL 0058, X 4.7.
26,27	Dorsal and posterior views of small pygidium, RL 0059, X 5.2.
28,29	Dorsal and posterior views of incomplete pygidium, Holotype, RL 0061, X 4.
30	Dorsal view of thoracic segment, RL 0066, X 4.
31,32	Oblique lateral and dorsal views of hypostome, RL 0067, X 4.
33	Interior view of free cheek, RL 0068, X 4.
34	Dorsal view of free cheek, RL 0065, X 4.
35	Oblique ventral view of incomplete cranidium, RL 0062, X 3.5.
36	Ventral view of small pygidium, RL 0063, X 5.
37	Dorsal view of small pygidium, RL 0060, X 5.2.
38-41	Ventral, lateral, posterior, and anterior views of hypostome, RL 0064, X 4.
42	Dorsal view of incomplete cranidium, RL 0057, X 8.

Figs. 43-58	Ceraurinella media n. sp. Middle Esbataottine Formation, Sunblood Range, all from A 385.
43-45	Dorsal, anterior, and lateral views of incomplete cranidium, Holotype, RL 0121, X 3.1.
46,47	Dorsal and posterior views of pygidium, RL 0125, X 2.7.
48	Dorsal view of free cheek, RL 0129, X 4.5.
49	Ventral view of hypostome, RL 0128, X 4.
50,51	Dorsal and oblique lateral views of hypostome, RL 0127, X 4.
52	Ventral view of incomplete cranidium, RL 0124, X 3.1.

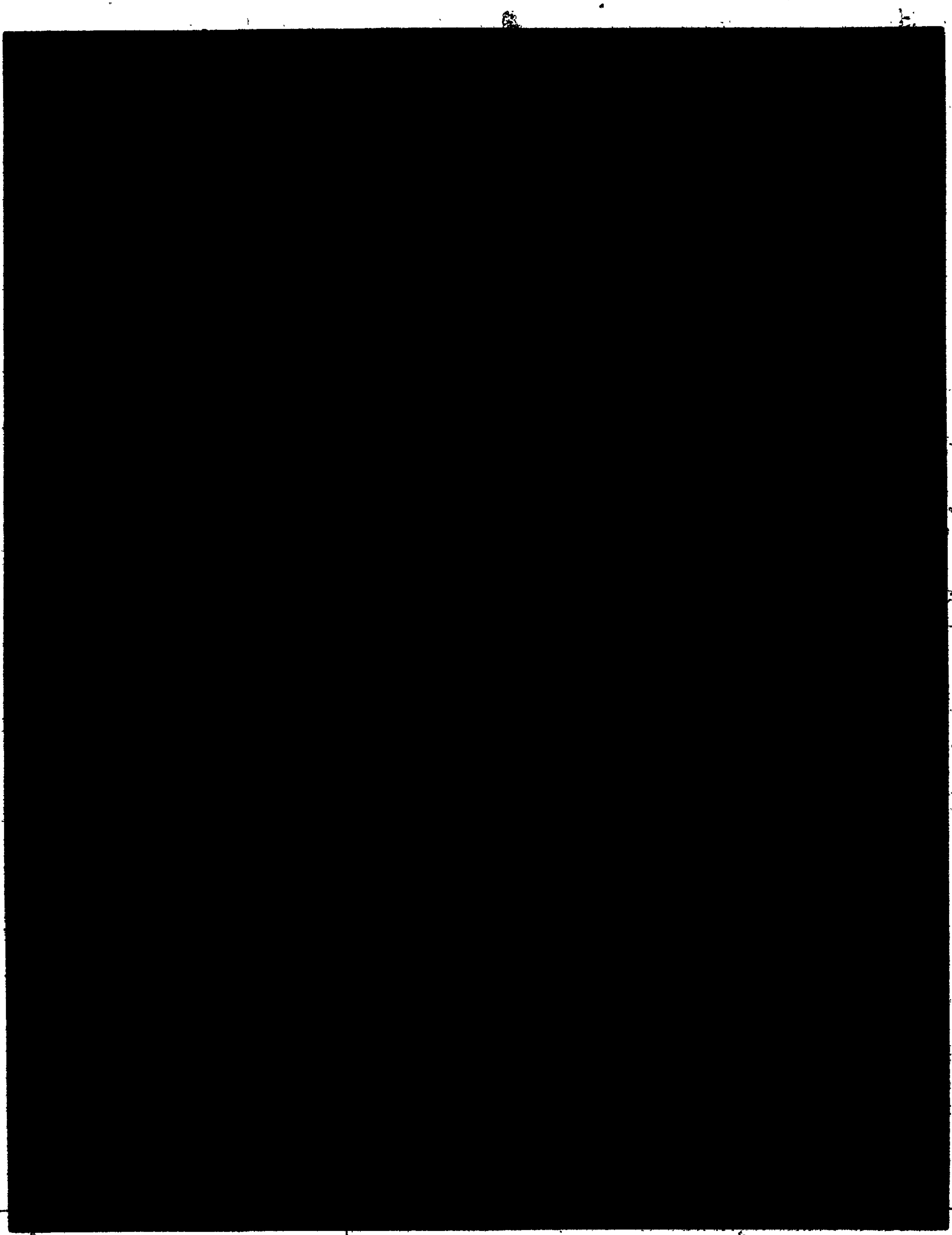

Plate 8

Plate 9

Figs. 1-31	Ceraurinella longispina n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 2038, except figs. 5-8, 17, 18, and 20 which are from A 615.
1-4,31	Dorsal, anterior, oblique posterior, and lateral views of cranidium, Holotype, RL 0011, X 4, and 6.6.
5,6	Dorsal and oblique anterior views of incomplete cranidium, RL 0143, X 5.2.
7,8	Dorsal and anterior views of incomplete cranidium, RL 0144, X 6.
9-11	Posterior, dorsal, and lateral views of pygidium, RL 0016, X 3.8.
12,13	Posterior and dorsal views of large pygidium, RL 0027, X 2.8.
14-16	Dorsal, lateral, and posterior views of pygidium, RL 0141, X 4.
17,18	Dorsal and posterior views of pygidium, GSC 40414, X 6.
19	Ventral view of pygidium, RL 0015, X 3.
20	Ventral view of hypostome, RL 0145, X 7.
21-23	Oblique lateral, dorsal, and posterior views of hypostome, RL 0018, X 5.
24	Lateral view of hypostome, RL 0019, X 5.
25	Ventral view of thoracic segment, RL 0023, X 3.
26,27	Dorsal and posterior views of small pygidium, RL 0014, X 5.3.
28	Oblique dorsal view of free cheek, RL 0022, X 5.
29	Interior view of free cheek, RL 0020, X 5.8.
30	Oblique dorsal view of free cheek, RL 0021, X 5.
Figs. 32-37	Ceraurinella media n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 2038.
32	Dorsal view of cranidium, RL 0013, X 5.
33-35	Dorsal, oblique anterior, and lateral views of incomplete cranidium, RL 0012, X 3.6.
36,37	Ventral and oblique anterior views of incomplete cranidium, RL 0017, X 3.8.

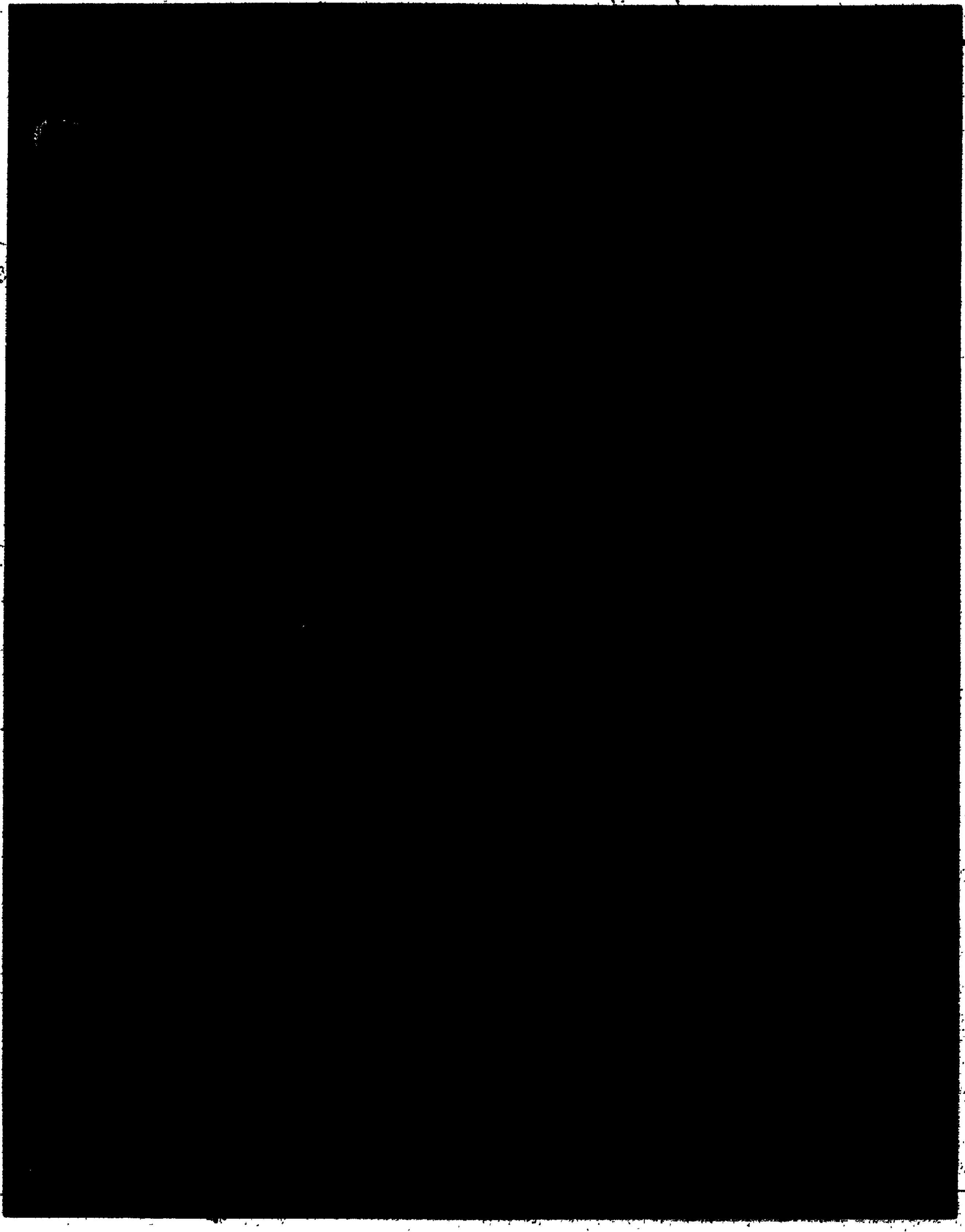

Plate 9

Plate 10

Figs. 1-34	*Ceraurinella arctica* n. sp. Esbataottine and Sunblood Formations, Sunblood Range and Mary Range. All from P 2050 except figs. 10, 11, and 17-19 which are from B 1510-1520.
1-5, 31-34	1-5, Dorsal, ventral, oblique posterior, posterior, and oblique lateral views of complete cephalon with attached hypostome, Holotype, X 3.8. 31, Oblique postero-ventral view showing attachment of hypostome; 32, Ventral view showing lateral doublure; 33, Oblique postero-ventral view showing rostral, hypostomal and connective sutures; 34, Dorsal view showing course of facial suture, X 6.4, Holotype, RL 0001.
6-9	Dorsal, anterior, posterior, and lateral views of cranidium, RL 0003, X 4.2.
10,11	Dorsal and anterior views of cranidium, RL 0132, X 4.5.
12,13	Posterior and ventral view of incomplete thoracic segment, RL 0008, X 2.8.
14-16	Dorsal, posterior, and oblique lateral views of pygidium, RL 0004, X 4.1.
17-19	Dorsal, lateral, and posterior views of pygidium, RL 0133, X 3.5.
20,21	Oblique anterior and ventral views of incomplete cranidium, RL 0002, X 2.8.
22,23	Dorsal and lateral views of incomplete thoracic segment, RL 0009, X 2.8.
24	Ventral view of pygidium, RL 0010, X 4.2.
25	Ventral view of hypostome, RL 0007, X 3.5.
26,27	Ventral and oblique lateral views of hypostome, RL 0006, X 4.7.
28	Interior view of free cheek, RL 0005, X 3.2.
29,30	Dorsal and ventral views of nearly complete specimen, RL 0119, X 8.

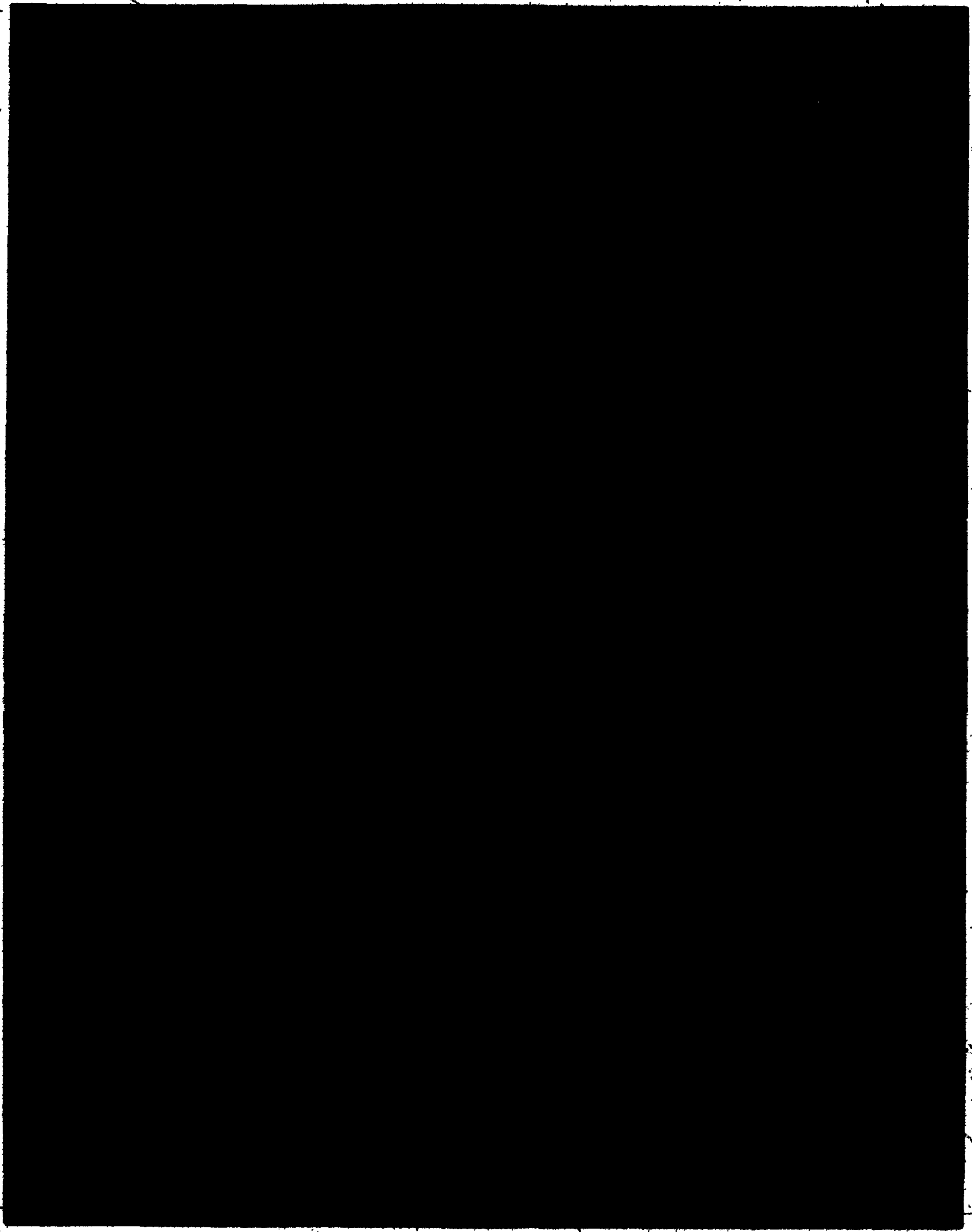

Plate 10

Plate 11

Figs. 1-30	<u>Ceraurinella</u> <u>necra</u> n. sp. Lower Whittaker Formation, Funeral Range, and Whittaker Range.
1-3	Dorsal, anterior, and lateral views of incomplete cranidium, RL 0045, X 4.3; C 570-590.
4,5,30	Dorsal and lateral views of incomplete cranidium, RL 0046, X 4.5, and X 8.6, C 570-590.
6-8	Dorsal, anterior, and lateral views of cranidium, RL 0107, X 4.5, I 1275.
9,10	Dorsal, and posterior views of pygidium, RL 0048, X 4.5, C 570-590.
11-13	Dorsal, posterior, and oblique lateral views of pygidium, Holotype, RL 0047, X 4.3, C 570-590.
14-16	Dorsal, posterior, and lateral views of incomplete pygidium, RL 0110, X 4.5, I 1275.
17	Dorsal view of incomplete cranidium, RL 0108, X 5, I 1275.
18,19	Ventral and oblique anterior views of incomplete cranidium, RL 0049, X 4.7, C 570-590.
20	Dorsal view of small pygidium, RL 0051, X 4.4, C 570-590.
21,22	Anterior and ventral views of pygidium, RL 0050, X 4.5, C 570-590.
23	Dorsal view of free cheek, RL 0055, X 4.5, C 570-590.
24	Interior view of free cheek, RL 0054, X 4.5, C 570-590.
25,26	Lateral and ventral views of hypostome, RL 0111, X 4.5, I 1275.
27	Dorsal view of hypostome, RL 0052, X 4.7, C 570-590.
28,29	Ventral and lateral views of hypostome, RL 0053, X 4.3, C 570-590.
Figs. 31-57	<u>Ceraurinella</u> <u>brevispina</u> n. sp. Lower Whittaker Formation, Funeral Range and Whittaker Range.
31-33	Dorsal, anterior, and lateral views of incomplete cranidium, GSC 40453, X 5, C 655.
34,35	Dorsal and lateral views of incomplete pygidium, RL 0043, X 5, C 655.
36	Ventral view of pygidium, RL 0042, X 5, C 655.
37,38	Dorsal and posterior views of pygidium, GSC 40454, X 5, C 655.
39	Dorsal view of pygidium, RL 0114, X 5, I 1410.
40,41	Posterior and dorsal views of pygidium, RL 0116, X 5.1, I 1590.

42 Ventral view of pygidium, RL 0117, X 5.1, I 1590.

43,44 Dorsal and posterior views of pygidium, RL 0106, X 5.6, Q 530.

45 Ventral view of thoracic segment, RL 0943, X 3.9, C 655.

46 Dorsal view of thoracic segment, RL 0942, X 3.9, C 655.

47,48 Ventral and lateral views of hypostome, RL 0113, X 5, I 1410.

49,50 Anterior and dorsal view of incomplete cranidium, RL 0115, X 5.1, I 1590.

51 Dorsal view of small cranidium, RL 0041, X 5.5, C 655.

52 Dorsal view of incomplete cranidium, RL 0103, X 5, H 1920.

53,54 Ventral and lateral views of hypostome, RL 0044, X 5, C 655.

55 Dorsal view of pygidium, RL 0104, X 4, H 1920.

56,57 Posterior and dorsal view of thoracic segment, RL 0105, X 3.4, H 1920.

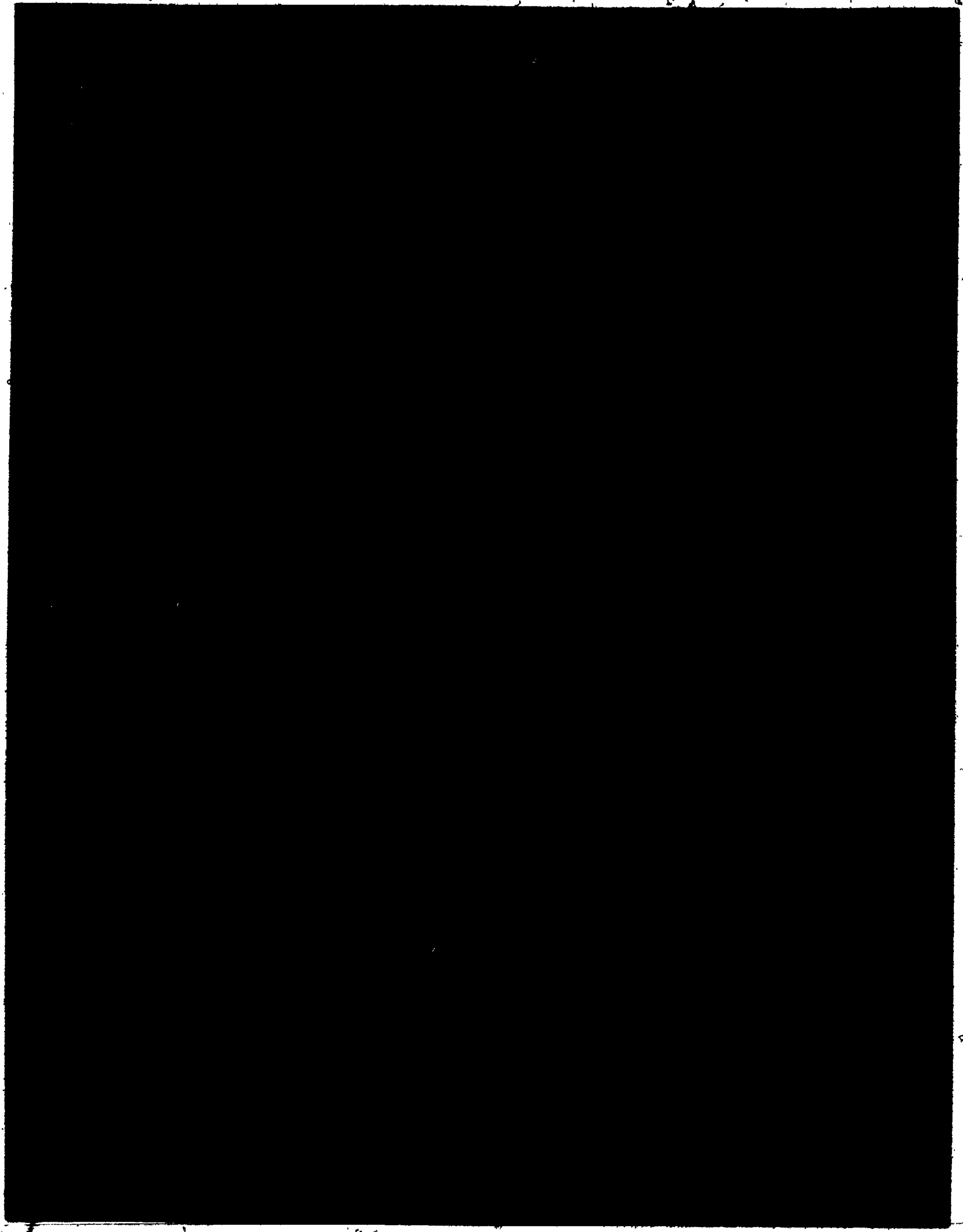

Plate 11

Plate 12

Figs. 1-44	<u>Ceraurus gabrielsi</u> n. sp. Middle and upper Esbataottine Formation, Sunblood Range. Figs. 1-36 from P 1685; figs. 37-44 from P 1931.
1-3	Dorsal, anterior, and oblique anterior views of incomplete cranidium, GSC 40425, X 2.4, and 5.
4	Dorsal view of incomplete cranidium, RL 0953, X 5.4.
5	Dorsal view of incomplete cranidium, RL 0954, X 5.4.
6-8	Dorsal, lateral, and anterior views of incomplete cranidium, RL 0676, X 3.4.
9	Ventral view of incomplete cranidium, RL 0677, X 4.
10,11	Dorsal and posterior views of pygidium, GSC 40426, X 2.8.
12-15	Dorsal, posterior, and lateral views of pygidium, RL 0680, X 6.7 and 3.7.
16	Ventral view of incomplete pygidium, RL 0678, X 3.
17	Dorsal view of pygidium, RL 0956, X 5.4.
18	Dorsal view of incomplete pygidium, RL 0955, X 4.
19	External view of rostral plate, RL 0675, X 5.4.
20	Internal view of rostral plate, RL 0958, X 4.
21,22	Ventral and lateral views of hypostome, RL 0681, X 3.2.
23	Ventral view of incomplete thoracic segment, RL 0960, X 3.
24	Dorsal view of free cheek, RL 0957, X 3.5.
25,34	Dorsal and lateral views of free cheek, RL 0683, X 3 and 7.
26	Interior view of free cheek, RL 0684, X 3.5.
27-29	Dorsal, posterior, and lateral views of thoracic segment, RL 0685, X 1.6, and 5.6.
30-33	Posterior, oblique lateral, oblique anterior, and dorsal view of hypostome, RL 0682, X 3.3.
35	Ventral view of thoracic segment, RL 0686, X 2.6.
36	Dorsal view of thoracic segment, RL 0959, X 3.5.
37	Ventral view of cranidium, RL 0767, X 2.7.
38-41	Dorsal, anterior, lateral, and oblique anterior views of cranidium, RL 0766, X 2.7, and 7.
42	Ventral view of hypostome, RL 0768, X 3.8.
43,44	Dorsal and posterior views of pygidium, RL 0770, X 3.8.

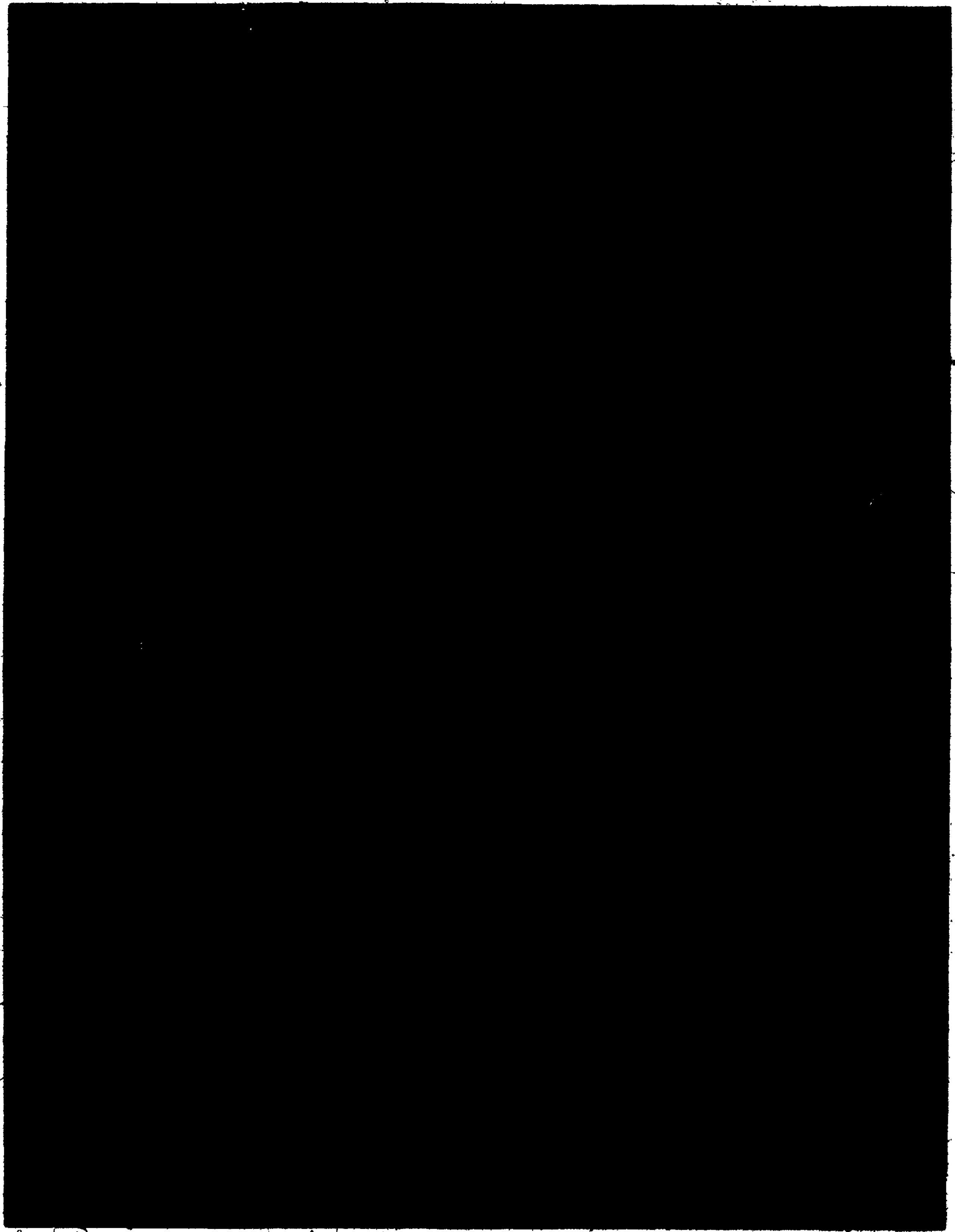

Plate 12

Plate 13

Figs. 1-49	Ceraurus gabrielsi n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 1945-1955, except figs. 22-24 which are from P 1931.
1-3	Dorsal, anterior, and lateral views of cranidium, Holotype, RL 0216, X 2.2.
4,5	Dorsal and anterior views of incomplete cranidium, RL 0217, X 2.7.
6,7	Dorsal [illegible] anterior view of cranidium, GSC 40435, X 2.5.
8	Dorsal view of cranidium, RL 0923, X 3.2.
9	Dorsal view of cranidium, RL 0929, X 3.2.
10,11	Ventral and posterior views of cranidium, RL 0219, X 3.3.
12	Ventral view of cranidium, RL 0922, X 2.3.
13	Dorsal view of small pygidium, RL 0223, X 5.
14-16	Dorsal, lateral, and posterior view of pygidium, RL 0220, X 2.8.
17	Dorsal view of pygidium, RL 0222, X 4.
18,19	Dorsal and lateral views of pygidium, GSC 40436, X 4.
20,21	Dorsal and posterior views of pygidium, RL 0924, X 4.
22-24	Posterior and dorsal views of large pygidium, RL 0769, X 2.7, and 4.5.
25	Dorsal view of pygidium, RL 0921, X 4, P 1945-1955.
26,27	Ventral and anterior views of pygidium, RL 0228, X 2.7.
28	Interior view of rostral plate, RL 0233, X 3.6.
29	Exterior view of rostral plate, RL 0232, X 3.6.
30	Dorsal view of small free cheek, RL 0231, X 5.
31-34	Ventral, anterior, posterior, and lateral views of hypostome, RL 0224, X 2.8.
35,36	Ventral and posterior views of hypostome, RL 0925, X 5.
37	Ventral view of small hypostome, RL 0227, X 5.
38	Ventral view of hypostome, RL 0225, X 3.3.
39-41	Dorsal, oblique exterior, and oblique interior views of hypostome, RL 0226, X 3.7, and 6.1.
42	Ventral view of thoracic segment, RL 0927, X 4.
43	Dorsal view of thoracic segment, RL 0928, X 4.
44	Dorsal view of thoracic segment, RL 0234, X 2.9.
45	Ventral view of thoracic segment, RL 0236, X 2.9.
46	Dorsal view of thoracic segment, RL 0235, X 2.9.
47	Interior view of free cheek, RL 0230, X 4.1.
48	Dorsal view of free cheek, RL 0926, X 5.
49	Dorsal view of free cheek, RL 0229, X 4.1.

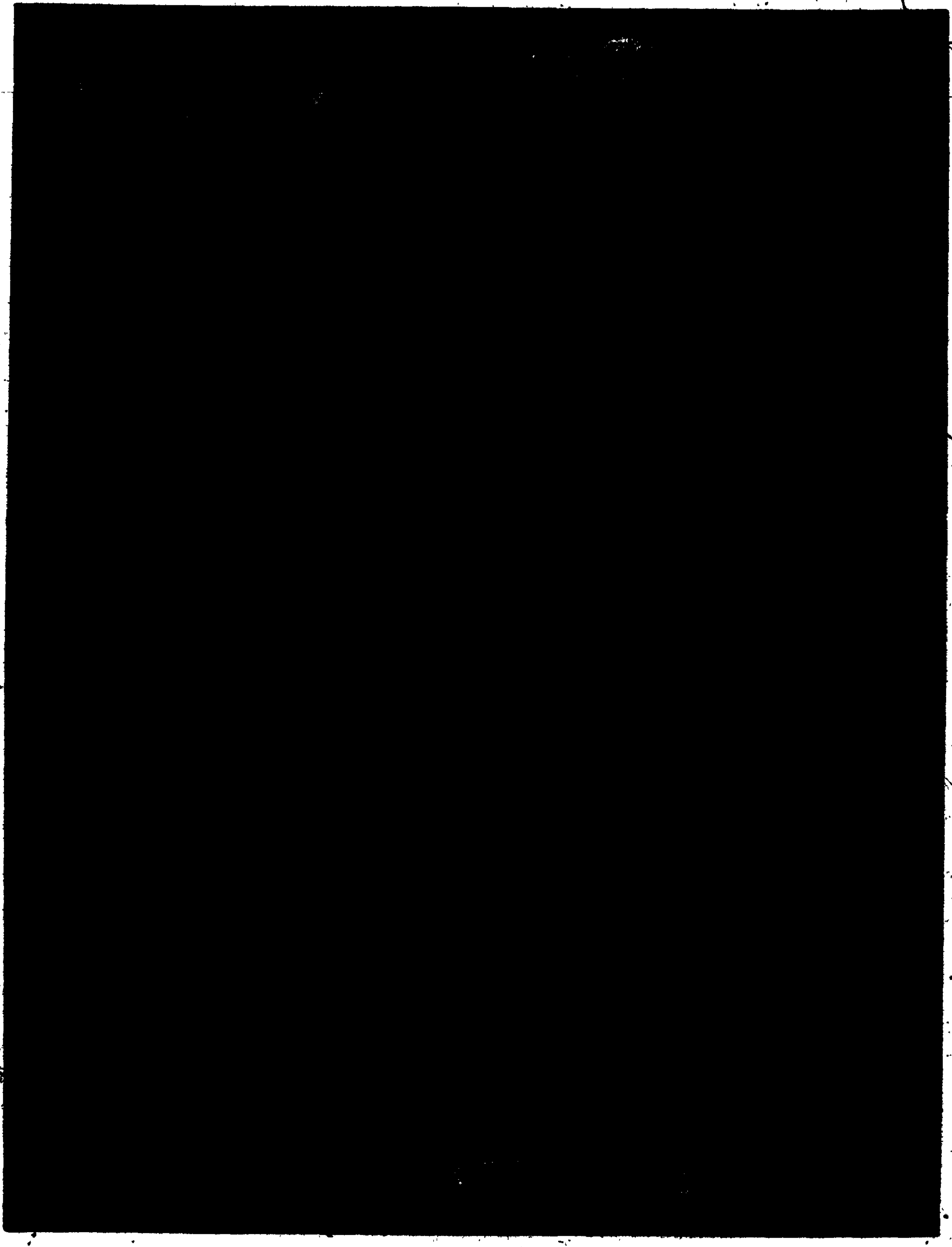

Plate 13

Plate 14

Figs. 1-8	*Ceraurus gabrielsi* n. sp. Upper Esbataottine Formation, Sunblood Range.
1,2	Dorsal and posterior views of thoracic segment, RL 0771, X 3, P 1931.
3	Oblique anterior view of cranidium, RL 0929, X 7, P 1945-1955 (same specimen as Pl. 13, fig. 9).
4	Oblique anterior view of cranidium, RL 0923, X 7, P 1945-1955 (same specimen as Pl. 13, fig. 8).
5	Dorsal view of incomplete cranidium, RL 0772, X 4.8, P 1870.
6-8	Lateral, posterior, and dorsal views of pygidium, RL 0773, X 4.8, P 1870.
Figs. 9-29	*Ceraurus blussoni* n. sp. Upper Sunblood Formation, Mary Range. All from B 1450.
9-11,29	Dorsal, anterior, and lateral views of incomplete cranidium, Holotype, RL 0237, X 2.1. Detail of cranidium, X 5.7.
12,13	Dorsal and anterior views of incomplete cranidium, RL 0930, X 3.
14	Dorsal view of incomplete cranidium, RL 0931, X 4.
15	Dorsal view of incomplete cranidium, RL 0240, X 4.3.
16,17	Ventral and lateral views of hypostome, RL 0241, X 3.3.
18	Dorsal view of free cheek, RL 0932, X 3.
19,20	Ventral and lateral views of hypostome, RL 0934, X 3.
21,22	Dorsal and posterior views of incomplete pygidium, RL 0933, X 3.
23	Dorsal view of incomplete thoracic segment, RL 0244, X 2.7.
24	Ventral view of incomplete cranidium, RL 0238, X 2.3.
25,26	Dorsal and posterior views of pygidium, RL 0239, X 3.1.
27	Ventral view of incomplete pygidium, RL 0242, X 2.7.
28	Dorsal view of free cheek, RL 0243, X 2.7.
Figs. 30-33	*Ceraurus maewestoides* n. sp. Lower Whittaker Formation, Dusky Range. From R 625. Oblique lateral, ventral, dorsal, and anterior views of cranidium, Holotype, RL 0581, X 5.1.

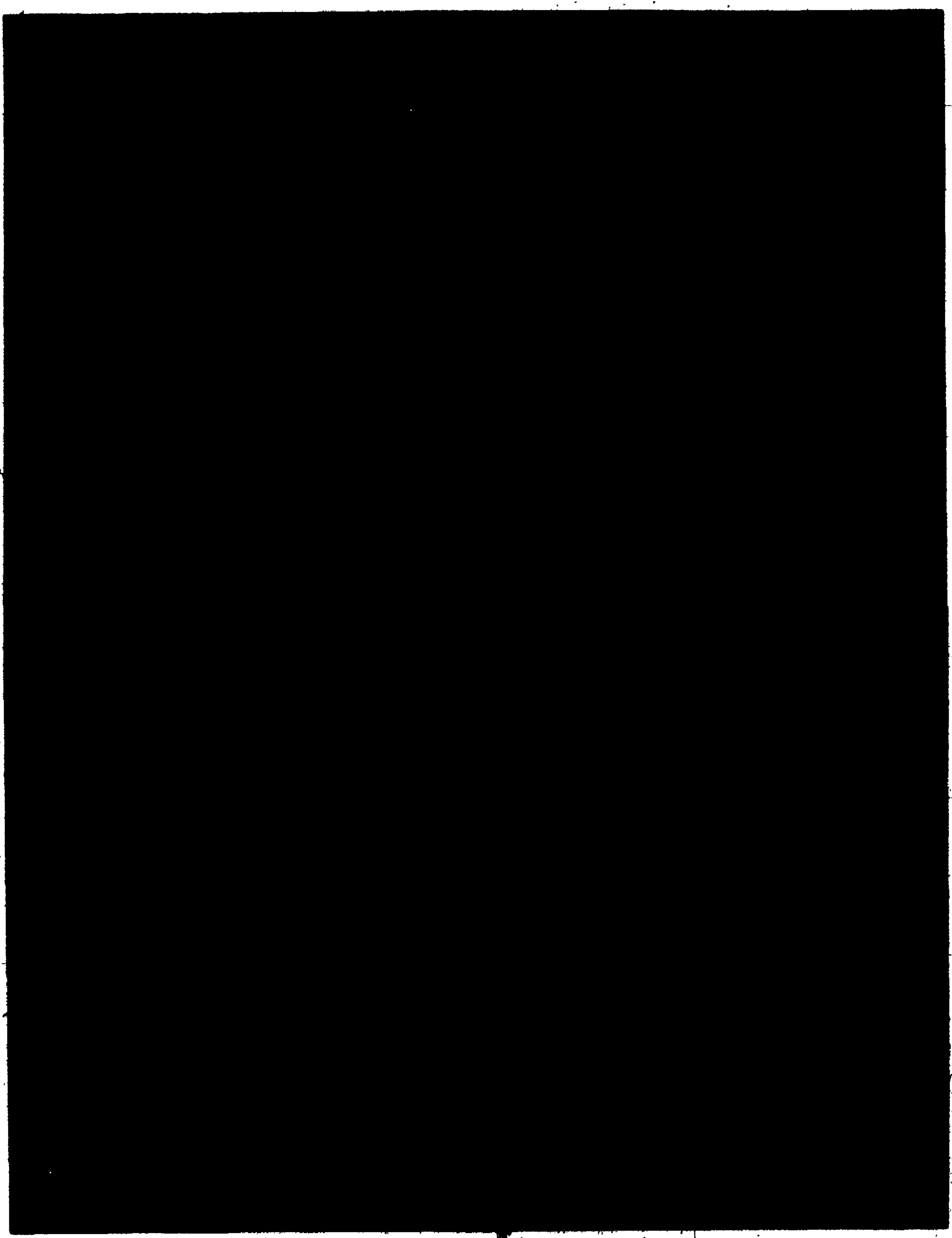

Plate 14

Plate 15

Figs. 1-25	Ceraurus hirsuitus n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 2038.
1,2	Dorsal and ventral views of incomplete cranidium, Holotype, GSC 40415, X 4.
3,4	Dorsal and anterior views of incomplete cranidium, RL 0944, X 2.2.
5,6	Oblique anterior and dorsal views of cranidium, RL 0247, X 2.2.
7	Dorsal view of incomplete cranidium, RL 0946, X 2.2.
8,9	Dorsal and posterior views of incomplete pygidium, GSC 40416, X 2.2.
10	Ventral view of incomplete cranidium, RL 0945, X 2.2.
11	Ventral view of incomplete pygidium, RL 0251, X 2.2.
12,25	Dorsal view of incomplete pygidium, RL 0250, X 2.2, and X 3.7, (note fine hair-like spines).
13,20	Dorsal and interior views of free cheek, RL 0948, X 4.
14	Ventral view of cranidium, RL 0248, X 3.
15	Dorsal view of cranidial fragment overgrown by bryozoans; shows total length of genal spine, RL 0947, X 2.2.
16-19	Dorsal, posterior, ventral, and oblique interior views of cranidium (note gall-like swelling at base of right genal spine), RL 0246, X 3.2.
21	Dorsal view of thoracic segment, RL 0025, X 3.
22,23	Dorsal and anterior view of thoracic segment, RL 0024, X 3.
24	Lateral view of thoracic segment, RL 0026, X 3.

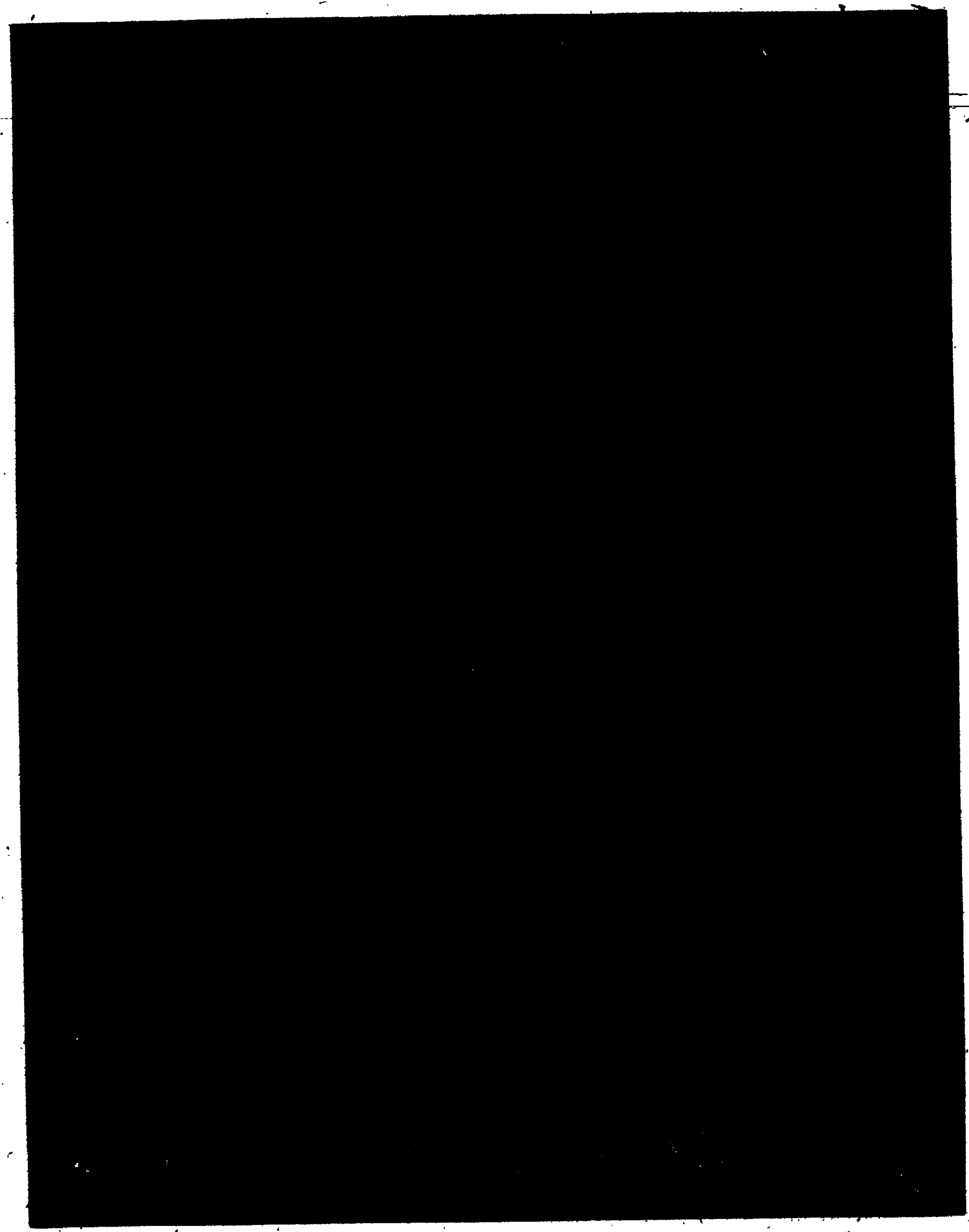

Plate 15

Plate 16

Figs. 1-44 *Ceraurus mackenziensis* n. sp. Lower Whittaker Formation, Funeral Range and Whittaker Range.

1-3 Dorsal, lateral, and anterior view of incomplete cranidium, Holotype, RL 0582, X 4.2, C 655.

4 Dorsal view of incomplete cranidium, RL 0650, X 5.4, H 1920.

5,6 Dorsal and anterior views of incomplete cranidium, GSC 40447, X 6, C 655.

7 Dorsal view of incomplete cranidium, RL 0936, X 6.6, C 655.

8,9 Dorsal and anterior views of incomplete cranidium, RL 0937, X 6.6, C 655.

10 Ventral view of incomplete cranidium, RL 0935, X 4.3, C 655.

11 Dorsal view of small incomplete cranidium, RL 0585, X 6.2, C 655.

12,13 Dorsal and lateral views of fragment of cranidium including complete genal spine, RL 0590, X 3.1, C 655.

14 Ventral view of incomplete cranidium, RL 0651, X 3.4, H 1920.

15,16 Ventral and oblique posterior views of incomplete cranidium, RL 0584, X 4.4, C 655.

17,18 Dorsal and posterior views of pygidium, GSC 40448, X 4.2, C 655.

19 Dorsal view of pygidium, RL 0939, X 6.6, C 655.

20 Dorsal view of pygidium, RL 0938, X 6.6, C 655.

21 Ventral view of pygidium, RL 0588, X 4.8, C 655.

22 Ventral view of pygidium, RL 0653, X 4.6, H 1920.

23-25 Dorsal, posterior, and lateral views of pygidium, RL 0606, X 3.6, J 220.

26,27 Dorsal and anterior views of incomplete cranidium, RL 0605, X 4, J 220.

28,29 Ventral and lateral views of hypostome, RL 0589, X 5.3, C 655.

30,31 Ventral and posterior views of hypostome, RL 0654, X 5.4, H 1920.

32,33 Dorsal and posterior views of pygidium, RL 0652, X 4.6, H 1920.

34,35 Ventral and lateral views of hypostome, RL 0607, X 6, J 220.

36,37 Dorsal and posterior views of hypostome, RL 0591, X 5.3, C 655.

38 Dorsal view of hypostome, RL 0941, X 6.6, C 655.

39 Ventral view of small hypostome, RL 0587, X 6.2, C 655.

40 Ventral view of hypostome, RL 0940, X 6.6, C 655.

41 Dorsal view of free cheek, RL 0593, X 5.5, C 655.

42 Dorsal view of free cheek, RL 0592, X 3.5, C 655.

43 Dorsal view of free cheek, RL 0608, X 3.5, J 220.

44 Ventral view of free cheek, RL 0594, X 3.4, C 655.

Figs. 45-57 *Ceraurus* *milleranus* Miller and Gurley. Lower Whittaker Formation, Dusky Range. All from R 625.

45-48 Ventral, dorsal, lateral, and anterior view of incomplete cranidium, RL 0575, X 5.1, and 3.4.

49,50 Dorsal and oblique lateral views of hypostome, RL 0580, X 5.

51,52 Ventral and lateral views of hypostome, RL 0579, X 5.

53,54 Dorsal and posterior views of pygidium, RL 0604, X 4.3.

55 Dorsal view of free cheek, RL 0576, X 4.

56,57 Posterior and dorsal views of pygidium, RL 0603, X 3.2.

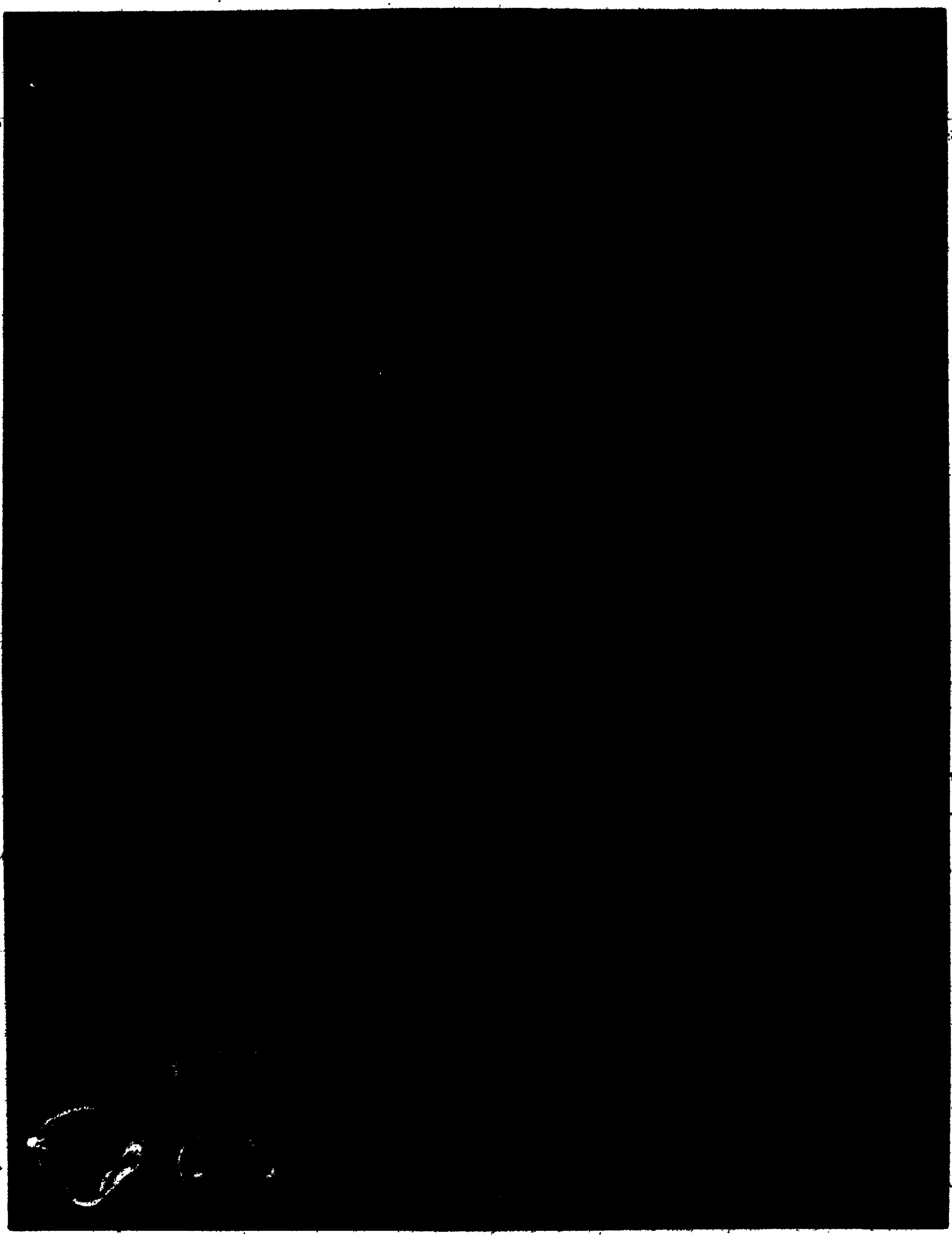

Plate 16

Plate 17

Figs. 1-47 Whittakerites planatus n. gen. and n. sp. Lower Whittaker Formation, Whittaker Range and Dusky Range.

1,2 Dorsal and anterior views of incomplete cranidium, RL 0733, X 4.3, I 1590.

3 Dorsal view of incomplete cranidium, RL 0734, X 4.3, I 1590.

4,5 Dorsal and ventral views of incomplete cranidium, Holotype, RL 0909, X 5, Q 530.

6,7 Dorsal and lateral views of incomplete cranidium, RL 0736, X 4.3, I 1590.

8 Dorsal view of incomplete cranidium, RL 0908, X 3, Q 530.

9 Dorsal view of incomplete cranidium, RL 0910, X 5, Q 530.

10 Dorsal view of small incomplete cranidium, RL 0911, X 5, Q 530.

11 Dorsal view of small incomplete cranidium, RL 0898, X 4.3, I 1590.

12 Dorsal view of small incomplete cranidium, RL 0912, X 5, Q 530.

13 Dorsal view of incomplete cranidium, RL 0896, X 4.3, I 1590.

14 Dorsal view of incomplete cranidium, RL 0897, X 4.3, I 1590.

15 Ventral view of incomplete cranidium, RL 0735, X 3.5, I 1590.

16 Dorsal view of incomplete cranidium, RL 0601, X 5.4, R 625.

17 Dorsal view of incomplete cranidium, RL 0602, X 5.4, R 625.

18-20 Dorsal, posterior, and lateral views of pygidium, RL 0900, X 4.3, I 1590.

21-23 Dorsal, lateral, and posterior views of pygidium, RL 0737, X 2.5, I 1590.

24 Dorsal view of pygidium, RL 0738, X 4.2, I 1590.

25 Ventral view of pygidium, RL 0915, X 5, Q 530.

26 Dorsal view of pygidium, RL 0899, X 4.3, I 1590.

27,28 Ventral and anterior views of pygidium, RL 0739, X 3.8, I 1590.

29 Dorsal view of pygidium, RL 0916, X 5, Q 530.

30 Dorsal view of pygidium, RL 0901, X 4.3, I 1590.

31 Dorsal view of small (meraspid?) pygidium, RL 0902, X 5.6, I 1590.

32,33 Ventral and lateral views of hypostome, RL 0741, X 4.7, I 1590.

34,35 Dorsal and oblique lateral views of hypostome, RL 0742, X 4.7, I 1590.

36 Ventral view [illegible] hypostome, RL 0904, X 5, I 1590.
37 Dorsal view of hypostome, RL 0905, X 5, I 1590.
38 Ventral view of hypostome, RL 0913, X 6, Q 530.
39 Dorsal view of hypostome, RL 0914, X 6, Q 530.
40,41 Dorsal and lateral views of free cheek, RL 0740, X 3, I 1590.
42 Dorsal view of free cheek, RL 0903, X 4.3, I 1590.
43 Interior view of free cheek, RL 0743, X 3, I 1590.
44,45 Lateral and dorsal views of incomplete thoracic segment, RL 0906, X 3, I 1590.
46,47 Ventral and posterior views of incomplete thoracic segments, RL 0907, X 3, I 1590.

Figs. 48-51 Cheirurinid indet. n. gen. and n. sp. Lower Whittaker Formation, Dusky Range. From R 625.
48-50 Dorsal, posterior, and lateral views of pygidium, RL 0577, X 4, R 625.
51 Ventral view of pygidium, RL 0578, X 4.

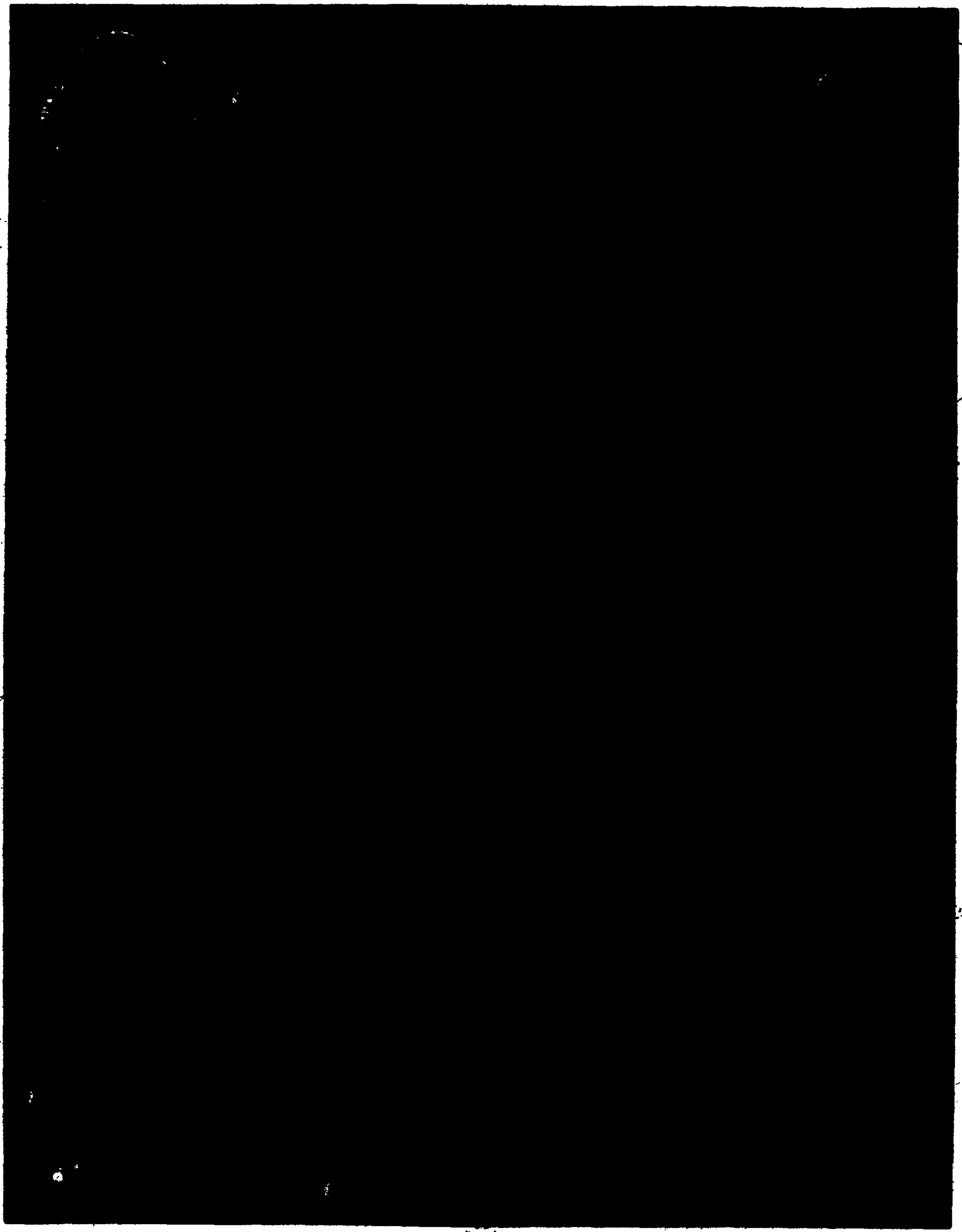

Plate 17

Plate 18

Figs. 1-12 Borealaspis whittakerensis n. gen. and n. sp. Lower Whittaker Formation, Funeral Range. All from C 655.

1-5 Dorsal, ventral, lateral, anterior, and oblique anterior views of incomplete cranidium, Holotype, GSC 40450, X 8.4, and 10.5.

6,7 Lateral and dorsal views of incomplete cranidium, RL 0610, X 5.1.

8 Dorsal view of incomplete pygidium, RL 0612, X 5.1.

9 Dorsal view of meraspid pygidium, RL 0613, X 6.3.

10 Ventral view of meraspid pygidium, RL 0614, X 6.3.

11,12 Anterior and dorsal views of incomplete cranidium, RL 0611, X 5.1.

Figs. 13-28 Borealaspis biformis n. gen. and n. sp. Lower Whittaker Formation, Funeral Range. All from C 570-590.

13-16 Dorsal, lateral, anterior, and ventral views of incomplete cranidium, Note occipital spine, Holotype, RL 0617, X 9.3.

17,18 Dorsal and ventral views of incomplete cranidium, Note absence of occipital spine, RL 0618, X 9.3.

19 Dorsal view of small incomplete cranidium, RL 0620, X 9.8.

20,21 Dorsal and lateral views of incomplete cranidium, RL 0619, X 5.

22,25,26 Oblique lateral, ventral, and lateral views of hypostome, RL 0622, X 6.9, and 3.7.

23,24 Oblique lateral and dorsal views of hypostome, RL 0623, X 4.5.

27 Dorsal view of incomplete pygidium, RL 0624, X 5.5.

28 Dorsal view of small incomplete cranidium, RL 0621, X 9.8.

Figs. 29-35 Borealaspis cf. biformis n. gen. and n. sp. Lower Whittaker Formation, Whittaker Range. Both from H 1920.

29-33 Dorsal, ventral, anterior, posterior, and oblique lateral views of incomplete cranidium, RL 0595, X 5.4.

34,35 Anterior and dorsal views of incomplete cranidium, RL 0596, X 6.

Figs. 36-41 *Ceraurus tuberosus* Troedsson. Lower Whittaker Formation, Whittaker Range. All from I·1275.

36-38 Dorsal, anterior, and lateral views of incomplete cranidium, RL 0949, X 5.8.
39 Ventral view of hypostome, RL 0952, X 5.8.
40 Dorsal view of pygidium, RL 0951, X 5.8.
41 Dorsal view of incomplete cranidium, RL 0950, X 5.8.

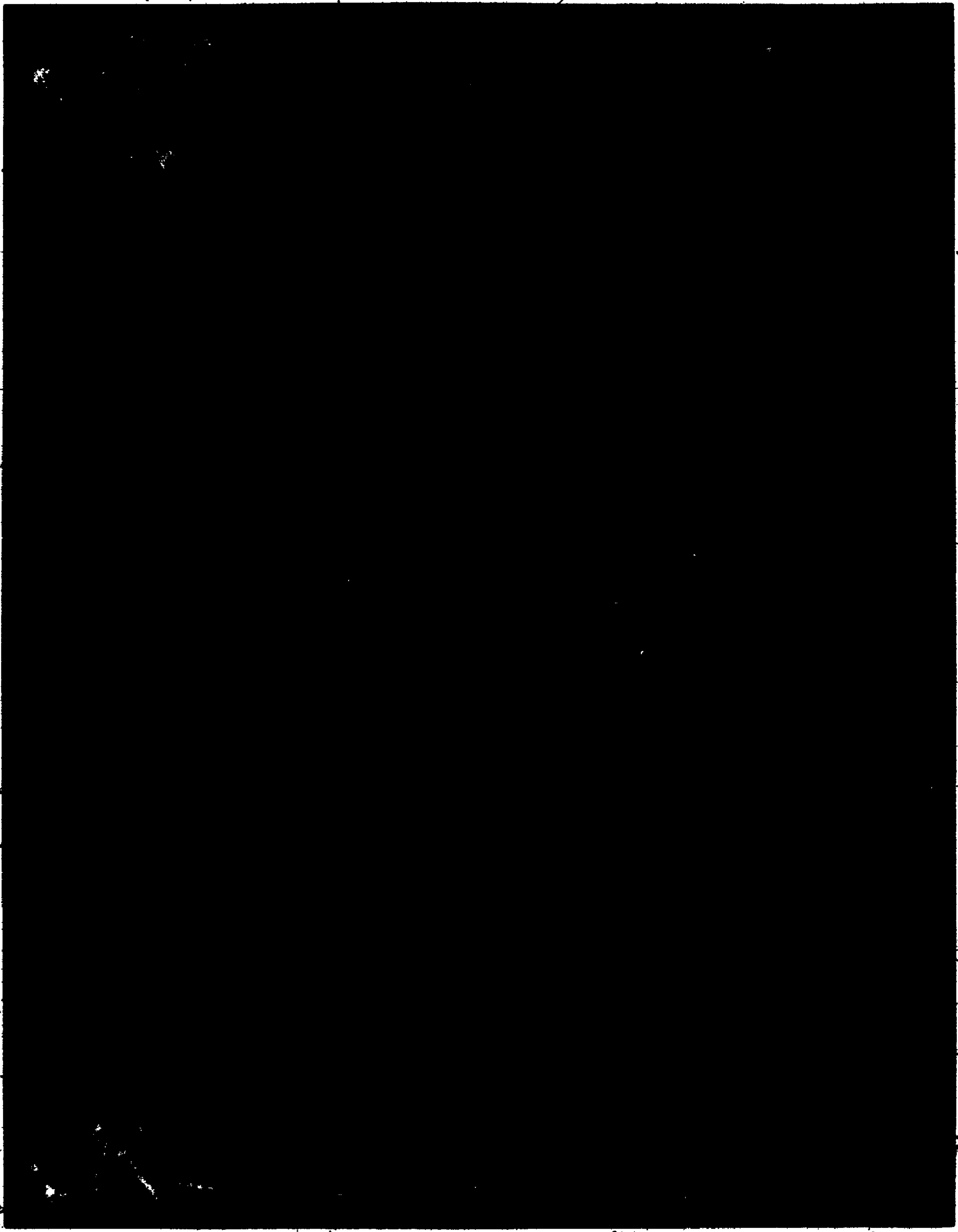

Plate 18

Plate 19

Figs. 1-3 *Ceraurinus marginatus* Barton. Southern Ontario. Figs. 1 and 3 from the top beds of the Cobourg Formation, 3 km east of Collingwood. Fig. 2 from the Cobourg Formation, Colborne Quarry.

1 Dorsal view of incomplete carapace, X 1.4.
2 Dorsal view of latex impression of internal mold of cranidium, X 2.
3 Dorsal view of partially crushed pygidium, X 1.4.

Figs. 4,5 *Remipyga icarus* (Billings). Whitehead Formation, Priest's Road, 3 km west of Perce, Gaspe Peninsula. Locality 1 of Cooper and Kindle (1936, p. 349).

4 Dorsal view of incomplete cranidium, GSC 9077, X 2.7 (paratype of *Ceraurinus elongatus* Cooper, in Schuchert and Cooper, 1930, Pl. 5, fig. 14).
5 Dorsal view of pygidium, GSC 21891, X 3 (photograph supplied by P.J. Lesperance).

Fig. 6 *Encrinuroides rarus* (Walcott). Platteville Group, Beloit, Wisconsin. Dorsal view of incomplete cranidium, Holotype, UC 12322, X 5 (illustrated by Raymond and Barton, 1913, Pl. 2, fig. 3).

Figs. 7,8 *Ceraurus mantranseris* Sinclair. "Unnamed limestone of Middle Trenton age" (Sinclair, 1947, p. 255), 3/4 km north of Roberval, Quebec.

7 Dorsal view of cranidium, Holotype, GSC 6801, X 5.8 (original of Sinclair, 1947, Pl. 1, fig. 3).
8 Dorsal view of pygidium, Paratype, GSC 7395, X 5.8 (original of Sinclair, 1947, Pl. 1, fig. 6).

Fig. 9 *Ceraurinella trentonensis* (Barton). Lower Trenton, Goat Island, Ontario. Dorsal view of slab with incomplete cranidium (Holotype) and hypostome, GSC 5836, X 3.2 (original of Barton, 1913, unnumbered plate, figs. 5, 6).

Fig. 10 *Ceraurinella tenuisculpta* (Bradley). Kimmswick Limestone, 3/4 km north of Batchtown, Illinois. Dorsal view of incomplete cranidium, Holotype, UC 20691, X 3 (original of Bradley, 1930, Pl. 30, fig. 14).

Figs. 11-15 Ceraurus globulobatus Bradley, Kimmswick Limestone, railroad station at Glen Park, Missouri.

11 Dorsal view of incomplete pygidium, UC 20695c, X 3 (original of Bradley, 1930, Pl. 30, fig. 40).

12 Dorsal view of incomplete cranidium, UC 28956, X 2.3 (original of Bradley, 1930, Pl. 30, fig. 33).

13 Dorsal view of incomplete cranidium, UC 20695a, X 3 (original of Bradley, 1930, Pl. 30, fig. 38).

14 Dorsal view of incomplete cranidium, UC 20719a, X 2.3 (original of Bradley, 1930, Pl. 30, fig. 42).

15 Dorsal view of plasticine impression of external mold of pygidium, UC 20695d, X 2.8 (original of Bradley, 1930, Pl. 30, fig. 39).

Figs. 16-18 Borealaspis numitor (Billings). Vaureal Formation, Makasti Bay, Anticosti Island. Anterior, lateral, and dorsal views of incomplete cranidium, Neotype, GSC 2199, X 2.5.

Figs. 19-22 Ceraurus milleranus Miller and Gurley.

19-21 Dorsal views of cephalon, entire carapace, and pygidium, Holotype, UC 5052, X 2.3. Maysville Group, Cincinnatti, Ohio (original of Raymond and Barton, 1913, Pl. 1, fig. 8; Slocum, 1913, Pl. 17, fig. 3).

22 Dorsal view of incomplete pygidium, P 16925, X 3. Lower Maquoketa Shale, Clermont, Iowa (original of Slocum, 1913, Pl. 17, fig. 2).

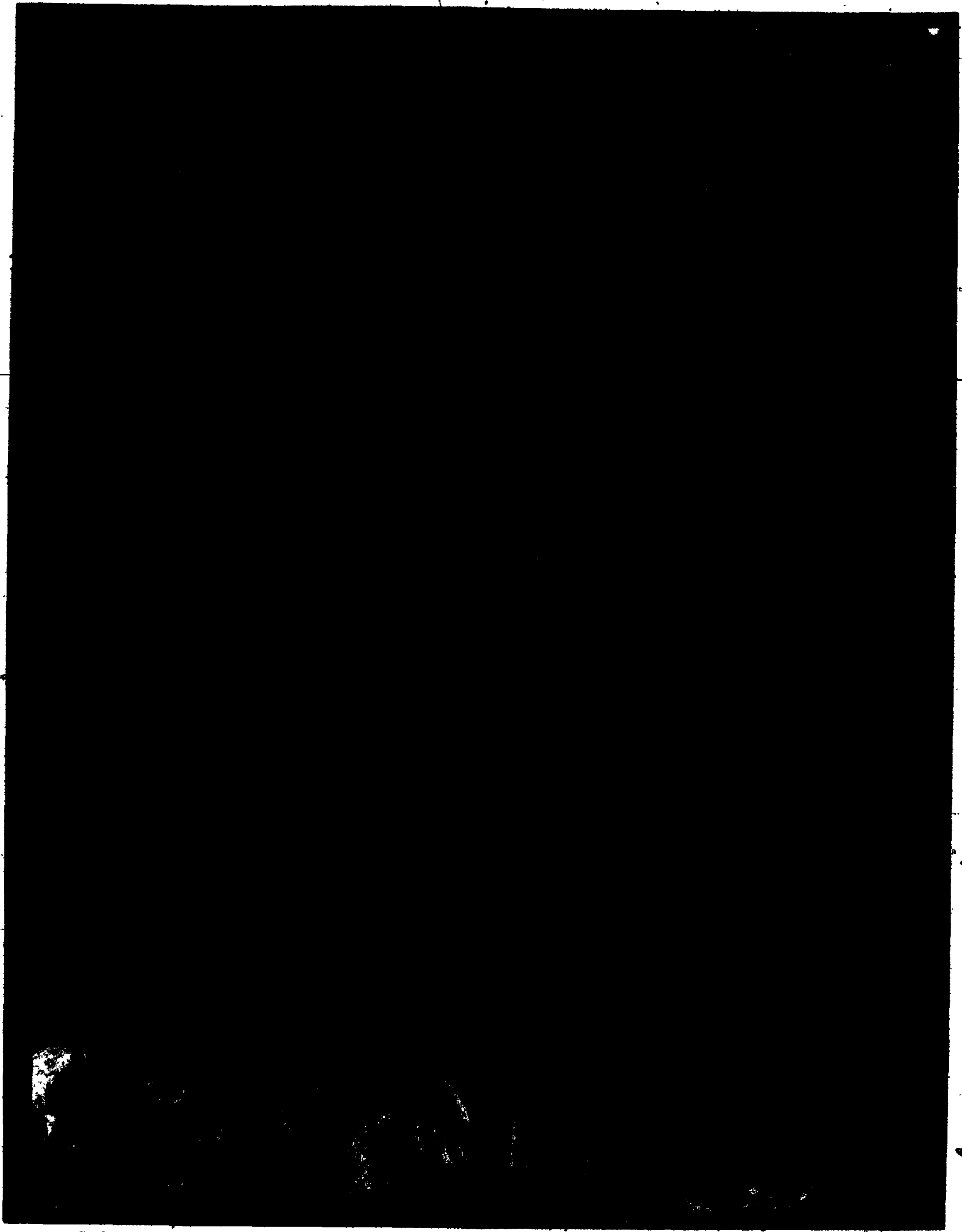

Plate 19

Plate 20

Figs. 1-32	*Remipyga serrata* n. sp. Lower Whittaker Formation, Whittaker Range and Funeral Range.
1-3	Dorsal, lateral, and anterior views of cranidium, GSC 40445, X 3.1, I 1590.
4	Ventral view of incomplete cranidium, RL 0322, X 3.6, C 655.
5-7	Dorsal, lateral, and anterior views of incomplete cranidium, RL 0321, X 4.4, C 655.
8	Dorsal view of small incomplete cranidium, RL 0326, X 3.8, C 655.
9	Dorsal view of incomplete cranidium, RL 0917, X 3.2, Q 530.
10,11	Dorsal and posterior views of pygidium, Holotype, GSC 40446, X 3.1, I 1590.
12,13	Dorsal and posterior views of pygidium, RL 0324, X 2.8, C 655.
14	Dorsal view of pygidium, RL 0317, X 4, I 1590.
15	Ventral view of pygidium, RL 0323, X 3, C 655.
16	Dorsal view of pygidium, RL 0316, X 4, I 1590.
17	Dorsal view of pygidium, RL 0325, X 3.8, C 655.
18	Ventral view of pygidium, RL 0315, X 3, I 1590.
19	Dorsal view of pygidium, RL 0919, X 4.4, Q 530.
20	Dorsal view of hypostome, RL 0318, X 5, I 1590.
21,22	Ventral and lateral views of hypostome, RL 0327, X 3, C 655.
23-25	Lateral, posterior, and ventral views of hypostome, RL 0918, X 5, Q 530.
26	Dorsal view of free cheek, RL 0920, X 3.5, Q 530.
27	Interior view of free cheek, RL 0319, X 3, I 1590.
28	Dorsal view of free cheek, RL 0320, X 3, I 1590.
29	Dorsal view of free cheek, RL 0329, X 3.6, C 655.
30	Dorsal view of incomplete thoracic segment, RL 0330, X 3.8, C 655.
31,32	Anterior and ventral views of incomplete thoracic segment, RL 0328, X 2.2, C 655.
Figs. 33-53	*Sphaerocoryphe robustus* Walcott. Lower Whittaker Formation, Whittaker Range and Funeral Range, all from C 655, except figs. 49-53 which are from H 1920.
33-38	Dorsal, anterior, oblique lateral, lateral, and ventral views of incomplete cranidium, GSC 40451, X 5, and 8.7.
39	Ventral view of incomplete cranidium, RL 0643, X 6.3.

40,41 Dorsal and posterior views of pygidium, RL 0644, X 7.

42 Ventral view of pygidium, RL 0645, X 8.5.

43 Dorsal view of small cranidium, RL 0642, X 8.5.

44,45 Dorsal and posterior views of incomplete pygidium, RL 0646, X 5.6.

46 Dorsal view of hypostome, RL 0648, X 8.5.

47,48 Ventral and posterior views of hypostome, RL 0647, X 8.5.

49-53 Ventral, dorsal, posterior, lateral, and oblique dorsal views of incomplete pygidium, GSC 40452, X 4.6, and 7.

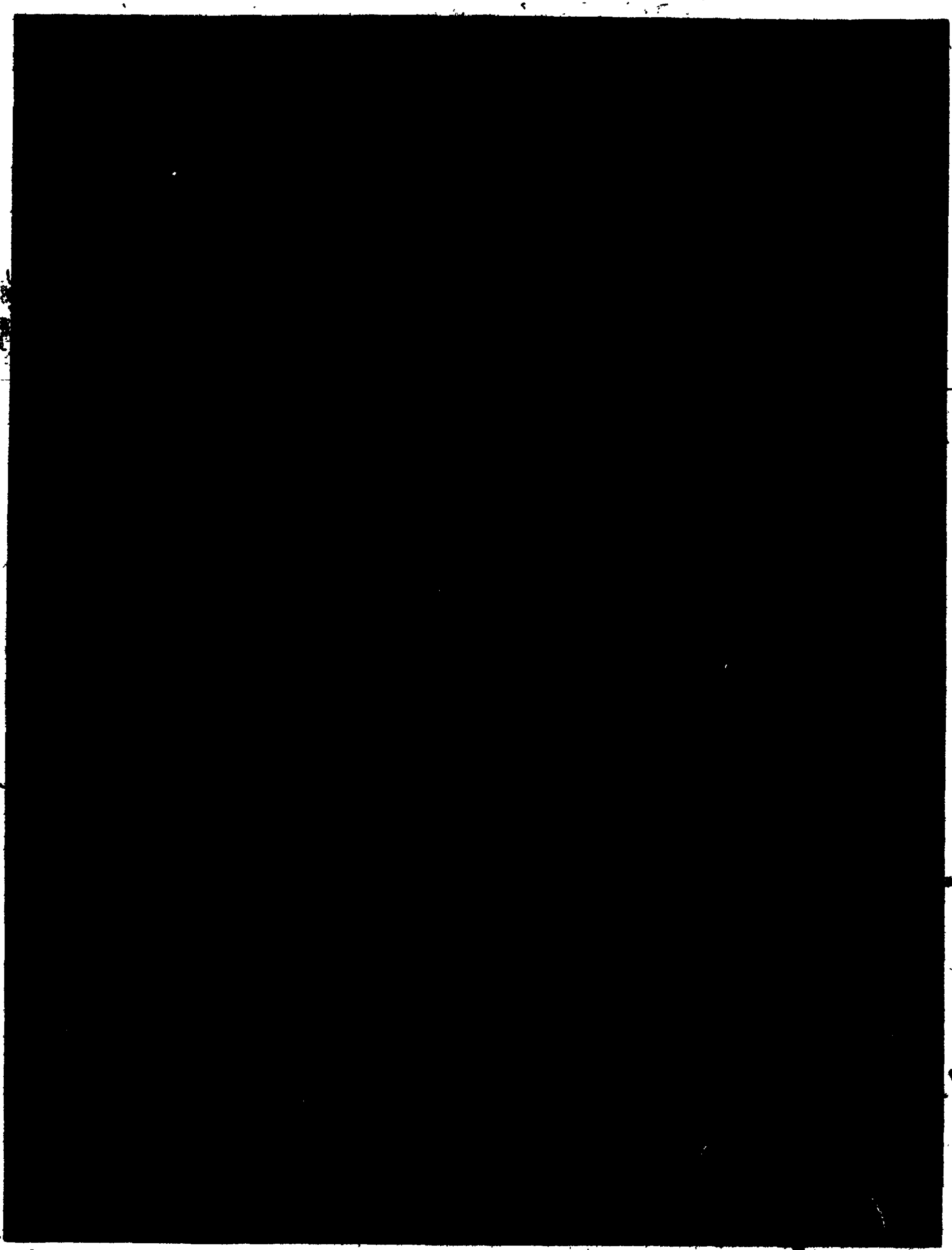

Plate 20

Plate 21

Figs. 1-41 **Acanthoparypha evitti** Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.

1-4 Dorsal, oblique, posterior, lateral, and anterior views of cranidium, Holotype, GSC 40403, X 5.3, P 1497.

5-7 Oblique lateral, ventral, and oblique posterior views of cranidium, RL 0147, X 4.1, P 1497.

8,41 Dorsal and oblique views of cranidium, RL 0871, X 5 and X 9, P 1512.

9 Lateral view of cranidium, RL 0886, X 5.2, A 125.

10 Dorsal view of small cranidium, UA 1360, X 7.5, A 125.

~~11 Dorsal view of small cranidium, UA 1330, X 7.5,~~ A 125.

12-14 Dorsal, posterior, and lateral views of pygidium, GSC 40404, X 8.3, P 1497.

15 Dorsal views of pygidium, UA 1328, X 7.5, A 140.

16 Dorsal view of pygidium, RL 0890, X 7.7, A 125.

17 Dorsal view of pygidium, UA 1331, X 7.5, A 125.

18 Dorsal view of incomplete thorax and pygidium, UA 1329, X 3, A 125.

19,20 Dorsal and ventral views of pygidium, UA 1332, X 5.5, A 125.

21 Dorsal view of pygidium, RL 0873, X 7.7, P 1512.

22 Ventral view of hypostome, UA 1334, X 7.5, A 125.

23,24 Dorsal and oblique posterior views of hypostome, RL 0264, X 7, A 125.

25 Ventral view of hypostome, RL 0874, X 7.7, P 1512.

26 Ventral view of hypostome, RL 0153, X 9, P 1497.

27,28 Dorsal and ventral views of hypostome, UA 1333, X 5.5, A 125.

29,30 Anterior and ventral views of pygidium, RL 0151, X 8.7, P 1497.

31 Ventral view of hypostome, UA 1335, X 5.5, A 125.

32 Oblique view of free cheek, RL 0156, X 6.3, P 1497.

33 Ventral view of thoracic segment, RL 0877, X 5, P 1512.

34 Ventral view of thoracic segment, RL 0863, X 6, P 1497.

35 Dorsal view of thoracic segment, RL 0154, X 7.9, P 1497.

36 Dorsal view of thoracic segment, UA 1338, X 7.5, A 125.

37 Dorsal view of thoracic segment, RL 0875, X 5, P 1512.
38 Dorsal view of small pygidium, UA 1336, X 33, A 125.
39 Interior view of free cheek, RL 0155, X 6.3, P 1497.
40 Oblique view of free cheek, UA 1337, X 5.5, A 125.

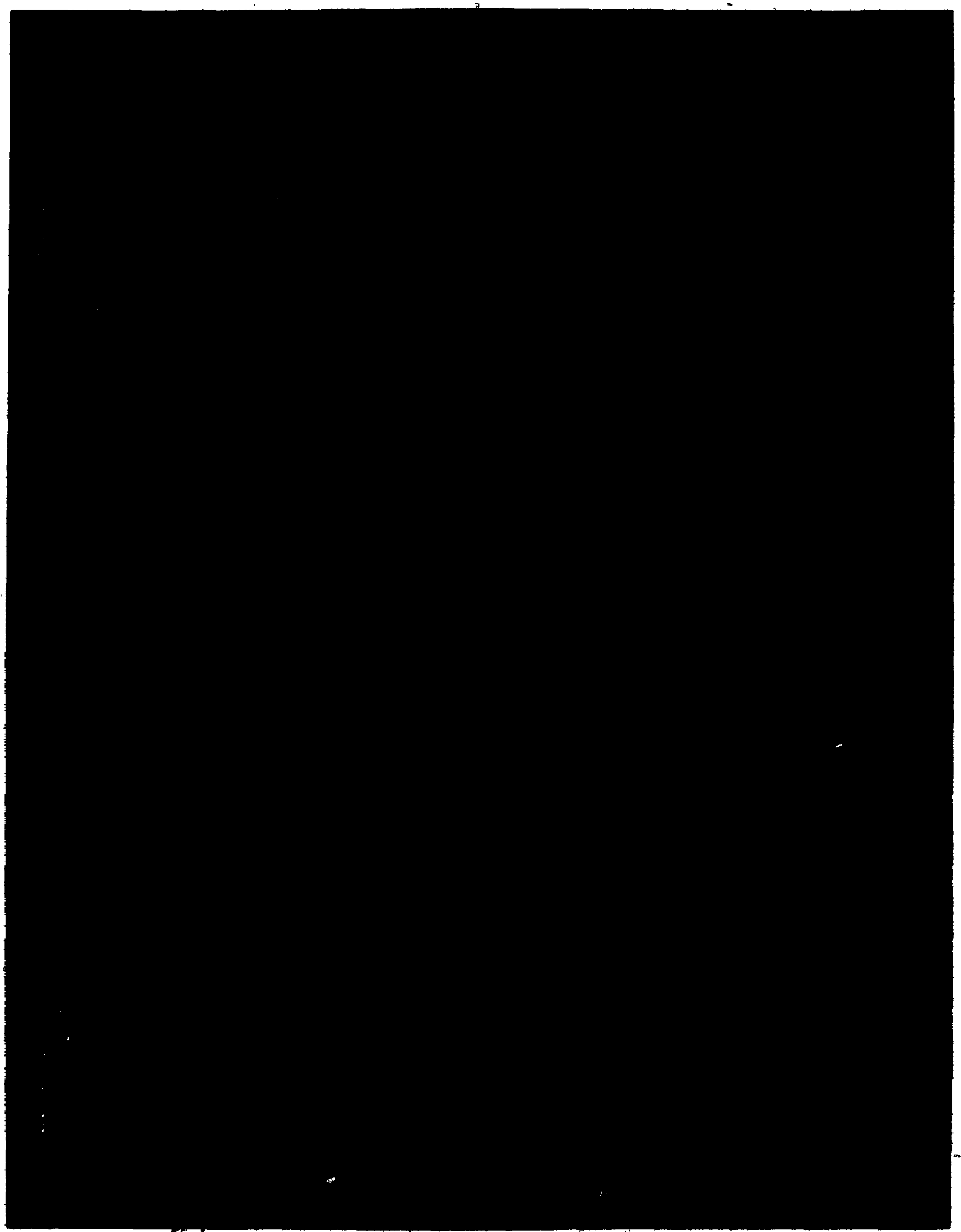

Plate 21

Plate 22

Figs. 1-42 *Holia secristi* Whittington and Evitt. Lower Esbataottine Formation, Sunblood Range.

1-3 Dorsal, lateral, and anterior views of incomplete cranidium, GSC 40390, X 6, P 1512.

4-7 Dorsal, lateral, anterior (X6), and oblique interior views(X7), of incomplete cranidium, RL 0494, P 1512.

8 Dorsal view of incomplete cranidium, UA 1346, X 7.5, A 125.

9 Dorsal view of incomplete cranidium, UA 1347, X 5.5, A 125.

10,11 Ventral and dorsal views of cranidium, UA 1348, X 5.5, A 115.

12 Ventral view of cranidium, RL 0497, X 6, P 1512.

13 Dorsal view of small cranidium, RL 0745, X 8.6, P 1485.

14 Dorsal view of cranidium, RL 0498, X 6.3, P 1512.

15 Dorsal view of small cranidium, RL 0499, X 6.6, P 1512.

16 Dorsal view of cranidium, RL 0744, X 8.6, P 1485.

17 Dorsal view of incomplete cranidium, RL 0496, X 6, P 1512.

18,19 Dorsal and ventral views of pygidium, UA 1349, X 5.5, A 115.

20-22 Posterior, dorsal, and lateral views of pygidium, GSC 40391, X 6, P 1512.

23,24 Ventral and lateral views of pygidium, RL 0500, X 5.5, P 1512.

25 Dorsal view of small pygidium, RL 0505, X 6, P 1512.

26 Dorsal view of transitory pygidium, UA 1533, X 7, A 115.

27,28 Ventral and posterior views of hypostome, RL 0506, X 7.7, P 1512.

29,35,36 Dorsal and ventral views of hypostome, X 5.5, Oblique views to show maculae and ornamentation, UA 1352, X 12, A 115.

30 Dorsal view of small pygidium, UA 1352, X 5.5, A 115.

31 Dorsal view of incomplete thoracic segment, UA 1353, X 7, A 140.

32 Dorsal view of incomplete thoracic segment, UA 1354, X 7.5, A 125.

33 Ventral view of hypostome, UA 1351, X 5.5, A 125.

34 Dorsal view of incomplete thoracic segment, UA 1356, X 7.5, A 125.

37-39 Dorsal, posterior and anterior views of incomplete thoracic segment, UA 1355, X 7.5, A 125.

40 Dorsal view of thoracic segment, RL 0504, X 8.3, P 1512.

41 Oblique dorsal view of free cheek, RL 0503, X 7.5, P 1512.

42 Interior view of free cheek, RL 0502, X 7.5, P 1512.

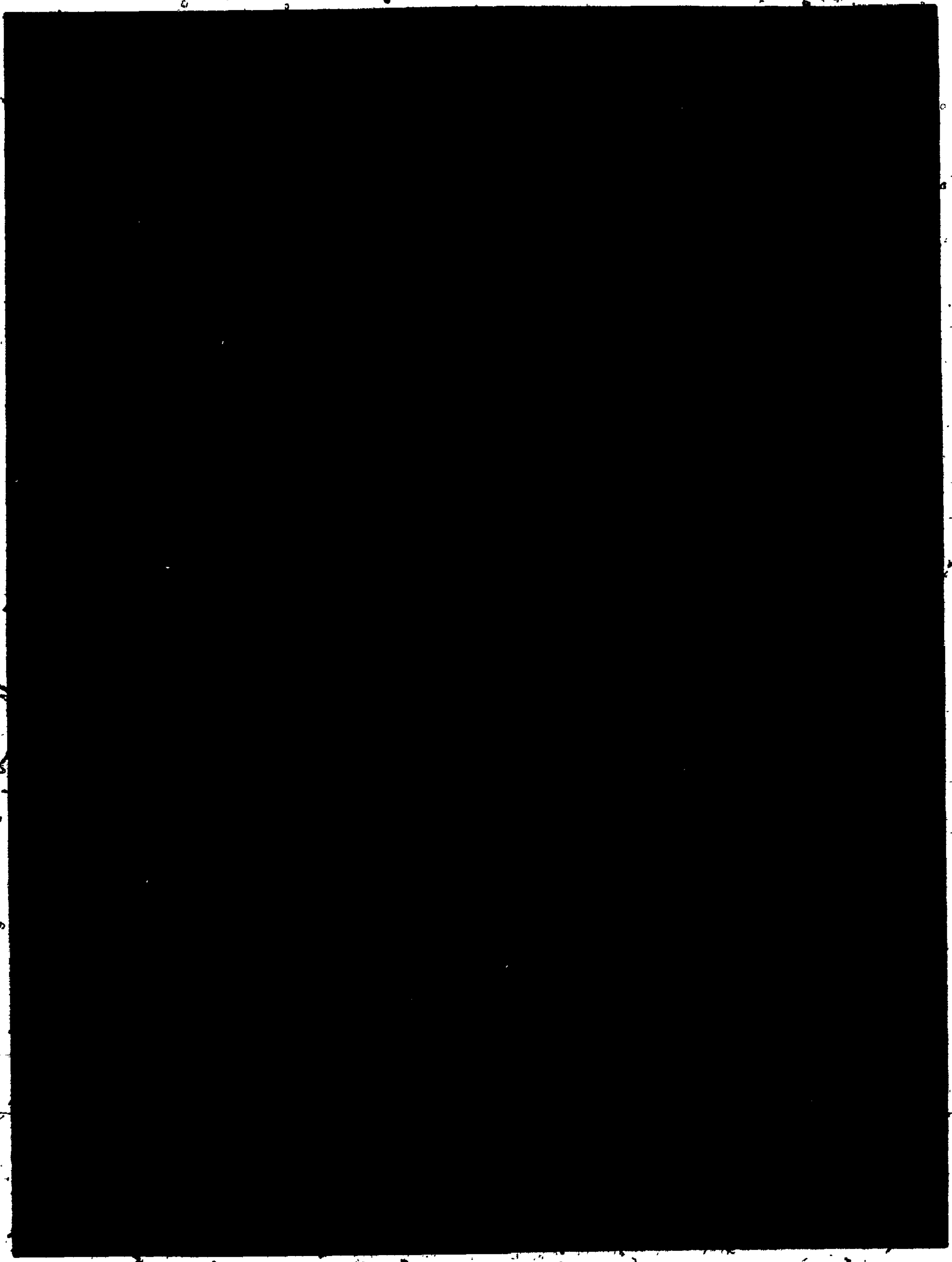

Plate 22

Plate 23

Figs. 1-15, 20-25	*Acanthoparypha echinoderma* Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.
1-4	Dorsal, posterior, lateral, and ventral views of incomplete thorax and pygidium, RL 0891, X 8.8, A 125.
5-9	Dorsal, lateral, and anterior views, X 5, and oblique lateral and interior views, X 8, of incomplete cephalon, Holotype, RL 0263, A 125.
10	Dorsal view of slightly distorted cranidium, RL 0862, X 6, P 1497.
11	Dorsal view of partial cranidium, RL 0534, X 7.3, P 1512.
12,13	Dorsal and lateral views of partial cranidium, RL 0533, X 6, P 1512.
14	Dorsal view of small pygidium, RL 0876, X 7, P 1512.
15	Dorsal view of small cranidium, RL 0535, X 7.9, P 1512.
20,21	Dorsal and posterior views of small pygidium, RL 0536, X 8, P 1512.
22	Dorsal view of thoracic segment (questionably assigned to this species), RL 0538, X 5.9, P 1512.
23	Ventral view of incomplete pygidium, RL 0537, X 8, P 1512.
24,25	Dorsal and ventral views of enrolled meraspid individual, UA 1840, X 5.5, A 115.
Figs. 16-19	*Pandaspinapyga dactyla* Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.
16,17	Dorsal and ventral views of incomplete pygidium, GSC 40407, X 2.2, P 1485.
18,19	Dorsal and ventral views of pygidium, Holotype, UA 1339, X 5.5, A 125.
Figs. 26-43	*Heliomeroides teres* Evitt. Lower Esbataottine Formation, Sunblood Range.
26-30	Dorsal, anterior, ventral, posterior, and lateral views of cranidium, GSC 40388, X 7.1, P 1485.
31	Dorsal view of small cranidium, RL 0865, X 10, P 1485.
32	Dorsal view of incomplete pygidium, UA 134[illegible] X 7, A 115.
33,34	Dorsal and posterior view of pygidium, GSC 40389, X 9, P 1485.
35	Dorsal view of incomplete thoracic segment, UA 1342, X 7.5, A 115.

36 Dorsal view of incomplete thoracic segment, RL 0867, X 10, P 1485.

37 Ventral view of incomplete thoracic segment, RL 0866, X 10, P 1485.

38,39 Dorsal and lateral views of small cranidium, RL 0792, X 7, P 1485.

40 Oblique view of free cheek, RL 0868, X 10, P 1485.

41 Dorsal view of small incomplete cranidium, UA 1343, X 7.5, A 115.

42 Oblique view of free cheek, UA 1344, X 7, A 115.

43 Dorsal view of meraspid cranidium, UA 1345, X 46, A 115.

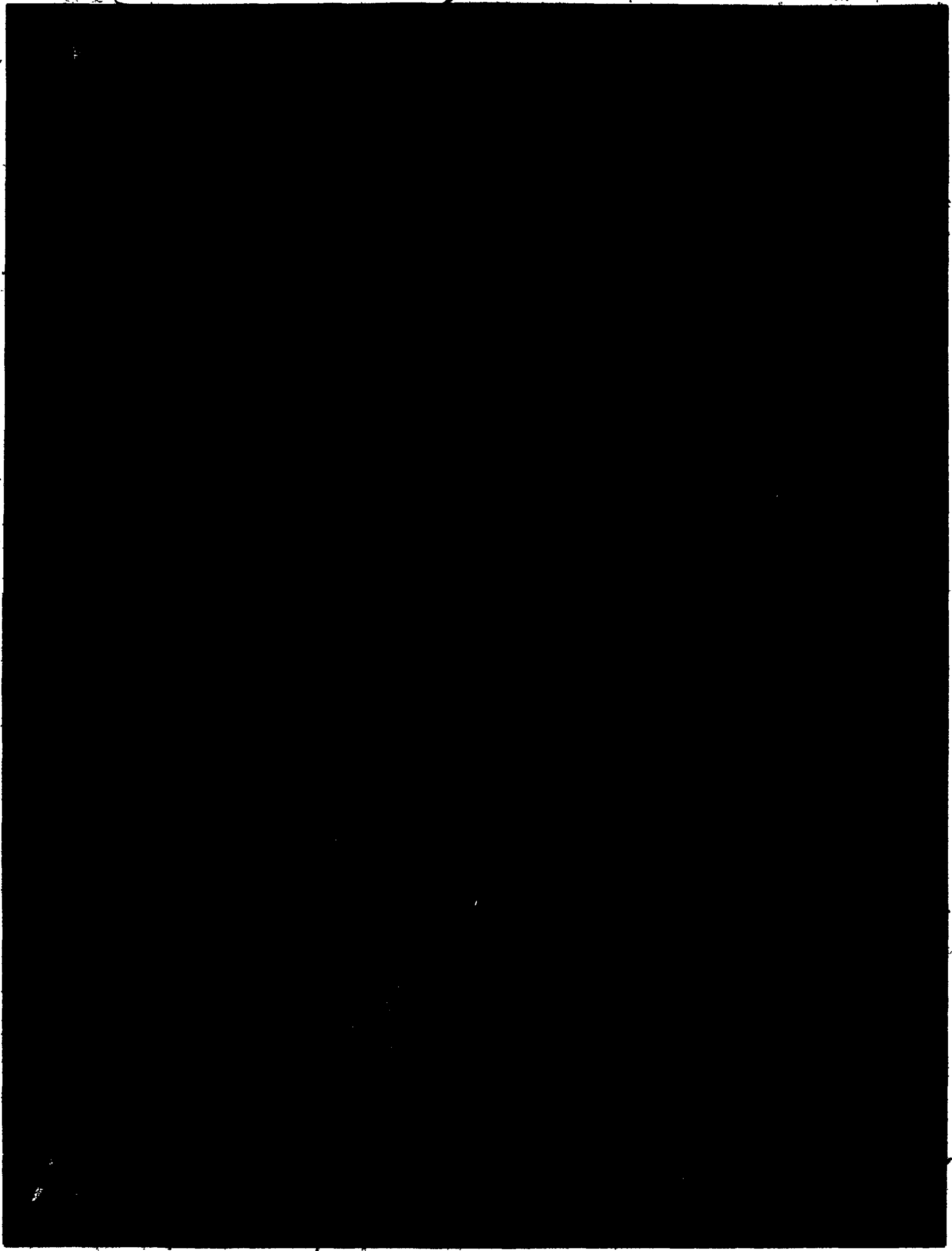

Plate 23

Plate 24

Figs. 1-19 Acanthoparypha? goniopyga n. sp. Lower Whittaker Formation. Funeral Range and Whittaker Range.

1-3 Dorsal, anterior, and lateral views of incomplete cranidium, RL 0259, X 4, H 1850.

4-6 Dorsal, lateral, and anterior views of incomplete cranidium, GSC 40449, X 6, C 655.

7-9 Dorsal, posterior, and lateral views of pygidium, Holotype, RL 0253, X 8, I 1275.

10 Dorsal view of free cheek, RL 0254, X 8, I 1275.

11 Dorsal view of free cheek, RL 0260, X 4, H 1850.

12 Dorsal view of incomplete cranidium, RL 0252 X 8, I 1275.

13,14 Dorsal and posterior views of pygidium, RL 0255, X 8, I 1275.

15 Dorsal view of incomplete cranidium, RL 0311, X 4.5, I 1410

16-18 Dorsal, posterior, and lateral views of pygidium, RL 0262, X 6, C 655.

19 Ventral view of incomplete thoracic segment, RL 0312, X 4.5, I 1410.

Figs. 20-29 Holia anacantha n. sp. Lower Whittaker Formation, Funeral Range. All from C 570-590.

20 Dorsal view of incomplete cranidium, RL 0347, X 6.2.

21 Dorsal view of small, incomplete cranidium, RL 0351, X 7.2.

22 Dorsal view of crushed cranidium, RL 0350, X 5.3.

23 Dorsal view of cranidial fragment showing base of genal spine, RL 0352, X 6.

24,25 Posterior and ventral views of incomplete pygidium, RL 0349, X 7.2.

26 Dorsal view of free cheek, RL 0353, X 7.

27-29 Lateral, dorsal, and posterior views of incomplete pygidium, Holotype, RL 0348, X 6.2.

Figs. 30-32 Pandaspinapyga cf. stubblefieldi (Bancroft). Upper Sunblood Formation, Sunblood Range. Both from P 1187.

30,31 Dorsal and posterior views of pygidium, RL 0257, X 8.

32 Dorsal view of fragment of cranidium, RL 0258, X 6.5.

Figs. 33-35 *Heliomera* cf. *sol* (Billings). Sunblood Formation, Mary Range. All from B 145. Dorsal, anterior, and lateral views of incomplete glabella, GSC 40334, X 4.8.

Figs. 36-58 *Sphaerexochus* *atacius* n. sp. Upper Esbataottine Formation, Sunblood Range. All from P 2038.

36-38,58 Dorsal (tilted), lateral, anterior, and dorsal views of cranidium, Holotype, GSC 40420, X 5.1, and 8.6.

39 Dorsal view of cranidium, RL 0470, X 5.5.

40 Dorsal view of small cranidium, RL 0472, X 6.2.

41 Dorsal view of small cranidium, RL 0473, X 6.2.

42,43 Posterior and dorsal views of pygidium, GSC 40421, X 5.6.

44 Dorsal view of pygidium, RL 0475, X 5.6.

45 Dorsal view of small pygidium, RL 0477, X 6.2.

46 Ventral view of pygidium, RL 0476, X 5.6.

47 Ventral view of hypostome, RL 0478, X 6.5.

48,49 Dorsal and posterior views of hypostome, RL 0479, X 6.2.

50 Oblique lateral view of free cheek, RL 0480, X 7.

51 Interior view of free cheek, RL 0481, X 8.3.

52,53 Posterior and dorsal view of thoracic segment, RL 0482, X 5.1.

54,55 Ventral and oblique lateral views of thoracic segment, RL 0483, X 5.

56,57 Ventral and posterior view of cranidium, RL 0471, X 5.

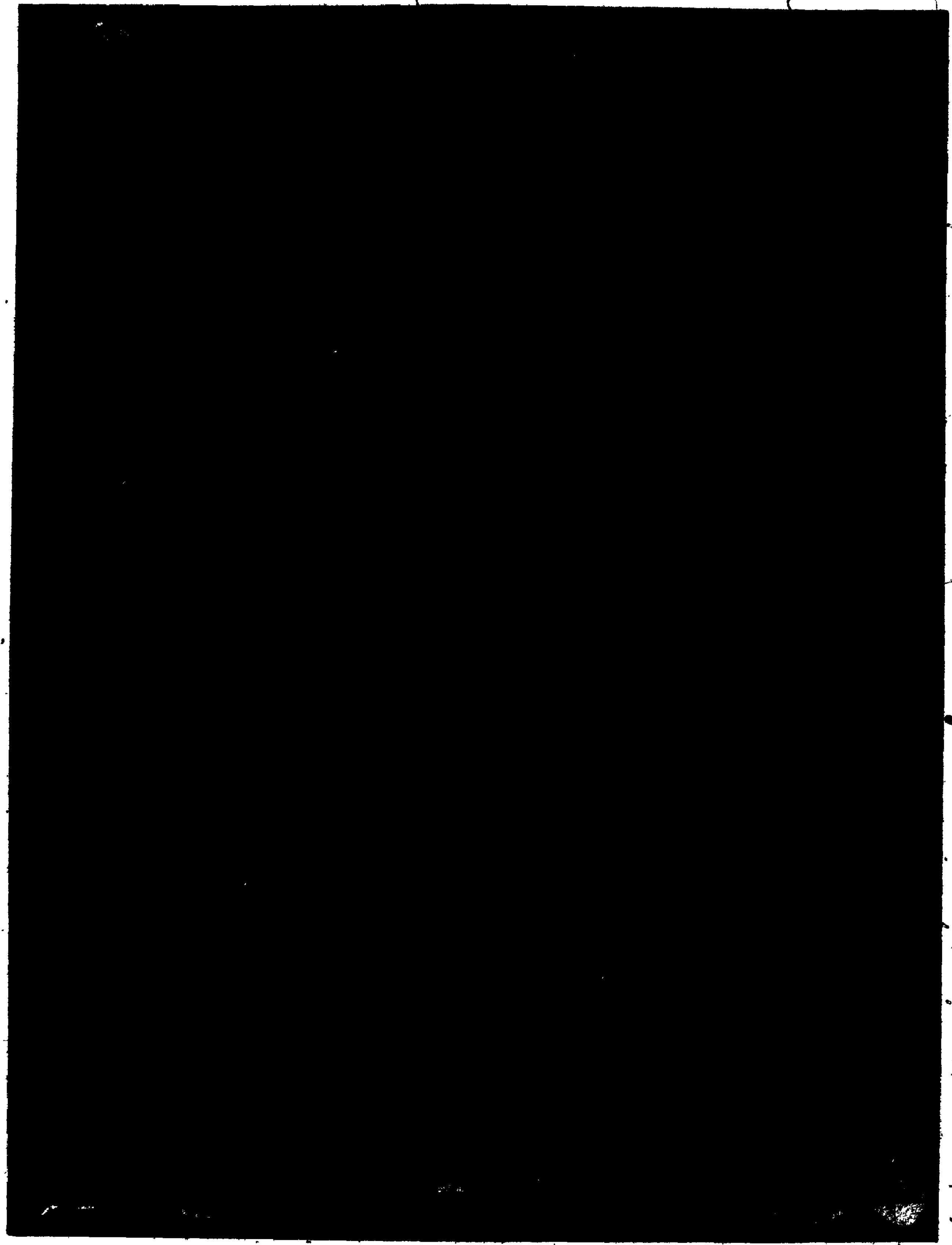

Plate 24

Plate 25

Figs. 1-48 *Sphaerexochus arenosus* Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.

1,2,45 Dorsal and lateral views(X 5.5) and detail of glabella,(X 12), UA 1384, A 125.

3,4 Dorsal (tilted) and lateral views of cranidium, UA 1385, X 5.5, A 125.

5 Posterior view of cranidium, UA 1386, X 5.5, A 125.

6,7,48 Oblique ventral and lateral views of incomplete cephalon, UA 1387, X 5.5, and X 12, A 115.

8,9 Anterior and lateral views of cranidium, GSC 40384, X 6.5, P 1497.

10-12 Ventral view showing position of rostral plate (X 15), lateral and oblique ventral (X 5.5), views of incomplete cephalon, Holotype, UA 1388, A 125.

13 Anterior view of small cephalon, UA 1389, X 5.5, A 115.

14,15 Dorsal (tilted) and anterior views of cranidium, RL 0510, X 6.6, P 1497.

16 Lateral view of cranidium, UA 1390, X 5.5, A 125.

17,18 Lateral and dorsal (tilted) views of cranidium, UA 1391, X 5.5, A 125.

19 Dorsal view of cranidium, UA 1392, X 5.5, A 125.

20 Dorsal view of pygidium, UA 1393, X 5.5, A 125.

21 Ventral view of cranidium, UA 1394, X 5.5, A 125.

22 Dorsal view of pygidium, UA 1396, X 5.5, A 125.

23 Ventral view of pygidium, UA 1397, X 5.5, A 125.

24 Dorsal view of pygidium and incomplete thorax, UA 1398, X 5.5, A 125.

25,26 Dorsal and ventral views of pygidium and two thoracic segments, UA 1399, X 5.5, A 125.

27 Lateral view of cephalon, UA 1395, X 5.5, A 115.

28,29 Ventral and dorsal views of pygidium, UA 1400, X 5.5, A 125.

30 Dorsal view of pygidium, UA 1401, X 5.5, A 115.

31 Dorsal view of pygidium, UA 1402, X 5.5, A 115.

32 Ventral view of hypostome, UA 1403, X 12, A 125.

33 Dorsal view of hypostome, UA 1404, X 12, A 125.

34 Anterior view of thoracic segment, UA 1405, X 5.5, A 125.

35 Interior view of free cheek, UA 1406, X 5.5, A 125.

36,46 Interior and lateral views of free cheek, UA 1407, X 5.5, and X 12, A 125.

37 Dorsal view of hypostome, UA 1408, X 12, A 125.

38 Ventral view of thoracic segment, RL 0518, X 7.2, P 1497.

39,40 Dorsal and posterior views of thoracic segment, UA 1409, X 5.5, A 115.

41 Ventral view of hypostome, RL 0514, X 7.7, P 1497.

42 Ventral view of hypostome,UA 1410, X 12, A 125.

43,44 Dorsal and posterior view of thoracic segment, RL 0517, X 7.2, P 1497.

47 Dorsal view of pygidium, UA 1411, X 39, A 125.

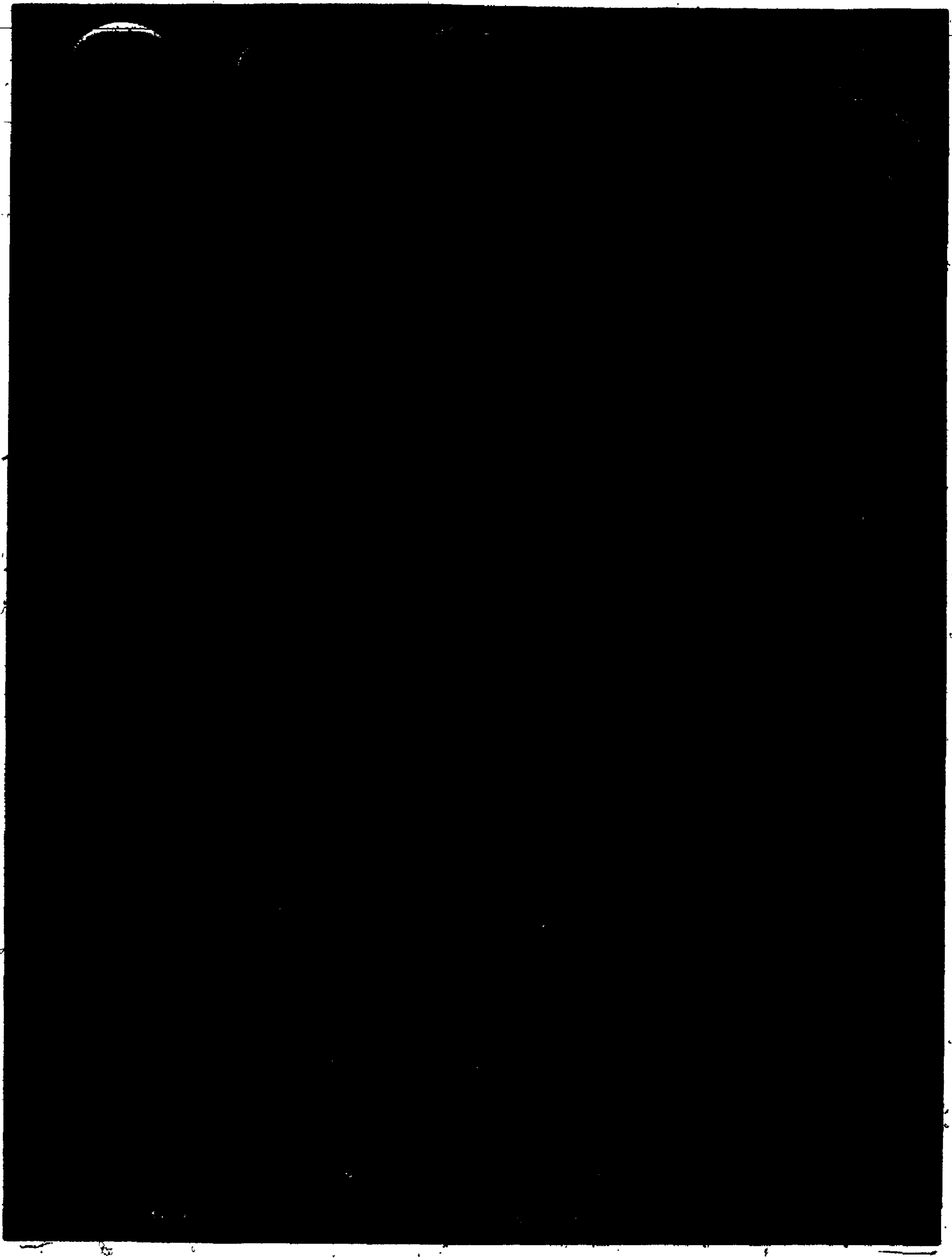

Plate 25

Plate 26

Figs. 1-14 *Cybellela? thor* n. sp. Sunblood Formation, southwest of South Nahanni River. All from GSC loc. 58678.

1-3 Dorsal, lateral, and ventral views of incomplete cranidium, Holotype, RL 0374, X 9.5.
4,5 Dorsal and anterior views of incomplete cranidium, RL 0374, X 9.5.
6 Dorsal view of incomplete cranidium, RL 0378, X 10.6.
7,8 Ventral and dorsal views of incomplete cranidium, RL 0376, X 9.5.
9-11 Posterior, lateral, and dorsal views of pygidium, RL 0380, X 8.1.
12 Oblique dorsal view of pygidium, RL 0377, X 8.6.
13,14 Lateral views of free cheek, RL 0379, X 7.

Figs. 15-36 *Cybeloides anna* n. sp. Upper Sunblood Formation, Sunblood Range. All from P 1187.

15,16,28 Anterior, dorsal, and detailed views of incomplete cranidium, Holotype, RL 0446, X 4.1 and 11.
17-19 Posterior, dorsal, and lateral views of pygidium, RL 0449, X 5.
20 Interior view of pygidium, RL 0450, X 5.2.
21 Oblique dorsal view of free cheek, RL 0455, X 5.1.
22,23 Ventral and lateral views of hypostome, RL 0452, X 6.
24 Dorsal view of thoracic segment (macropleura), RL 0458, X 5.
25 Ventral view of thoracic segment, RL 0457, X 5.
26,27 Dorsal and lateral views of incomplete cranidium, RL 0447, X 4.1.
29 Oblique dorsal view of small pygidium, RL 0451, X 6.6.
30 Exterior view of rostral plate, RL 0454, X 6.3.
31,32,36 Ventral and oblique posterior views of incomplete cranidium, RL 0448, X 4.1, and 7.3.
33,34 Dorsal and oblique anterior views of incomplete hypostome, RL 0453, X 6.
35 Interior view of free cheek, RL 0456, X 5.

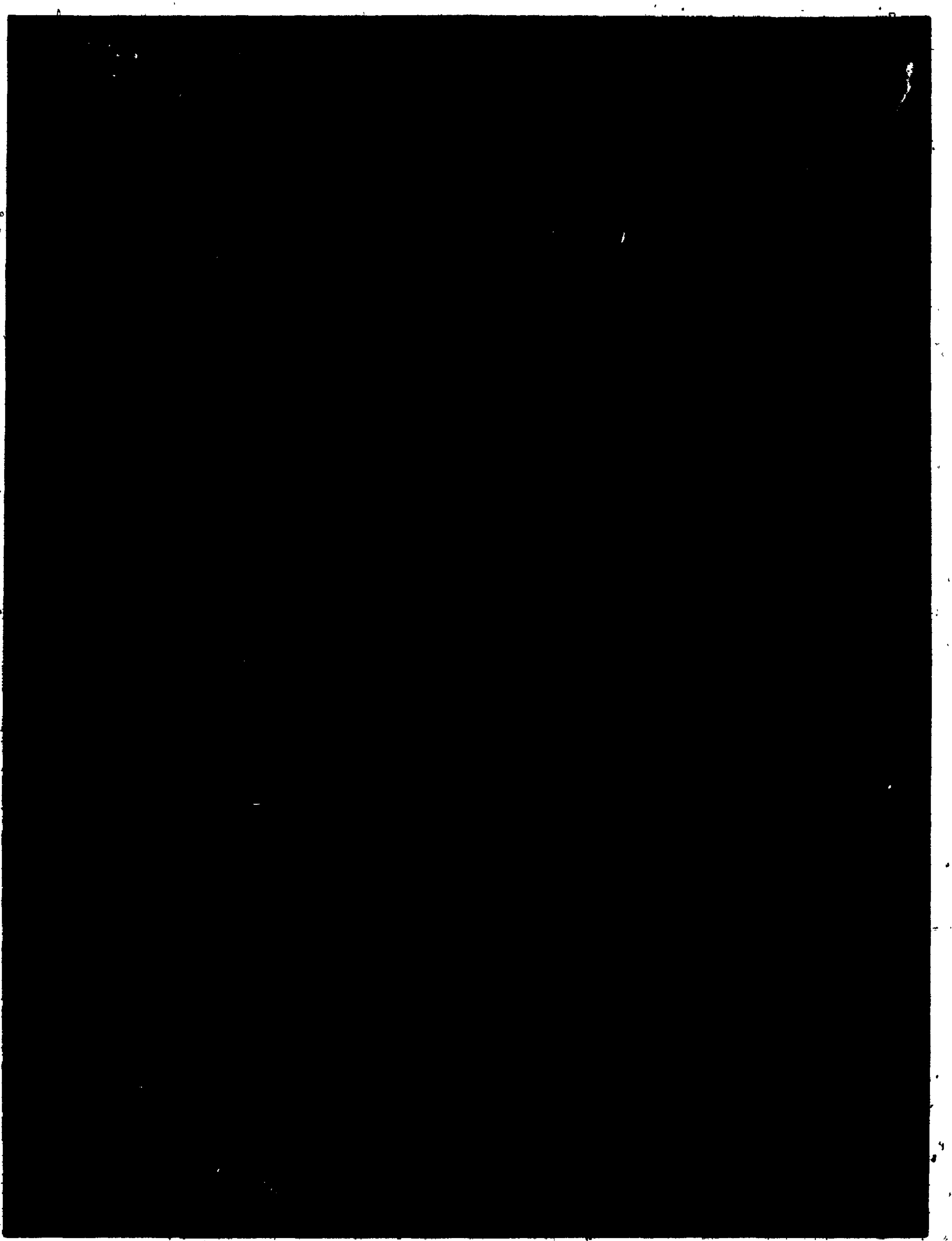

Plate 426

Plate 27

Figs. 1-43	*Cybeloides cimelia* Chatterton and Ludvigsen, ms. Lower Esbataottine Formation, Sunblood Range.
1,2	Dorsal and lateral views of cranidium, UA 1357, X 5.5, A 125.
3	Dorsal view of incomplete cranidium and two thoracic segments, UA 1359, X 5.5, A 115.
4-6	Anterior, lateral, and dorsal views of cranidium, GSC 40401, X 4.1, P 1497.
7-10	Anterior, dorsal, oblique posterior, and oblique lateral views of cranidium, Holotype, UA 1358, X 5.5, A 115.
11	Anterior view of incomplete cranidium, RL 0855, X 7, P 1485.
12	Dorsal view of incomplete cranidium, UA 1361, X 5.5, A 115.
13	Ventral view of cranidium, RL 0460, X 4.1, P 1497.
14	Oblique view of free cheek, RL 0463, X 6.3, P 1497.
15	Oblique view of free cheek, UA 1362, X 5.5, A 125.
16	Dorsal view of incomplete cranidium, UA 1363, X 5.5, A 125.
17	Oblique view of free cheek, UA 1364, X 5.5, A 115.
18	Interior view of free cheek, RL 0464, X 6, P 1497.
19-21	Dorsal, oblique, and lateral views of pygidium, UA 1365, X 5.5, A 115.
22,23	Lateral and oblique dorsal views of pygidium, UA 1366, X 5.5, A 115.
24,25	Ventral and lateral views of hypostome, RL 0465, X 6, P 1497.
26	Ventral view of hypostome, UA 1367, X 5.5, A 115.
27	Ventral view of pygidium, RL 0462, X 6, P 1497.
28-30	Dorsal, lateral, and posterior views of pygidium, GSC 40402, X 6, P 1497.
31,32	Dorsal and anterior views of thoracic segment, RL 0846, X 6.5, P 1485.
33,34	Posterior and dorsal views of thoracic segment, RL 0467, X 5, P 1497.
35	Ventral view of hypostome, UA 1369, X 5.5, A 125.
36	Oblique ventral view of hypostome, UA 1371, X 5.5, A 125.
37,38	Dorsal and posterior view of thoracic segment, RL 0847, X 6.5, P 1485.

39,40 Ventral and lateral view of thoracic segment, RL 0848, X 6.5, P 1485.

41 Dorsal view of thoracic segment, UA 1370, X 5.5, A 115.

42 Ventral view of thoracic segment, RL 0466, X 5, P 1497.

43 Dorsal view of thoracic segment with macropleural spine, UA 1368, X 5.5, A 115.

6 OF/DE 6

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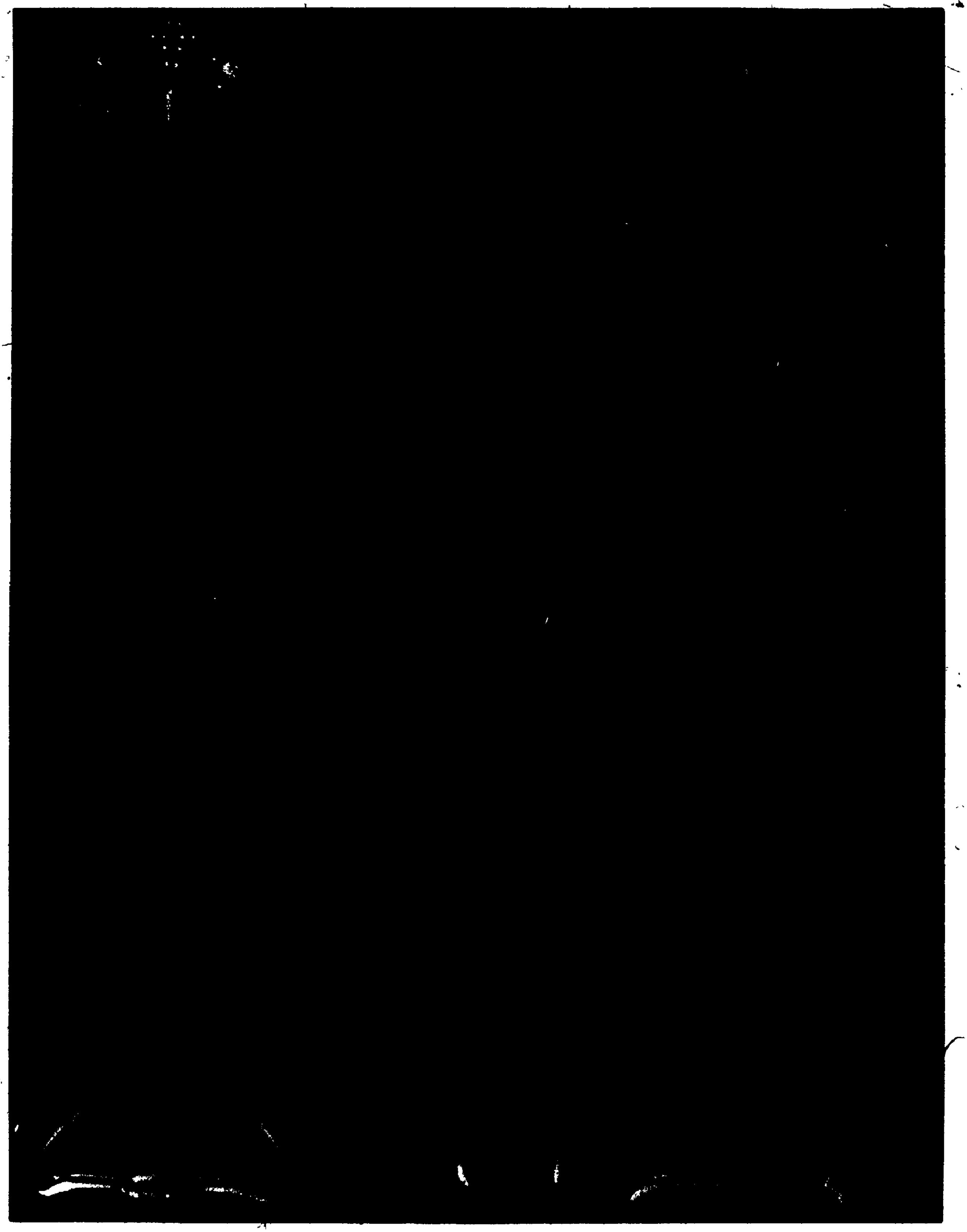

Plate 27

Plate 28

Figs. 1-41	Cybeloides cimelia Chatterton and Ludvigsen, ms. Esbataottine Formation, Sunblood Range and Flood Creek.
1-3	Anterior, dorsal, and lateral views of incomplete cranidium, GSC 40417, X 3.3, P 2038. Note bryozoan overgrowth on occipital spine.
4,5	Ventral and oblique posterior views of incomplete cranidium, RL 0435, X 3.1, P 2038.
6	Dorsal view of incomplete cranidium, RL 0436, X 3.3, P 2038.
7,8	Dorsal and oblique anterior views of glabella, RL 0445, X 7.2, P 2038. Note bisected tubercle pair on anterior margin.
9-11	Lateral, posterior, and dorsal views of pygidium, GSC 40418, X 4.1, P 2038.
12	Interior view of free cheek, RL 0443, X 4, P 2038.
13,14	Dorsal and lateral views of free cheek, RL 0438, X 4, P 2038.
15,16	Dorsal and posterior views of thoracic segment, RL 0441, X 4.3, P 2038.
17-19	Posterior, dorsal, and lateral views of thoracic segment, RL 0443, X 4, P 2038.
20-22	Ventral, lateral, and posterior views of hypostome, RL 0439, X 5.6, P 2038.
23,24	Dorsal and oblique anterior views of hypostome, RL 0440, X 5, P 2038.
25	Lateral view of thoracic segment, RL 0444, X 3.6, P 2038.
26	Dorsal view of incomplete cranidium, RL 0663, X 3, G 3195.
27,28	Dorsal and lateral views of pygidium, RL 0664, X 5.3, G 3195.
29	Dorsal view of free cheek, RL 0665, X 6, G 3195.
30	Ventral view of hypostome, RL 0666, X 6, G 3195.
31	Dorsal view of incomplete cranidium, RL 0855, X 7, P 1485, (same specimen as Pl. 27, fig. 11).
32	Ventral view of incomplete cranidium, RL 0857, X 8, P 1485.
33	Dorsal view of thoracic segment (macropleura), RL 0858, X 5, P 1485.
34	Oblique dorsal view of free cheek, RL 0859, X 7, P 1485.
35,36	Lateral and dorsal views of pygidium, RL 0861, X 8, P 1485.
37	Dorsal view of thoracic segment, RL 0860, X 7, P 1485.

38 Dorsal view of incomplete cranidium, RL 1052, X 6.2, A 365.

39 Oblique dorsal view of pygidium, RL 1053, X 6.2, A 365.

40 Ventral view of hypostome, RL 1055, X 6.2, A 365.

41 Oblique lateral view of free cheek, RL 1054, X 6.2, A 365.

Figs. 42-48 *Encrinuroides rarus* (Walcott). Upper Esbataottine Formation, Sunblood Range.

42,43 Anterior and dorsal views of incomplete cranidium, RL 1051, X 5.5, A 385.

44 Dorsal view of pygidium, RL 1050, X 6, A 615.

45-47 Dorsal, posterior, and lateral views of pygidium, RL 1049, X 6, A 615.

48 Dorsal view of incomplete cranidium, RL 1048, X 6, A 615.

Figs. 49,50 *Kawina* sp. Sunblood Formation, Sunblood Range. From P 55. Dorsal and posterior views of pygidium, RL 0627, X 7.3.

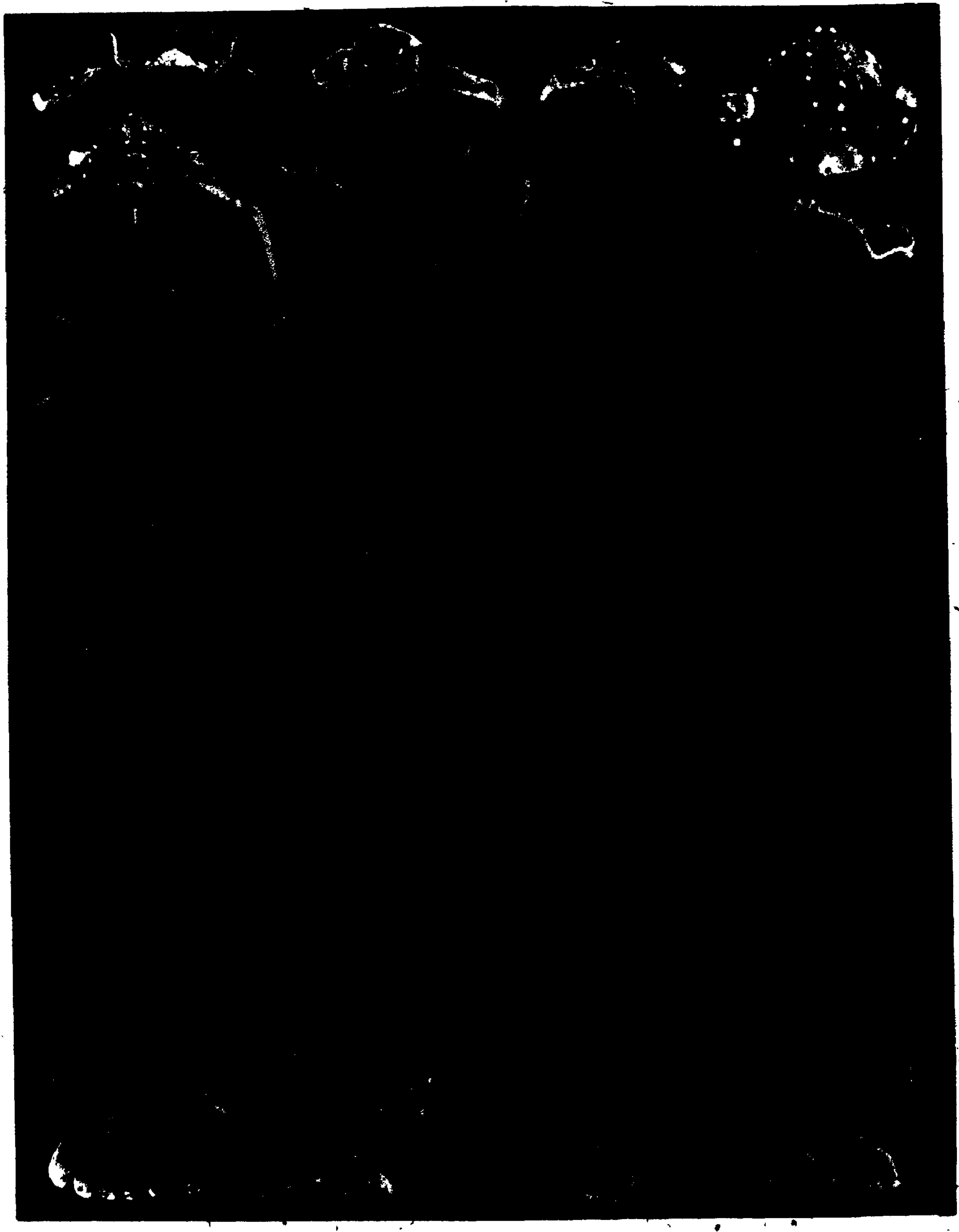

Plate 28

Plate 29

Figs. 1-43	Encrinuroides rarus (Walcott). Lower Esbataottine Formation, Sunblood Range.
1	Dorsal view of cranidium, UA 1372, X 5.5, A 125.
2	Dorsal view of cranidium, UA 1373, X 5.5, A 125.
3-8	Lateral, anterior, dorsal, ventral (X 4.2), oblique lateral (X 5.5), and oblique interior (X 5.7) views of incomplete cephalon, RL 0266, P 1497.
9,10	Dorsal and ventral view of hypostome, UA 1375, X 5.5, A 125.
11	Oblique view of free cheek, UA 1374, X 5.5, A 125.
12	Interior view of free cheek, UA 1376, X 5.5, A 125.
13-15	Oblique dorsal, posterior, and lateral views of pygidium, UA 1378, X 5.5, A 125.
16-18	Dorsal, posterior, and lateral views of pygidium, GSC 40406, X 4.6, P 1497.
19	Ventral view of pygidium, UA 1380, X 5.5, A 125.
20	Dorsal view of cranidium, UA 1377, X 5.5, A 125.
21	Oblique view of free cheek, UA 1379, X 5.5, A 125.
22	Ventral view of pygidium, RL 0269, X 4.8, P 1497.
23,24	Dorsal and anterior views of cranidium, GSC 40405, X 4.6, P 1497.
25-27	Ventral, lateral, and posterior views of hypostome, UA 1381, X 5.5, A 125.
28-30	Ventral, lateral, and posterior views of hypostome, RL 0270, X 6, P 1497.
31-33	Oblique dorsal, lateral, and dorsal views of pygidium, UA 1382, X 5.5, A 125.
34-36	Posterior, oblique lateral, and oblique anterior views of hypostome, RL 0271, X 8.4, P 1497.
37,38	Anterior and dorsal views of thoracic segment, RL 0272, X 5, P 1497.
39-41	Posterior, anterior, and dorsal views of thoracic segment, UA 1383, X 5.5, A 125.
42,43	Anterior and ventral views of thoracic segment, RL 0273, X 5, P 1497.
Figs. 44-46	Sphaerocoryphe cf. pemphis Lane. Lower Esbataottine Formation, Sunblood Range. Both from A 115.
44,45	Lateral and dorsal views of incomplete cranidium, X 7.
46	Ventral view of hypostome, X 7.

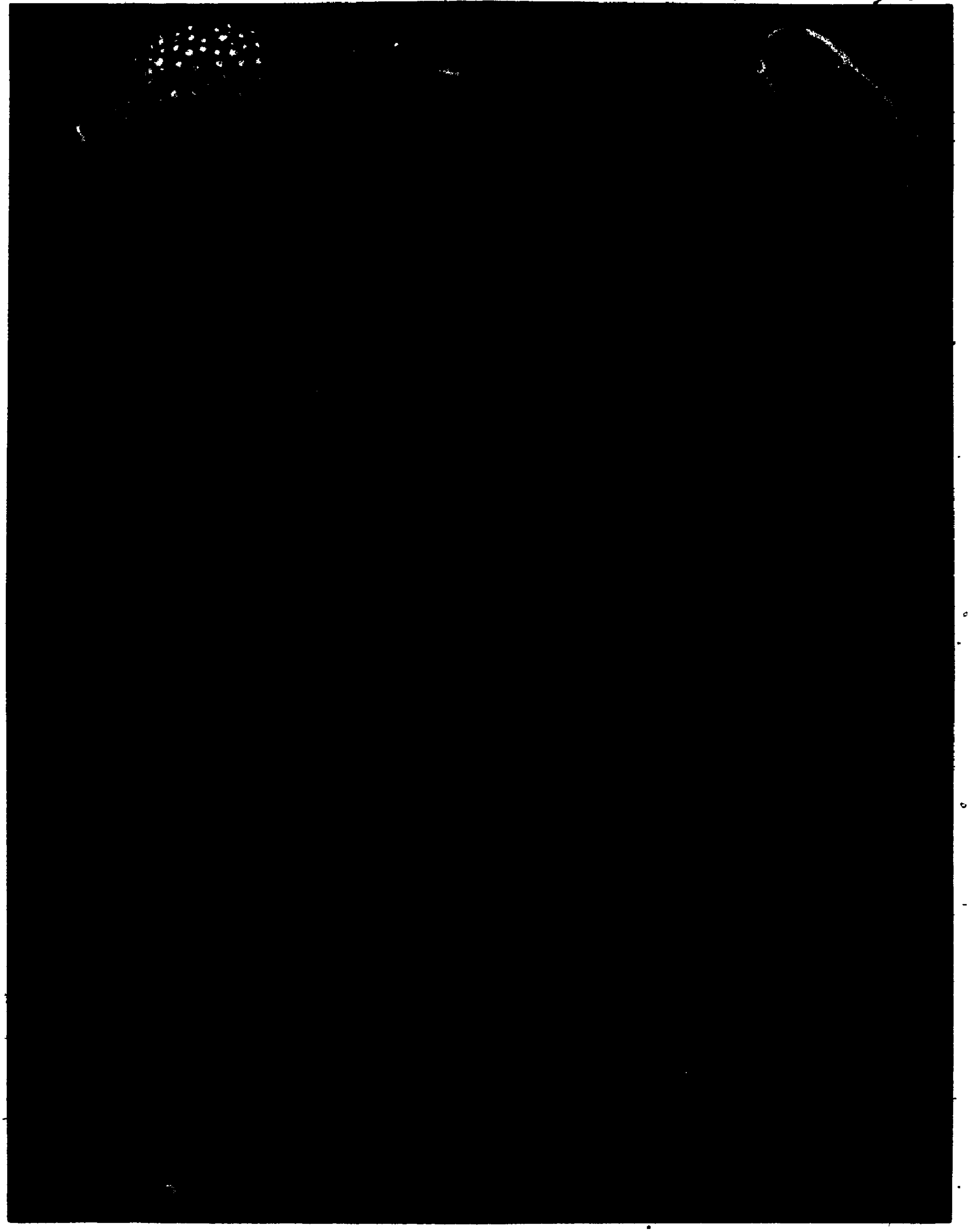

Plate 29

APPENDIX I

Diagrammatic lithology sections of Sections A, B, C, D, E, G, H, I, J, K, M, O, P, Q, and R. Formational assignments and level of fossil collections are indicated.

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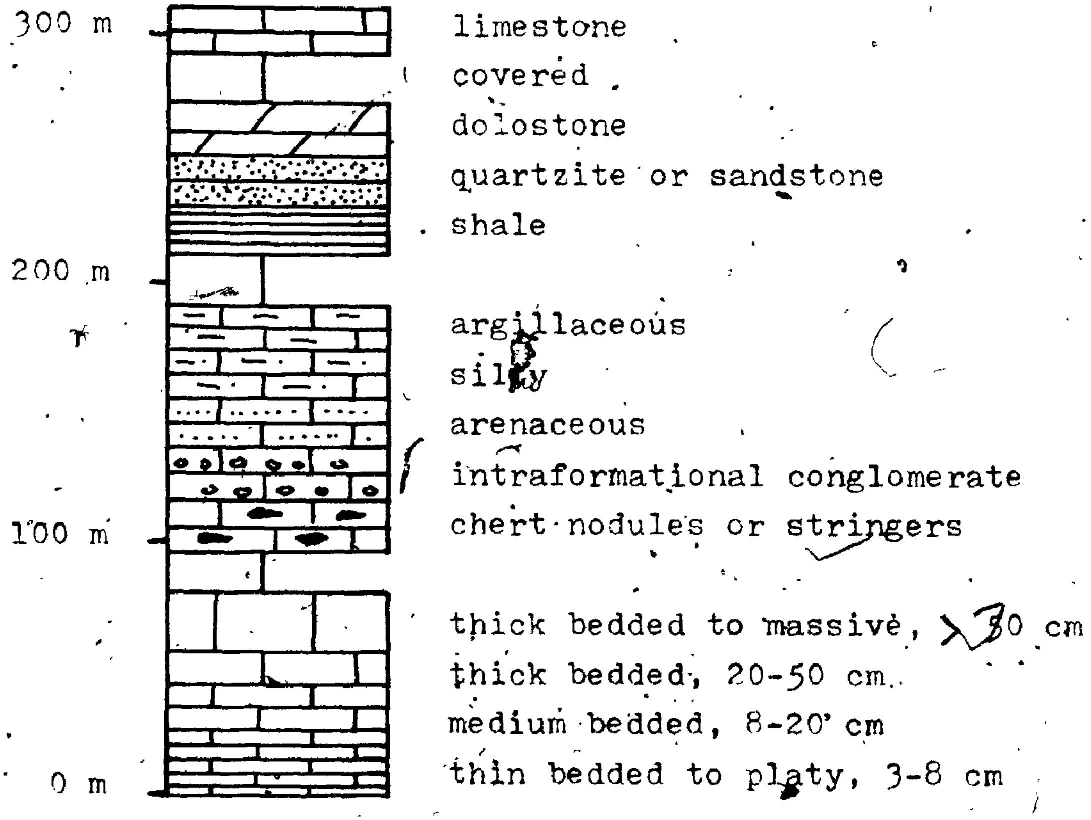
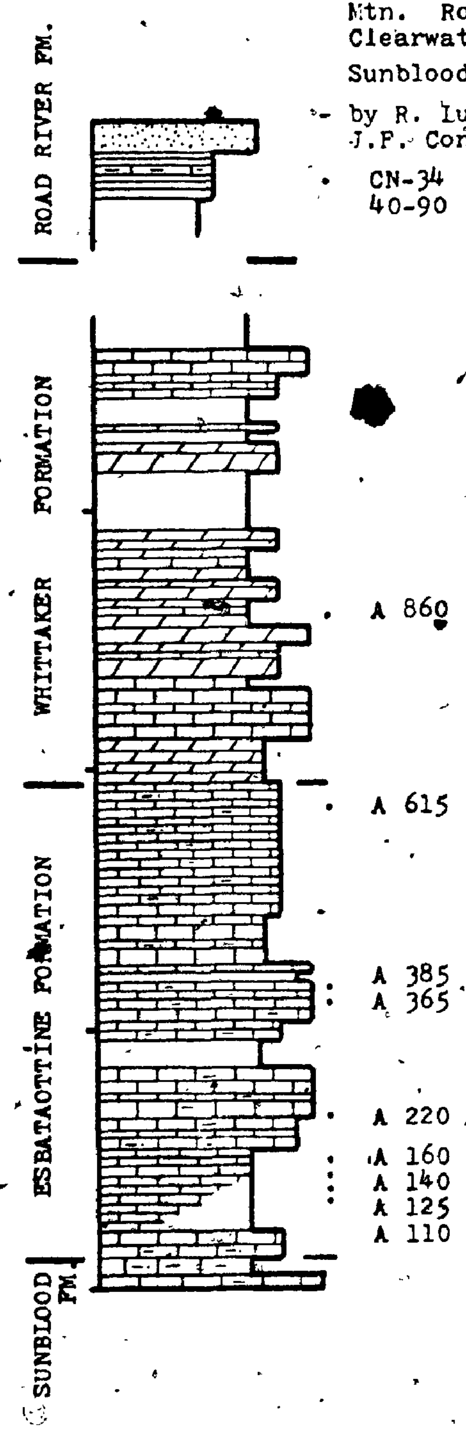


SECTION A SUNBLOOD RANGE

61° 31' N, 125° 44' W July, 1971

Air photo ref: A17440-19

- section started in top beds of Sunblood Fm., at cairn on Sunblood Mtn. Road River Fm. measured along Clearwater Creek, 10 km. SW of Sunblood Mtn.
- by R. Ludvigsen, J.W. Harrington, J.P. Conrad, B.D.E. Chatterton



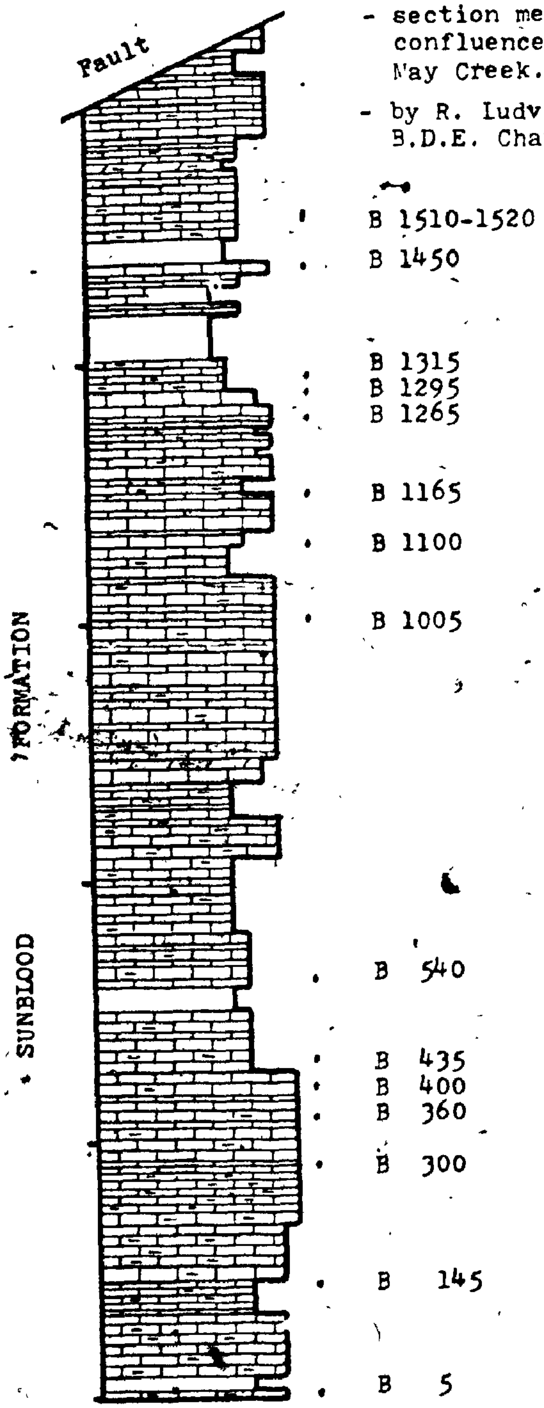
00464

SECTION B MARY RANGE

61° 19' N, 125° 23' W July, 1971

Air photo ref: A 17440-149

- section measured 10 km. SW of confluence of Mary River and May Creek.
- by R. Ludvigsen, B. Skinner, B.D.E. Chatterton

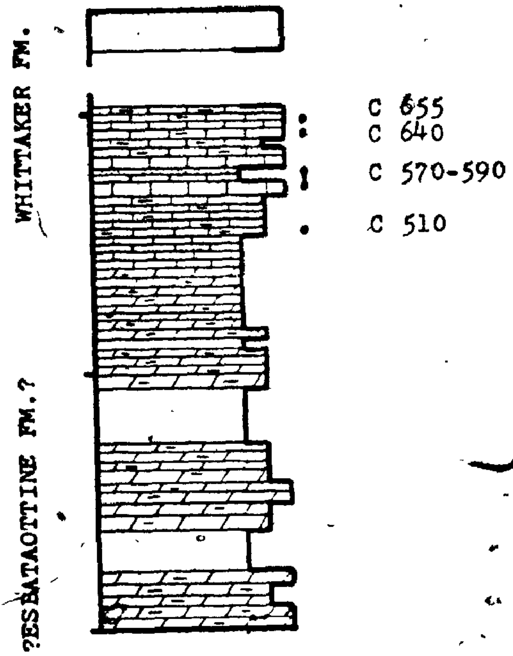


SECTION C FUNERAL RANGE

61° 31' N, 124° 52' W July, 1971

Air photo ref: A 12333-258

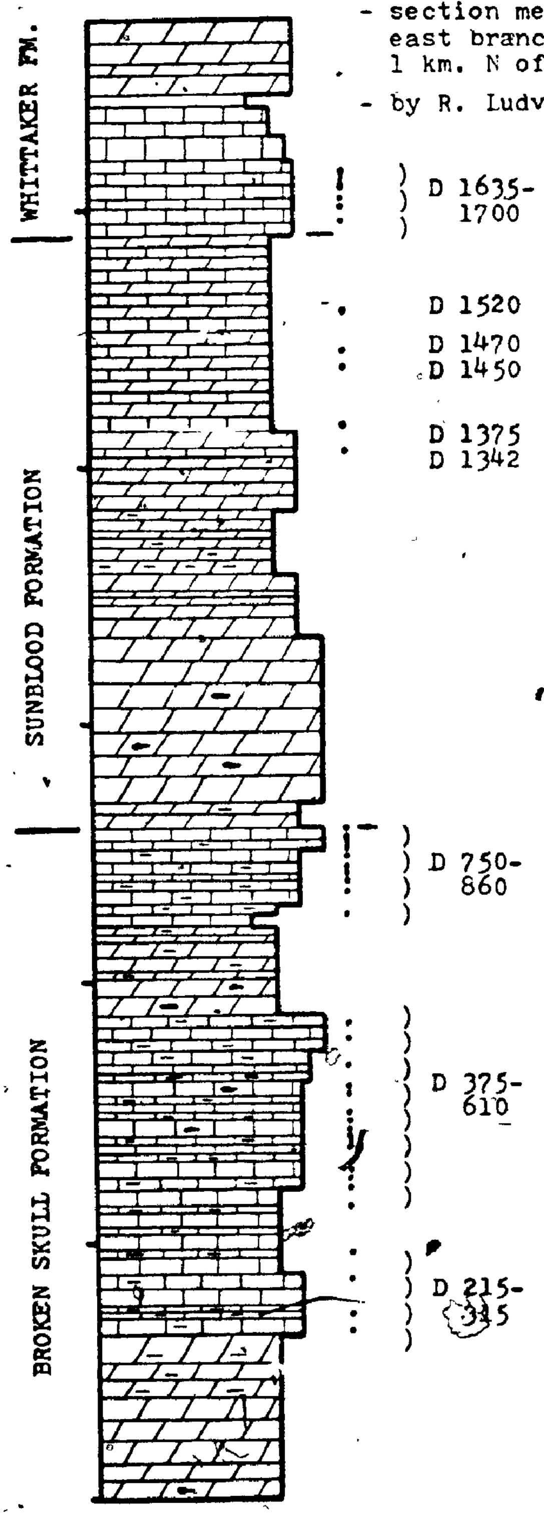
- section measured 6 km. west of Prairie Creek; started in core of drag fold above Gate Fault.
- by R. Ludvigsen, B.D.E. Chatterton



SECTION D NATLA RIVER

63° 09' N, 127° 58' W Aug., 1972

- section measured 10 km. E of east branch of Natla River, 1 km. N of peak 7257'.
- by R. Ludvigsen, D.G. Perry

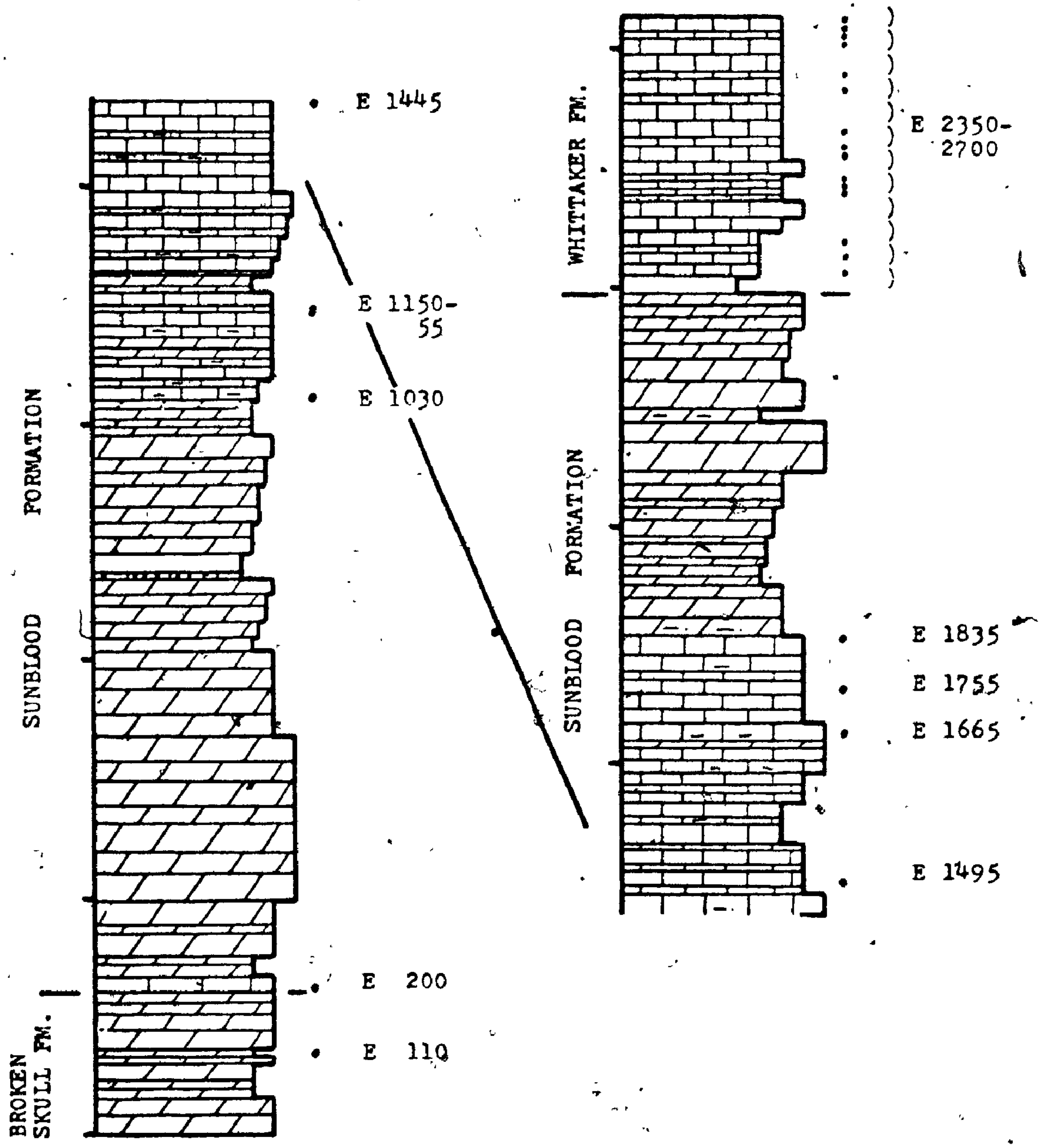


00467

SECTION E GLACIER LAKE

62° 10' N, 127° 25' W Aug., 1972

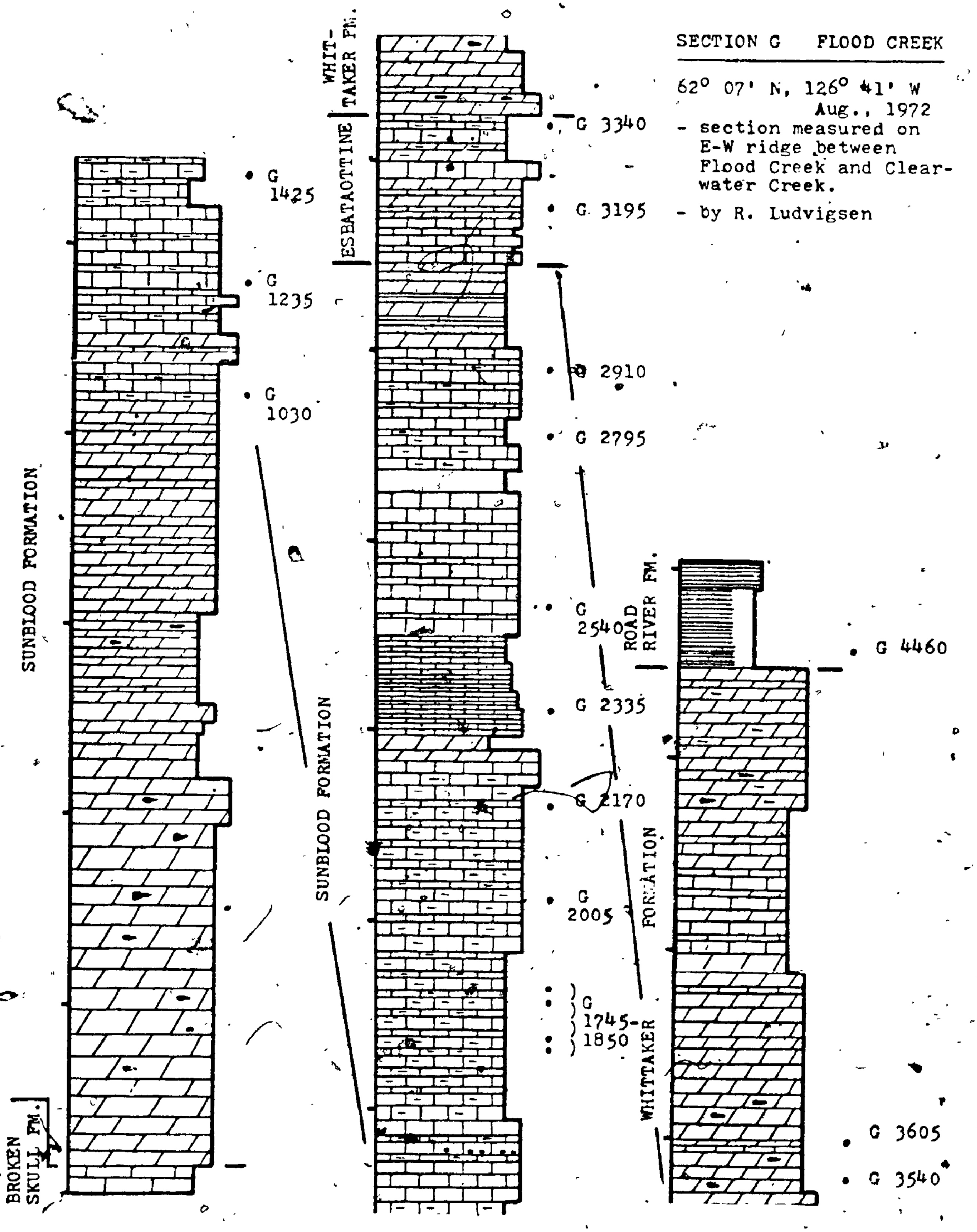
- section measured on scarp above South Nahanni River, 13 km. NE of Glacier Lake
- by R. Ludvigsen



00468

SECTION G FLOOD CREEK

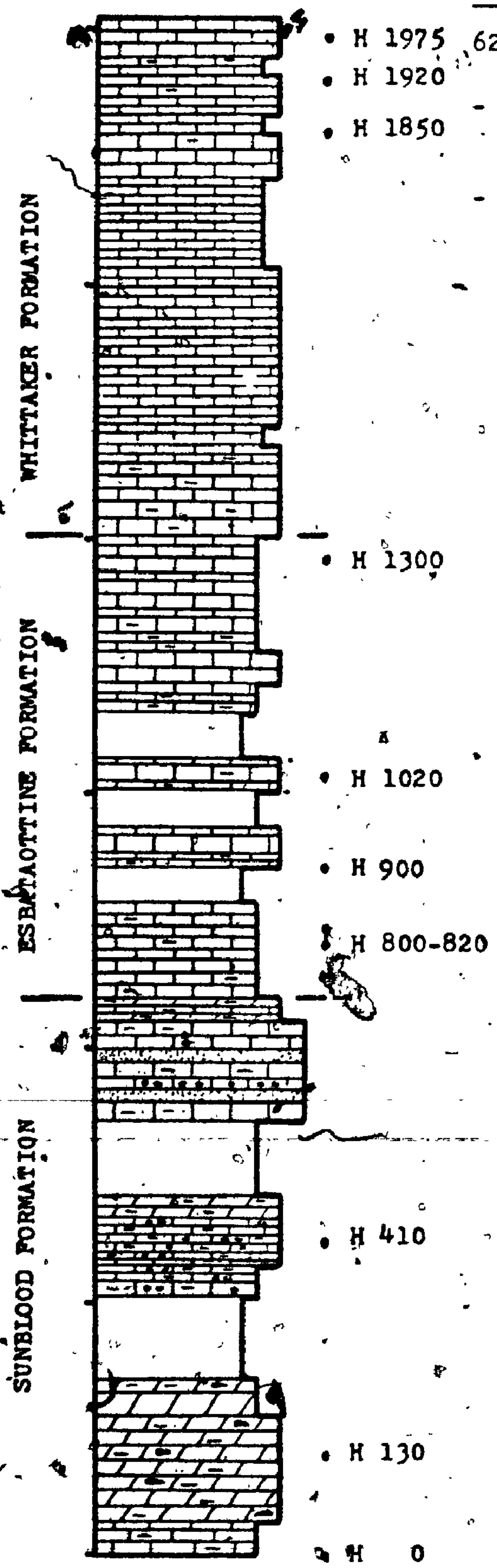
62° 07' N, 126° 41' W
Aug., 1972
- section measured on E-W ridge between Flood Creek and Clearwater Creek.
- by R. Ludvigsen



SECTION H WHITTAKER RANGE

62° 31' N, 124° 51' W
June, 1972.

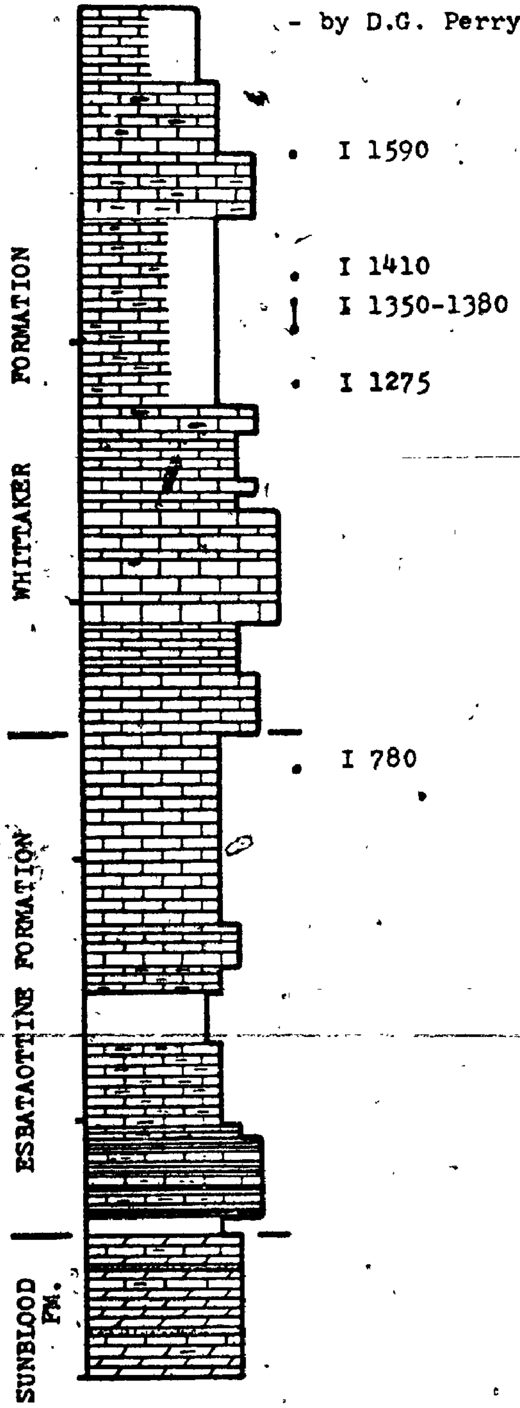
- section measured 5 km. NW of north tip of Trench Lake.
- by R. Ludvigsen, B.D.E. Chatterton



SECTION I WHITTAKER RANGE

62° 29' N, 124° 47' W June, 1972

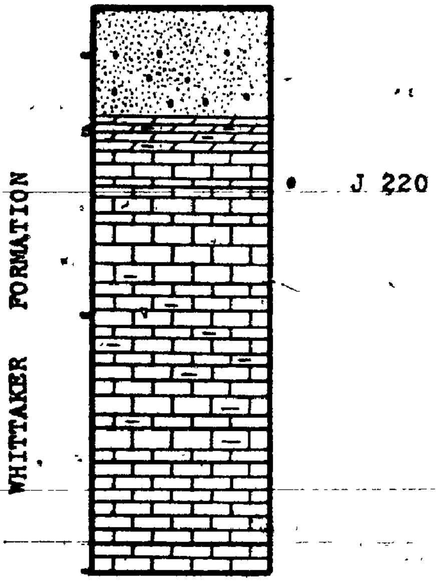
- section measured 6 km. W of Trench Lake.
- by D.G. Perry, A.C. Lenz



SECTION J FUNERAL RANGE

61°29' N, 125° 03' W July, 1971

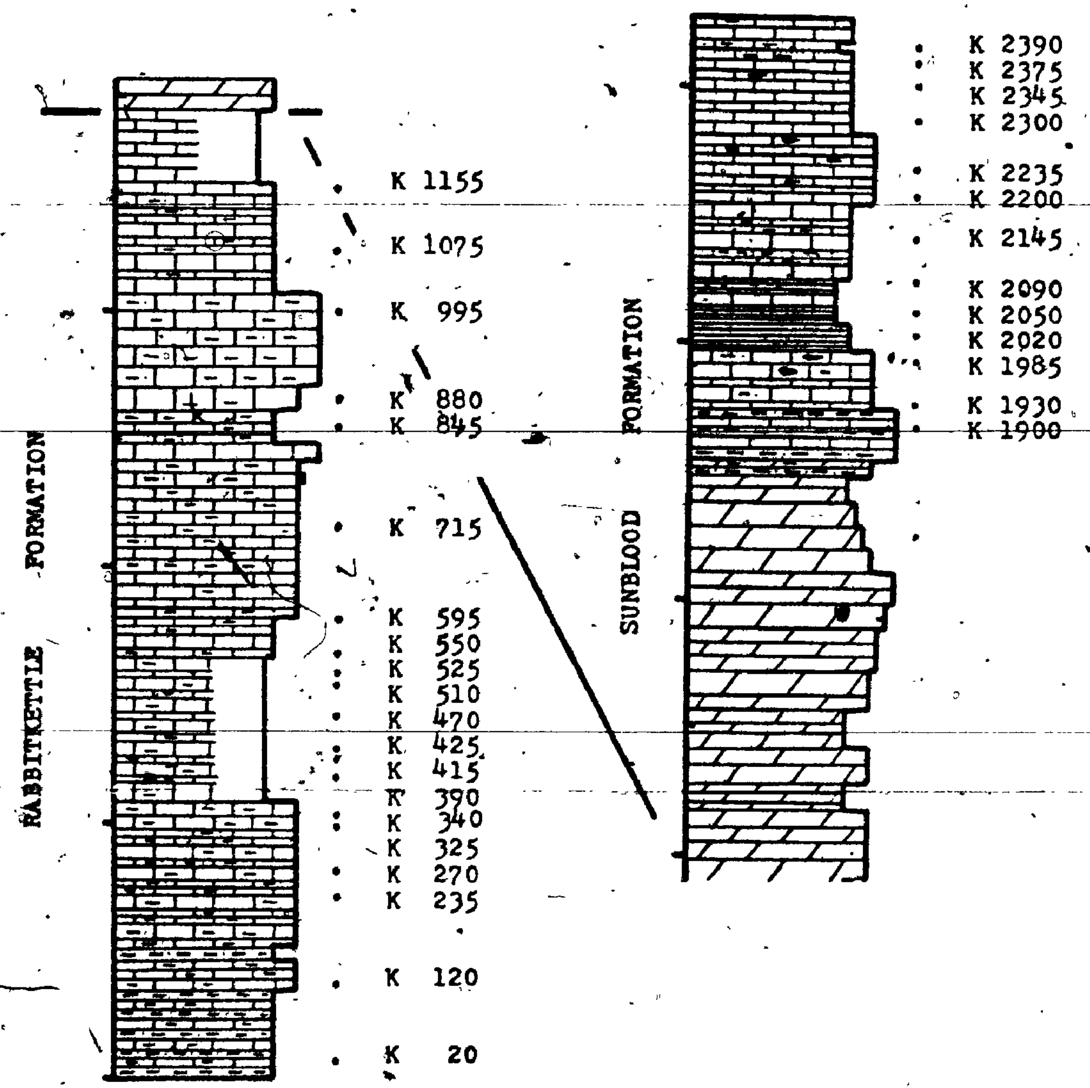
- section measured 11 km. NE of The Gate of the South Nahanni River.
- by B.D.E. Chatterton, J.E. Conrad



SECTION K BROKEN SKULL RIVER

62° 55' N, 128° 25' W Aug., 1972

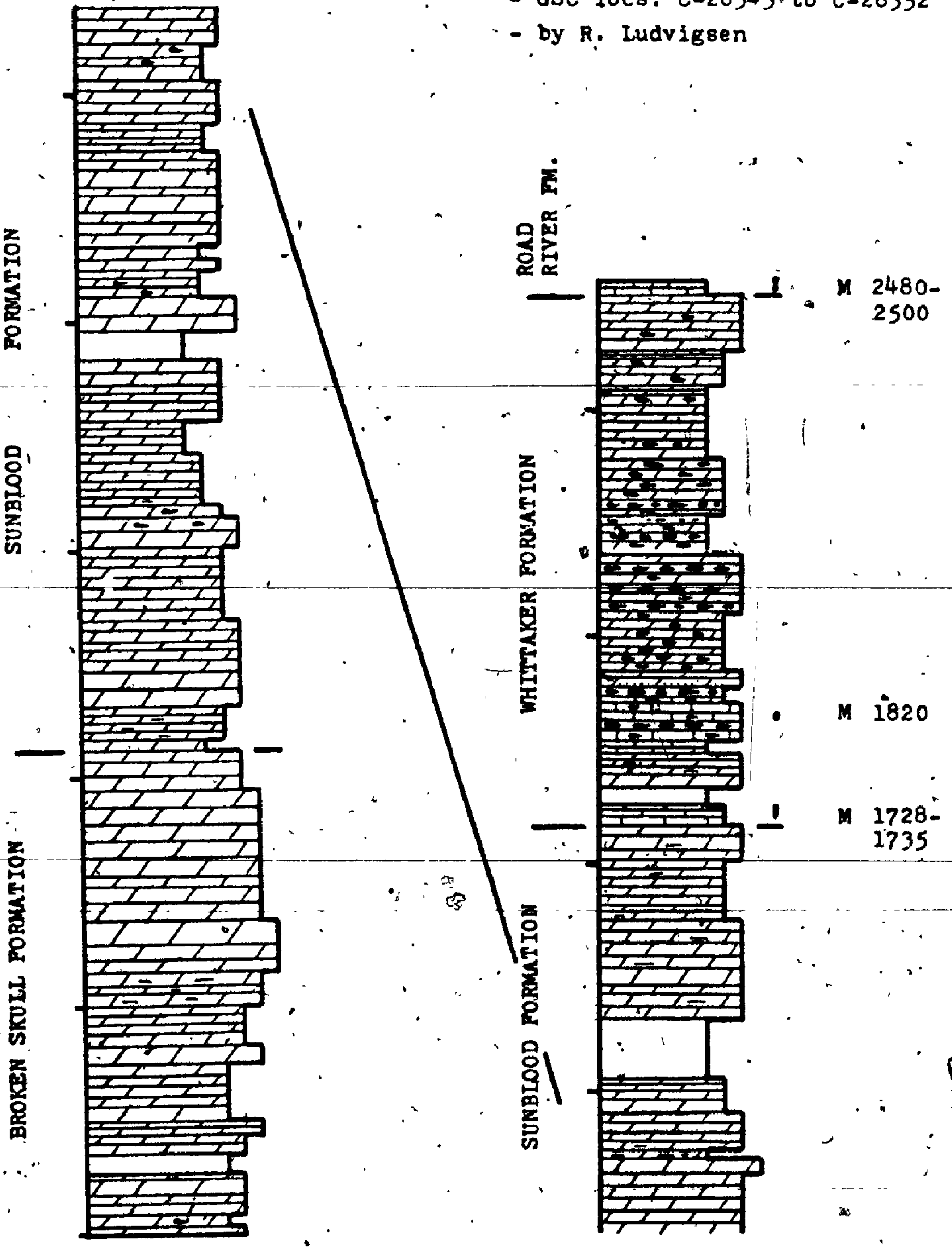
- section measured 8 km. S of Broken Skull River and 20 km. SE of Divide Lake.
- by R. Ludvigsen



SECTION N GRIZZLY BEAR LAKE

62° 42' N, 127° 56' W July, 1973

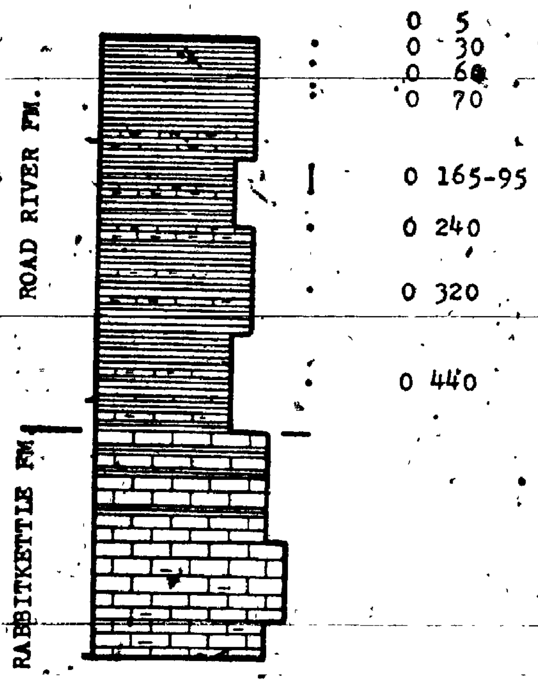
- measured on N-S ridge 5 km. W of Grizzly Bear Lake
- GSC locs. C-26345 to C-26352
- by R. Ludvigsen



SECTION O SUMMIT LAKE

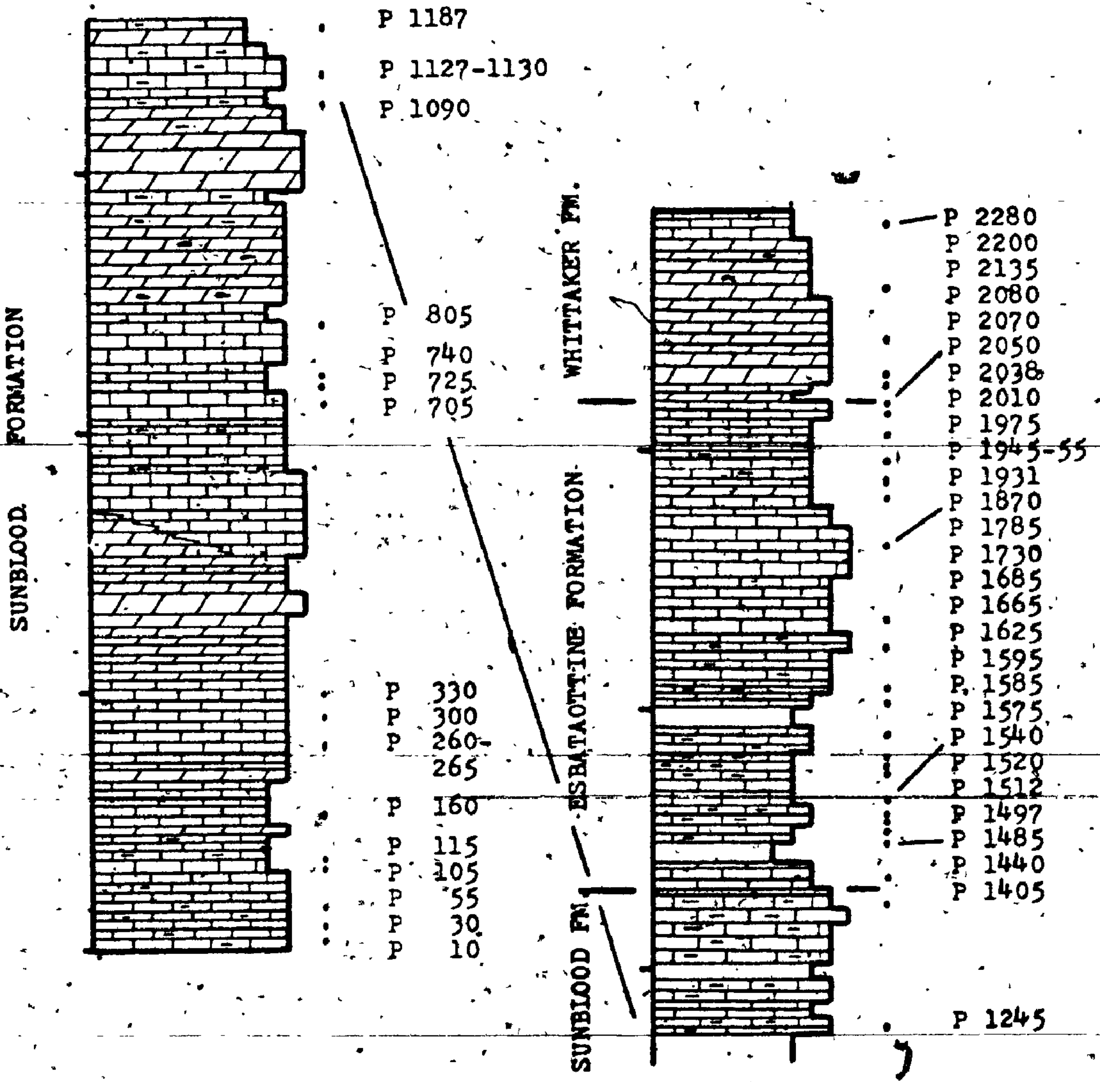
62° 28' N, 129° 04' W Aug., 1973.

- measured 21 km. NE of Summit Lake.
- by R. Ludvigsen



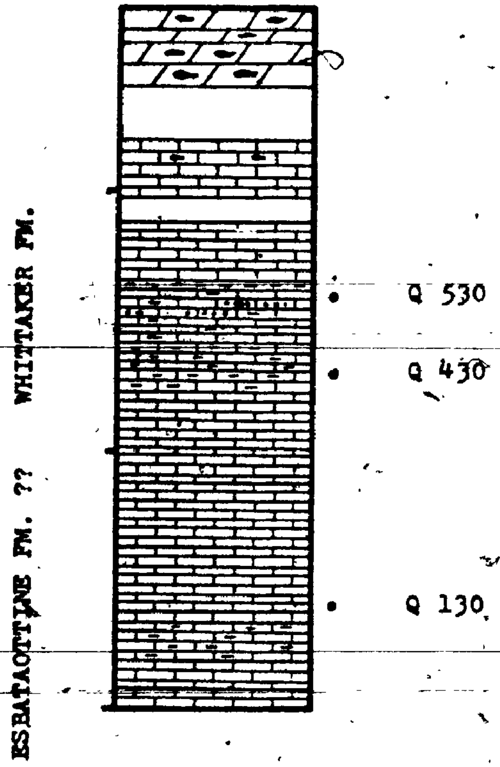
SECTION P **SUNBLOOD RANGE**

61° 43' N, 125° 56' W Aug., 1973
- measured 16 km. NW of Sunblood Mtn
- GSC locs. C-26296 to C-26344
- by R. Ludvigsen



SECTION Q WHITTAKER RANGE

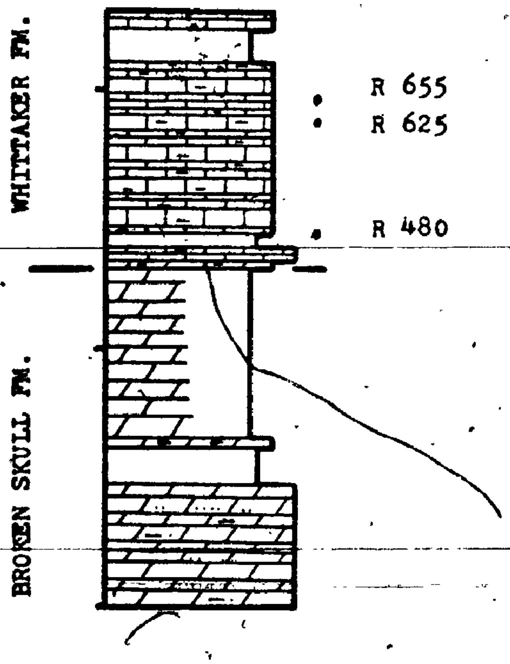
62° 28' N, 124° 48' W July, 1972
- measured 7 km. W of Trench Lake.
- by J.P. Conrad, D.G. Perry



SECTION R DUSKY RANGE

63° 17' N, 125° 21' W June, 1972

- measured 16 km. W of Dahadinni River.
- by R. Ludvigsen, R. Christie



APPENDIX II

Summary of Late Cambrian to Late Ordovician biostratigraphic information from collections of Sections A, B, C, D, E, G, H, I, J, K, M, O, P, Q, and R incorporating trilobite zones (this thesis), informal biostratigraphic units (Ludvigsen, 1975), conodont faunas (Tipnis, personal communication, 1975), and ostracod faunas (Copeland, 1974).

See Appendix I and Text-figure 1 for location of sections and horizons of fossil collections. Text-figure 32 shows abbreviations used.

Section P includes Geological Survey of Canada locality numbers (C-00000).

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Trilobite zones	Biostratigraphic units (Ludvigsen, 1975)	Conodont faunas (Tipnis)	Ostracod faunas (Copeland, 1974)
Whittakerites planatus (plan)	Bighornia-Thaerodonta fauna (B-T) Cryptolithus-Anataphrus fauna (C-A)		
Ceraurus mackenziensis (mack)	Hesperorthis-Oepikina fauna (H-O)	Fauna 9	Barneveld-Wilderness fauna (B-Wild)
Ceraurinella necra (necr)			
Ceraurinella longispina (long)	Doleroides fauna (Do)	Fauna 8	Wilderness fauna (Wild)
Ceraurus gabrielsi (gabr)		Fauna 7	
Bathyurus ulu (ulu)			Porterfield fauna (Port)
Ceraurinella nahanniensis (naha)	Mimella fauna (Mim)	Fauna 6	
Bathyurus granulosus (gran)	Bathyurus sp. 1 fauna (B. sp. 1)	Fauna 5	Chazy? fauna (Chazy)
Orthidiella-"Goniotelina" fauna (O-"G")	Orthidiella-"Goniotelina" fauna (O-"G")	Fauna 4 Faunas 3 & 2 Fauna 1	Whiterock fauna (Wtrk)
	Hesperonomia fauna (Hes)	Fauna E Arenigian	
	trilobite zones D to G_2	Fauna D	
		Trem.	
	Saukia Zone trilobites	Cambrian	

Text-figure 32.

Relationship of trilobite zones (this thesis), informal biostratigraphic units (Ludvigsen, 1975), conodont faunas (Tipnis, personal communication, 1975), and ostracod faunas (Copeland, 1974). Abbreviations used in Appendix II are in brackets.

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SECTION A	SUNBLOOD RANGE				
ROAD RIVER	CN-34 40-90		*C*-*A* f.		
WHITTAKER	A 860		*H*-*O* f.	8	
ESBATAOTTINE	A 615	*long* Z.	*Do* f.	7 or 8	
	A 385	*gabr* Z.	*Do* f.		
	A 365	*gabr* Z.	*Do* f.	7	Port f.
	A 240-247	*ulu* Z.			
	A 220	*ulu* Z	*Do* f.		Port f.
	A 160	*naha* Z.			
	A 140	*naha* Z.			
	A 125	*naha* Z.	*Mim* f.		Port f.
	A 115	*naha* Z.		6	
SUNBLOOD	35 m below top			5 or 6	
SECTION B	MARY RANGE				
SUNBLOOD	B 1510-1520	*long* Z.	*Do* f.		
	B 1450	*gabr* Z.	*Do* f.	7	Wild f.
	B 1315	*gran* Z.	*B*. sp. 1 f.	6	
	B 1295	*gran* Z.	*B*. sp. 1 f.	6?	
	B 1265	*gran* Z.	*B*. sp. 1 f.		
	B 1112			5 or 6	
	B 1100			5 or 6	
	B 1005			5	Port f.
	B 795-860			5	
	B 400	*O*-"*G*" f.	*O*-"*G*" f.	4 or 5	
	B 360	*O*-"*G*" f.	*O*-"*G*" f.	4	
	B 310			4	
	B 145	*O*-"*G*" f.	*O*-"*G*" f.		

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SECTION C	FUNERAL RANGE				
WHITTAKER	C 655	mack Z.	S-C f.	9	B-Wild f.
	C 640	mack Z.	S-C f.	9	B-Wild f.
	C 570-590	necr Z.	S-C f.	9	B-Wild f.
	C 510			9	
SECTION D	NATLA RIVER				
WHITTAKER	D 1680		B-T f.	9	
	D 1665		B-T f.	9	
	D 1635		B-T f.	9	
SUNBLOOD	D 1470			??	
	D 1375	gabr Z.	Do f.	6 or 7	
	D 1342	gabr Z.	Do f.		
BROKEN SKULL	D 750- D 860		Hes f.	Arenig	
	D 210- D 610		Zones D to G2	Arenig	
SECTION E	GLACIER LAKE				
WHITTAKER	E 2350- E 2700		?Do f.	8 or 9	
SUNBLOOD	~~E 1835~~			~~6 or 7~~	
	E 1665			5 or 6	
	E 1495			3	
	E 1150[illegible]155			2	
	E 1075			M to U Arenig	
	~~E 1030~~			~~Arenig?~~	
BROKEN SKULL	E 200		Hes f.		
	E 110		Hes f.		

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SECTION G - FLOOD CREEK					
ROAD RIVER	G 4460		C-A f.		
WHITTAKER	G 3605		H-O f.		
	G 3540		H-O f.		
ESBATAOTTINE	G 3340	long Z.			
	G 3195	long Z.	Do f.	7	
SUNBLOOD	G 2910				Chazy f.
	G 2795	gran Z.	B. sp. 1 f.	6	Chazy f.
	G 2335			4	
	G 2170			4	Wtrk f.
	G 2005			4	Wtrk f.
	G 1850			3	Wtrk f.
	G 1825			3	Wtrk f.
	G 1760			3	
	G 1745				Wtrk f.
	G 1425			2	Wtrk f.
	G 1030			2	
SECTION H - WHITTAKER RANGE					
WHITTAKER	H 1975	mack Z.	S-C f.	9	B-Wild f.
	H 1920	mack Z.	S-C f.		B-Wild f.
	H 1850	mack Z.	S-C f.	9	B-Wild f.
ESBATAOTTINE	H 1300	gabr Z.	Do f.		Wild f.
	H 1020	gabr Z.		7	
	H 900	gabr Z.			
	H 800-820	naha Z.	Mim f.	6 or 7	
SUNBLOOD	H 410	?gran Z.			
	H 130	O-"G" f.	O-"G" f.		
	H 0	O-"G" f.	O-"G" f.	1	

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SECTION I	WHITTAKER RANGE				
WHITTAKER	I 1590	plan Z.	S-C f.	9	
	I 1410	mack Z.	S-C f.	9	B-Wild f.
	I 1350-1380	mack Z.	S-C f.		
	I 1275	necr Z.	S-C f.		B-Wild f.
ESBATAOTTINE	I 780	gabr Z.	Do f.		Port f.
SECTION J	FUNERAL RANGE				
WHITTAKER	J 220	mack Z.	S-C f.	9	B. Wild f.
SECTION K	BROKEN SKULL RIVER				
SUNBLOOD	K 2375			Whiterock	
	K 2300			U. Arenig	
	K 2200			M- U-Arenig	
	K 2145			M. Arenig	
	K 2090			L. Arenig	
	K 2050			L. Arenig	
	K 2020			L. Arenig	
	K 1900			?Arenig	
RABBIT-KETTLE	K 995			L. Trem.	
	K 880			L. Trem.	
	K 715			U. Cam. or L. Ord.	
	K 20- K 525		Saukia Zone	U. Cam.	

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SECTION M	GRIZZLY BEAR LAKE				
ROAD RIVER	M 2480-2500		M. Sil.		
WHITTAKER	M 1820		*B-T* f.	9	
	M 1728-1735		*B-T* f.	9	
~~SECTION O~~	~~SUMMIT LAKE~~				
	O 30		Silurian		
	O 70		*gracilis* Zone		
	O 440		*fructicosus* Zone		
SECTION P	SUNBLOOD RANGE				
WHITTAKER	P 2280 (C-26296)		*H-O* f.	8 or 9	
ESBATAOTTINE	P 2050 (C-26301)	*long* Z.	*Do* f.		Wild f.
	P 2038 (C-26302)	*long* Z.	*Do* f.		Wild f.
	P 2010 (C-26303)	*long* Z.	*Do* f.		
	P 1975 (C-26304)			7 or 8	
	P 1945-1955 (C-26305)	*gabr* Z.	*Do* f.		Wild f.
	P 1931 (C-26306)	*gabr* Z.	*Do* f.		Wild f.
	P 1870 (C-26307)	*gabr* Z.		7 or 8	
	P 1785 (C-26308)	*gabr* Z.	*Do* f.		
	P 1685 (C-26310)	*gabr* Z.			
	P 1665 (C-26311)	*gabr* Z.	*Do* f.	7	Port f.

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
ESBATAOTTINE	P 1625 (C-26312)	*ulu* Z.		7	
	P 1595 (C-26313)	*ulu* Z.			Port f.
	P 1585 (C-26314)	*ulu* Z.	*Mim* f.		Port f.
	P 1575 (C-26315)	*ulu* Z.	*Mim* f.		Port f.
	P 1540 (C-26316)		*Mim* f.	6 or 7	
	P 1520 (C-26317)	*naha* Z.			
	P 1512 (C-26318)	*naha* Z.		6 or 7	Port f.
	P 1497 (C-26319)	*naha* Z.	*Mim* f.		Port f.
	P 1485 (C-26320)	*naha* Z.	*Mim* f.	6 or 7	Port f.
	P 1440 (C-26321)	*naha* Z.			
SUNBLOOD	P 1405 (C-26322)			6	Port f.
	P 1245 (C-26323)			5 or 6	
	P 1187 (C-26325)	*gran* Z.	*B.* sp. 1 f.		Chazy f.
	P 1130 (C-26326)	*gran* Z.	*B.* sp. 1 f.		Chazy f.
	P 1127 (C-26327)	*gran* Z.	*B.*sp. 1 f.	5	Chazy f.
	P 1090 (C-26328)	*gran* Z.	*B.* sp. 1 f.		Chazy f.
	P 740 (C-26330)				Chazy f.
	P 725 (C-26331)			5	
	P 705 (C-26332)			5	

Formation	Collection name	Trilobite	Biostrat. units	Conodont	Ostracod
SUNBLOOD	P 525			5	
	P 330 (C-26333)				Wtrk f.
	P 300 (C-26334)			4 or 5	Wtrk f.
	P 160 (C-26338)			4	
	P 115 (C-26339)	O-"G" f.	O-"G" f.		
	P 105 (C-26340)	O-"G" f.	O-"G" f.	4	Wtrk f.
	P 55 (C-26341)	O-"G" f.	O-"G" f.		Wtrk f.
	P 30 (C-26342)	O-"G" f.	O-"G" f.		Wtrk f.
	P 25 (C-26343)			4	
	P 10 (C-26344)	O-"G" f.	O-"G" f.		Wtrk f.
SECTION Q	WHITTAKER RANGE				
WHITTAKER	Q 530	plan Z.	S-C f.		B-Wild f.
	Q 430	mack Z.	S-C f.		
ESBATAOTTINE	Q 130	gabr Z.			Port f.
SECTION R	DUSKY RANGE				
WHITTAKER	R 655	plan Z.	S-C f.	8-12	
	R 625	plan Z.	S-C f.	8-12	B-Wild f.
	R 480		B-T f.		

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APPENDIX III

Ludvigsen, Rolf. 1975.

Ordovician formations and faunas, southern Mackenzie Mountains.

Canadian Journal of Earth Sciences, v. 12, no. 4, p. 663-697.

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