Life Sciences Contributions 134

Upper Cambrian and Lower Ordovician Trilobite Biostratigraphy of the Rabbitkettle Formation, Western District of Mackenzie

Rolf Ludvigsen



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ROLF LUDVIGSEN

Upper Cambrian and Lower Ordovician Trilobite Biostratigraphy of the Rabbitkettle Formation, Western District of Mackenzie

This paper is dedicated to the memory of David G. Perry of Vancouver, Robert K. Jull of Windsor, and Zoltan Hadnagy of Calgary—three close friends and colleagues who died in a helicopter accident in western Alberta on August 2, 1979.



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Upper Cambrian and Lower Ordovician Trilobite Biostratigraphy of the Rabbitkettle Formation, Western District of Mackenzie

Abstract

Two measured sections of the upper Rabbitkettle Formation in the western District of Mackenzie are separated by a thrust fault. These sections provide a record of silicified trilobite faunas across the Cambrian-Ordovician boundary in open marine carbonate rocks along the deeper portion of the shelf—a North American palaeogeographic setting not previously extensively sampled for macrofossils.

A new biostratigraphy is proposed for the Trempealeauan to Lower Tremadocian interval in this setting. A Yukonaspis Zone with three divisions (in ascending order, Yukonaspis kindlei Fauna, Bowmania americana Fauna, and Elkanaspis corrugata Fauna) is based on eurekiine, entomaspid, and olenid trilobites. The Yukonaspis Zone is of Trempealeauan age and is considered equivalent to the Saukia Zone. A Parabolinella Zone with three divisions (in ascending order, Missisquoia mackenziensis Fauna, Missisquoia depressa Subzone, and Apoplanias rejectus Fauna) is based on olenid, missisquoid, and leiostegiid trilobites. The Parabolinella Zone is of Early Tremadocian age and is considered to be largely equivalent to the Missisquoia Zone. The Symphysurina brevispicata Subzone of the Symphysurina Zone (Early Tremadocian) is represented by a single collection.

The base of the Ordovician System is drawn at the first appearance of *Parabolinella* at the base of the *Parabolinella* Zone. This horizon probably correlates closely with the base of the Tremadocian and it may be slightly older than the base of the Ordovician as recognized elsewhere in the North American Province (that is, the base of the *Missisquoia* Zone).

The coincident base of the "Hystricurid" Biomere and a Grand Cycle occurs at the base of the *Elkanaspis corrugata* Fauna of the *Yukonaspis* Zone (correlative with the base of the *Corbinia apopsis* Subzone of the *Saukia* Zone) at the abrupt appearance of black laminated lime mudstones above light grey, burrowed lime wackestones. The mudstones contain a new fauna dominated by kingstoniid (?), olenid, and kainellid trilobites. This horizon, located 70 m below the top of the Rabbitkettle Formation, is a biogeographic boundary which separates the shelf-biogeographic region below from the slopebiogeographic region above. The extinction, immigration, speciation, and diversity patterns that define the Ptychaspid-"Hystricurid" Biomere boundary are explained with reference to the diversity-area relationships inherent in the equilibrium model of biogeography.

Forty-six species of trilobites are described and illustrated. Four new genera are proposed (Larifugula, Kathleenella, Naustia, and Elkanaspis). Eleven species are new (Parabolinella panosa, Larifugula triangulata, "Calvinella" palpebra, Kathleenella subula, Kathleenella hamulata, Eurekia bacata, Naustia papilio, Elkanaspis futile, Elkanaspis corrugata, Missisquoia mackenziensis, and Tatonaspis diorbita.

"Acidaspis" ulrichi Bassler is a junior synonym of Bowmania americana (Walcott), which is reassigned to the Entomaspidae. "Leiobienvillia" leonensis Winston and Nicholls is assigned to a new kingstoniid (?) genus, Larifugula. Liostracinoides Raymond and Kathleenella gen. nov. are assigned to the Euptychaspidinae. Yukonaspis Kobayashi is assigned to the Eurekiinae and Ptychopleurites Kobayashi to the Pagodiinae.

Introduction

In 1972, as a part of a thesis project on silicified Middle Ordovician trilobites of the southern District of Mackenzie, I measured and collected a 750 m-thick section (Section K, Fig. 1) near the headwaters of the Broken Skull River. I had hoped to sample the fossiliferous deeper-water equivalents of the Sunblood, Esbataottine, and lower Whittaker formations that are exposed farther to the east in the Mackenzie Mountains ((Ludvigsen, 1975; 1979b). This hope was not realized. Black argillaceous limestones and cherts of the upper part of this section, which were assigned to the Road River Formation, proved to be equivalent to the lower part of the Sunblood Formation, but these strata yielded only inarticulate brachiopods and conodonts (Tipnis et al., 1979). The lower part of Section K, below a conspicuous lower black dolostone member of the Road River Formation, was assigned to the Rabbitkettle Formation and these strata proved more interesting because they contained a number of collections with abundant silicified trilobites of types not seen in Ordovician strata to the east. Etching of these samples in the laboratory yielded 12 collections of Late Cambrian trilobites. Two collections from higher in the section contained abundant and well-preserved specimens of Parabolinella, Missisquoia, and Geragnostus of apparently earliest Ordovician age. Section K, therefore, was potentially of considerable importance in providing a detailed trilobite biostratigraphy across the Cambrian-Ordovician boundary in this area of northern Canada. The samples acquired in 1972, however, were too widely spaced to allow definite conclusions about the distribution of trilobites across this boundary.

An opportunity to revisit Section K came in 1977 and, at that time, the 240 m stratigraphic interval of the upper Rabbitkettle Formation was systematically sampled. The new section was designated Section KK. Thirty-five bulk limestone

samples, varying in weight from 2 kg to more than 20 kg, were collected. All but four of these yielded silicified trilobites.

The sequence of collections forms the basis for a new trilobite biostratigraphy of the boundary interval between the Cambrian and the Ordovician in an outer platform, open marine setting in western North America. A companion paper on conodont biostratigraphy of the same sequence of samples has already been published (Landing et al., 1980).

Although the present paper is based on a single measured section, the critical boundary interval was sampled twice. This was made possible by a fortuitously placed and previously unrecognized thrust fault. The collections also provide a trilobite and conodont record across the Ptychaspid-"Hystricurid" Biomere boundary and a new model is proposed to account for the extinction, immigration, speciation, and diversity patterns which define this level in North America.



Fig. 1 Map of western District of Mackenzie showing location of Section K near the headwaters of the Broken Skull River. Base of measured section is to the west. Section KK covers the middle part of line of Section K.

Regional Setting and Stratigraphy

Section K is located near the western margin of the Mackenzie Platform—a stable tectonic feature that received dominantly shallow-water sediments from the Helikian to the Late Devonian (Gabrielse, 1967). Flanking the Mackenzie Platform to the west is the epicontinental Selwyn Basin which is characterized by thick sequences of fine clastic rocks. The southwestern margin of the Selwyn Basin is bordered by the Pelly-Cassiar Platform which was initiated in the Late Cambrian as a site of andesitic volcanism and, in the Silurian and Devonian, was the locus of shallow-water carbonate sedimentation (Tempelman-Kluit, 1977). Tempelman-Kluit and Blusson (1977) and Tempelman-Kluit (1977) have provided evidence that, prior to mid-Cretaceous right-lateral movement on the Tintina Fault, the Pelly-Cassiar Platform was a narrow belt at the shelf-slope break at least 1000 km long. The Yukon Crystalline Terrane and its southern extension, the Omineca Crystalline Belt, comprise severely metamorphosed and tectionized sedimentary rocks that are probably in part equivalent to the unmetamorphosed Lower Palaeozoic sedimentary rocks on the shelf (Tempelman-Kluit, 1977: fig. 45.2). The relationship of these Lower Palaeozoic tectonic elements is shown in Fig. 2.

Three carbonate formations of Late Cambrian and Early Ordovician age are exposed across the Mackenzie Platform between latitudes 62°N and 64°N. From east to west, these are the Franklin Mountain Formation in the Mackenzie River Valley, the Broken Skull Formation in the eastern and central Mackenzie Mountains, and the Rabbitkettle Formation in the western Mackenzie Mountains and the Selwyn Mountains (Aitken et al., 1973; Gabrielse et al., 1973; Norford and Macqueen, 1975). These formations are not well dated. The Franklin Mountain Formation contains brachiopods, molluscs, and trilobites of Dresbachian to middle Canadian age (Norford and Macqueen, 1975: 12; Aitken et al., 1973: 31). The Broken Skull Formation contains trilobite, brachiopod, and conodont faunas which range in age from late Franconian to late Canadian (Gabrielse et al., 1973: 49, Ludvigsen, 1975; Tipnis et al., 1979). Only a single fossil collection has been recovered from typical exposures of the Rabbitkettle Formation in the Selwyn Mountains. This is a trilobite collection of Franconian age (Gabrielse et al., 1973: 51). In the Howards Pass area, near Summit Lake, some 50 km southwest of Section K, the Rabbitkettle is conformably overlain by the Road River Formation which here contains early Arenigian graptolites near its base (Ludvigsen, 1975: 675). In other areas, the lower Road River Formation appears to be a facies equivalent of the Rabbitkettle Formation.

The thick package of predominantly carbonate rocks of the Mackenzie Platform rests unconformably on Middle Cambrian and older formations. This is the "sub-Franconian unconformity" of Gabrielse et al. (1973) and the "sub-Dresbachian unconformity" of Aitken et al. (1973).

The outcrop belts defined by the Franklin Mountain, Broken Skull, Rabbitkettle, and lowermost Road River formations are approximately parallel to one another and parallel to the western margin of the Mackenzie Platform. A generalized palaeoenvironment may be interpreted for each formation.

Norford and Macqueen (1975) have presented a detailed discussion of the lithologic character and palaeoenvironment of the Franklin Mountain Formation at its type area in the Mackenzie River Valley. Here, the formation consists of laminated to



Fig. 2 Early Palaeozoic tectonic elements of the northern Cordillera. Reconstruction was made by restoring 450 km of right lateral displacement on the Tintina Fault (Tempelman-Kluit, 1977). Section K is located near the western margin of the Mackenzie Platform. Line of cross-section in Fig. 3 is indicated.

thickly bedded dolostones which range from coarsely to very finely crystalline. The middle part of the formation is characterized by rhythmic alternations of oolitic or bioclastic grainstones/packstones and banded, very finely crystalline and silty dolostones. The middle and upper parts of the formation are characterized by well-developed hemispheric stromatolites and stromatolitic dolostones. The Franklin Mountain Formation clearly represents deposition in shallow subtidal and intertidal environments along the interior portions of the Mackenzie Platform.

The basal portion of the Broken Skull Formation in the Mackenzie Mountains (Gabrielse et al., 1973: 45–48) consists of sandy dolomitic mudstones, siltstones, and dolostones with mudcracks, cross-beds, and trace fossils. The bulk of the formation comprises thick bedded to flaggy limestones and dolostones that are variably silty and sandy and weather in shades of buff, grey, and brown. Planar and cross-laminations are occasionally present and some beds contain abundant pisolites. The Broken Skull Formation probably represents deposition in a wide range of palaeoenvironments, from intertidal to moderately deep subtidal. On balance, it appears to be somewhat deeper than the Franklin Mountain Formation.

The Rabbitkettle Formation is a thick sequence of monotonous thin-bedded to massive silty limestones and calcareous siltstones exposed in the Selwyn Mountains (Blusson, 1968: 13, 14; Gabrielse et al., 1973: 48). The limestones are finely grained and characterized by planar and wavy banding of silty layers, some of which are graded (Gabrielse et al., 1973: pls. 19, 20). An upper member of the Rabbitkettle consisting of finely laminated, dark grey to black muddy limestones and shales is herein reassigned to the Road River Formation. The palaeoenvironment of the Rabbitkettle Formation is poorly understood. Presumably, it represents relatively deep-water deposition in open marine settings along the western portion of the Mackenzie Platform and, perhaps, in part on the decline into the Selwyn Basin.

The Upper Cambrian and Lower Ordovician parts of the Road River Formation have been studied by Cecile (1978) in the Misty Creek Embayment of the Selwyn Basin, some 200 km north-northeast of Section K. In this area, the Road River consists of thin bedded, yellowish weathering muddy limestones according to Cecile. He noted (1978: 374) that these strata "have all the characteristics of a slope facies: including slumps, *in situ* slump breccias, carbonate clast conglomerates and breccias, trains of ripple-drift cross laminae, lensed and scoured bedding".

A diagrammatic cross-section of Upper Cambrian and Lower Ordovician rocks from the interior portion of the Mackenzie Platform to the Yukon Crystalline Terrane is shown in Fig. 3.

According to recent mapping of the Nahanni Sheet by Gordey (1980), the stratigraphic succession in the vicinity of the Section K consists of a conformable sequence of Upper Hadrynian to Lower Ordovician rocks (that is, the Backbone Ranges, Sekwi, Rockslide, Rabbitkettle, and Broken Skull formations) which is disconformably overlain by Upper Ordovician to Devonian rocks (that is, the Whittaker and Road River formations). The Rabbitkettle Formation as recognized in this paper apparently corresponds to the Rabbitkettle Formation as mapped by Gordey. I believe, however, that the name Broken Skull Formation is inappropriately applied to the dark grey to black dolostones and black argillaceous limestones which overlie the Rabbitkettle in this area. These strata are, herein, assigned to the Road River Formation (Figs. 4, 5).



Fig. 3 Diagrammatic cross-section of Trempealeauan formations from the Mackenzie Platform in the east to the Yukon Crystalline Terrane in the west (Fig. 2). Not to scale.

Biostratigraphy

Cambrian

Winston and Nicholls (1967) proposed a four-fold subzonal division of the Saukia Zone for shallow-water carbonate rocks in central Texas which was based largely on saukiid and eurekiine trilobites. They named the upper three subzones and Longacre (1970) later named the lowest subzone. This biostratigraphic scheme has been applied, in part or in its entirety, to successions in Oklahoma (Stitt, 1971b, 1977), Alberta (Derby et al., 1972), and New York (Taylor and Halley, 1974). Biofacies differentiation among latest Cambrian trilobites hampers the utility of the four-fold subzonal division of the Saukia Zone outside the interior portions of the Middle Carbonate Belt of Palmer (1960a). These subzones cannot be recognized within the Inner Detrital Belt developed in the upper Mississippi Valley where the Saukia Zone and its divisions (Bell et al., 1956) are based largely on dikelocephalid and saukiid trilobites that have not been found in Texas and Oklahoma (Stitt, 1977: 15). Nor can the subzones be applied to coeval shelf-edge carbonate rocks carrying Hungaia associations in Newfoundland, Quebec, Vermont, and Alaska. In addition, the striking biofacies change at the Upper Cambrian shelf-slope break outlined by Taylor for western United States prevents the recognition of the Saukia Zone in autochthonous Trempealeauan Outer Detrital Belt sediments and Taylor (1976) assigned the slope trilobites in central Nevada to the Hedinaspis Local Range Zone (Franconian and Trempealeauan).

Upper Cambrian strata of the Rabbitkettle Formation exposed at Section KK carry trilobites that show affinities to both those of the *Saukia* Zone and those of the *Hungaia* associations. Significant differences, notably the virtual absence of saukiid trilobites, preclude the application of the Texas/Oklahoma biostratigraphic

SERIES	SELWYN BASIN		MACKENZIE	PLATFORM	
STAGES	Bonnet Plume map-area	Selwyn Mountains	Mackenzie	Mountains	Mackenzie River Valley
LLANDEILIAN				SUNBLOOD FORMATION	
ARENIGIAN		ROAD RIVER FORMATION	ROAD RIVER FORMATION		
TREMADOCIAN	ROAD RIVER FORMATION	Section KK-	BROKEN SKULL	<u>, , , , , , , , , , , , , , , , , , , </u>	
TREMPEALEAUA		RABBITKETTLE FORMATION	RABBIT- KETTLE FORMATION	FORMATION	FRANKLIN MOUNTAIN FORMATION
	1				
v	CECILE (1978)	BLUSSON (1968)	THIS PAPER	LUDVIGSEN (1975	NORFORD & MACQUEEN (1975

Fig. 4 Correlation chart of Upper Cambrian and Lower Ordovician formations across the Mackenzie Platform to the Selwyn Basin.

nomenclature to the District of Mackenzie succession. Instead, a *Yukonaspis* Zone comprising three informal biostratigraphic units is proposed for these deep platform carbonate rocks. The *Yukonaspis* Zone and its three faunas are based largely on eurekiine, entomaspidid, and olenid trilobites. This biostratigraphic terminology is probably more widely applicable to Trempealeauan platform margin rocks in western and, possibly, eastern North America than is the *Saukia* Zone and its subzones.

It is evident from the preceding discussion and from Rowell et al. (1973, fig. 11) that it is no longer possible to accept only a single standard biostratigraphic system for latest Cambrian trilobites of North America. Robison (1976, text-fig. 5) reached similar conclusions for Middle Cambrian trilobites of western North America. It will be necessary to take cognizance of as many as four parallel zonal schemes of Trempealeauan trilobites to effectively account for the environmental heterogeneity of these faunas:

- 1. A *Saukia* Zone and its array of subzones for the Inner Detrital Belt and the inner parts of the Middle Carbonate Belt.
- 2. A *Yukonaspis* Zone and its eventual subzones for the outer parts of the Middle Carbonate Belt.
- 3. A zone or zones based on elements of the *Hungaia* associations for shelf-edge carbonate sites.
- 4. A zone or zones based on elements of the *Hedinaspis* Local Range Zone for the Outer Detrital Belt.

The *Yukonaspis* Zone and its three faunas from the upper Rabbitkettle Formation at Section KK are defined below.

Yukonaspis Zone (177 m–60 m of composite Section KK)

The lower 117 m of composite Section KK are dominated by species of Yukonaspis, Eurekia, Kathleenella gen. nov., Larifugula gen. nov., Idiomesus, Bowmania, Elkanaspis gen. nov., and Geragnostus. Other genera are less common— Euptychaspis, Rhaptagnostus, Heterocaryon, Leiocoryphe, Tatonaspis, Euloma, Naustia gen. nov., Pseudagnostus, Triarthropsis, Liostracinoides, Plethometopus, Bienvillia, Parabolinites. This generic assemblage constitutes the Yukonaspis Zone. Specifically, the zone is defined by the body of strata from the first appearance of Yukonaspis to the first appearance of Parabolinella. Only three genera of the Yukonaspis Zone (that is, Geragnostus, Plethometopus, and Parabolinites) continue into the superjacent zone.

The Yukonaspis Zone of the District of Mackenzie is undoubtedly equivalent to, at least, the middle and upper parts of the Saukia Zone of Texas and Oklahoma. Many of the Yukonaspis Zone genera are confined to the Saukia Zone. The upper boundaries of the Yukonaspis and Saukia Zones must be closely correlative because Larifugula leonensis (Winston and Nicholls) is confined to the highest fauna of the Yukonaspis Zone and the highest subzone of the Saukia Zone. In addition, the base of the Cordylodus oklahomensis Zone (= C. proavus Zone) occurs a short distance below the top of both the Yukonaspis Zone appears to be an outer carbonate platform equivalent of the Saukia Zone which is typically developed in carbonate and clastic rocks higher on the platform.



Fig. 5 Graphic lithology log of upper Rabbitkettle Formation and lower Road River Formation at Section K showing location of samples obtained in 1972 (K prefix). The thrust fault was not recognized when Section K was measured. The upper 240 m of the Rabbitkettle was remeasured in 1977 and designated Section KK. Location of 1977 samples are indicated (KK prefix).

The *Yukonaspis* Zone may also be recognized in the Road River Formation, Bonnet Plume map-area (GSC loc. C-7562; Aitken et al., 1973: 73). It occurs on Jones Ridge and Squaw Mountain, east-central Alaska (the Trempealeauan-2 Fauna of Palmer, 1968) and within the Cow Head Group, western Newfoundland (C.H. Kindle Collection, Geological Survey of Canada, Ottawa).

A tripartite division of the *Yukonaspis* Zone is proposed below and is shown in Figs. 6 and 7.

Yukonaspis kindlei Fauna (177 m–96 m of composite Section KK). The lower 81 m of composite Section KK (Fig. 7) comprise the Yukonaspis kindlei Fauna. Its base is defined at the first appearance of the nominate species and it extends upward to the first appearance of Bowmania americana. The following species occur in the Y. kindlei Fauna (Note: in this and in following faunal lists, those species that continue from the subjacent fauna are indicated by - and those that continue into the superjacent fauna are indicated by +):



Fig. 6 Correlation of the foot wall and the hanging wall of the unnamed thrust fault in the upper Rabbitkettle Formation. The thrust fault repeats at 58 m interval. The boundaries of biostratigraphic units are shown. The collections from the two fault blocks were combined to form composite Section KK.

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"Calvinella" palpebra sp. nov. + ceratopygid indet. Elkanaspis futile gen. et sp. nov. Euloma (Plecteuloma) sp. Euptychaspis typicalis Ulrich Eurekia bacata sp. nov. Eurekia ulrichi (Rasetti) + Eurekia spp. Geragnostus sp. + Heterocaryon tuberculatum Rasetti + Idiomesus intermedius Rasetti Idiomesus tantillus Raymond Kathleenella hamulata gen. et sp. nov. + Kathleenella subula gen. et sp. nov. + Larifugula triangulata gen. et sp. nov. + Leiocoryphe spp. Meteoraspis? sp. Naustia papilio gen. et sp. nov. Pseudagnostus (Pseudagnostina) sp. Rhaptagnostus clarki (Kobayashi) saukiid indet. Tatonaspis diorbita sp. nov. Triarthropsis limbata Rasetti Yukonaspis kindlei Kobayashi

The Yukonaspis kindlei Fauna is probably correlative to most of the Saukiella junia Subzone of Texas and Oklahoma (Longacre, 1970; Stitt, 1977), but the correlation is not entirely satisfactory because none of the species of the Y. kindlei Fauna is confined to the S. junia Subzone. Euptychaspis typicalis, however, is most commonly found in the S. junia Subzone of the southern United States. A firmer correlation can be made with the Trempealeauan-2 Fauna of east-central Alaska (Palmer, 1968) based on the co-occurrence of Eurekia ulrichi, Rhaptagnostus clarki, and Yukonaspis kindlei. Four species of the Y. kindlei Fauna (that is, Eurekia ulrichi, Heterocaryon tuberculatum, Idiomesus intermedius, and I. tantillus) also occur in Vermont (Raymond, 1924, 1937) and Quebec (Rasetti, 1944, 1945) and the Y. kindlei Fauna is undoubtedly equivalent to parts of the Hungaia assemblages of these areas.

Bowmania americana Fauna (96 m–70 m of composite Section KK). The next 26 m of composite Section KK (Fig. 7) comprise the Bowmania americana Fauna. Its base is defined by the first appearance of the nominate species and its top is defined by the first appearance of Elkanaspis corrugata. The following species occur in the B. americana Fauna:

Bowmania americana (Walcott)

- ceratopygid indet.
 Elkanaspis? sp.
- + Eurekia spp.
- Heterocaryon tuberculatum Rasetti

- Idiomesus intermedius Rasetti
- Kathleenella subula gen. et sp. nov.
- + Larifugula triangulata gen. et sp. nov.
- Leiocoryphe spp.
 Liostracinoides vermontanus Raymond
 + Plethometopus obtusus Rasetti
 - + Yukonaspis sp.

The Bowmania americana Fauna appears to be correlative to most of the Saukiella serotina Subzone of the Saukia Zone. In the well-sampled Upper Cambrian sections of Texas and Oklahoma (Longacre, 1970; Stitt, 1971b), B. americana is confined to the S. serotina Subzone. Only four of the twelve species that comprise the B. americana Fauna in the Rabbitkettle Formation are restricted to this biostratigraphic unit; seven continue from the subjacent fauna and four continue into the superjacent fauna.



Fig. 7 Occurrences of 46 species of trilobites in composite Section KK of the upper Rabbitkettle Formation.

Elkanaspis corrugata Fauna (70 m-60 m of composite Section KK). The abrupt appearance of dark lime mudstones and olenid trilobites at the 70 m level of the composite section signals a new lithologic and faunal sequence in the Rabbitkettle Formation. The lower 10 m are assigned to the *Elkanaspis corrugata* Fauna. Its base is defined by the first appearance of the nominate species and its top by the first appearance of *Missisquoia mackenziensis*. The following species occur in the *Elkanaspis corrugata* Fauna:

- Bienvillia cf. corax (Billings) Elkanaspis corrugata gen. et sp. nov.
- Eurekia spp.
 Idiomesus levisensis (Rasetti)
 Larifugula leonensis (Winston and Nicholls)
- Larifugula triangulata gen. et sp. nov. Missisquoia sp.
- + Parabolinites cf. williamsoni (Belt)
- + Plethometopus obtusus Rasetti
- Yukonaspis sp.

Larifugula leonensis is restricted to the Elkanaspis corrugata Fauna in the District of Mackenzie and to the Corbinia apopsis Subzone of the Saukia Zone in Texas, Oklahoma, and Utah (Winston and Nicholls, 1967; Stitt, 1971b, 1977; Hintze et al., 1980) and these biostratigraphic units are undoubtedly wholly or partially correlative. The only other species that occur in both the *E. corrugata* Fauna and the *C. apopsis* Subzone are *Idiomesus levisensis* and *Plethometopus obtusus*, but these species have wider teilzones in both Oklahoma and the District of Mackenzie.

The base of the *E. corrugata* Fauna marks the arrival of olenids (*Parabolinites* and *Bienvillia*) and missisquoiids (*Missisquoia*) in the Rabbitkettle Formation (Fig. 8). Trilobites of these families assume increasing importance and abundance in the next four biostratigraphic units recognized in Section KK.

Ordovician

Winston and Nicholls (1967) proposed the *Missisquoia* Zone as a basal Ordovician biostratigraphic unit in the Middle Carbonate Belt of central Texas and recognized a succeeding *Symphysurina* Zone (first defined by Hintze, 1953 in Nevada and Utah). These zones were also recognized in similar rocks of Oklahoma by Stitt (1971b) who later (Stitt, 1977) redefined the base of the *Symphysurina* Zone and divided the zones into two subzones each; from base to top, *Missisquoia depressa*, *M. typicalis*, *Symphysurina* occur in the upper Rabbitkettle Formation, but in these dark grey to black, argillaceous lime mudstones the trilobite assemblages are strongly dominated by the olenid trilobites *Parabolinella* and *Apoplanias* (Figs. 7 and 16). The rocks are suggestive of Cambrian and Ordovician assemblages known from shallow settings at high palaeolatitude sites or from deep settings at low palaeolatitude sites (Taylor, 1977). A *Parabolinella* Zone with three divisions is proposed for the lowermost

Ordovician rocks of the Rabbitkettle Formation at Section KK. This zone appears to be the Outer Detrital Belt equivalent of the *Missisquoia* Zone. The *Parabolinella* Zone holds promise as a biostratigraphic index for basal Ordovician rocks in shelf-edge or off-shelf localities where *Missisquoia* is rare or absent. A single poorly preserved free cheek of *Symphysurina* cf. *brevispicata* Hintze above the *Parabolinella* Zone indicates the presence of the *Symphysurina* Zone in the higher beds of the Rabbitkettle Formation.

Parabolinella Zone (60 m-25 m of composite Section KK)

Parabolinella is a common to very abundant trilobite through a 17 m interval of the upper Rabbitkettle Formation at Section KK. The abundance is locally quite



Fig. 8 Stratigraphic ranges of 31 trilobite genera in composite Section KK.

remarkable. Nearly 500 cranidia of *Parabolinella* cf. *prolata* were recovered from four collections of the *Missisquoia depressa* Subzone (see Fig. 16). The *Parabolinella* Zone is established for the interval from the base of the *Missisquoia mackenziensis* Fauna to the base of the *Symphysurina* Zone; that is, from the first occurrence of *Parabolinella* to the first occurrence of *Symphysurina* cf. *brevispicata*.

The Parabolinella Zone is dominated by species of Parabolinella, Geragnostus, Missisquoia, Ptychopleurites, and Apoplanias. Other genera are rare. Plethometopus, Parabolinites, and Levisaspis have been recovered from one or two collections each. The Parabolinella Zone is undoubtedly largely correlative with the Missisquoia Zone. The two zones share a Missisquoia depressa Subzone in their lower parts, both contain Apoplanias rejectus in their upper parts, and both are overlain by the Symphysurina brevispicata Subzone of the Symphysurina Zone. The lower boundary of the Parabolinella Zone may be slightly older than the base of the Missisquoia Zone. The Missisquoia mackenziensis Fauna, the lowest fauna of the Parabolinella Zone, is not known from Oklahoma where the Missisquoia Zone starts with the Missisquoia depressa Subzone, but it could well be represented in the 1 or 2 m unfossiliferous interval between the Saukia and Missisquoia Zones in the Arbuckle and Wichita mountains.

A tripartite division of the *Parabolinella* Zone is proposed below and is shown diagrammatically in Fig. 9.

Missisquoia mackenziensis Fauna (60 m-57 m of composite Section KK). Two collections from the lowest few metres of the *Parabolinella* Zone in the Rabbitkettle Formation are dominated by species of *Parabolinella*, *Geragnostus*, and *Missisquoia*. This is the *Missisquoia mackenziensis* Fauna which contains the following species.

- + Geragnostus (Micragnostus) subobesus (Kobayashi) Missisquoia mackenziensis sp. nov.
- Parabolinites cf. williamsoni (Belt)
 Parabolinella panosa sp. nov.
- + Parabolinella cf. prolata Robison and Pantoja-Alor
- + Plethometopus obtusus Rasetti

This association of mainly new species cannot be correlated to other faunal successions in the Cambrian-Ordovician boundary interval in North America. It has greater affinity for younger faunas than for older faunas and its occurrence above the *Yukonaspis* Zone and below the *Missisquoia depressa* Subzone (previously considered the basal biostratigraphic unit of the North American Ordovician; Stitt, 1977) suggests that the *Missisquoia mackenziensis* Fauna is the oldest Ordovician trilobite fauna discovered so far on this continent.

Missisquoia depressa Subzone (57 m-44 m of composite Section KK). The next 13 m of the composite section comprise the *Missisquoia depressa* Subzone of the *Parabolinella* Zone. This subzone is defined in the same manner as is the *Missisquoia depressa* Subzone of the *Missisquoia* Zone in Oklahoma (Stitt, 1977); that is, from the first occurrence of *M. depressa* to the first occurrence of *Apoplanias rejectus*. The following species characterize this subzone:

- Geragnostus (Micragnostus) subobesus (Kobayashi) Levisaspis glabrus (Shaw) Missisquoia depressa Stitt Parabolinella hecuba (Walcott)
- Parabolinella cf. prolata Robison and Pantoja-Alor
- Plethometopus obtusus Rasetti
 Ptychopleurites brevifrons (Kobayashi)

This subzone shares *Missisquoia depressa* and *Ptychopleurites brevifrons* with the *M. depressa* Subzone of Oklahoma (Stitt, 1977) and *P. brevifrons* and *Geragnostus* (*Micragnostus*) subobesus with the *Ptychopleurites* Fauna of east-central Alaska (Kobayashi, 1936a) and it is certainly correlative with these two biostratigraphic units (Fig. 9). The presence of *Missisquoia depressa* (see Systematic Palaeontology) and a species of *Geragnostus* (*Micragnostus*) that is very similar to *G.* (*M.*) subobesus in the Fengshan Formation of Hopeh Province, China suggests that the *Mictosaukia orientalis* Assemblage of Zhou and Zhang (1978) is of Early Ordovician age and correlative with the *M. depressa* Subzone of North America. The Parabolina assemblage in the lower Tinu Formation of southern Mexico (Robison and Pantoja-Alor, 1968) contains Parabolinella prolata, *P. hecuba*, and a species of *Mictosaukia*. This assemblage may also be correlative to the *M. depressa* Subzone.

Apoplanias rejectus Fauna (44 m-25 m of composite Section KK). Two collections above the *Missisquoia depressa* Subzone in the Rabbitkettle Formation have yielded low diversity olenid assemblages. The *Apoplanias rejectus* Fauna is defined from the first occurrence of *A. rejectus* to the first occurrence of *Symphysurina* cf. *brevispicata*. Only two species occur in this fauna.

+ Apoplanias rejectus Lochman Parabolinella sp.

Apoplanias rejectus is a scarce trilobite in the Missisquoia typicalis and Symphysurina brevispicata subzones of Oklahoma (Stitt, 1971b, 1977). In the Rabbitkettle Formation, A. rejectus occurs in both the A. rejectus Fauna and the Symphysurina brevispicata Subzone. A correlation of the A. rejectus Fauna with the M. typicalis Subzone is proposed. A. rejectus also occurs a few metres above Saukia Zone trilobites in the subsurface Deadwood Formation of Montana (Lochman, 1964a) and in the Basal Silty Member of the Survey Peak Formation of Alberta (Dean, 1978). Lochman (1964a) defined an A. rejectus faunule for the occurrences in Montana. This faunule is, at least in part, correlative with the A. rejectus Fauna.

Symphysurina Zone (25 m–0 m of composite Section KK)

I follow Stitt's (1977: 32) definition of the base of the *Symphysurina* Zone in placing this boundary at the first occurrence of *Symphysurina* cf. *brevispicata* Hintze. Only a single collection from high in the Rabbitkettle Formation is assigned to this zone. This collection differs markedly from other *Symphysurina* Zone assemblages in being dominated by olenid trilobites of the genus *Apoplanias* and by lacking hystricurine trilobites.

Symphysurina brevispicata Subzone (25 m of composite Section KK). A single collection 25 m below the top of the Rabbitkettle Formation is assigned to the Symphysurina brevispicata Subzone. Only two species occur in this fauna, in addition to very poorly preserved specimens of Geragnostus.

- Apoplanias rejectus Lochman Symphysurina cf. brevispicata Hintze

These trilobites are generally poorly preserved, but the assemblage is very similar to those of the more diverse *Symphysurina brevispicata* Subzone of Oklahoma (Stitt, 1977) and the Rabbitkettle collection is confidently assigned to that subzone.

Note on Construction of Composite Section KK

An unnamed thrust located 102 m below the top of the Rabbitkettle Formation at Section KK repeats a 58 m interval of the upper part of the formation such that the interval KK 102 to KK 160 of the foot wall is duplicated by the interval KK 44 to KK 102 of the hanging wall. The repetition of strata was initially suspected in the field in 1977 by the repeat of the 15 m thick wavy banded unit above a thin recessive interval at KK 120 and KK 60 (Fig. 4). The field observations were later corroborated when it was determined that the *Bowmania americana* Fauna, the *Elkanaspis corrugata* Fauna, the *Missisquoia depressa* Subzone, and the *Apoplanias rejectus* Fauna occur in both the hanging and foot walls of the thrust (Fig. 6). The *Yukonaspis kindlei* Fauna occurs only in the foot wall and the *Symphysurina brevispicata* Subzone only in the hanging wall. The thin *Missisquoia mackenziensis* Fauna was recovered only from the foot wall; the correlative beds in the hanging wall (between KK 56 and KK 64) were not sampled.

A correlation of the foot and hanging walls of the thrust permits the compilation of a composite Section KK (Fig. 7). The trilobite biostratigraphy and the trilobite occurrences in the section on Systematic Palaeontology are keyed to this composite section. Thus, the 240-m-thick Section KK as originally measured (Fig. 5) is reduced to a true stratigraphic thickness of about 180 m (Fig. 7).

Cambrian-Ordovician Boundary

In North America, the base of the Ordovician System has traditionally been placed at the base of the Canadian Series (Twenhofel, 1954). More recently, the base of the Canadian Series has been specified to occur at the base of the *Missisquoia depressa* Subzone, the lower subzone of the *Missisquoia* Zone in Oklahoma (Stitt, 1977). The Canadian Series, however, can be interpreted to be based either on the Levis Formation, near Quebec City, or on the "Calciferous Sandrock" (Beekmantown Group) of New York State and eastern Quebec (see Fahraeus, 1977: 982, 983). Neither of these stratigraphic units includes a *Missisquoia* Zone at its base. The Levis

Formation (Tremadocian? and Arenigian) is part of the Taconic Allochthon and nowhere is it seen in conformable contact with Upper Cambrian rocks and the Beekmantown Group has recently been revised downward to include lower Upper Cambrian rocks of the Potsdam Formation (Fisher, 1977: 37, 38). In eastern New York State, the *Missisquoia* Zone in the Whitehall Formation (Taylor and Halley, 1974) occurs well up in the Beekmantown. Therefore, the base of the Canadian Series (if based on the Beekmantown) falls well below the base of the Ordovician as defined in Oklahoma and Texas by Stitt (1977) and Winston and Nicholls (1967). The Canadian cannot be used as a lower series of the Ordovician System in North America.

In Europe and elsewhere, the base of the Ordovician has been drawn variously at the base of the Arenigian Series, at the base of the "Upper Tremadocian" Series, or at the base of the Tremadocian Series (Henningsmoen, 1973). The base of the Tremadocian has become the most widely used level and that is herein accepted to constitute the extra-North American base of the Ordovician.

Over the past decade, the base of the Tremadocian has been correlated to a number of horizons within the North American Upper Cambrian and Lower Ordovician faunal succession. These include (1) the base of the *Saukia* Zone (Wolfart, 1970; Whittington and Hughes, 1974), (2) the base of the *Corbinia apopsis* Subzone of the *Saukia* Zone (Stitt et al., 1976; Jaanusson, 1979), (3) the base of the *Missisquoia depressa* Subzone of the *Missisquoia* Zone (Landing et al., 1978), and (4) near the base of the *Symphysurina* Zone (Fortey and Skevington, 1980). I concur with the conclusion of Jaanusson (1979: 138) that, "the overlap between the Tremadocian and the Trempealeauan, if present at all, seems to be inconsiderable" and suggest that the base of the Tremadocian Series correlates to a horizon close to the base of the *Missisquoia* Zone.

In the type area of the Tremadocian at Harlech Dome in north Wales, the contact of the Tremadoc Slates with the underlying Dolgelly Beds is everywhere marked by an unconformity, or it is a fault contact (Cowie et al., 1972; Henningsmoen, 1973). Only two unfaulted basal contacts were known to Stubblefield (1956: 37). At the more complete of these, at Ogof-ddu east of Ciccieth, the basal Tremadoc is marked by a bed of phosphate nodules followed by 6 m of striped mudstones with sporadic *Dictyonema flabelliforme sociale* below the main *D. f. sociale* "Band". The underlying Dolgelly Beds contain trilobites of the *Peltura scarabaeoides* and other zones (Rushton, 1974: 67).

Because the *Dictyonema flabelliforme* Zone in northern Wales has few trilobites, it is necessary to employ a reference section in order to relate the graptolite biostratigraphy of the Lower Tremadocian in the type area to the olenid trilobite biostratigraphy of the Lower Tremadocian of Europe and parts of North America. The thick Tremadocian section at Rio Santa Victoria, Province of Salta, northern Argentina is such a section. According to the data presented by Harrington and Leanza (1957: 8, 9, fig. 2), the 725-m-thick *Parabolina argentina* Zone is dominated by *Jujuyaspis keideli* Kobayashi and *Parabolinella argentinensis* Kobayashi. These two species enter 255 m above the base of the zone and are followed some 15 m higher by *Dictyonema flabelliforme sociale* and *D. f. flabelliforme*. These data suggest that the base of the Tremadocian in the Rio Santa Victoria section should be drawn at the 255 m level at the appearance of *J. keideli* and *P. argentinensis* and not at the base of the *P. argentina* Zone as proposed by Harrington and Leanza (1957). The 255 m level in the *Parabolina argentina* Zone provides a useful reference for the base of the Tremadocian; one that can be correlated closely to the succession in northern Europe because *Jujuyaspis keideli* occurs with *D. f. sociale* and *D. f. parabola* near the base of the *D. flabelliforme* Zone at Oslo (Henningsmoen, 1957: 264). It may also be correlated to the Mexican succession because *Parabolinella argentinensis*, *P. prolata* Robison and Pantoja-Alor, and *P. hecuba* (Walcott) occur with *Parabolina* cf. *argentina* (Kayser) and *Mictosaukia* in the *Parabolina* Assemblage of the Tinu Formation of southern Mexico (Robison and Pantoja-Alor, 1968, figs. 2–4).

Parabolinella does not occur at or near the base of the Tremadocian in northern Europe (Henningsmoen, 1957), but three observations suggest that this widespread olenid genus has potential as a contributor to the definition of the Cambrian-Ordovician boundary: (1) a species of Parabolinella appears just below the first occurrence of D. flabelliforme in Argentina, (2) four species of Parabolinella occur in Lower Tremadocian rocks of southern Mexico, and (3) species of Parabolinella have never been definitely identified in pre-Tremadocian rocks. The supposed Cambrian occurrences of this genus from North America cited by Henningsmoen



Fig. 9 Correlation of biostratigraphic successions across the Cambrian-Ordovician boundary in the District of Mackenzie, Oklahoma, Alaska, and Vermont. Correlation of the Hungaia assemblage is largely based on conodont biostratigraphy by Landing (1978, 1979).

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(1957: 133) have either been wrongly dated or been based on species that since have been reassigned to other genera (see also Landing et al., 1978).

Most previous investigators have defined the Cambrian-Ordovician boundary in North America at the base of the Missisquoia Zone (Winston and Nicholls, 1967; Stitt, 1971b; Derby et al., 1972); specifically at the base of the *Missisquoia depressa* Subzone of the Missisquoia Zone (Stitt, 1977; Hintze et al., 1980). This subzone has been recognized with certainty only in two stratigraphic sections in Oklahoma; one in the Arbuckle Mountains and one in the Wichita Mountains (Stitt, 1971b, 1977). Here, the base of the *M. depressa* Subzone lies 1.2 m and 1.8 m above the highest occurrence of Corbinia apopsis Subzone trilobites. Hintze et al. (1980) reported the M. depressa Subzone from a single collection in western Utah. Here, the base of the *M. depressa* Subzone lies 1.5 m above the highest occurrence of *C. apopsis*. Thus, in Oklahoma and Utah, the initial appearance of *Missisquoia* is at the base of the M. depressa Subzone, a metre or two above the highest occurrence of such "Cambrian" genera as Corbinia, Idiomesus, Larifugula, and Triarthropsis. Parabolinella does not occur in the Oklahoma and Utah sections, but in Vermont, central Texas, and Nevada (Shaw, 1951; Winston and Nicholls, 1967; Taylor, 1976) this genus first appears in the Missisquoia Zone.

Section KK through the upper part of the Rabbitkettle Formation contains abundant representatives of both *Missisquoia* and *Parabolinella*, including *M. depressa*, *P. cf. prolata*, and *P. hecuba*. In this section, the base of the *Missisquoia depressa* Subzone of the *Parabolinella* Zone corresponds neither to the first appearance of *Missisquoia* nor to the first appearance of *Parabolinella*. In the foot-wall portion of Section KK, *Missisquoia* first appears immediately above the base of the "Hystricurid" Biomere at the base of the *Elkanaspis corrugata* Fauna of the *Yukonaspis* Zone (13.5 m below the first occurrence of *M. depressa*) and *Parabolinella* Zone (3.5 m below the first occurrence of *M. depressa*). The multi-element condont species *Cordylodus oklahomensis* (senior synonym of the form species *C. proavus*; Landing et al., 1980) first appears high in the *Elkanaspis corrugata* Fauna (4.5 m below the first occurrence of *M. depressa*).

The important first and last faunal appearances in the Cambrian-Ordovician boundary interval of the foot-wall portion of Section KK are shown in Table 1.

The chief drawback to a definition of a systemic boundary at the base of the *Missisquoia depressa* Subzone is the difficulty posed by attempts at inter- and intra-continental correlation. This boundary cannot be correlated directly with trilobite successions in Europe (Landing et al., 1978) and, on this continent, it can be specified only in four sections—two in Oklahoma and one each in Utah and the District of Mackenzie. By changing the criterion for recognition from that of the lowest occurrence of *Missisquoia* at the base of the *Missisquoia* Zone to that of the lowest occurrence of *Parabolinella* at the base of the *Parabolinella* Zone, it is possible to improve the correlation potential of this horizon with only a very minor change in its actual placement. Stitt (1977: 26) defined the base of the *M. depressa* Subzone at the first occurrence of *M. depressa* Stitt, *Plethopeltis arbucklensis* Stitt, and *Ptychopleurites brevifrons* (Kobayashi). In the District of Mackenzie, such a level defines the upper boundary of the 3-m-thick *Missisquoia* and *Parabolinella*. A boundary located at the first appearance of *Missisquoia mackenziensis* sp. nov.,

Table 1	Faunal events recorded in the Cambrian-Ordovician boundary inte	val of the foot-wall portion of Section KK (see Fig. 6).
106.0 m	Base of <i>Apoplanias rejectus</i> Fauna	entry of A. rejectus
109.0 m	Highest collection of Missisquoia depressa Subzone	exit of M . depressa, Parabolinella cf. prolata, and Geragnostus (M .) subobesus
119.5 m	Base of Missisquoia depressa Subzone	entry of M. depressa and Ptychopleurites brevifrons
123.0 m	Base of Missisquoia mackenziensis Fauna, base of Parabolinella Zone, and base of ORDOVICIAN	entry of M . mackenziensis, P . cf. prolata, and G . (M .) subobesus and exit of Parabolinites cf. williamsoni
124.0 m	Highest collection of Elkanaspis corrugata Fauna and Yukonaspis Zone	entry of Cordylodus oklahomensis and exit of Larifugula, Eurekia, Yukonaspis, and Idiomesus
133.0 m	Base of Elkanaspis corrugata Fauna	entry of Missisquoia, Bienvillia, P. cf. williamsoni, E. corrugata, and Larifugula leonensis
135.0 m	Base of "Hystricurid" Biomere	

Parabolinella cf. prolata Robison and Pantoja-Alor, P. panosa sp. nov., and Geragnostus (Micragnostus) subobesus (Kobayashi) at the base of the M. mackenziensis Fauna, the lowest division of the Parabolinella Zone, is very close to the commonly accepted base of the North American Ordovician and it has the advantage of being correlatable to a level at, or close to, the base of the Tremadocian in the Rio Santa Victoria section in Argentina. The base of the Parabolinella Zone also corresponds to the highest occurrence of such "Cambrian" genera as Larifugula, Idiomesus, Yukonaspis, and Eurekia.

I suggest that the base of the *Dictyonema flabelliforme* Zone and the base of the *Parabolinella* Zone are closely correlative and, in combination, these define an operational base to the Tremadocian Series and the Ordovician System.

Lithofacies and Environment

The upper Rabbitkettle Formation at Section KK is, at first glance, remarkably uniform. It is a platy bedded to medium bedded unit of grey limestone with thin, buff, yellow, brown, or brick-red weathering silty and argillaceous partings. These impart a pronounced banded aspect to the outcrops. Despite the platy nature of many of the beds, the unit weathers massive (Fig. 10A). The only apparent differentiation in the 180 m of strata at composite Section KK is a lower 120 m unit of planar banded limestone and an upper 60 m unit of undulose banded limestone (Fig. 5).

The impression of uniformity of these strata was quickly dispelled when the limestones were examined in thin sections, by acetate peels and in polished hand samples. Such investigations demonstrated that major textural and colour changes correspond to changes in trilobite composition and a study of the carbonate rock textures was undertaken in order to get a fuller picture of the environmental significance of the rocks and the faunas.

Below, the textures of the limestones in four segments of composite Section KK are discussed. The boundary coincidence of the lithofacies segments and the trilobite biostratigraphic divisions demonstrate that the benthic trilobite associations dealt with in this paper are packages of taxa whose composition and relative abundance are controlled by both environmental and temporal factors. This conclusion, of course, provides constraints on the use of these faunas (and, indeed, most other trilobite biostratigraphic units) in correlation.

180 to 96 m of Composite Section

The most commonly encountered lithology in the lower part of Section KK is light to medium grey lime mudstones and wackestones that are finely interbedded with yellow-brown laminated silty layers (Fig. 10B). The lime mudstone/wackestone beds are a few centimetres thick and typically discontinuous laterally. They are terminated at near-vertical incursions or by broad waves of the laminated silt-rich layers. These mud supported limestones generally lack internal features, but occasionally show vague parallel laminations and rare horizontal burrows. This lithofacies apparently

records deposition on the seaward side of a carbonate shoal in water depths exceeding that of effective wave base. In the Rabbitkettle Formation, this lithofacies yielded only a few trilobites. Most of the silicified trilobites of the *Yukonaspis kindlei* Fauna came from irregularly interbedded 5- to 10-cm-thick beds of light grey to medium grey lime grainstone or packstone in which the major allochems are trilobites, pelmatozoan ossicles, and ooids. Some of these grain-supported allochem limestones show crude grading (Fig. 12A) and they were probably deposited by non-turbid traction currents which periodically swept off the higher parts of the carbonate shelf.



Fig. 10 Outcrop photographs of the upper Rabbitkettle Formation at Section KK.

- A Upper Cambrian part of Rabbitkettle. Dotted line separates the *Yukonaspis kindlei* Fauna below from the *Bowmania americana* Fauna above. Location of photograph in Fig. 10B is indicated by "b". Figure in left centre provides scale.
- B Thinly bedded medium grey lime mudstones separated by yellow-brown finely laminated silty layers. About 50 cm of strata are shown. *Yukonaspis kindlei* Fauna.

96 to 70 m of Composite Section

The silty lime mudstone/wackestone facies which dominates the lower part of Section KK persists into higher rocks carrying the *Bowmania americana* Fauna, but here the facies assumes a subordinate role. The bulk of this 26 m interval comprises medium to thick bedded, dove-grey, porcelaneous, burrowed, and pelletoid lime wackestones with wispy silt laminations (Figs. 12B, 14). Such a facies suggests deposition on an open, low-relief shelf in quiet, moderately shallow, and well-oxygenated water below effective wave base. Similar burrowed lime wackestone facies have been described from the Nevada/Utah area, in lower Dresbachian strata by Lohmann (1976), and in lower Franconian strata by Brady and Rowell (1976). In the Mackenzie Mountains, the burrowed lime wackestone facies forms the top of the Ptychaspid Biomere; in Nevada/Utah, it occurs at the top of the Marjumiid Biomere and at the top of the Pterocephalid Biomere.

70 to 57 m of Composite Section

At the 70 m level in composite Section KK, at the base of the Elkanaspis corrugata Fauna, the grey burrowed lime wackestone facies is replaced sharply by a sequence of thinly bedded, dark grey to black, non-burrowed lime mudstones and finely laminated clay and silt-rich layers. Many of these beds display sedimentary boudinage (Figs. 11B, 13D) and most of the lime mudstones have vague parallel laminations (Fig. 12c). The striking colour change between the *Bowmania americana* interval and the *E. corrugata* interval is best appreciated in polished hand samples (Fig. 14). The black laminated mudstone facies was deposited in waters that were deeper, colder, or less oxygenated than were the underlying lithofacies and it is best assigned to the Outer Detrital Belt of Palmer (1960a). A similar dark grey to black laminated lime mudstone facies was described from lower Dresbachian strata of Nevada/Utah by Lohmann (1976). The black laminated mudstone facies of the upper Rabbitkettle Formation is also very similar to the autochthonous slope lithofacies of black, shaly lime mudstone and wackestone described by Taylor and Cook (1976) and Cook and Taylor (1977) from the Franconian and Trempealeauan Hales Limestone of Nevada.

Fig. 11 Outcrop photographs of the upper Rabbitkettle Formation at Section KK.

- A Uppermost Cambrian and lower Ordovician parts of Rabbitkettle. View is across unnamed thrust fault (white dotted line) that repeats Cambrian-Ordovician boundary at base of *Parabolinella* Zone (dashed double line). Location of photographs in Figs. 11B and 11C is indicated by "b" and "c".
- B Thinly bedded dark grey to black lime mudstones and laminated silty layers (note sedimentary boudinage). Hammer in Fig. 11c provides scale. *Elkanospis corrugata* Fauna.
- c Rubbly bedded dark grey lime mudstones. Missisquoia depressa Subzone.



base of PARABOLINELLA Zone

С





25

57 to 0 m of Composite Section

The higher parts of the upper Rabbitkettle Formation at Section KK, assigned to the *Missisquoia depressa* Subzone to *Symphysurina brevispicata* Subzone, consist of a series of medium to thin beds of dark grey, broadly laminated lime mudstones separated by thin undulose silty and argillaceous laminae (Figs. 11C, 13). In places, adjacent silty laminae meet to produce irregular boudins. Like the underlying facies, the undulose lime mudstone facies is best assigned to the Outer Detrital Belt. It is similar in many respects to the silty lime mudstone/wackestone facies occurring in the lower part of the upper Rabbitkettle, but it differs consistently by being darker in colour, by having thicker and irregular nodular bedding, by lacking burrows, by lacking grain-supported allochem limestones, and by containing abundant, *in situ* trilobites. In this lithofacies the silicified trilobites are found in both the silty laminae and in the dark mudstone.

Conclusion

The 180 m composite section through the upper Rabbitkettle Formation records finely alternating carbonate mud and terrigenous silt deposition on the seaward side of the broad Mackenzie Platform and adjacent to the Selwyn Basin (Fig. 3). With the exception of occasional thin beds of grainstone and packstone low in the section, lime sands are absent, suggesting a depositional setting far removed from high-energy carbonate shoal complexes. Despite the occurrence of dark lime mudstones of slope aspect in the upper part of the composite section, no portion of the upper Rabbitkettle is judged to have been deposited on the slope. Typical slope features are found in the Road River Formation, depositionally seaward of the Rabbitkettle Formation (Fig. 3; Cecile, 1978).

A similar sequence of lithofacies has been documented by Lohmann (1976) for platform-margin and deep platform settings in the lower Dresbachian interval of the Great Basin of Nevada and Utah. Lohmann outlined a platform-margin, high energy complex of grainstone and packstone, in part stromatolitic and oolitic, deposited above wave base, and a deep platform, low energy complex composed of three, progressively deeper, lithofacies: a burrowed wackestone lithofacies, a nodular mudstone lithofacies, and a laminated mudstone lithofacies. By correlating the tops of shallowing-upward cycles across the platform margin and by assuming comparable sediment compaction in sand and mud-size sediment, Lohmann was able to estimate palaeoslopes of 0.3 to 2.4 m/km for this portion of the shelf and water depths for each of the lithofacies. He concluded that the high energy complex of grainstones and packstones accumulated in waters shallower than 15 m and that the low energy complex of mudstones and wackestones accumulated below effective wave base from 15 m to greater than 30 m. Of particular importance is Lohmann's conclusion that a lithofacies such as the black laminated mudstone facies, generally considered to be "deep water", could have been deposited in water depths not much greater than 30 m.

If the water depths estimated for similar, and presumably environmentally correlative, lithofacies in Nevada/Utah are used as guides, then it is possible to propose tentative palaeobathymetries for the two main lithofacies segments of the



Fig. 12 Negative prints of acetate peels of limestones from the upper Rabbitkettle Formation. All are cut perpendicular to bedding with the exception of Fig. 12B which is cut parallel to bedding. Bar represents 1 cm. Arrow indicates stratigraphic top.

- A Trilobite-rich lime grainstone/packstone showing crude grading. Yukonaspis kindlei Fauna, K 525.
- B Burrowed lime wackestone. Bowmania americana Fauna, KK 156.
- c Broadly laminated lime mudstone. Elkanaspis corrugata Fauna, KK 64.
- D Lime mudstone with sedimentary boudinage; light-coloured and laminated bands are clay-rich. *Missisquoia mackenziensis* Fauna, KK 122.5.



- Fig. 13 Negative prints of acetate peels of limestones from the upper Rabbitkettle Formation. All are cut perpendicular to bedding. Bar represents 1 cm. Arrow indicates stratigraphic top.
 - A,B Wavy bedded lime mudstones with clay-rich seams. *Missisquoia depressa* Subzone, KK 119.5 and K 880.
 - c Wavy bedded lime mudstone with clay-rich seams. Apoplanias rejectus Fauna, KK 106.
 - D Lime mudstone. Symphysurina brevispicata Subzone, KK 25.



Fig. 14 Lithologic, textural, and colour spectra across the Ptychaspid-"Hystricurid" Biomere boundary and the Cambrian-Ordovician boundary displayed by selected polished and oiled hand samples cut perpendicular to bedding. Sample from *B. americana* Fauna is a dove-grey, burrowed, and thickly bedded lime wackestone deformed by steeply dipping tension fractures. Samples from *E. corrugata* Fauna and higher intervals comprise dark grey to black, nonburrowed, crudely laminated, and thinly and irregularly bedded lime mudstones.

upper Rabbitkettle Formation at Section KK. The light to medium grey and burrowed lime mudstone and wackestone facies with minor grainstone or packstone beds in the lower part of the composite section (180–70 m) were probably deposited in water depths of 15 to 30 m and below wave base. This interval is assigned to the Middle Carbonate Belt of Palmer (1960a) and it records a gradual shallowing caused by progradation of the grey burrowed wackestone facies. The dark grey to black and non-burrowed lime mudstone facies in the upper part of the composite section (70–0 m) was probably deposited in water depths deeper than 30 m, but probably not much deeper. This interval is assigned to the Outer Detrital Belt of Palmer (1960a).

Grand Cycle Boundary

Aitken (1966) defined the Grand Cycle as a large scale asymmetric depositional cycle consisting of a lower shaly half-cycle gradually overlain by an upper carbonate half-cycle. The lower and upper boundaries are sharp. Grand Cycles are substantial stratigraphic units. In the southern Canadian Rocky Mountains, each cycle extends through 275 to 800 m of strata and Aitken (1978) showed that the Grand Cycle pattern can be mapped along the Cambrian platform from northern British Columbia to Utah, a distance of some 2000 km. Aitken (1966) outlined eight Grand Cycles from Middle Cambrian to Middle Ordovician rocks in the southern Canadian Rocky Mountains and attributed the cyclicity to regular and periodic shifts of Palmer's (1960a) facies belts—the lower shaly half-cycle comprises either the Outer Detrital (OD) Belt or the Inner Detrital (ID) Belt and the upper carbonate half-cycle comprises the Middle Carbonate (MC) Belt.

In his recent analysis of Grand Cycle patterns, Aitken (1978: 532, 533, figs. 8, 9) provided environmental interpretations and lithofacies maps of these cyclical deposits in the area between Jasper and Salt Lake City. According to this synthesis, the higher levels of the MC Belt of a Grand Cycle comprise a broad, outer peritidal carbonate complex which expands cratonwards by progradation and a narrow, inner subtidal carbonate mud lithofacies which grades cratonwards into fine and coarse clastics of the ID Belt. A rapid transgression drowns all or part of the MC Belt and the terrigenous muds are distributed by currents across most or all of the previous MC Belt. These clastics record the initial deposits of the succeeding Grand Cycle. The supply of terrigenous mud decreases as the transgression continues and carbonate deposition initiates again on sites near the edge of the platform. To put it simply, the Grand Cycle records the gradual expansion and rapid contraction (or collapse) of the MC Belt.

In the well-studied stratigraphic succession at Sunwapta Pass, Jasper National Park, Aitken (1966) placed the base of a Grand Cycle at the appearance of recessive shales and calcareous siltstones (ID Belt) of the Survey Peak Formation above thick-bedded limestones with large domal stromatolites (MC Belt) of the Mistaya Formation. Here, the base of the Survey Peak corresponds to the base of the *Corbinia apopsis* Subzone of the *Saukia* Zone (Dean, 1978).

The sharp vertical juxtaposition of the MC Belt and the OD Belt in the upper Rabbitkettle Formation that was documented previously invites comparison with the Grand Cycle pattern. At the 70 m level in composite Section KK, grey burrowed
wackestones of the MC Belt are abruptly succeeded by dark grey to black, non-burrowed lime mudstones of the OD Belt. This level is concluded to be a Grand Cycle boundary (Fig. 14). The base of the Grand Cycle in Section KK corresponds to the base of the Elkanaspis corrugata Fauna of the Yukonaspis Zone and is synchronous with the base of the Grand Cycle in the Sunwapta Pass section (Fig. 9). It is reasonable to suppose that the grey limestones of the upper Mistaya and the upper Rabbitkettle are parts of the same continous MC Belt and that the distinct lithologic aspects of these carbonate units reflect merely different palaeobathymetric positions-the upper Mistaya was part of the carbonate shoal complex and the upper Rabbitkettle (between 180 and 70 m of the composite section) was deposited in deeper water on the seaward side of such a complex. The rapid deepening at the Grand Cycle base will result in different lithologic records at different positions along this palaeobathymetric profile. In the southern Rocky Mountains the stromatolitic limestones of the Mistaya Formation are succeeded by shales and siltstones of the Survey Peak Formation (ID Belt); whereas in the Mackenzie Mountains the lime wackestones of the Rabbitkettle Formation are succeeded at the 70 m level by dark lime mudstones (OD Belt). A single Grand Cycle boundary, therefore, will be of the ID/MC type on the shallow platform margin and of the OD/MC type on the deep platform.

Aitken (1978) proposed that the cyclicity pattern of Grand Cycles was induced externally—a rapid transgression causing a shift from carbonate to fine clastic deposition. Matti and McKee (1976) and Palmer and Halley (1979: 54, fig. 34) have proposed alternate models for large scale carbonate-clastic cycles. These two models differ in detail, but both were presented as largely internally controlled and self-regulating systems because the cyclicity was interpreted to be a natural consequence of active carbonate production on a slowly subsiding shelf during a period of a gradual rise in sea level. The Palmer and Halley model may be restated in a slightly modified format as follows:

- a) A shallow subtidal carbonate-producing belt becomes established on a slowly subsiding shelf which is also receiving a steady supply of terrigenous clastics. This carbonate factory supports the entire MC Belt and supplies, not only *in situ* sediment to the subtidal zone, but also transported sediment to the peritidal zone and to the deep shelf as peri-platform ooze (McIlreath and James, 1978).
- b) The MC Belt progrades landward and seaward because carbonate sediments generally accumulate at a greater rate than subsidence (James, 1977) and eventually to sea level to form shoal and peritidal carbonate complexes and, possibly, carbonate islands. These complexes are net consumers of carbonate sediment.
- c) The peritidal and shoal complexes continue to prograde across the shallow subtidal carbonate factory so that the quantity of carbonate sediment is diminished. At a critical level, the area occupied by the carbonate factory becomes too small to maintain the now very broad carbonate platform and, because subsidence and sea-level rise continues apace, the entire MC Belt either founders or is displaced and reduced markedly in size.
- d) Terrigenous clastics of the ID Belt now spread out across the inner portions of the MC Belt while dark limestones and shales of the OD Belt encroach upon the outer portions.

This internally controlled model adequately accounts for the asymmetric cyclicity of Grand Cycles and, in particular, provides plausible explanations for the nonuniform lithofacies successions across a single Grand Cycle boundary at different localities in western North America.

The shut-down of the carbonate factory, coupled with the gradual eustatic sea-level rise and continued subsidence, results in a moderate deepening across the shelf. On the outer part of the shelf this deepening could have been sufficient to permit the spread of cold oceanic and oxygen-poor waters onto the relatively shallow shelf. Cook and Taylor (1975) and Taylor and Forester (1979) have presented evidence for the existence of a two-layered thermally stratified ocean in the Lower Palaeozoic—warm-water thermosphere and cold-water psychrosphere. A Grand Cycle boundary on the outer part of the shelf, therefore, may separate warm-water environments, below, from cold-water environments, above.

The Biomere Concept

The biomere was defined as an Upper Cambrian biostratigraphic unit of stage magnitude that is bounded by abrupt and diachronous nonevolutionary changes in the polymerid trilobites and that is characterized by an internal pattern of increasing species diversities and increasing species ranges (Palmer, 1965a,b; Stitt, 1975). This concept has stimulated considerable interest in recent years, both among biostratigraphers concerned with correlation of Cambrian rocks and fossils and among palaeontologists interested in the possible evolutionary implications of such a closed system of limited stratigraphic extent which is bounded by significant extinction horizons.

At present, four biomeres have been named. These extend from the late Middle Cambrian to the Early Ordovician—the Marjumiid, Pterocephaliid, Ptychaspid, and "Hystricurid" biomeres (Fig. 15; Stitt, 1977, figs. 3, 4). Of these, only the Pterocephaliid and Ptychaspid biomeres have been fully documented (Palmer, 1965b; Longacre, 1970; Stitt, 1971b, 1977). The upper boundary of the "Hystricurid" Biomere remains to be defined. Each biomere typically spans 250 m to 350 m of strata and each apparently lasted for 5 Ma to 7.5 Ma (Palmer, 1979: 40).

Both Palmer (1965a, 1979) and Stitt (1971b, 1975, 1977) have maintained that biomere boundaries cannot be located by physical criteria in a rock column because they are not associated with unconformities or with drastic lithologic changes. This conclusion was disputed by Johnson (1974) who noted that Palmer's own (1965b) data for the base of the Pterocephaliid Biomere showed a lithologic change in each of 10 columnar sections in Nevada and Utah. Moreover, Miller (1978: 16–21) devoted an entire chapter to a discussion of lithologic changes at the revised base of the "'Hystricurid'' Biomere in North America.

Palmer's (1965a) contention that the biomere differs from other biostratigraphic units by its diachronous boundaries was disputed by Henderson (1976) who maintained that the data for diachrony of the base of the Pterocephaliid Biomere are not conclusive. In this regard it is important to recognize that all subsequent graphical depictions have shown biomere boundaries at isochronous zonal boundaries (Stitt, 1977, fig. 4; Palmer, 1979, fig. 1); this suggests that any diachrony of a biomere boundary cannot be resolved by the available biostratigraphic framework.

A biomere is a biostratigraphic unit and, as such, it comprises a sequence of strata which is unified by its fossil content. Its distribution is controlled by temporal, environmental, and biogeographic factors and, therefore, any explanation of the biomere pattern must address not only the vertical faunal changes in terms of composition, diversity, and range, but also lateral and vertical faunal (biofacies) and lithologic (lithofacies) relationships, as well as possible biogeographic influences. Previous explanations of the biomere pattern have been based almost exclusively on the vertical distribution of trilobites in separate measured sections. Biofacies and lithofacies changes have not been considered. Thus, in the most comprehensive statement on the biomere pattern to date, Stitt (1975) interpreted the Ptychaspid Biomere as an adaptive radiation of a single trilobite community (emphasis added). This radiation, apparently fuelled by increasing environmental stability, came to a halt as environmental deterioration caused extensive extinction at the biomere top

_ ^_	ΛΟΕ5/ 5EKTE5		
LOWER <	TREMADOCIAN	SYMPHYSURINA	"HYSTRICURID" BIOMERE
		MISSISQUOIA	
UPPER CAMBRIAN	TREMPEALEAUAN	<u>C.</u> apopsis	
		SAUKIA	PTYCHASPID BIOMERE
	FRANCONIAN	ELLIPSOCEPHALOIDES	
		IDAHOIA	
		TAENICEPHALUS	
		ELVINIA	PTEROCEPHALIID BIOMERE
	DRESBACHIAN	DUNDERBERGIA	
		PREHOUSIA	
		DICANTHOPYGE	
		APHELASPIS	
		CREPICEPHALUS	MARJUMIID BIOMERE
		CEDARIA	
RIAN		BOLASPIDELLA	
AIDC		BATHYURISCUS -	
لركما		ELRATHINA	

STACES/SERIES TRUORITE ZONIES RIGMEDES

Fig. 15 Sequence of upper Middle Cambrian, Upper Cambrian, and lower Lower Ordovician trilobite zones (based largely on successions in southwestern United States) and boundaries of the four named biomeres. The lower boundaries of the Ptychaspid and "Hystricurid" Biomeres are shown as revised by Palmer (1979).

(see also Bretsky and Lorenz, 1970; Ashton and Rowell, 1975; Stitt, 1977; and Eldredge, 1977 for a concise review).

As Eldredge (1977: 313) noted, "Stitt's [(1971a, 1975)] explanatory models of the ecologic and evolutionary dynamics accounting for biomere patterns are imaginative but cannot be taken as demonstrated until some more definitive, testable hypotheses are formulated and tested with the data." Nonetheless, Stitt's (1975) interpretation of the biomere as an adaptive radiation which issued from a few ancestral species was accepted by Stanley (1979: 246-250) who then used Palmer's (1965b) data for the Pterocephaliid Biomere to calculate remarkably high rates of diversification for Late Cambrian trilobites-rates that far exceed those of ammonites, graptoloids, and mammals (Stanley, 1979, fig. 9-1)! In the face of such anomalously high rates of diversification, it would seem prudent to critically examine the basic tenet of monophyly (or pauciphyly) for the species proliferation pattern of the biomere. Stanley's calculation of rates of diversification for 27 species of trilobites near the middle of the Pterocephaliid Biomere was based on the assumption of either a single ancestral species or as many as five ancestral species. However, the Pterocephaliid Biomere includes eight families of trilobites and the Ptychaspid Biomere eleven families or more and such numbers would seemingly provide a logical estimate for the minimum numbers of ancestral species. If an adaptive radiation model is to be applied to the biomere pattern, then the reasonable postulate of as many as ten ancestral species would bring the rate of diversification of these trilobites more in line with those of other faunal groups (Stanley, 1979, fig. 9-1).

The concept of the biomere as an *in situ* adaptive radiation of a single trilobite community has never been demonstrated, nor has it ever been seriously questioned. A full critique of this idea is beyond the scope of the present paper, but the faunal and lithologic spectra across the Ptychaspid-"Hystricurid" Biomere boundary at Section KK, combined with an evaluation of the boundary interval at other localities in western North America, cast serious doubt on a strict evolutionary interpretation of the biomere pattern. Instead, these data suggest that each biomere consists of a succession of biofacies and lithofacies and that the change in faunal diversity and composition are responses to changes in the environment. The environmental or facies packages seen in superpositional sequence will, of course, also be expressed laterally or geographically and, in this context, the biomere emerges as a manifestation of dynamic biogeography.

Ptychaspid-''Hystricurid'' Biomere Boundary

Stitt (1975) placed the lower and upper boundaries of the Ptychaspid Biomere at the base of the *Taenicephalus* Zone and the base of the *Missisquoia* Zone, respectively, and considered the *Corbinia apopsis* Subzone to be the highest (stage 4) division of the Ptychaspid Biomere. Palmer (1979) argued convincingly that both of these boundaries should be lowered slightly to or near the base of the *Irvingella major* Subzone and to or near the base of the *C. apopsis* Subzone, so that the *C. apopsis* Subzone becomes the lowest (stage 1) division of the "Hystricurid" Biomere (Fig. 15). Palmer's relocation of these boundaries placed the biomere concept in a new

light. Stitt's (1975: 385) final stage of "evolutionary desperation" now becomes an initial stage of immigration of new taxa and proliferation of old taxa. The biomere boundary is no longer primarily an extinction level. Furthermore, the base of the "Hystricurid" Biomere is now coincident with major changes in the conodonts (Miller, 1978), as well as coincident with significant lithofacies changes on the outer parts of the platform.

Palmer (1979: 33) stated that a biomere commences with a brief crisis period during which rare elements of the soon-to-be-dominant new fauna are associated with opportunistic bursts of both new and old faunal elements. Applying these criteria to the faunal record in the upper Rabbitkettle Formation at Section KK, it is clear that the *Elkanaspis corrugata* Fauna, the highest division of the *Yukonaspis* Zone, constitutes such a crisis interval. The base of this interval is marked by the disappearance of *Bowmania* and *Kathleenella*; the first appearance of *Parabolinites*, *Bienvillia*, and *Missisquoia*; minor increase in *Idiomesus* and *Elkanaspis*; and significant increase in *Larifugula*. *Eurekia*, *Yukonaspis*, *Geragnostus*, and *Plethometopus* continue from the underlying *Bowmania americana* Fauna; the last two continue into the overlying *Parabolinella* Zone (Fig. 16).

The base of the *Elkanaspis corrugata* Fauna is the base of the "Hystricurid" Biomere in Section KK and this level is correlative with the base of the *Corbinia apopsis* Subzone which constitutes the base of the "Hystricurid" Biomere in Oklahoma (Stitt, 1977; Palmer, 1979), Texas (Longacre, 1970), Alberta (Dean, 1978), and Utah (Hintze et al., 1980).

The level defined by the base of the *Elkanaspis corrugata* Fauna and the base of the *Corbinia apopsis* Subzone is not only the base of a biomere, it is also the base of a Grand Cycle. The boundary coincidence of two major stratigraphic units, one based on fossils and one based on lithostratigraphy, encourages ecologic and biogeographic explanations for the biomere boundary events.

The boundary between the Ptychaspid and "Hystricurid" biomeres in the upper Rabbitkettle Formation can profitably be viewed as a boundary between trilobite biofacies: a lower biofacies dominated by *Bowmania*, *Kathleenella*, and *Yukonaspis* that occurs in light to medium grey and burrowed lime wackestones and an upper biofacies dominated by *Larifugula*, *Parabolinites*, and *Elkanaspis* that occurs in black and nonburrowed lime mudstones (Fig. 16). The lower biofacies has clear affinity for associations that lived on the broad Upper Cambrian shelf and the upper biofacies has characteristics in common with associations that lived on the Upper Cambrian and Lower Ordovician slope.

The faunal succession across the biomere boundary in Section KK shown in Fig. 16 is very similar to the vertical biofacies transition from the nileid to the olenid communities in the Lower Ordovician of Spitsbergen (Fortey, 1975, figs. 4, 6) and to the lateral transition from Biofacies III to IV in the Middle Ordovician of the District of Mackenzie (Ludvigsen, 1979a, figs. 12, 13). I suggest that the resemblance is significant and it implies that there is nothing uniquely Cambrian about the biomere pattern.

Biofacies and community studies of Late Cambrian benthic faunas in North America have only just been started. The only study that deals with such biofacies at a scale appropriate for the present problem is that of Taylor (1977) which defined an undifferentiated shelf trilobite biofacies for the Inner Detrital (ID) and Middle Carbonate (MC) belts and two slope biofacies from the outer MC Belt and Outer Detrital (OD) Belt along a 3000 km transect of Trempealeauan rocks from Wisconsin to Nevada.

Using Taylor's (1977, table 3) occurrence data of 41 genera, supplemented by Stitt's (1971b, 1977) and Longacre's (1970) data from Oklahoma and Texas, and the data from the present study, it is possible to outline approximately the major features of trilobite biofacies development for the interval immediately below the Ptychaspid-''Hystricurid'' Biomere boundary. At least four trilobite associations may be defined for these upper Trempealeauan rocks:

- (1) The ID Belt in the upper Mississippi Valley contains abundant dikelocephalid, saukiid, and eurekiine trilobites. These biofacies are here designated "di-kelocephalid associations".
- (2) The inner MC Belt in Oklahoma and, possibly, Texas and New York State contain abundant plethopeltid (particularly *Stenopilus*), eurekiine, euptychaspidine, and saukiid trilobites. These diverse biofacies are here designated "plethopeltid-eurekiine associations".



Fig. 16 Percentage abundances of 19 genera of trilobites across the Ptychaspid-"Hystricurid" Biomere boundary in the upper Rabbitkettle Formation at composite Section KK. Open limestone symbol represents light grey, burrowed lime wackestones; stippled limestone symbol represents dark grey to black, nonburrowed lime mudstones. Stratigraphic interval extends from the lower *Bowmania americana* Fauna to the upper *Missisquoia depressa* Subzone. Note the expansion of *Larifugula* and the appearance of the olenids *Parabolinites* and *Bienvillia* immediately above the biomere boundary.

- (3) The outer MC Belt in the District of Mackenzie and, possibly, Nevada and Utah contains abundant entomaspid (particularly *Bowmania*), eurekiine, euptychaspidine, and kainellid trilobites. These biofacies are here designated "*Bowmania* associations".
- (4) The OD Belt in Nevada contains olenid, papyriaspid, asaphid, and kainellid trilobites. These faunas are of Franconian to mid-Trempealeauan age (Taylor, 1976), but they could well extend into the late Trempealeauan. They are included here under the name "*Hedinaspis* associations".

The diverse *Hungaia* faunas, best known from boulders in slope facies of Trempealeauan age in Quebec and Newfoundland, are not included in this synthesis because of the uncertain provenance of these transported blocks. They may have been derived from shelf-edge or upper slope reef mounds, a facies that could have been widespread in marginal settings around North America (James, 1980).

The interval immediately above the base of the "Hystricurid" Biomere in western North America includes two associations that are probably attributable to biofacies developments:

- (5) The MC Belt in Oklahoma, Texas, and Utah contains trilobite faunas that are dominated by the eurekiine *Corbinia*, but also includes kainellid, kingstoniid (?), catillicephalid, and plethometopid trilobites. These biofacies are here designated "*Corbinia* associations".
- (6) Lithofacies of OD Belt aspect on the outer shelf in the District of Mackenzie contain trilobite faunas that are dominated by the kingstoniid (?) *Larifugula* and the olenid *Parabolinites*. Minor elements include kainellid, eurekiine, shumardiid, and missisquoiid trilobites. These biofacies are here designated "*Larifugula* associations".

Faunas from a basal "Hystricurid" Biomere position in the ID Belt are not definitely known.

Higher levels in the "Hystricurid" Biomere include two contrasting trilobite biofacies developments:

- (7) The MC Belt in Oklahoma, Texas, and Utah contains trilobite faunas that are strongly dominated by the plethopeltid *Plethopeltis* and the missisquoiid *Missisquoia*. Rare elements include agnostid, leiostegiid, and olenid trilobites. These biofacies are here called "*Plethopeltis* associations".
- (8) Lithofacies of OD Belt aspect on the outer shelf in the District of Mackenzie and Vermont contain trilobite faunas that are dominated by the olenid *Parabolinella*, the agnostid *Geragnostus*, and by *Missisquoia*. Minor elements include plethopeltid, leiostegiid, norwoodiid and, in Vermont, asaphid trilobites. These biofacies are here called "*Parabolinella* associations".

Each of the eight trilobite associations outlined above comprises one or more trilobite biofacies. These associations can be placed on a space-time framework along an Inner Detrital Belt to Outer Detrital Belt transect from the Late Trempealeauan to the Early Tremadocian (Fig. 17A) and their positions followed across the coincident biomere and Grand Cycle boundary (Fig. 17B). This way of examining the biomere

boundary events differs from those of previous investigators in that it emphasizes that migration and extinction are ecologic and biogeographic events that occur in communities and environments, and not primarily at stratigraphic levels in measured sections.

During Saukiella serotina Subzone and Bowmania americana Fauna time a succession of trilobite-dominated assemblages lived on a variety of carbonate and terrigenous clastic substrates on a broad, warm water shelf about 2000 to 3000 km wide (Fig. 17A). The shelf extended farther into the marginal shale basin than the previous time interval because this interval represents the time of maximum progradation of carbonates near the top of the Grand Cycle (see Aitken, 1978, figs. 8.4 and 9.6 for similar conditions near the tops of older Grand Cycles). This was also the time of maximum species diversity of trilobites. The bathymetry of this broad shelf was controlled largely by offshore peritidal and shoal complexes consisting of a variety of subenvironments which contained the biofacies assigned to the "plethopeltid-eurekiine associations". The carbonate shoal complexes formed the bulk of the MC Belt and they flanked an inshore basin of subtidal and peritidal carbonate and clastic sediments which contained the "dikelocephalid associations". "Bowmania associations" occur in subtidal carbonate mud environments seaward of the carbonate shoal complexes. Carbonate mounds or reefs with Hungaia faunas may have occupied the same general position. Seaward of the MC Belt occurred dark lime and terrigenous muds with the "Hedinaspis associations". This slope assemblage apparently inhabited deep, cold, and poorly oxygenated waters below the thermocline (Taylor and Cook, 1976).

Cessation of carbonate deposition over large parts of the shelf at the Grand Cycle top initiated a chain reaction of faunal events which defines the biomere boundary (Fig. 17B).

During *Corbinia apopsis* Subzone and *Elkanaspis corrugata* Fauna time the MC Belt became much narrower and, possibly, confined to separate and discontinuous regions. Clastic deposition continued apace, encroached upon the MC Belt from shoreward and seaward directions, and probably merged in a number of places.

The appearance of terrigenous clastics and lime grainstones in otherwise uniform lime mudstone successions in the uppermost Cambrian of southwestern United States was taken by Miller (1978) to be evidence for a short-lived sea-level drop during the C. apopsis Subzone followed by a sea-level rise during the Missisquoia depressa Subzone. An alternate explanation of the same data is provided above. The model of cessation of carbonate deposition and displacement of facies belts that is proposed

- Fig. 17 Inferred lithofacies and biofacies developments across the coincident Ptychaspid-"Hystricurid" biomere and Grand Cycle boundary in western and southern North America.
 - A Schematic cross-section of near-shore to off-platform rocks showing position of eight trilobite associations and three lithofacies belts in the biomere and Grand Cycle boundary interval. Note size decrease of the Middle Carbonate (MC) Belt at the biomere and Grand Cycle boundary and mixture of Outer Detrital (OD) Belt and Inner Detrital (ID) Belt sediments in front of the MC Belt. See text for discussion.
 - B A series of schematic block diagrams showing positions of lithofacies belts and trilobite associations for the interval below and above the biomere and Grand Cycle boundary. Note the spread of OD Belt and ID Belt sediments and the size decrease of the MC Belt in the basal "Hystricurid" Biomere interval. Positions of key locations are indicated on the upper block diagram (note that this is not a map). See text for discussion.



here is preferred because it is simpler and, furthermore, strongly supported by the lithofacies relationships seen at the edge of the platform.

Breaching of the carbonate shoal complexes at the base of the "Hystricurid" Biomere permitted the migration of modified slope biofacies to positions on the platform and permitted access of deep platform biofacies to the interior portions of the platform. The "Larifugula associations" of the Elkanaspis corrugata Fauna are amalgams of slope trilobites (Parabolinites, Bienvillia, and possibly Elkanaspis), "exotic" elements (that is, trilobites with an extra-North American origin; possibly Missisquoia), and elements of the underlying "Bowmania associations" (primarily Larifugula, Yukonaspis, Eurekia, and Idiomesus). The "Corbinia associations" of the Corbinia apopsis Subzone are amalgams of deep platform trilobites from both the "Bowmania associations" and the Hungaia faunas (Larifugula, Liostracinoides, Apatokephaloides, and Triarthropsis) and elements of the underlying "plethometopid-eurekiine associations" (Corbinia, Stenopilus, and Acheilops).

The "*Corbinia* associations" are typically found in the reduced MC Belt and in adjacent parts of the ID Belt whereas the "*Larifugula* associations" occur in the OD Belt on the outer part of the platform. Differentiation of the OD Belt from the ID Belt is sometimes impractical in those areas where the intervening MC Belt is missing.

The biofacies associations of the basal "Hystricurid" Biomere gave rise to successor associations in slightly younger rocks assigned to the *Missisquoia depressa* Subzone of the *Missisquoia* and *Parabolinella* zones. The "Larifugula associations" are followed in the OD Belt on the outer platform by the "Parabolinella associations" which comprise slope trilobites (Parabolinella and Geragnostus) and probable exotic elements (*Missisquoia* and Ptychopleurites). The "Corbinia associations" which comprise trilobites from the underlying associations (*Plethopeltis associations*" which comprise trilobites from the underlying associations (*Plethopeltis associations*. The "Plethopeltis associations" are succeeded by trilobites dominated by Symphysurina and Hystricuris of uncertain provenance.

The coincident biomere and Grand Cycle boundary separates distinct lithofacies and biofacies across an Upper Cambrian environmental profile and, thus, it is expressed differently in inner platform settings than in outer platform settings. On the inner platform, the boundary is of the MC/MC type or the ID/MC type and it is expressed by both significant generic extinction and by a decrease in species diversity from the "plethopeltid-eurekiine associations" below to the "Corbinia associations" above. Here, the biomere boundary event affects highly diverse trilobite associations and the source of the new elements above the boundary is the outer platform. On the outer platform the boundary is of the OD/MC type and it is expressed by minor generic extinction and by a minor increase in species diversity from the "Bowmania associations" below to the "Larifugula associations" above. Here, the biomere boundary event affects less diverse trilobite associations and the main source of the new elements above the boundary is and the main source of the new elements above the boundary is the slope.

Cook and Taylor (1975) and Taylor (1977) have demonstrated that the abrupt change in trilobite faunas at the Upper Cambrian shelf-slope break is a palaeobiogeographic boundary that separates the warm-water North American Province from the cold-water Chiangnan Province. The Grand Cycle boundary is expressed by a shift of this palaeobiogeographic boundary (Fig. 17) and the coincident biomere boundary is characterized by extinction, immigration, species diversity changes, and biofacies reorganization. These are items of biogeography, which suggests that biogeographic models, rather than evolutionary models, should be applied to the faunal dynamics at the biomere boundary.

One of the more promising of such models is the equilibrium model of biogeography of MacArthur and Wilson (1967) which states that the size of the biota in a region represents a dynamic equilibrium of extinction of existing species and immigration of new species. Because extinction increases as population size decreases and because smaller regions, in general, support smaller populations, then if the size of a biogeographic region is decreased, the model predicts that extinction rates will increase and the diversity of the region will be lowered. Conversely, if the size of a biogeographic region is increased, the diversity of the region will be raised with increasing rates of immigration and speciation. The equilibrium model was originally applied to species changes in small areas over ecologic time, but Simberloff (1972, 1974) has suggested that it may fruitfully be applied to geologic time in areas as large as continents, and be expressed on generic and higher levels.

An equilibrium model of biogeography showing the faunal dynamics across a biomere boundary is summarized in Fig. 18. Here, the two biogeographic regions are shown to comprise belts with cold-water, geographically widespread trilobites on the slope and warm-water, geographically restricted trilobites on the shelf. A thermocline separates the biogeographic regions. An expansion of the slope-biogeographic region and concomitant contraction of the shelf-biogeographic region defines the biomere boundary.

Most of the genera that were able to cross the biomere boundary became extinct within or at the top of the *Elkanaspis corrugata* Fauna and the *Corbinia apopsis* Subzone. Whether these extinctions were synchronous cannot be determined within



THERMOCLINE

Fig. 18 Equilibrium model of biogeography applied to the faunal dynamics on a space-time diagram across a biomere and Grand Cycle boundary. The expansion of the slope-biogeographic region and contraction of the shelf-biogeographic region define the biomere boundary and these area changes cause the extinction, immigration, and specification events above the boundary.

the present biostratigraphic framework. The biomere boundary was originally defined as an extinction level (Palmer, 1965a) and it is perhaps understandable why later investigators have assumed that by identifying the cause of the extinction they have discovered the cause for the biomere boundary. Thus, Stitt (1975, 1977) suggested that the trilobites became extinct because the temperature of the shelf seas declined and Johnson (1974) and Miller (1978) attributed the extinction to a sudden regression. The application of the equilibrium model of biogeography to the biomere problem suggests another explanation for the extinction of "Cambrian" genera in the vicinity of the revised Ptychaspid-"Hystricurid" Biomere boundary. On the inner shelf, the extinction of Saukia Zone trilobites in the Corbinia apopsis Subzone may be explained as a simple consequence of the decrease in the area of the shelfbiogeographic region caused by the partial cessation of carbonate production and deposition at the base of a Grand Cycle. There is no need to identify specific causes. A different situation existed on the outer shelf. Most of the Yukonaspis Zone trilobites that crossed the biomere boundary became extinct at the top of the Elkanaspis corrugata Fauna. Here, the biomere boundary also represents a boundary between biogeographic regions. Again, it is doubtful that a special explanation is required for the extinction of these trilobites. Their failure to speciate in a new biogeographic region is sufficient reason.

In the preceding pages I have attempted to demonstrate that the boundary between the Ptychaspid and "Hystricurid" biomeres is at the same level as a Grand Cycle boundary on the outer part of the platform in western North America. I do not suggest that the lower boundary of each of the older biomeres is necessarily coincident with a Grand Cycle boundary or that each biomere has a corresponding Grand Cycle, but this possibility cannot be discounted.* The boundary coincidence of a fossil-based unit and a rock-based unit has important implications, not only for the biomere boundary itself, but also for the nature of the internal differentiation of this biostratigraphic unit. The Grand Cycle/biomere boundary is a rapid facies shift which affects a lateral sequence of environmentally controlled trilobite biofacies, each with its own composition and diversity. It is evident from Walther's Principle that these biofacies must have some superpositional relationship within the biomere. The idea of the biomere pattern as a faunal response to a Grand Cycle is attractive in its simplicity; that is, changing composition and an increase in trilobite diversity and longevity through the biomere is controlled by the lateral progradation of the MC Belt and the formation and expansion of shoal complexes. But whether the biomere is merely an analogue (Palmer, 1979: 39) or a homologue of the Grand Cycle remains to be demonstrated. The common occurrence of internally controlled (autogenic) faunal and lithic successions in Phanerozoic strata, such as the ecologic successions of Walker and Alberstadt (1975), lends support to a fundamental unity of the biomere

^{*} Large-scale facies shifts of the OD Belt over the MC Belt, similar to the shift at the base of the "Hystricurid" Biomere at Section KK, have been shown to occur in Nevada and Utah near the base of the Marjumiid Biomere (Robison, 1976, text-fig. 2), the Pterocephaliid Biomere (Palmer, 1971, fig. 16 E,F), and the Ptychaspid Biomere (Taylor, 1977, text-fig. 5; Brady and Rowell, 1976, p. 160), as well as in the southern Canadian Rocky Mountains (Aitken et al., 1972, figs. 3, 4).

and Grand Cycle. It is of more than passing interest to note that the faunal attributes of the four *ecologic* stages of Ordovician to Cretaceous reefs (Walker and Alberstadt, 1975: 240–243) closely resemble those of the four *evolutionary* stages of the Ptychaspid Biomere (Stitt, 1975: 383–386); even their descriptions are remarkably similar. There are certainly important differences in scale, setting, duration, and fossil groups between the Grand Cycle/biomere and an ecologic reef succession, but the ecologic controls on these asymmetric cyclical units may well be identical.

The main conclusion of the present investigation is that the biomere is an ecologic and biogeographic phenomenom, not primarily an adaptive radiation. Attempts to apply a strict evolutionary explanation to the biomere pattern have been misdirected. The recognition that the base of the "Hystricurid" Biomere is defined by area changes in the shelf- and slope-biogeographic regions permits this biomere boundary event to be explained in terms of the equilibrium model of biogeography. The application of this model to biomere boundaries removes much of the supposed uniqueness of these abrupt faunal events. Similar shifts in slope and shelf lithofacies and biofacies with similar speciation, immigration, and extinction responses are known throughout the Phanerozoic record.

Systematic Palaeontology

Repositories

The illustrated specimens from the Rabbitkettle Formation are housed at the Department of Invertebrate Palaeontology, Royal Ontario Museum, Toronto (ROM prefix). Other illustrated specimens from the Yukon-Alaska border, Texas, and Vermont are housed at the Geological Survey of Canada, Ottawa (GSC prefix), National Museum of Natural History, Washington (USNM prefix), and Peabody Museum of Natural History, Yale University, New Haven (YPM prefix).

Measurements

Most of the silicified specimens from the Rabbitkettle Formation are small and fragile and measurements cannot be made in a conventional manner. All cited dimensions were measured on photographs of known magnification. Abbreviations used when giving measurements are: exsag.—exsagittal, sag.—sagittal, and tr.—transverse.

Order Miomera Jaekel Suborder Agnostina Salter Family Agnostidae M'Coy, 1849 Subfamily Agnostinae M'Coy, 1849

Genus Geragnostus Howell, 1935

Type Species

Agnostus sidenbladhi Linnarsson, 1869 from the Tremadocian of Sweden (by original designation).

Geragnostus sp. Fig. 69A–C

Occurrences

Rabbitkettle Formation, Broken Skull River (five collections between 114 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Remarks

Geragnostus sp. is characterized by a transverse pygidium with very wide borders which carry a pair of minute posterolateral spines. The first and second transverse furrows on the pygidial axis are very shallow and the axial pygidial node is small. The anterior furrow on the glabella is faint and expressed only medially. Both the cephalon and pygidium are finely granulose.

Subgenus Micragnostus Howell, 1935

Type Species

Agnostus calvus Lake, 1906 from the Tremadocian of Wales (by original designation).

Geragnostus (Micragnostus) subobesus (Kobayashi, 1936a) Figs. 19, 47A-P, 70M

Agnostus subobesus Kobayashi, 1936a: 161, pl. 21, figs. 1, 2.

Occurrences

Jones Ridge Limestone, Jones Ridge, east-central Alaska, *Ptychopleurites* Fauna (Kobayashi, 1936a; Palmer, 1968). Rabbitkettle Formation, Broken Skull River (10

collections between 46 m and 60 m below top of formation), *Missisquoia depressa* Subzone and *Missisquoia mackenziensis* Fauna.

Lectotype (here designated)

A cephalon from the Jones Ridge Limestone, east-central Alaska illustrated by Kobayashi (1936a, pl. 21, fig. 1) and herein (Fig. 70M).

Description

Cephalon is subcircular in outline, slightly wider than long and strongly convex. Maximum height is about 60 per cent width (tr.). Borders are wide and flat; marginal furrows are well incised. Acrolobe is evenly convex, unconstricted, and inflated; it is of the same width (tr. and sag.) around glabella. A median preglabellar furrow does not occur. Glabella occupies 80 per cent cephalic length and about 40 per cent cephalic width; it is parallel sided and evenly rounded anteriorly. Glabella comprises a transversely suboval and inflated anterior lobe separated from a rectangular and strongly inflated posterior lobe by a forwardly concave anterior furrow. An axial glabellar node which is faint and drop shaped is located slightly in front of mid-length of the posterior lobe. Basal lobes are rather small, triangular, and only moderately inflated. Genal angles are small blunt spines, between which the posterior margin is straight in dorsal view. In posterior view, posterior margin rises in U-shaped notch between basal lobes.

Anterior thoracic segment is rectangular, three and a half times as wide (tr.) as long. Convex axis occupies 70 per cent of width of segment; it comprises three



Fig. 19 Geragnostus (Micragnostus) subobesus (Kobayashi, 1936a). Reconstruction of cephalon and pygidium. Bar represents 1 mm.

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lobes—a trapezoidal and inflated central lobe which is separated by a pair of posteriorly diverging furrows from two drop-shaped lateral lobes.

Pygidium is subquadrate in outline, slightly wider than long and strongly convex. Maximum height is about 60 per cent of width (tr.). Borders are flat and widest posterolaterally, marginal furrows are well incised. Acrolobe is evenly convex and unconstricted; it narrows towards rear. Axis is inflated and nearly parallel sided; it occupies 85 to 90 per cent pygidial length and about 40 per cent pygidial width. Anterior lateral furrows isolate lateral lobes of first segment. Second axial segment does not extend as far laterally; it is defined posteriorly by faint and nearly transverse furrow. An elongate axial pygidial node separates second axial lobes; it may extend forwardly to articulating furrow as a low ridge. Posterior axial lobe is semicircular and inflated: its length (sag.) equals that of the anterior two segments combined. A pair of inwardly curving posterolateral spines are located just in front of a transverse line posing through posterior margin of axis.

Remarks

The type collection of Agnostus subobesus Kobayashi from the Jones Ridge Limestone, east-central Alaska consists of a well-preserved cephalon (here designated the lectotype, Fig. 70M) and a poorly preserved and exfoliated pygidium. Kobayashi (1936a) suggested that the Alaska species belonged in the group of agnostids typified by Homagnostus obesus (see Henningsmoen, 1958, pl. 5, figs. 13–16). As Robison and Pantoja-Alor (1968: 775) have noted, differentiation with the Geragnostus-Homagnostus plexus of species in the Late Cambrian and Early Ordovician is difficult because diagnostic characters tend to intergrade. Kobayashi's species is assigned to Micragnostus Howell, 1935 based on its similarity to Micragnostus calvus (Lake) and I follow Shergold (1971: 23) in considering Micragnostus a subgenus of Geragnostus.

Few species of *Geragnostus* attain the degree of convexity shown by both the cephalon and pygidium of G. (M.) subobesus. This species is perhaps closest to G. (M.) intermedius Palmer which occurs in the Franconian of Alaska and Oklahoma (Palmer, 1968; Stitt, 1977) and the early Tremadocian of Mexico (Robison and Pantoja-Alor, 1968). G. (M.) subobesus differs in having a higher degree of convexity, a parallel-sided glabella, a forwardly concave anterior glabellar furrow, and a narrower pygidial axis.

Geragnostus (Micragnostus) chiushensis (Kobayashi) which occurs with Missisquoia depressa Stitt (senior synonym of Tangshanaspis zhaogezhuangensis Zhou and Zhang) in the Mictosaukia orientalis Assemblage in Hopeh Province, China (Zhou and Zhang, 1978) is very similar to G. (M.) subobesus. The Chinese form appears to have a more prominent axial glabellar node. It is not known whether it has the convexity characteristic of the North American form.

The species illustrated as G. (M.) bisectus (Matthew) from the Missisquoia Zone of Vermont by Shaw (1951, pl. 23, figs. 11–18) is inflated to nearly the same degree as G. (M.) subobesus. The Vermont form differs in possessing narrower cephalic and pygidial borders and in lacking an axial glabellar node.

Geragnostus reductus (Winston and Nicholls, 1967) from the Missisquoia and Symphysurina zones of Texas and Oklahoma (Fig. 70D-G) differs from the present

species in being much less inflated, in having a shorter and tapered glabella and pygidial axis, and in having constricted cephalia and pygidial acrolobes. The latter feature led Shergold (1975: 55) to tentatively assign G. reductus to Geragnostus (Strictagnostus) Shergold.

Family Diplagnostidae Whitehouse, 1936 Subfamily Pseudagnostinae Whitehouse, 1936

Genus Pseudagnostus Jaekel, 1909

Type Species

Agnostus cyclopyge Tullberg, 1880 from the Upper Cambrian of Sweden (by original designation).

Subgenus Pseudagnostina Palmer, 1962

Type Species

Pseudagnostina contracta Palmer, 1962 from the Dresbachian of Nevada and Alabama (by original designation).

Pseudagnostus (Pseudagnostina) sp. Figs. 20, 47Q, R

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 165 m below top of formation), Yukonaspis kindlei Fauna.



Fig. 20 Pseudagnostus (Pseudagnostina) sp. Reconstruction of pygidium. Bar represents 1 mm.

Remarks

Pseudagnostus (Pseudagnostina) sp. is characterized by a subquadrate pygidium with deep marginal furrows and an unconstricted and evenly inflated acrolobe. Lateral rim is broad and somewhat rounded (tr.). Accessory furrows and deuterolobe are not differentiated. Axial furrows are nearly parallel and extend to the rear of a prominent axial pygidial node. A faint transverse furrow extends inwards from axial furrow at half length of node. Short posterolateral spines are directed backwards. On the cephalon, rim is broad, axis is parallel sided, transverse anterior furrow is concave forwardly, and median glabellar furrow is absent.

In lacking both a median preglabellar furrow and a distinctly outlined deuterolobe on the pygidium, these specimens belong in the Contracta group of *Pseudagnostus* as defined by Shergold (1977). They are most similar to P. (P.) contracta Palmer, but differ slightly in having a forwardly concave transverse anterior furrow on the glabella and a deeper transverse furrow on the pygidial axis.

P. (*Pseudagnostina*) has previously been known only from the early Late Cambrian (Dresbachian, Mindyallan, and Kushanian) of North America, Australia, and eastern Asia (Shergold, 1977: 84). The occurrence in the Rabbitkettle Formation is the first from the Late Cambrian (Trempealeauan).

Genus Rhaptagnostus Whitehouse, 1936

Type Species

Agnostus cyclopygeformis Sun, 1924 from the Upper Cambrian Kaoli Limestone, Shantung, China (by original designation).

Rhaptagnostus clarki (Kobayashi, 1935) Fig. 520–s

Pseudagnostus (Plethagnostus) clarki Kobayashi, 1935: 47, pl. 9, figs. 1, 2. Pseudagnostus laevis Palmer, 1955: 97, pl. 19, figs. 8, 9, 11, 12. Pseudagnostus clarki—Palmer, 1968: 29, pl. 15, figs. 10, 13, 14. Pseudagnostus clarki—Shergold, 1975: 61, pl. 1, 2, figs. 1, 2, pl. 3, 4, 5. Rhaptagnostus clarki—Shergold, 1977: 86, pl. 15, figs. 14, 15.

Occurrences

Jones Ridge Limestone, east-central Alaska, Trempealeauan-1 and Trempealeauan-2 Faunas (Palmer, 1968). Windfall Formation, Eureka District, Nevada, Trempealeauan (Palmer, 1955). "Chatsworth Limestone", Queensland, Australia, Pre-Payntonian A and Pre-Payntonian B (Shergold, 1975). Rabbitkettle Formation, Broken Skull River (two collections between 152 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Lectotype

A pygidium from the Jones Ridge Limestone, east-central Alaska illustrated by Palmer (1968, pl. 15, fig. 13) and Shergold (1977, pl. 15, fig. 15).

Remarks

The recent discussions in Palmer (1968: 29) and Shergold (1975: 61; 1977: 86) adequately characterize this effaced pseudagnostine species. Of the five subspecies established by Shergold (1977), the Rabbitkettle specimens are closest to *Rhaptagnostus clarki clarki* (Kobayashi) from the Trempealeauan of east-central Alaska, but differ from this subspecies in having a slightly wider pygidium with the posterolateral spines located slightly farther toward the rear.

Order Ptychopariida Suborder Ptychopariina Superfamily Ptychopariacea Family Ptychopariidae Matthew, 1887 Subfamily Eulominae Kobayashi, 1955

Genus Euloma Angelin, 1854

Type Species

Euloma laeve Angelin, 1854 from the Lower Ordovician of Östergötland, Sweden (subsequent designation by Vogdes, 1925).

Subgenus Plecteuloma Shergold, 1975

Type Species

Euloma (Plecteuloma) strix Shergold, 1975 from the "Chatsworth Limestone", Queensland (by original designation).

Euloma (Plecteuloma) sp. Fig. 57v

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 165 m below top of formation), Yukonaspis kindlei Fauna.

Description

This small eulomine cranidium is probably an immature specimen. It measures about 2 mm between anterior and posterior margins and has a rectangular glabella with two oblique, lateral furrows. Preglabellar field is long. Straight anterior border furrow is interrupted medially by a minute plectrum. Small palpebral lobes are located about half-way out on cheeks; faint palpebral ridges run into axial furrows. Facial sutures diverge slightly in front of eyes and markedly behind.

Remarks

Euloma (*Plecteuloma*) has hitherto been known only from the Late Cambrian of Australia. The small eulomine cranidium with a minute plectrum from the Rabbitkettle Formation establishes the presence of this subgenus in the Late Cambrian of North America.

Superfamily Conocoryphacea Family Shumardiidae Lake, 1907

Genus Idiomesus Raymond, 1924

Type Species

Idiomesus tantillus Raymond, 1924 from the Gorge Formation, Highgate Falls, Vermont (by original designation).

Remarks

Since its definition, *Idiomesus* has been classified with *Shumardia* Billings in the family Shumardiidae. The discovery of the pygidium of I. *intermedius* lends support to this assignment which previously was based on cranidial features only. The

pygidium is similar in outline and general aspect to those of "Shumardia" pusilla (Sars) and "Shumardia" exopthalma Ross, 1967. Both of these species possess pygidia that are quite distinct from that of Shumardia and they are probably not congeneric with S. granulosa, the type species of Shumardia (Dean, 1973: 8), although both are undoubtedly assignable to the family Shumardiidae.

Contrary to the statement of Poulsen (*in* Moore, 1959: 245), *Shumardia* and "*Shumardia*" both possess facial sutures (Whittington, 1965: 328, pl. 16, fig. 17; Young, 1973, pl. 1, figs. 1, 5, 6). These are marginal in position and, in "S." *exopthalma*, they isolate yoked free cheeks. Very similar facial sutures occur in *Idiomesus tantillus* Raymond (Fig. 54Q, R).

Idiomesus tantillus Raymond, 1924 Fig. 54P–U

Idiomesus tantillus Raymond, 1924: 397, pl. 12, fig. 10. Idiomesus tantillus-Rasetti, 1946: 538, pl. 1, figs. 1-3.

Occurrences

Gorge Formation, Highgate Falls, Vermont, Zones 2 and 3—Hungaia Assemblage (Raymond, 1924; Rasetti, 1946). Rabbitkettle Formation, Broken Skull River (single collection at 165 m below top of formation), Yukonaspis kindlei Fauna.

Holotype

A cranidium from the Gorge Formation, Highgate Falls, Vermont illustrated by a drawing in Raymond (1924, pl. 12, fig. 10).

Remarks

Even though the Rabbitkettle material is coarsely silicified, it shows certain features not displayed by the Vermont material studied by Raymond and Rasetti.

One specimen (Fig. 54P–R) is a cephalon missing only the right free cheek. This cephalon shows a narrow (tr.) lateral border furrow running along the inner side of the facial suture. This furrow is a forward continuation of the deeper posterior border furrow and it extends as far forward as the front part of the glabella. The lateral border is wide (lateral view) and slightly inflated; it descends vertically and is, in part, curved under the cephalon. The lateral border becomes wider towards the bluntly rounded genal corner which bears one (or perhaps two) minute spines. The anterior border is curved under frontal part of cephalon. The free cheeks are yoked and the border carries poorly defined terrace lines. In anterior view the facial sutures are seen to descend gently in both anterior and posterior directions from high points located on front part of cheek.

Idiomesus tantillus Raymond differs from the remaining four species of *Idiomesus* from North America (Taylor, 1976: 685) in possessing a relatively narrow glabella which is poorly defined and widest anteriorly, and which is crossed, or partly crossed, by 1s furrow. Other glabellar furrows are not developed.

Idiomesus levisensis (Rasetti, 1944) Fig. 57N, O

Idiomesus levisensis-Taylor, 1976: 686, pl. 3, figs. 12, 13 (see for synonymy).

Occurrences

Levis Formation, North Ridge, Levis, Quebec, Hungaia Assemblage (Rasetti, 1944). Wilberns Formation, central Texas, Saukiella pyrene to Saukiella serotina subzones (Longacre, 1970). Snowy Range Formation, Bridger Mountains, Montana, Illaenurus Zone (Grant, 1965). Hales Limestone, Hot Creek Range, Nevada, Hedinaspis Zone (Taylor, 1976). Rabbitkettle Formation, Broken Skull River (three collections between 61 m and 70 m below top of formation), Elkanaspis corrugata Fauna.

Syntypes

Two cranidia from an Upper Cambrian boulder, North Ridge, Levis, Quebec illustrated by Rasetti (1944, pl. 37, figs. 8, 9).

Remarks

Taylor (1976) has demonstrated that minor differences separate the two similar and contemporaneous species, *Idiomesus levisensis* (Rasetti) and *I. intermedius* Rasetti. These differences are best seen in small cranidia. A few small specimens from the *Elkanaspis corrugata* Fauna display the complete 1s furrow and pitlike 2s and 3s furrows that apparently are characteristic of *I. levisensis*.

Idiomesus intermedius Rasetti, 1959 Fig. 57 G–M

Idiomesus intermedius Rasetti, 1959: 393, pl. 51, figs. 25, 26. Idiomesus intermedius—Winston and Nicholls, 1967: 73, pl. 10, fig. 21. Idiomesus intermedius—Longacre, 1970: 55, pl. 4, figs. 13, 14. Idiomesus levisensis (Rasetti), Stitt, 1971b: 45, pl. 5, figs. 1–5.

Occurrences

Conococheague Limestone, Maryland, Saukia Zone (Rasetti, 1959). Wilberns Formation, central Texas, Saukiella junia to Corbinia apopsis subzones (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Wichita and Arbuckle Mountains, Oklahoma, Rasettia magna to Corbinia apopsis subzones (Stitt, 1971b, 1977). Notch Peak Formation, Utah, Saukiella serotina Subzone (Hintze et al., 1980). Rabbitkettle Formation, Broken Skull River (11 collections between 80 m and 165 m below top of formation), Bowmania americana Fauna and Yukonaspis kindlei Fauna.

Holotype

A cranidium from the Conococheague Limestone, Washington County, Maryland illustrated by Rasetti (1959, pl. 51, fig. 25).

Description

The discussion by Taylor (1976: 686, text-fig. 7) effectively describes the cranidium of *Idiomesus intermedius*. The pygidium is described here for the first time.

Pygidium is semicircular in outline with a transverse or slightly re-entrant posterior margin; length is about two-thirds width (tr.). Axis is convex, less than one-third pygidial width, and it extends to posterior border furrow. Three axial rings and a terminal piece are separated by sharply incised and narrow (sag.) furrows. In longitudinal profile each ring comprises a low, asymmetric cuesta with its steep flank facing forward. Pleural field is flat, it is crossed by four narrow (exsag.) pleural furrows. Border furrows are complete and firmly impressed. Lateral and posterior borders are narrow and rimlike; they stand well above the pleural field and their outer portions descend steeply to margin.

Superfamily Crepicephalacea Family Tricepicephalidae Palmer, 1954

Genus Meteoraspis Resser, 1935

Type Species

Ptychoparia? metra Walcott, 1890 from the Upper Cambrian of Texas (by original designation).

Meteoraspis? sp. Fig. 68R-T

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 177 m below top of formation), Yukonaspis kindlei Fauna.

Description

Cranidium possesses a rather long glabella outlined by deep and parallel axial furrows that die out before reaching a very deep and forwardly bowed border furrow. The occipital furrow is straight and sharply incised. Lateral glabellar furrows are not present. The eyes are located far out on the cheeks, at or just behind mid-length of cranidium. The posterior limbs are bent backward. The anterior border furrow houses a pair of large and very deep pits whose presence cannot be detected on the dorsal side. On the ventral side, they protrude as large rectangular knobs whose long axes are aligned along the anterior border furrow.

Remarks

The identification of these peculiar cranidia is extremely tentative and is based merely on the presence of the pair of deep pits in the anterior border furrow. Tricrepicephalids have not been recorded in rocks younger than Dresbachian. In general proportions, *Meteoraspis*? sp. is vaguely similar to species such as *Meteoraspis mutica* Rasetti, 1961, but differs markedly in lacking a preglabellar furrow. The similarity could well be spurious.

The only other post-Dresbachian trilobite with a pair of deep pits in the anterior border furrow is *Bifodina* Robison and Pantoja-Alor, 1968 from the early Tremadocian of Mexico. This genus, however, has a forwardly tapering glabella, a preglabellar furrow, a broad frontal area, and a shallow and broad anterior border furrow.

Superfamily Olenacea Burmeister, 1843 Family Olenidae Burmeister, 1843

Remarks

Fortey (1974: 13) provided a brief diagnosis of this family in which he placed prime emphasis on the yoked cheeks united by a narrow doublure, the simple diagonal pleural furrows on the thoracic segments, and the very thin exoskeleton. The yoked cheeks of *Apoplanias* and the general cephalic similarity of this genus to *Parabolinella* suggest that Lochman (1964a) was correct in assigning this taxon to the Olenidae.

Subfamily Oleninae Burmeister, 1843 (= Triarthrinae Ulrich, *in* Bridge, 1931)

Remarks

Poulsen (*in* Moore, 1959) assigned *Parabolina* and *Parabolinites* to the Oleninae and *Parabolinella* and *Angelina* to the Triarthrinae. These genera are similar (Henningsmoen, 1957: 156; Robison and Pantoja-Alor, 1968: 785) and should be classified in the same subfamily. Indeed, I can discern no characters in the diagnoses of the Oleninae and Triarthrinae (Poulsen, *in* Moore, 1959: 262, 267) that would justify separation of these taxa and I agree with Henningsmoen (1957: 96) that the Triarthrinae is a junior synonym of the Oleninae.

Genus Parabolinites Henningsmoen, 1957

Type Species

Parabolinella laticauda Westergaard, 1922 from the Upper Cambrian of Sweden (by original designation).

Remarks

Henningsmoen (1957: 129) separated *Parabolinites* from *Parabolina* Salter on the basis of the greater sagittal length of the preglabellar field and on the non-spinose pygidium of *Parabolinites laticaudus*. In his diagnosis of *Parabolina* (1957: 113), he stated that this genus comprises species with and without pygidial spines. Of the 13 species of *Parabolina* with known pygidia which were treated by Henningsmoen (1957: 114–129), 12 have three (rarely two) to five pairs of spines, one has a single pair of spines, and one lacks pygidial spines. *Parabolina argentina* (Kayser), the species which supposedly lacks spines, does, in fact, possess three pairs of short, sharp spines on the pygidial characters to the larger group of *Parabolina* species.

Henningsmoen was apparently following Matthew (1903) when he described the pygidium of *Parabolina dawsoni* Matthew as having a single pair of short spines. The type collection of *P. dawsoni* from the *Peltura* Zone at Escasonie, Cape Breton Island (ROM 327CM, 1199CM, 1201CM, and 1208CM) includes two pygidia, neither of which possesses a spine pair such as that illustrated by Matthew (1903, pl. 17, fig.

6f). One of the pygidia shows a very slight protuberance at the anterior part of the pygidial border similar to that of another pygidium of *P. dawsoni* illustrated by Hutchinson (1952, pl. 3, fig. 12). In both cranidial and, now, pygidial features, *Parabolina dawsoni* is very similar to its contemporary, *Parabolinites laticaudus* from Sweden, and Matthew's species should be reassigned to *Parabolinites*. This leaves *Parabolina* with a well-defined set of diagnostic characters, including three (rarely two) to five pairs of marginal spines on the pygidium.

In addition to the type species and *P. dawsoni*, *Parabolinites* includes *Parabolinella williamsoni* (Belt, 1868) (= *Parabolinella caesa* Lake, 1913) from the upper Dolgelly Beds of northern Wales and possibly also *Olenus longispinus* (Belt, 1868) from the same stratigraphic and geographic location. These four species are approximately the same age; that is, *Peltura minor* or *P. scarabaeoides* zones. The youngest member of the genus, *Parabolinites* cf. *williamsoni* from the Rabbitkettle Formation, is of latest Trempealeauan and earliest Tremadocian age.

Parabolinites cf. williamsoni (Belt, 1868) Figs. 21, 50P, S, 51A-K

Conocoryphe? Williamsonii Belt, 1868: 9, pl. 2, figs. 7–11. Parabolinella williamsoni—Lake, 1908: 64, pl. 6, fig. 12. Parabolinella williamsoni—Lake, 1913: 65, pl. 7, fig. 1. Parabolinella caesa Lake, 1913: 66, pl. 7, fig. 2. Parabolinites? williamsonii—Henningsmoen, 1957: 131. Parabolinella? caesa—Henningsmoen, 1957: 140.

Occurrences

Rabbitkettle Formation, Broken Skull River (five collections between 60 m and 70 m below top of formation), *Missisquoia mackenziensis* Fauna and *Elkanaspis corrugata*



Fig. 21 Parabolinites cf. williamsoni (Belt, 1868). Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Fauna. Parabolinites williamsoni (Belt) occurs in the upper Dolgelly Beds of northern Wales (late Merionethian, Rushton, 1974: 67).

Description

Cephalon is semicircular in outline and strongly arched (tr. and sag.); it is surrounded by firmly impressed border furrows and narrow, convex borders whose lateral portions continue posteriorly as slender genal spines of unknown length. Convex glabella narrows only very slightly towards the front, it occupies somewhat less than one-third width of cephalon. It is outlined by deep and narrow (tr.) axial furrows which, in front of palpebral ridges, merge with forwardly arched preglabellar furrow. Occipital furrow is shallow, but distinct; laterally it bifurcates. Occipital ring carries median tubercle. Three pairs of firmly impressed lateral glabellar furrows do not connect with axial furrows; 1s is sigmoid, located at about glabellar mid-length; 2s and 3s are forwardly convex, located close together on anterior quarter of glabella. Preglabellar field is one-fifth the length (sag.) of glabella and, in large cranidia, is steeply sloping to anterior border furrow; in small cranidia, it declines gently. Palpebral lobe is large, well raised over genal field; it is located half-way out on the cheek, opposite 2s and 3s. It is confluent with short (exsag.) and raised transverse palpebral ridge which is bounded on both sides by furrows. Posterior branch of facial suture proceeds obliquely backwards and outwards along somewhat sigmoid path. Anterior branch proceeds nearly straight forward in small cranidia and is divergent in large cranidia. Genal and preglabellar fields are covered by irregular, but generally radial, scrobiculate and ropy caecal network. Cephalic borders bear prosopon of fine parallel terrace lines.

Hypostome is quadrate, longer than wide, and convex (sag.). Inflated central body is slightly waisted anteriorly and is circumscribed by deep border furrows. Anterior wings are not fully preserved, but apparently are triangular. Anterior margin is gently arched forwardly and is steeply raised over anterior border furrow. Lateral border is arched above a deep antennal notch. Posterior border is very narrow (sag.).

Pygidium is transversely semielliptical in outline and moderately arched (tr.). Narrow, convex axis tapers slightly; it consists of six rings and a short blunt terminal piece; and it extends to posterior border furrow. Pleural field is crossed by five, sharply incised interpleural furrows that are hooked backwardly adjacent to border furrow. Five pleural furrows are confined to distal part of pleural field. Both interpleural and pleural furrows terminate against shallow border furrow which defines narrow and rather flat pygidial border.

Remarks

Lake (1908, 1913) described and illustrated a large and incomplete external mould of an olenid trilobite which he identified as *Parabolinella williamsoni* (Belt, 1868). According to Lake, this species is characterized by a large, anteriorly rounded glabella with two oblique pairs of lateral furrows and a relatively large pygidium with four interpleural furrows. Lake (1913: 66) also described a similar species, Parabolinella caesa Lake, which he separated from P. williamsoni "with some hesitation" on the basis of the presence of three pairs of lateral glabellar furrows. Both of these species occur in the upper Dolgelly Beds (Peltura scarabaeoides Zone, late Merionethian; Rushton, 1974) of northern Wales. Henningsmoen (1957: 131, 140) assigned P. williamsoni to Parabolinites? and P. caesa to Parabolinella?. Lake (1913), however, noted that these species are closely allied and both differ significantly from other species of Parabolinella in having much larger pygidia. I suggest that the two Welsh species are conspecific and referable to Parabolinites. The minor differences apparent in Lake's descriptions and illustrations are probably attributable to preservational differences (similar differences are seen in the cranidia of P. cf. williamsoni from the Rabbitkettle Formation; compare pl. 6, fig. 12 and pl. 7, fig. 2 of Lake with Fig. 50s and Fig. 51c of this paper).

The similarity between *Parabolinites williamsoni* from the late Merionethian of Wales and P. cf. *williamsoni* from the latest Trempealeauan/earliest Tremadocian of the District of Mackenzie is best seen in the pygidia (compare Lake, 1913, pl. 7, fig. 1 and this paper, Fig. 511). *P. williamsoni* has one or two fewer axial ring furrows and interpleural furrows than P. cf. *williamsoni*, but the pygidial outline, the shape of the tapering axes, and the aspect of the shallow border furrows and flat borders appear to be identical.

The large pygidium and narrow glabella of *Parabolinites* cf. williamsoni distinguish this species from P. laticaudus and P. dawsoni. The glabella of P. cf. williamsoni is also narrower (tr.) than that of P. williamsoni.

Genus Parabolinella Brögger, 1882

Type Species

Parabolinella limitis Brögger, 1882 from the Ceratopyge Shale (Tremadocian) of Oslo, Norway (subsequent designation by Bassler, 1915).

Diagnosis

A genus of olenine trilobites possessing a parallel-sided to slightly forwardly tapered glabella with two or three pairs of oblique lateral glabellar furrows; 1s furrow bifurcates laterally. Preglabellar field is relatively long; its posterior flank is variably inflated. Palpebral lobes are located close to glabella, opposite 3p lobe. Facial sutures are subparallel to slightly divergent in front of eyes. Genal spines are long and slender. Pygidium is small, transverse; axis consists of two axial rings and a blunt terminal piece.

Remarks

One feature that has been overlooked by previous framers of diagnoses of *Parabolinella* (Henningsmoen, 1957: 132; Poulsen, *in* Moore, 1959: 267; Robison

and Pantoja-Alor, 1968: 789) is the variable inflation of the preglabellar field. In uncompressed specimens this inflation may be no more than a rounded rim in front of the preglabellar furrow (for example, in *P. cf. prolata*, Figs. 48A–C, 49A–C) or it may involve the entire preglabellar field (for example, in *P. hecuba* [Walcott], Fig. 52E; Robison and Pantoja-Alor, 1968, pl. 102, fig. 12; Harrington and Leanza, 1957, fig. 39–2c; *P. panosa* sp. nov., Fig. 50Q). This feature may also be seen in flattened specimens (for example, in *P. argentinensis* Kobayashi, Robison and Pantoja-Alor, 1968, pl. 102, fig. 2; *P. limitis* Brögger, Henningsmoen, 1957, pl. 12, fig. 3; *P. triarthra* [Callaway], Henningsmoen, 1957, pl. 12, fig. 6; Lake, 1913, pl. 7, fig. 8).

Inflation of the preglabellar field is not seen in the species of *Parabolinites* that may otherwise be confused with *Parabolinella* (for example, in *Parabolinites* williamsoni [Belt] Lake, 1908, pl. 6, fig. 12; *P. dawsoni* Matthew, 1903, pl. 17, fig. 6a; and *P. cf. williamsoni* [Belt], Fig. 51G).

According to the diagnosis above, *Parabolinella* is confined to the Tremadocian of northern Europe (Henningsmoen, 1957), South America (Harrington and Leanza, 1957), Mexico (Robison and Pantoja-Alor, 1968), Maritime Canada (Hutchinson, 1952), and western North America. Tjernvik (1956) reported questionable occurrences of *Parabolinella* from the early Arenigian of Sweden. The supposed Cambrian occurrences of *Parabolinella* from North America cited by Henningsmoen (1957: 133) have either been wrongly dated or been based on species that since have been reassigned to other genera.

The occurrences of *Parabolinella* in Vermont, Alaska, Nevada, Texas, Mexico, Newfoundland, and District of Mackenzie appear to be in Lower Tremadocian rocks correlative with the *Parabolinella*, *Missisquoia*, or *Symphysurina* zones. The presence of *Parabolinella* in higher Lower Ordovician rocks or in Upper Cambrian rocks in North America has not been demonstrated.

Parabolinella cf. prolata Robison and Pantoja-Alor, 1968 Figs. 22, 48, 49, 50M, N

Parabolinella prolata Robison and Pantoja-Alor, 1968: 789, pl. 102, figs. 3, 6, 9.



Fig. 22 Parabolinella cf. prolata Robison and Pantoja-Alor, 1968. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Occurrences

Rabbitkettle Formation, Broken Skull River (10 collections between 46 and 60 m below top of formation), *Missisquoia depressa* Subzone and *Missisquoia mackenziensis* Fauna. *Parabolinella prolata* occurs in the *Parabolina* assemblage (Lower Tremadocian) of the Tinu Formation, Mexico.

Description

Cephalon is semicircular in outline and about half as high as wide (tr.). Glabella rises steeply out of axial furrows; it is one-third the width (sag.) and three-quarters the length (sag.) of cephalon; and it narrows slightly towards front from widest point at occipital ring. Preglabellar furrow is sharply incised and has moderate forward curvature. A triangular depressed area is formed at juncture of preglabellar and axial furrows. Occipital furrow is well-incised medially; it bifurcates and shallows laterally. Occipital lobe thus comprises three poorly outlined lobes: a lenticular central lobe bearing prominent median tubercle and two triangular lateral lobes. Two pairs of lateral glabellar furrows are oblique and firmly impressed, neither reaches axial furrow; 1s bifurcates laterally and 2s is located in line with palpebral lobes. Preglabellar field is relatively long (sag.) and steeply sloping towards anterior border furrow; its anterior edge comprises a narrow (sag.) inflated rim which extends from in front of axial furrows. In lateral view, crest of glabella slopes evenly downward from horizontal posterior portion; preglabellar field continues this curvature, but at a slightly higher level. Anterior border furrow is sharply incised and marked by closely spaced pits; it is continuous in even curve with lateral border furrows. Narrow convex anterior and lateral borders are continued posteriorly as long straight and gradually tapering genal spines. Posterior border is somewhat wider (exsag.) and less convex than lateral border. Palpebral lobes are large and located half-way out on cheek opposite anterior glabellar lobe. A faint curved palpebral furrow defines interior edge. Posterior branch of facial suture proceeds obliquely backward and outward before swinging exsagitally to cross posterior border. Anterior branch of facial suture proceeds straight forward (or very slightly inward) in large cephala and then inward along anterior border to define yoked cheeks. In smaller cephala, anterior sutures may diverge. In anterior view, the ventral margin of cephalon rises in a broad low arch towards midline. On interior convex doublure extends to border furrows. Inner edge of anterior doublure is very finely toothed so that each tooth connects with a pit in the anterior border furrow (see Fortey, 1974, fig. 4 C for an identical structure in another olenid). Cephalon is covered by extremely fine granules. Borders carry prosopon of fine terrace lines arranged parallel to margin. Similar, but transverse and irregular prosopon occurs on preglabellar field.

Hypostome has large, oval, and greatly inflated central body. Middle furrow parallels lateral margin; it terminates medially in transversely directed macula. Anterior wing is wide (tr.) and triangular. Anterior margin is moderately curved. Lateral border is narrow and convex. Posterior border and margin are poorly preserved.

Number of thoracic segments is unknown. Axis is highly convex; it is crossed by well-incised articulating furrow and surmounted by prominent median tubercle. Interior third of pleura is horizontal; outer two-thirds declines at 40 degrees along straight path. Pleura is crossed at very low angle by pleural furrow which nearly reaches pointed terminus. Spine tip is encased by flat doublure which carries fine terrace lines. With the exception of articulating half ring, articulating devices are not seen on thoracic segments.

Pygidium is elliptical in outline, three times as wide as long (sag.). Moderately convex axis consists of two rings and a blunt terminal piece; it extends to border furrow. Pleural region is crossed by two deep pleural furrows and two shallow interpleural furrows, both furrow types terminate against narrow and flat border. In posterior view, ventral margin of pygidium is arched beneath axis. Narrow doublure carries fine terrace lines.

Remarks

Parabolinella cf. *prolata* Robison and Pantoja-Alor is, by far, the most abundant trilobite in the *Parabolinella* Zone of the upper Rabbitkettle Formation at Section KK and accounts for the bulk of the *Parabolinella* frequency histogram in Fig. 16.

Among species represented by noncompressed material, *Parabolinella* cf. *prolata* is most similar to *P. prolata* and the poorly known *P. punctolineata* Kobayashi, 1936a from the Lower Tremadocian of Mexico and the Alaska-Yukon border, respectively. From both of these species, *P.* cf. *prolata* is distinguished by the presence of a narrow inflated rim which defines the front edge of both the preglabellar furrow and the axial furrow and by the slightly more anteriorly located eyes.

A surprising feature of *Parabolinella* cf. *prolata* is the high degree of convexity of both the cephalon and the thoracic segments. The ratio of height at the axis to transverse width is about 5:10 for the cephalon and 4:10 for a segment near mid-length of thorax. If a thin-shelled trilobite such as this species is flattened in shale, extensive deformation of morphological features and significant alterations of proportions will result. Nonetheless, tentative comparisons may be made with some species of *Parabolinella* preserved in flattened states. The compressed cranidia of *P*. limitis Brögger, P. rugosa Brögger, P. triarthra (Callaway), and P. argentinensis Kobayashi illustrated by Hutchinson (1952), Henningsmoen (1957), Harrington and Leanza (1957), and Robison and Pantoja-Alor (1968) all possess rectangular glabellae that are only slightly longer (sag.) than wide (tr.), three pairs of lateral glabellar furrows, and relatively small eyes. The course of the anterior facial suture varies in these species from slightly divergent in *P. triarthra* to markedly divergent in P. argentinensis. P. cf. prolata differs from these species in having a slightly tapering glabella that is generally longer than wide, but the proportions vary considerably (compare Fig. 48A and 48F, Fig. 49A and 49M), and in having only two pairs of lateral glabellar furrows.

Parabolinella hecuba (Walcott, 1924)

Figs. 23, 52A-I

Moxomia hecuba Walcott, 1924: 59, pl. 12, fig. 3. Moxomia angulata (Hall and Whitfield), Walcott, 1925: 107, pl. 22, figs. 8, 9. Moxomia angulata—Henningsmoen, 1957: 160, fig. 19. Parabolinella hecuba—Harrington and Leanza, 1957: 107, fig. 39 2a-e. Parabolinella tumifrons Robison and Pantoja-Alor, 1968: 790, pl. 102, figs. 10-16. [non] Parabolinella hecuba—Ross, 1970: 71, pl. 10, figs. 10-13.

Occurrences

Chushina Formation, Mount Robson area, British Columbia (Walcott, 1924, 1925). Tiñu Formation, southern Mexico, Lower Tremadocian *Parabolina* assemblage (Robison and Pantoja-Alor, 1968). Rabbitkettle Formation, Broken Skull River (two collections 48 m and 50 m below top of formation), *Missisquoia depressa* Subzone.

Holotype

An incomplete cranidium from the Chushina Formation, British Columbia, illustrated by Walcott (1925, pl. 22, figs. 8, 9) and by Harrington and Leanza (1957, fig. 39 2c-e).

Remarks

Walcott (1924: 59) established a new genus *Moxomia* with the terse diagnosis, "*Moxomia* is characterized by the quadrate glabella and cranidium and the small eyes situated far forward." The designated type species, *M. hecuba* Walcott from the



Fig. 23 Parabolinella hecuba (Walcott, 1924). Reconstruction of cranidium (prosopon omitted). Bar represents 1 mm.

Ozarkian of British Columbia, was not described and was merely illustrated by a line drawing. The following year, Walcott (1925: 107), without explanation, changed the type species of *Moxomia* to *Crepicephalus* (*Bathyurus*?) *angulatus* Hall and Whitfield, 1877, and provided a more complete diagnosis of the genus. His illustration of *Moxomia angulata*, however, was a retouched photograph of the same specimen from British Columbia that he had illustrated the previous year by a line drawing as *Moxomia hecuba* and not the holotype of *Moxomia angulata* from the Pogonip Group, White Pine District, Nevada.

Harrington and Leanza (1957: 107) examined the types of both *Moxomia hecuba* Walcott, 1924, and *Moxomia angulata* (Hall and Whitfield, 1877). They concluded that Hall and Whitfield's species probably belongs in *Dunderbergia* and that Walcott's species is congeneric with *Parabolinella limitis* Brögger, the type species of *Parabolinella*.

A complete description of the cranidium of *Parabolinella hecuba* (as *P. tumifrons* Robison and Pantoja-Alor) was presented by Robison and Pantoja-Alor (1968: 790). These authors suggested that *P. tumifrons* differs from *P. hecuba* in having a more tapered and more elongate glabella, more anteriorly situated eyes, and convergent rather than divergent facial sutures. The present material from the Rabbitkettle Formation includes cranidia with both broad glabellae with little forward taper similar to *P. hecuba* (Fig. 52A) and with elongate glabellae with moderate forward taper similar to *P. tumifrons* (Fig. 52F). Because the material from British Columbia, Mexico, and the District of Mackenzie shares the tumid and steeply sloping preglabellar field and a sigmoid 1s furrow, it is united under the name *P. hecuba*. The eye position appears to be similar in these cranidia and the direction of the anterior facial sutures varies only a few degrees on either side of exsagittal.

The cranidium from the Goodwin Limestone in Nevada that was identified as *Parabolinella hecuba* by Ross (1970: 71, pl. 10, figs. 10-13) lacks the tumid and steeply downsloping preglabellar field of the holotype and it is probably not conspecific with *P. hecuba*.

Parabolinella panosa sp. nov. Fig. 50A–L, O, Q, R

Diagnosis

A small species of *Parabolinella* with deep axial furrows; a long, narrow, and inflated glabella bearing three pairs of very shallow and short (tr.) lateral furrows; large palpebral lobes located opposite 2s and 3s furrows; faint occipital furrow; and a tumid preglabellar field.

Occurrences

Rabbitkettle Formation, Broken Skull River (two collections 59.5 m and 60 m below top of formation), *Missisquoia mackenziensis* Fauna.

Holotype

A cranidium (ROM 37731) from KK 122.5 (59.5 m below top of Rabbitkettle Formation) illustrated in Fig. 50Q, R.

Name

From panosus—like bread (Latin) in reference to the loaf shape of the glabella.

Remarks

Parabolinella panosa sp. nov. is represented by well-preserved material of small size in two collections from the *Missisquoia mackenziensis* Fauna. If cranidia of the same size are compared (2.5–3.5 mm, sagittal length), *P. panosa* (Fig. 500, Q) differs from *P.* cf. prolata (Figs. 49D, M, 50N) in having a longer (sag.) and more inflated glabella which has only faint traces of lateral furrows and a tumid preglabellar field. The pygidia of the two species appear to be identical. The tumid and steeply sloping preglabellar field of *P. panosa* is reminiscent of that of *P. hecuba* (Walcott). That latter species has a broader (tr.) glabella and deeper lateral glabellar furrows.

An incomplete ontogenetic sequence of *P. panosa* is preserved in rather coarsely crystalline silica. A few of the better specimens are shown in Fig. 50A–J. An early meraspid specimen (Fig. 50C) demonstrates that immature olenids, at least, were capable of sphaeroidal enrollment (see Bergström, 1973: 21). A conspicuous row of long and slightly curved spines runs along the axes of meraspid specimens from the occipital ring to the first segment in front of the transitory pygidium (Fig. 50E).

Parabolinella sp. Fig. 52J–N

Occurrences

Rabbitkettle Formation, Broken Skull River (single collection 43 m below top of formation), Apoplanias rejectus Fauna.

Remarks

A single collection from the *Apoplanias rejectus* Fauna has yielded cranidia of a *Parabolinella* in which the lateral glabellar furrows are nearly effaced. Two kinds of cranidia are present. One type (Fig. 52J) has a relatively broad glabella and a preglabellar furrow that is shallower than the axial furrows. The other type (Fig. 52L, M), has a relatively narrow glabella and a preglabellar furrow of the same depth as the

axial furrows. It is possible that these types represent distinct species, but it is equally possible that they comprise a single variable effaced species related to, and possibly derived from, *Parabolinella hecuba* (Walcott) which occurs a few metres below *Parabolinella* sp. Both cranidial types have close counterparts in *P. hecuba* (compare Fig. 52J with Fig. 52A and Fig. 52L, M with Fig. 52F, H).

Genus Apoplanias Lochman, 1964a

Type Species

Apoplanias rejectus Lochman, 1964a from the Lower Ordovician part of the Deadwood Formation, Montana (by original designation).

Diagnosis

A genus of olenine trilobite possessing a forwardly tapering glabella with a truncate front margin and two pairs of deep and oblique lateral glabellar furrows; preglabellar field is long (sag.) and gently declining; palpebral lobes are large and located close to glabella near its mid-length. Pygidium is short (sag.) and inverted V-shaped in posterior view; high axis is crossed by single axial ring furrow; posterior margin carries three pairs of flattened spines which decrease in size towards rear.

Remarks

Lochman's (1964a) assignment of pygidia to *Apoplanias rejectus* appears to be incorrect. The two nonspinose pygidia attributed to this species (pl. 15, figs. 15, 17) came from a different drill hole than the one that yielded the holotype cranidium. These pygidia are associated with two cranidia that Lochman assigned to *A. rejectus*, but these differ from the holotype in possessing palpebral lobes that are located far from the glabella and, apparently, in lacking lateral glabellar furrows. These cranidia and pygidia are excluded from *A. rejectus*. It is explicit from the synonymy of *A. rejectus*, below, and from the association of cranidia and pygidia in collections from the Rabbitkettle Formation, that *A. rejectus* possessed a spinose pygidium.

Apoplanias rejectus seems to be restricted to the upper Missisquoia Zone and lower Symphysurina Zone and this olenine is clearly similar and presumably closely related to the contemporaneous and younger species, Highgatella cordilleri (Lochman, 1964b). The cranidium of H. cordilleri differs from that of A. rejectus in having wider (tr.) fixed cheeks, deeper lateral glabellar furrows, a distinct third pair of glabellar furrows, an inflated preglabellar field, and pronounced pitting in the anterior border furrow. Although Lochman (1964b: 464) stated that the pygidium of H. cordilleri was not known, she tentatively assigned a meraspid pygidium to this species (pl. 63, fig. 35). I agree with Hu (1971: 104) that this pygidium probably belongs to a species of Symphysurina.

Apoplanias rejectus Lochman, 1964a Figs. 51M–T, 69K–Q

Apoplanias rejectus Lochman, 1964a: 57, pl. 14, figs. 26–31 (only). Apoplanias rejectus—Stitt, 1971b: 46, pl. 8, fig. 16. Highgatella facila Hu, 1971: 103, pl. 21, figs. 1–26. Highgatella facila—Hu, 1973: 90, pl. 1, figs. 25–28, 30–32. Apoplanias rejectus—Stitt, 1977: 45, pl. 4, figs. 8, 9.

Occurrences

Deadwood Formation, Montana, Wyoming, South Dakota, Lower Ordovician (Lochman, 1964a; Hu, 1971, 1973). Signal Mountain Limestone, Wichita and Arbuckle Mountains, Oklahoma, *Missisquoia typicalis* and *Symphysurina brevispicata* subzones (Stitt, 1971b, 1977). Survey Peak Formation, western Alberta, *Missisquoia* Zone (Derby et al., 1972; Dean, 1978). Rabbitkettle Formation, Broken Skull River (three collections between 25 m and 44 m below top of formation), *Symphysurina brevispicata* Subzone and *Apoplanias rejectus* Fauna.

Holotype

An incomplete cranidium from the Deadwood Formation, Montana illustrated by Lochman (1964a, pl. 14, figs. 26, 28).

Remarks

The available material of this olenine from the upper part of the Rabbitkettle Formation is badly deformed for the main part. Some of the better preserved cranidia (Figs. 510, 69K, L) conform well to those of *Apoplanias rejectus* from the Williston Basin and Oklahoma.

The pygidium associated with the A. rejectus cranidium (Fig. 69M–O) is transverse in dorsal view and inverted V-shaped in posterior view; it carries a highly convex and bluntly rounded axis with a single axial ring and a semicircular terminal piece. The pleural field descends steeply and it is crossed by two firmly impressed pleural furrows. The posterior margin of the pygidium bears three pairs of short flattened spines which decrease in size towards the rear. I suggest that this pygidium belongs to A. rejectus despite Lochman's (1964a) assignment of two nonspinose pygidia to this species. Very similar spinose pygidia from the Deadwood Formation of Wyoming were assigned to a new species, Highgatella facila, by Hu (1971). Because the cranidia of H. facila are indistinguishable from those of A. rejectus from Montana, Oklahoma, and the District of Mackenzie, Hu's species is considered to be a junior subjective synonym of A. rejectus.
Genus Bienvillia Clark, 1924

Type Species

Dikelocephalus? corax Billings, 1865 from the Levis Formation, Point Levis, Quebec (by original designation).

Bienvillia cf. corax (Billings, 1865) Fig. 57s

Bienvillia corax—Henningsmoen, 1957: 143, pl. 1, fig. 6 (see for synonymy).

Occurrences

Rabbitkettle Formation, Broken Skull River (two collections 64 m and 70 m below top of formation), *Elkanaspis corrugata* Fauna.

Remarks

The silicified cranidia from the Rabbitkettle Formation are much smaller than the holotype of *Bienvillia corax* illustrated by Rasetti (1944, pl. 36, fig. 51) and because they are incomplete and somewhat wrinkled, the comparison with *B. corax* is tentative. Three pairs of lateral glabellar furrows are evident in *B.* cf. *corax*; the posterior pairs extend from the axial furrows and connect across the glabella in a chevron shape. The anterior pair extends from near the mid-line towards, but does not reach, the anterolateral corner of glabella. The illustrated cranidium of *B. cf. corax* in having a transverse preglabellar field.

Superfamily Solenopleuracea Family Entomaspidae Ulrich, *in* Bridge, 1931 (= Family Heterocaryonidae Hupé, 1953; emend. Gilman Clark and Shaw, 1968)

Assigned Genera

Entomaspis Ulrich, in Bridge, 1931; Bowmania Walcott, 1925; Heterocaryon Raymond, 1937; Hypothetica Ross, 1951; and, possibly Conococheaguea Rasetti, 1959.

In his diagnosis of the Entomaspidae, Rasetti (*in* Moore, 1959) emphasized the closely aligned, oblique, and backwardly directed anterior and posterior branches of the facial suture and the narrow strip of free cheek which connects the eye to the cephalic border of *Entomaspis radiatus* Ulrich. The backwardly directed anterior branch of the facial suture certainly lends a singular aspect to the *Entomaspis* cephalon and that, coupled with the wide flat border, apparently encouraged comparisons with both harpids and trinucleids (Rasetti, 1952; Hupé, 1953). Rasetti (1952: 801) hypothesized that *Entomaspis* formed part of the lineage leading to the Trinucleidae and both Rasetti (*in* Moore, 1959) and Hupé (1953) included the Entomaspidae in the Harpina.

The general similarity of *Entomaspis* and the Harpina does not necessarily mean that these taxa are closely related. I suggest that *Entomaspis* has much more in common with *Bowmania* and *Heterocaryon* and should be classified with these genera.

The possibility that *Entomaspis* is related to genera that were previously assigned to the Heterocaryonidae Hupé was first suggested by Winston and Nicholls (1967: 89) who stated that *Bowmania sagitta* Winston and Nicholls is probably intermediate between *B. americana* (Walcott) and *Entomaspis radiatus* (see also Stitt, 1977: 41).

My recognition that the yoked and spiny cheeks previously assigned to Acidaspis ulrichi Bassler actually belong to Bowmania americana lends further credence to a close relationship of Bowmania and Entomaspis. It is possible to transform a Bowmania cephalon to an Entomaspis cephalon by fusing the lateral array of cephalic spines and by shifting the anterior facial sutures forward to the edge of the cephalon and by shifting the preocular sutures outward and backward. This hypothetical transformation does not imply that Bowmania necessarily gave rise to Entomaspis.

This study also demonstrates that the pygidia of both *Bowmania* and *Heterocaryon* are very similar to those assigned to *Entomaspis radiatus*. In addition, the pygidium which formed the basis for *Entomaspis bridgei* Rasetti, 1952 is more similar to *Bowmania* than it is to *Entomaspis* and Rasetti's species should be assigned to the former genus.

I conclude that the Heterocaryonidae Hupé should be synonymized with the Entomaspidae Ulrich.

Rasetti (1952) discussed the possible relationship of the entomaspids to the trinucleids. Two entomaspid genera, *Entomaspis* and *Bowmania*, also exhibit marked similarity to *Doremataspis* Öpik, 1967 from the Mindyallan (early Late Cambrian) of Queensland which Öpik assigned to the family Liostracinidae Raymond (compare Öpik, 1967, fig. 138 and Rasetti, 1952, figs. 1, 3 and this paper, Fig. 24). These genera possess similarly shaped cephala and glabellae with similar markings. The difference in the degree of divergence of the anterior branches of the facial suture in the three genera is striking, but in this feature *Doremataspis* is intermediate between *Bowmania* and *Entomaspis*. Whether the cephalic similarity between this liostracinid and the entomaspids is indicative of close phyletic connection is uncertain. The pygidium attributed to *Doremataspis* has little in common with those of the entomaspids and its cephalon is distinguished by a pair of bacculae and by the presence of a very large rostral plate that extends for nearly the full width of the cephalon.

Genus Bowmania Walcott, 1925

Type Species

Arethusina americana Walcott, 1884 from Upper Cambrian rocks of the Eureka District, Nevada (by original designation).

Revised Diagnosis

A genus of Entomaspidae with a glabella of parabolic outline, deep axial furrows, and two or three lateral glabellar furrows. Preglabellar field is long and forwardly declined. Widely set eyes are located opposite mid-length of glabella. Palpebral ridges are prominent. Anterior and posterior branches of facial suture curve outward from the eye; anteriorly, suture runs along and bisects slightly convex anterior border. Free cheeks are yoked. Genal spines are long and backwardly directed. Lateral and anterior flanks of cephalon carry prominent fringe of marginal spines whose lengths decrease posteriorly. Pygidium is small, broadly triangular, and three times as wide as long. Prominent axis with five or six rings is slightly tapering. Horizontal pleural portion has four or five interpleural furrows and faint pleural furrows. A narrow raised rim forms anterior and posterior border of pygidium.

Bowmania americana (Walcott, 1884)

Figs. 24, 53K-s, 54A-O

Arethusina americana Walcott, 1884: 62, pl. 9, fig. 27. Acidaspis ulrichi Bassler, 1919: 355, pl. 37, figs. 6–8. Bowmania americana—Walcott, 1925: 73, pl. 15, figs. 15, 16. Bowmannia americana [sic]—Hupé, 1953: 150, fig. 132–2. ''Acidaspis'' cf. ulrichi—Kindle and Whittington, 1958: 332. ''Acidaspis'' ulrichi—Rasetti, 1959: 393, pl. 51, fig. 27. ''Acidaspis'' ulrichi—Kindle and Whittington, 1959: 17. Bowmania americana—Winston and Nicholls, 1967: 89, pl. 10, fig. 18. Bowmania americana—Longacre, 1970: 56. Bowmania americana—Stitt, 1971b: 22, pl. 7, figs. 7–9.

Occurrences

Upper Cambrian, Eureka District, Nevada (Walcott, 1884). Wilberns Formation, central Texas, *Saukiella serotina* Subzone (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Arbuckle Mountains, Oklahoma, *Saukiella serotina* Subzone (Stitt, 1971b). Notch Peak Formation, Utah, *Saukiella serotina* Subzone (Hintze et al., 1980). Lime Kiln Member of Frederick Limestone,

Maryland, Saukiella serotina Subzone (Rasetti, 1959; M.E. Taylor, in Reinhardt, 1974). Cow Head Group, Broom Point, western Newfoundland, Hungaia Assemblage (Kindle and Whittington, 1959; C.H. Kindle Collection at Geological Survey of Canada, Ottawa). Rabbitkettle Formation, Broken Skull River (seven collections between 75 m and 96 m below top of formation), Bowmania americana Fauna.

Holotype

An incomplete cranidium from the Hamburg Limestone (?), Dunderberg Mine, Eureka District, Nevada illustrated by Walcott (1884, pl. 9, fig. 27), Walcott (1925, pl. 15, figs. 15, 16).

Description

Cephalon (exclusive of genal and marginal spines) is semicircular in outline and moderately convex. Glabella is inflated and parabolic in outline. Its length is one-half that of cephalon and its width is less than one-third that of cephalon at level of eyes. Broad preglabellar field curves steeply to anterior border furrow. Deep axial furrows are connected in even curve with narrow and sharply incised preglabellar furrow. Three short and approximately equally spaced lateral glabellar furrows extend inward and backward. Occipital ring is relatively long (sag.) and is surmounted by large curved median spine. Occipital furrow is complete and slightly backwardly curving. Eyes are located at about half length of glabella; a little more than one-half the distance out on the cheeks. Crescentic palpebral lobe is continuous adaxially with prominent palpebral ridge which extends across fixed cheek with slight forward curvature to join axial furrow at level of 3s furrow. Cephalic borders are relatively long (sag.) and very gently convex anteriorly; become narrower and convex laterally and posteriorly; they are demarcated by deep border furrows which connect in semicircular continuum. Posterior branch of facial suture curves outward and backward to cut posterior margin inside base of genal spine. Anterior branch of facial suture curves laterally a short distance before turning in to cross anterior border furrow. It continues along anterior border in a path parallel with anterior margin. Genal spine is long, gradually tapering, backwardly directed with faint adaxial curvature distally, and circular in cross-section. Its interior flank contains a single row of small, closely spaced spines. Outside margin of entire cephalon is fringed by a single row of long, slim, horizontally disposed spines that number about 50 in total. Anterior spines are about as long as glabella, forwardly pointed with slight lateral curvature distally. Posteriorly, these spines decrease in length and are progressively swept backward. Each of the marginal spines is circular in cross-section and each projects abruptly from the tubelike anterior and lateral borders and the genal spines.

Cephalon inside border furrows is covered by sparsely distributed tubercles, some of which are perforated.

Pygidium is semielliptical in outline and three times as wide as long. Convex axis extends to posterior border and is outlined by deep, straight, and slightly converging axial furrows. It comprises five well-defined axial rings and a terminal piece. Flat

pleural field is crossed by four or five deep interpleural furrows and an equal number of faint pleural furrows. These furrows extend to, and terminate against, narrow and raised posterior border which rims edge of pygidium. Posterior margin of pygidium is vertical to slightly overhanging.

Remarks

The holotype of *Bowmania americana* (Walcott) is an incomplete cranidium of moderate convexity. It measures about 6.5 mm in sagittal length and it possesses backwardly swept palpebral ridges. This cranidium differs somewhat from most of the silicified cranidia from the Rabbitkettle Formation assigned to *B. americana*. These are, for the most part, smaller and tend to have steeply curving preglabellar fields and prominent median occipital spines. Whether the holotype has a median occipital spine cannot be determined because the central part of the occipital ring is exfoliated. In addition, the palpebral ridges of the silicified specimens tend to be directed only slightly posterior of transverse—but this feature is difficult to evaluate



Fig. 24 Bowmania americana (Walcott, 1884). Reconstruction of cephalon and pygidium. Bar represents 1 mm.

because each of the cranidia is somewhat sheared and wrinkled. Significantly, the largest silicified cranidium recovered (sagittal length 5.0 mm, Fig. 53L) is very similar to the holotype from Nevada. The differences between the Rabbitkettle specimens and the holotype may well be attributable to size and preservation. The cranidia of *B. americana* from Oklahoma (Stitt, 1971b, pl. 7, figs. 7–9) are smaller than the holotype and rather similar to the Rabbitkettle specimens.

Longacre (1970: 56) suggested that the separation of *Bowmania americana* from *B*. pennsylvanica Rasetti, 1959 may be artificial and Stitt (1971b: 22) implied that *B*. americana is gradational with *B*. sagitta Winston and Nicholls, 1967. These species of *Bowmania* are confined to the Saukiella serotina Subzone in both Oklahoma and Texas and, because each has considerable morphologic variation, it may eventually be necessary to unite them under the name *B*. americana. In this regard, it should be noted that the type material of *B*. pennsylvanica occurs in the same collection as "Acidaspis" ulrichi in Maryland (Rasetti, 1959). Cook and Taylor (1977, fig. 2) indicated a nearly complete overlap of the stratigraphic ranges of Bowmania and "Acidaspis" in the upper Whipple Cave Formation of the Egan Range, Nevada.

Genus Heterocaryon Raymond, 1937

Type Species

Heterocaryon platystigma Raymond, 1937 from Zone 1 (Hungaia Assemblage), Highgate Falls, Vermont (by original designation).

Heterocaryon tuberculatum Rasetti, 1944 Figs. 25, 55A-N

Heterocaryon tuberculatum Rasetti, 1944: 241, pl. 36, fig. 55.
Heterocaryon cf. tuberculatum—Winston and Nicholls, 1967: 76, pl. 11, figs. 15, 18.
Heterocaryon cf. tuberculatum—Longacre, 1970: 57.
Heterocaryon tuberculatum—Stitt, 1971b: 22, pl. 7, fig. 11.

Occurrences

Levis Formation, North Ridge, Levis, Quebec, Hungaia Assemblage (Rasetti, 1944). Wilberns Formation, central Texas, Saukiella serotina Subzone (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Wichita and Arbuckle mountains Oklahoma, Rasettia magna to Saukiella serotina subzones (Stitt, 1971b, 1977). Notch Peak Formation, Utah, Saukiella serotina Subzone (Hintze et al., 1980). Rabbitkettle Formation, Broken Skull River (eight collections between 90 m and 177 m below top of formation), Bowmania americana Fauna and Yukonaspis kindlei Fauna.

Holotype

An incomplete cranidium from the Levis Formation, Levis, Quebec illustrated by Rasetti (1944, pl. 36, fig. 55).

Description

Cephalon is crescentic in outline and strongly convex (sag. and tr.). Glabella is large, inflated, and oval in outline. It expands somewhat towards the front and is about one-third the width and four-fifths the sagittal length of cephalon. Preglabellar field is short and nearly vertically disposed. Axial furrows are deep and are continuous with evenly rounded and shallow preglabellar furrow. Three short (tr.) lateral glabellar furrows are approximately equally spaced and are barely perceptible. Occipital ring is short (sag.); occipital furrow is nearly straight. Eyes are located far out on cheek, opposite 3s furrow. Palpebral lobe is distinct and nearly exsagittally directed. Palpebral ridge is faint and narrow (exsag.). It curves across wide and inflated fixed cheek to join axial furrow at midlength of 4p lobe. Cephalic borders are tubelike; border furrows are deep. Posterolateral corner is extended into short, backwardly and slightly upwardly curving genal spine. Anterior branch of facial suture runs forward and inward in even curve on to anterior border. Posterior branch of suture runs backward and outward. Entire cephalon is densely covered by tubercles, some of which are perforated.

Pygidium is broadly triangular and two and a half times as wide as long. Axis consists of four or five highly arched rings and a blunt terminal piece. Deep axial furrows converge posteriorly. Flat pleural field is crossed by four distinct interpleural furrows. Faint pleural furrows may be seen on some specimens. Five pairs of flattened spines and a larger median unpaired spine project back and over vertical posterior margin of pygidium. Each spine has an oval base, above which it expands and is flattened in line with pygidial margin. Each spine has a saddle-shaped tip in plan view. Pygidium bears sparsely distributed perforate tubercles, including one or two pairs of each axial ring.



Fig. 25 *Heterocaryon tuberculatum* Rasetti, 1944. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

The type species, *Heterocaryon platystigma* Raymond (1937, pl. 3, fig. 13; see also Gilman Clark and Shaw, 1968, pl. 125, figs. 4–6), differs from *H. tuberculatum* in having a shorter and highly inflated glabella with deep and oblique 1s furrows and a longer and concave preglabellar field.

The similarity of the pygidia of *Bowmania americana*, *Heterocaryon tuber*culatum, and *Entomaspis radiatus* provides strong support for their inclusion in the same family.

Family Catillicephalidae Raymond, 1938

Genus Triarthropsis Ulrich, in Bridge, 1931

Type Species

Triarthropsis nitida Ulrich, in Bridge, 1931 from the Eminence Dolomite (Trempealeauan), Eminence, Missouri (by monotypy).

Triarthropsis limbata Rasetti, 1959 Fig. 57U

Triarthropsis limbata Rasetti, 1959: 382, pl. 52, figs. 1–8. Triarthropsis limbata—Stitt, 1971b: 16, pl. 7, fig. 3.

Occurrences

Conococheague Limestone, Maryland, Saukia Zone (Rasetti, 1959). Signal Mountain Limestone, Wichita and Arbuckle mountains, Oklahoma, Saukiella junia to Corbinia apopsis subzones (Stitt, 1971b, 1977). Rabbitkettle Formation, Broken Skull River (single collection 165 m below top of formation), Yukonaspis kindlei Fauna.

Holotype

A cranidium from the upper Conococheague Limestone, Washington County, Maryland illustrated by Rasetti (1959, pl. 52, figs. 1, 2).

The specimens from the Rabbitkettle Formation possess wide fixed cheeks, large palpebral lobes, shallow axial and preglabellar furrows, and long (sag.) preglabellar fields. They appear to conform to Rasetti's (1959) description and illustrations of T. *limbata*.

? Family Kingstoniidae Kobayashi, 1933

Genus Larifugula gen. nov.

Type Species

Larifugula triangulata sp. nov. from the Upper Cambrian part of the Rabbitkettle Formation.

Diagnosis

A small genus of kingstoniid (?) trilobite possessing an anteriorly expanding or subrectangular glabella with two pairs of faint lateral furrows. Occipital ring bears a long slender median spine. Preglabellar field is long and evenly downcurved to weak anterior border furrow. Palpebral lobes are small and slightly raised; they are located opposite frontal glabellar lobe. Genal spines are long, slender, and gently curved. Facial sutures follow outwardly arcuate path from posterior margin to eye and then forward to join median connective suture on sagittal line—thus outlining a subtriangular to semicircular cranidium. Pygidia are subtriangular to subcircular in outline with variably developed axes, pleural fields, and borders.

Name

From *larifuga*—vagabond (Latin) in reference to the widespread occurrences of this small trilobite. Feminine.

Assigned Species

The type species occurs in the Yukonaspis kindlei Fauna to Elkanaspis corrugata Fauna interval in the Rabbitkettle Formation. The only other species assigned to the new genus is Larifugula leonensis (Winston and Nicholls, 1967) which occurs in the Corbinia apopsis Subzone in Texas, Oklahoma, and Nevada and in the Elkanaspis corrugata Fauna in the District of Mackenzie.

Taylor (1977: 408) remarked in a footnote that the supposed olenid *Leiobienvillia leonensis* Winston and Nicholls, 1967 probably represents an undescribed genus. Examination of the type material of *L. leonensis* from Texas (Fig. 70H–L) confirms that this trilobite is neither congeneric with *Leiobienvillia laevigata* Rasetti, 1954 nor an olenid. *L. leonensis* and a new species from the Rabbitkettle Formation are here assigned to a new genus, *Larifugula*, whose affiliation may lie with the kingstoniids.

Larifugula differs from *Leiobienvillia* Rasetti in having an ovate glabella, deeper cephalic furrows, an anterior border furrow, an occipital spine, and a subtriangular cranidium (compare Fig. 26A and Rasetti, 1954, fig. 3).

The cranidium of the new genus shares some features with three genera that Raymond defined for one or two small and poorly preserved cranidia from the Upper Cambrian of Vermont. These are Zacompsus Raymond, 1924 (type species, Z. clarki), Pseudosalteria Raymond, 1924 (type species, P. laevis), and Strotocephala (type species, S. howelli). Of these, Zacompsus is most similar to Larifugula in having an anteriorly expanding and bulb-shaped glabella. Raymond's genus differs from the new genus by possessing prominent palpebral ridges and, apparently, by lacking an anterior border furrow and an occipital spine. Pseudosalteria and Strotocephala have semicircular cranidia with faintly outlined and subcircular glabellae, anteriorly placed eyes, and very faint occipital and posterior border furrows. In addition, Strotocephala do not appear to differ from Leiobienvillia and these taxa should probably be united under the senior name, Pseudosalteria.

Larifugula shares a number of cranidial and pygidial features with the Dresbachian/Franconian genus Bynumia Walcott, 1924 and with the Trempealeauan genus Bynumiella Resser, 1942 and this similarity is the basis for the tentative assignment of Larifugula to the Kingstoniidae. The three genera share a triangular cranidial outline and similarly placed palpebral lobes of the same size. The pygidium of Bynumia bears a faintly ribbed axis and lacks both border furrows and furrows on the pleural region. On the interior, the pygidium of Bynumia eumus Walcott (= B. venusta Resser, B. robsonensis Resser, and B. sawbackensis Resser; see Greggs, 1962: 116, 117) from the Sullivan Formation, Banff National Park (Resser, 1942, pl. 9, figs. 24–26, 34, 44) displays five or six pleurae that terminate against a "quasi-border". B. eumus, therefore, appears to possess an exterior pygidial morphology similar to the exterior of the Larifugula triangulata pygidium and an interior morphology similar to the exterior of the L. leonensis pygidium. Exfoliated pygidia of Kingstonia alabamensis Resser (see Palmer, 1962, pl. 6, fig. 12) also display a morphology similar to that of L. leonensis.

Larifugula can be distinguished from Bynumia by possessing deeper cephalic furrows, an unfurrowed glabella that expands anteriorly, an occipital spine, and long slender genal spines. The anteriorly expanding and unfurrowed glabella and the occipital spine also distinguish it from Bynumiella, but it is significant that Greggs (1962: 120) noted that B. typicalis Resser, 1942 from the Saukia Zone of the Bison Creek Formation, Banff National Park, bears two pairs of shallow lateral glabellar furrows and a short, sharp medial tubercle on the occipital ring. These features bring Bynumiella close to Larifugula.

The Lower Ordovician genus Yumenaspis Chang and Fan (type species Y. yumenensis Chang and Fan; see Lu et al., 1965, pl. 132, figs. 1–6) has a cranidium that is rather similar to that of Larifugula. It differs from Larifugula in having a glabella that expands markedly towards the front, a broad (tr.) anterior border on the cranidium, prominent palpebral ridges, eyes located closer to the glabella, and in lacking an occipital spine. In addition, the ribbed pygidium attributed to Yumenaspis is broadly triangular and bears a marginal rim.

Larifugula triangulata gen. et sp. nov. Figs. 26A; 56A–O, Q–S

Diagnosis

A species of *Larifugula* with an anteriorly expanding and drop-shaped glabella and a subtriangular pygidium bearing a convex axis with two rings and a long terminal piece and an unfurrowed pleural region which slopes evenly to margin.

Occurrences

Rabbitkettle Formation, Broken Skull River (eight collections between 61 m and 165 m below top of formation), *Elkanaspis corrugata* Fauna, *Bowmania americana* Fauna, *Yukonaspis kindlei* Fauna.

Holotype

A cranidium (ROM 37643) from K 550 illustrated on Fig. 56A-C.

Name

From *triangulus*—having three angles (Latin) in reference to the shape of the pygidium.

Preservation

These silicified specimens are extremely small; the largest cranidium measures 2.0 mm (exclusive of occipital spine) and the largest pygidium only 0.7 mm in sagittal length. In addition, the specimens from the *Elkanaspis corrugata* Fauna have exceedingly thin and wrinkled shells. Some of these specimens show small-scale deformation that could be mistaken for true morphologic features; for example, the

prominent "palpebral ridge" on the left side of the cranidium in Fig. 56G. The specimens are difficult to handle and a number were destroyed in attempts to remove them from their mounting pins after photography.

Description

Cephalon is crescentic in outline and moderately vaulted. Glabella is oval to bulb-shaped and it expands somewhat towards front; it is outlined by deep axial furrows and variably developed and shallow preglabellar furrow. Two pairs of short (tr.) lateral glabellar furrows extend inward a short distance. Occipital furrow is faint to effaced. Occipital ring is triangular; it protrudes well beyond the posterolateral edge of cephalon. A long slim occipital spine extends nearly straight back; it is almost as long (sag.) as glabella. Preglabellar field slopes evenly to the faint anterior border furrow which is generally defined by no more than a change in slope. In many cranidia a poorly differentiated median longitudinal ridge traverses preglabellar field to narrow (tr.) anterior border. Small palpebral lobe is raised slightly above cheek at weakly incised palpebral furrow; it is located opposite widest part of glabella, at two-thirds glabellar length. Deep and transverse posterior border furrow defines narrow and convex posterior border. It continues on to free cheek and swings forward and shallows markedly as it becomes lateral border furrow. Genal spine is oval in cross-section and is about as long as glabella; it is slender and curves slightly inward. Anterior branch of facial suture swings forward along outwardly curved path to meet median connective suture on sagittal line. Posterior path of suture proceeds backward and outward to cross posterior margin at right angle. Surface of cephalon is smooth; occipital and genal spines carry fine terrace lines which run parallel to their margins.

Minute pygidium is triangular in outline and moderately vaulted (tr.). Narrow axis consists of two short (sag.) rings and long, tapering terminal piece; it extends to just in front of posterior margin. Pleural region is unribbed, but most specimens carry a



Fig. 26

- A Larifugula triangulata gen. et sp. nov. Reconstruction of cranidium and pygidium. Bar represents 1 mm.
- B Larifugula leonensis (Winston and Nicholls, 1967). Reconstruction of cranidium and pygidium. Same scale as 26A.

few irregular transverse undulations; its interior portion is nearly flat, distally it declines steeply to lateral margin. Pleural region carries irregular fine terrace lines that are oriented parallel to lateral margin.

Remarks

The cranidium of Larifugula triangulata gen. et sp. nov. differs from that of L. *leonensis* (Winston and Nicholls) in having an anteriorly expanding, drop-shaped glabella and fainter occipital, preglabellar, and anterior border furrows. The pygidia of the two species differ considerably. That of L. triangulata is subtriangular in outline and lacks a border; that of L. leonensis is semicircular in outline and bears a narrow and outwardly concave border which has an inner raised rim (Fig. 26).

Larifugula leonensis (Winston and Nicholls, 1967) Figs. 26B, 56P, 670–R, 70H–L

Leiobienvillia leonensis Winston and Nicholls, 1967: 75, pl. 11, figs. 16, 20, 21. Leiobienvillia leonensis—Longacre, 1970: 18. Leiobienvillia leonensis—Stitt, 1971b: 26, pl. 7, fig. 12.

Occurrences

Wilberns Formation, central Texas, *Corbinia apopsis* Subzone (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Wichita and Arbuckle mountains, Oklahoma, *Corbinia apopsis* Subzone (Stitt, 1971b, 1977). Notch Peak Formation, Utah, *Corbinia apopsis* Subzone (Hintze et al., 1980). Survey Peak Formation, western Alberta, *Corbinia apopsis* Subzone (Derby et al., 1972). Rabbitkettle Formation, Broken Skull River (two collections 61 m and 70 m below top of formation), *Elkanaspis corrugata* Fauna.

Holotype

A cranidium from the Wilberns Formation, central Texas illustrated by Winston and Nicholls (1967, pl. 11, fig. 20) and herein (Fig. 70H–J).

Remarks

The holotype cranidium of *Larifugula leonensis* (Winston and Nicholls) from Texas (Fig. 70H–J) is slightly larger and somewhat more inflated than the cranidia from the Rabbitkettle Formation which are assigned to this species (Figs. 56P, 67P, Q). The single deformed pygidium of *L. leonensis* from the Rabbitkettle (Fig. 67R) is more

transverse than the paratype pygidium from Texas (Fig. 70K).

A fragmentary thorax of L. *leonensis* (Fig. 670) consists of six articulated segments. Each segment comprises an arched axis, a horizontal inner portion of the pleura, and a gently declined outer portion. A transverse pleural furrow continues nearly to the tip of the segment. A long median spine projects posteriorly from the axis of one of the segments. This spine carries a longitudinal prosopon of very fine ridges; identical to that on the occipital spine.

Family Plethopeltidae Raymond, 1925

Genus Plethometopus Ulrich, in Bridge, 1931

Type Species

Bathyurus armatus Billings, 1860 from the Levis Formation, Point Levis, Quebec (by original designation).

Remarks

Plethometopus differs from the related genus *Plethopeltis* Raymond, 1913 in the absence of axial furrows in front of the eyes and the absence of an anterior border furrow (Longacre, 1970: 19; Taylor and Halley, 1974: 25).

The Rabbitkettle material of P. obtusus Rasetti extends the range of Plethometopus into the lower part of the Missisquoia depressa Subzone. Previously, the youngest record of the genus was in the Corbinia apopsis Subzone in Texas and Oklahoma. Stitt (1977: 28, 29) demonstrated that Plethopeltis, previously thought to be restricted to the Trempealeauan (Lochman-Balk, 1970, fig. 7), also extends as high as the M. depressa Subzone in Oklahoma.

Plethometopus obtusus Rasetti, 1945 Figs. 27, 56T–V

Plethometopus obtusus—Taylor and Halley, 1974: 24, pl. 1, figs. 11–14 (see for synonymy).

Occurrences

Levis Formation, Levis, Quebec, Hungaia Assemblage (Rasetti, 1945). Conococheague Formation, Maryland, Saukia Zone (Rasetti, 1959). Wilberns Formation, central Texas, Saukiella serotina and Corbinia apopsis subzones (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Wichita and Arbuckle mountains, Oklahoma, Saukiella serotina and Corbinia apopsis subzones (Stitt, 1971b, 1977). Whitehall Formation, New York, Saukiella serotina Subzone (Taylor and Halley, 1974). Rabbitkettle Formation, Broken Skull River (five collections between 55 m and 77 m below top of formation), Missisquoia depressa Subzone, Missisquoia mackenziensis Fauna, Elkanaspis corrugata Fauna, and Bowmania americana Fauna.

Holotype

A cranidium from an Upper Cambrian boulder, North Ridge, Levis, Quebec illustrated by Rasetti (1945, pl. 62, fig. 1).

Remarks

The characteristic features of *Plethometopus obtusus* Rasetti and the differences with other species of *Plethometopus* have recently been discussed by Longacre (1970: 19), Stitt (1971: 35) and Taylor and Halley (1974: 24). The Rabbitkettle cranidia agree, in all respects, with the type and other attributed cranidia of *P. obtusus*.

Genus Leiocoryphe Clark, 1924

Type Species

Leiocoryphe gemma Clark, 1924 from an Upper Cambrian boulder, Levis, Quebec (by original designation).





Leiocoryphe spp. Fig. 57A–F

Occurrences

Rabbitkettle Formation, Broken Skull River (seven collections between 86.5 m and 177 m below top of formation), *Bowmania americana* Fauna and *Yukonaspis kindlei* Fauna.

Remarks

In the Rabbitkettle Formation, *Leiocoryphe* is represented by a few small cranidia and pygidia. On the basis of the associated pygidia, the generic identification is firm. I have not attempted to identify these specimens to the species level. Some cranidia (Fig. 57A, B) are subtriangular in outline and inflated above and over the anterior margin. These cranidia are associated with typical pod-shaped *Leiocoryphe* pygidia. (Fig. 57F) whose anterior margin is located on the anteroventral edge (note position of articulating furrow in the anterior view in Fig. 57E). Other cranidia (Fig. 57C) are transverse and only slightly inflated. Associated pygidia (Fig. 57D) are nearly flat and equally transverse. These are similar to the specimens assigned to *L. platycephala* Kobayashi, 1935 (for example, by Stitt, 1971b, pl. 4, figs. 9, 10, 12).

Superfamily Norwoodiacea Family Norwoodiidae Walcott, 1916

Genus Levisaspis Rasetti, 1943

Type Species

Levisaspis typicalis Rasetti, 1943 from Lower Ordovician limestone conglomerate at North Ridge, Levis, Quebec (by original designation).

Remarks

Shaw (1951: 105) considered *Levisaspis* to be a subgenus of *Holcacephalus* Resser. Later, he (Shaw, 1953: 145) proposed that *Levisaspis* be considered a junior synonym of *Hardyoides* Kobayashi, an arrangement also favoured by Lochman (*in* Moore, 1959: 302). Palmer (1965b) reviewed the classification of *Holcacephalus*, *Levisaspis*, and *Hardyoides* and concluded (p. 54) that *Levisaspis* is not congeneric with *Hardyoides* and that *Holcacephalus* belongs to a separate family from *Levisaspis* and *Hardyoides*. Herein, *Levisaspis* is considered to have full generic status within the Norwoodiidae.

Levisaspis glabrus (Shaw, 1951) Figs. 28, 680–Q

Holcacephalus (Hardyoides) glabrus Shaw, 1951: 106, pl. 24, figs. 1–3 (only). Hardyoides glabrus—Shaw, 1953: 145, pl. 18, figs. 20, 21. Levisaspis glabrus—Palmer, 1965: 54.

Occurrences

Gorge Formation, Highgate Falls, Vermont. *Missisquoia* Zone (Shaw, 1951). Rabbitkettle Formation, Broken Skull River (two collections 45 m and 45.5 m below top of formation). *Missisquoia depressa* Subzone.

Holotype

A cranidium from the Gorge Formation, Highgate Falls, Vermont illustrated by Shaw (1951, pl. 24, fig. 1).

Description

Cranidium crescentic in outline, twice as wide as long, and convex. Genal corners bear fixigenal spines of unknown length. Axial furrows deep; continuous with shallow preglabellar furrow. Evenly inflated glabella is subrectangular in outline with rounded anterolateral corners. Occipital ring is short (sag.), defined by faintly incised occipital furrow. A single pair of short (exsag.) lateral glabellar furrows extends inwardly a short distance. Preglabellar field is nearly vertically disposed towards deep and narrow (sag.) anterior border furrow which defines narrow, rimlike and slightly curving (tr.) anterior border. Distinct and tubelike palpebral ridge curves outward from anterolateral corner of glabella; terminates as small, convex palpebral lobe.





Facial suture is proparian; its posterior course is laterally curving; anteriorly, it curves slightly adaxially. Dorsal surface of cranidium is finely granulose.

Remarks

Levisaspis glabrus differs from the only other known species, L. typicalis Rasetti, in having a shorter preglabellar field, more convex palpebral ridges, eyes located closer to the glabella, and, possibly, longer fixigenal spines.

The holotype of L. glabrus was illustrated only in lateral view by Shaw (1951) so some uncertainty exists about the morphology of this species. Even though the illustrated Rabbitkettle specimen has a glabella that is less rounded anteriorly, it is considered to be conspecific with the two paratype heads of L. glabrus from Vermont.

Superfamily Dikelocephalacea Family Saukiidae Ulrich and Resser, 1933

Genus Calvinella Walcott, 1914

Type Species

Dikelocephalus spiniger Hall, 1863 from the Trempealeau Formation, Trempealeau, Wisconsin (by original designation).

Remarks

Longacre (1970: 45) and Taylor and Halley (1974: 27) have summarized the features that have been used to distinguish *Calvinella* from other saukiid genera (unequally divided pygidial pleurae, occipital spine, granular prosopon on the cranidium). Taylor and Halley emphasized that these features are of doubtful taxonomic significance because some are shared with *Tellerina* Ulrich and Resser, 1933 and *Prosaukia* Ulrich and Resser, 1933 and these authors further noted that these saukiid generic names should be used advisedly until such time as their respective type species have been fully re-evaluated.

Diagnosis

A species of "*Calvinella*" with wide (tr.), long (exsag.) and crescentic palpebral lobes located close to the glabella and two pairs of lateral glabellar furrows. Small cranidia possess slender occipital spines; these are reduced to tubercles in large cranidia.

Occurrence

Rabbitkettle Formation, Broken Skull River (two collections 165 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A cranidium (ROM 37466) from K 510 (177 m below top of Rabbitkettle Formation) illustrated on Fig. 58C, D.



Fig. 29 *"Calvinella" palpebra* sp. nov. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Name

From *palpebra*—eyelid (Latin) in reference to the large and conspicuous palpebral lobes.

Remarks

"Calvinella" palpebra sp. nov. is so similar to "Calvinella" prethoparia Longacre, 1970 that a comparison with that well-described species (Longacre, 1970; Taylor and Halley, 1974) is presented in lieu of a description. The Rabbitkettle material of "Calvinella" is much smaller than the Texas and New York material. In spite of the size difference, "C." palpebra is seen to have consistently larger palpebral lobes that are located closer to the glabella than does "C." prethoparia (compare the cranidia of increasing sizes illustrated by Longacre, 1970, pl. 6, figs. 10, 9, 7 with those in this paper, Fig. 58I, D, 69E). "C." palpebra has only two pairs of lateral glabellar furrows, of which 1s is complete across the glabella in only the largest available cranidia. "C." prethoparia has three pairs of furrows, of which 1s extends across the glabella in both small and large cranidia.

> saukiid indet. Fig. 57P-R

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 165 m below top of formation), Yukonaspis kindlei Fauna.

Remarks

Several saukiid specimens occur in a single collection from the Rabbitkettle Formation. A fragmentary cranidium (Fig. 57Q, R) is unlike that of any saukiid genus in North America in having an inflated rectangular glabella; straight, narrow (sag.), and bandlike 1s and 2s furrows that are complete across the glabella; a narrow anterior border furrow that undercuts front part of the glabella; and a pair of small, anteriorly directed spines located on the vertical anterior border. In the nature of the front part, this cranidium has affinity to the Australasian genus *Lophosaukia* Shergold, 1971, but that genus has a triangular crest, and not a pair of spines, on the anterior border.

An associated pygidium (Fig. 57P) is similar to those of North American saukiids. It is semicircular in outline and has a convex axis of, at least, five rings, which terminates as a pointed post-axial ridge. The pleural field declines gradually to a broad border and it is crossed by six backwardly curving interpleural furrows. The pleurae are subequally divided by pleural furrows. Such a pygidium could belong to *Calvinella* Walcott, 1914 or *Tellerina* Ulrich and Resser, 1933. It is unlikely that these specimens are conspecific or even congeneric.

Family Ptychaspididae Raymond, 1925 Subfamily Euptychaspidinae Hupé, 1953 (*pro* Euptychaspidae Hupé, 1953)

Diagnosis

Ptychaspididae with deep axial furrows, faintly to firmly impressed anterior border furrow, short preglabellar field, generally wide (tr.) fixed cheeks, and short (exsag.) raised palpebral lobes defined by deep palpebral furrows and lacking distinct palpebral ridges. Pygidium is elliptical to triangular in outline; axis is short (sag.), axial rings are few in number; border is broad and declined.

Assigned Genera

Euptychaspis Ulrich, in Bridge, 1931; Liostracinoides Raymond, 1937; Kathleenella gen. nov.

Remarks

Hupé (1953) established the family Euptychaspidae for *Euptychaspis* Ulrich, *Keithia* Raymond, and *Keithiella* Rasetti. This family was synonymized with the Ptychaspididae by Lochman-Balk (*in* Moore, 1959). I propose to retain the name Euptychaspidinae Hupé for ptychaspidids with a preglabellar field, small eyes, inflated fixed cheeks lacking conspicuous palpebral ridges, and characteristic pygidia with broad and declined borders.

Liostracinoides Raymond was assigned to the family Liostracinidae by Raymond (1937), Hupé (1953) and Howell (in Moore, 1959). Öpik (1967: 387) has pointed out that the only feature of the type species, Liostracinoides vermontanus, that allies it to Liostracina Monke and related genera is the longitudinal preglabellar furrow—a feature that occurs in a number of unrelated trilobites. An examination of the holotype cranidium of L. vermontanus suggests that this rare genus belongs in the Euptychaspidinae.

The euptychaspidines are confined to the Trempealeauan. The earliest known member, *Kathleenella frontalis* (Longacre), occurs in the *Saukiella pyrene* Subzone of Texas and in the correlative *Rasettia magna* Subzone of Oklahoma. An early species of *Kathleenella* probably gave rise to *Euptychaspis* (see Longacre, 1970: 41), which first appears in the *Saukiella junia* Subzone of Texas and Oklahoma and the *Yukonaspis kindlei* Fauna of the Mackenzie Mountains. *Liostracinoides*, as well, was

probably derived from an early Trempealeauan species of Kathleenella because L. vermontanus is most similar to K. hamulata sp. nov. from low in the Y. kindlei Fauna. Both Kathleenella and Euptychaspis persist to the top of the Ptychaspid Biomere in Texas, Oklahoma, and the Northwest Territories (that is, to the base of the Corbinia apopsis Subzone and the base of the Elkanaspis corrugata Fauna). Of the euptychaspidines, only Liostracinoides texana (Longacre) continues across the Ptychaspid-"Hystricurid" Biomere boundary into the C. apopsis Subzone.

Kathleenella and the subfamily Euptychaspidinae were probably derived from *Ptychaspis* or another ptychaspidine genus during the late Franconian (see Longacre, 1970, text-fig. 1).

Both Winston and Nicholls (1967) and Longacre (1970) suggested that *Macronoda* Lochman, 1964 represents an offshoot from *Euptychaspis* and Longacre even suggested that the two genera are synonymous. The elongate and triangular pygidium attributed to *Macronoda prima* by Lochman (1964a, pl. 53, figs. 15, 18, 19, 21, 22) is markedly dissimilar to that of *Euptychaspis typicalis*. If the *M. prima* pygidium is correctly assigned, then it is unlikely that *Macronoda* and *Euptychaspis* belong to the same subfamily.

Genus Euptychaspis Ulrich, in Bridge, 1931

Type Species

Euptychaspis typicalis Ulrich, *in* Bridge, 1931 from the Eminence Dolomite (Trempealeauan), Eminence, Missouri (by original designation).

Euptychaspis typicalis Ulrich, in Bridge, 1931 Figs. 30, 58K-w

Euptychaspis typicalis—Taylor and Halley, 1974: 26, pl. 2, figs. 4–11 (see for synonymy).

Occurrences

Eminence Dolomite, Missouri, Saukia Zone (Ulrich, in Bridge, 1931). Conococheague Formation, Maryland, Saukia Zone (Rasetti, 1959). Wilberns Formation, central Texas, Saukiella junia Subzone (Winston and Nicholls, 1967; Longacre, 1970). Signal Mountain Limestone, Wichita and Arbuckle mountains, Oklahoma, Saukiella junia and Saukiella serotina subzones (Stitt, 1971b, 1977). Notch Peak Formation, Utah, Saukiella junia Subzone (Hintze et al., 1980). Whitehall Formation, New York, Saukiella serotina Subzone (Taylor and Halley, 1974). Rabbitkettle Formation, Broken Skull River (three collections between 152 m and 177 m below top of formation), Yukonaspis kindlei Fauna.

Syntypes

Two cranidia from the Eminence Dolomite, Missouri illustrated by Ulrich (*in* Bridge, 1931, pl. 29, figs. 5–7).

Remarks

Little can be added to Taylor and Halley's (1974) exhaustive description of cranidia, pygidia, and free cheeks of *Euptychaspis typicalis* from New York. The silicified Rabbitkettle material shows the palpebral lobes, the occipital ring, and the prosopon of this trilobite to perfection. The palpebral lobe is semicircular in outline with its long axis directed exsagittally. Its mid-point contains a single minute perforation. Identical structures occur in the Ordovician trilobites *Ceraurinella*, *Encrinuroides*, and *Cybeloides* (Chatterton and Ludvigsen, 1976, pl. 8, fig. 5, pl. 15, fig. 2; Ludvigsen, 1979b, pl. 20, fig. 28). Such perforations were probably occupied by sensory setae.

The triangular occipital spine of E. *typicalis* can now be seen to be a composite spine composed of a median ridge that arises directly from the depressed occipital ring and which lies in a triangular trough formed by foldlike projections of the posterior cephalic border.

The silicified free cheek (Fig. 580) suggests that *Euptychaspis* has a median connective suture crossing the narrow anterior cephalic doublure and the reconstruction (Fig. 30) has been drawn on that basis.

The identical prosopon of reticulate ridges seen on the silicified cranidia and pygidia removes any doubt about the correctness of Taylor and Halley's (1974: 26) assignment of the single exfoliated (?) pygidium to *E. typicalis*.



Fig. 30 *Euptychaspis typicalis* Ulrich, *in* Bridge, 1931. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Longacre (1970: 42) stated that *Euptychaspis typicalis* from central Texas possesses a short (sag.) and flat anterior border and Taylor and Halley (1974: 26) noted that same feature in some cranidia of *E. typicalis* from New York and on one of Ulrich's syntypes from Missouri. Each of the silicified cranidia from the Rabbitkettle Formation possesses an anterior border furrow and a short anterior border which is commonly no more than a narrow rim. In view of the difficulty in exposing this feature in nonsilicified material (Longacre, 1970: p. 42), it seems probable that all cranidia of the type species of *Euptychaspis* possess anterior border furrows and anterior border furrows and anterior border furrows and anterior border furrows and the type species of *Euptychaspis* possess anterior border furrows and anterior border furrows and anterior borders.

Genus Kathleenella gen. nov.

Type Species

Kathleenella subula gen. et sp. nov. from the Upper Cambrian part of the Rabbitkettle Formation, District of Mackenzie.

Diagnosis

A genus of euptychaspine trilobite possessing a subrectangular glabella with two or three pairs of straight lateral glabellar furrows. Preglabellar field is short and anterior border furrow is deep. Cephalon has slim genal spines and an anterior prow in front of glabella. Palpebral lobes are knoblike and located anterior of mid-length of glabella. Fixed cheeks are wide. Occipital ring carries simple, curved spine. Pygidium is triangular; it comprises a high axis flanked by depressed and triangular pleural field and a broad and gradually sloping border.

Name

For my wife, Kathleen MacKinnon. Feminine.

Other Species

Kathleenella hamulata gen. et sp. nov. and Euptychaspis frontalis Longacre, 1970.

Remarks

The new genus is established to accommodate two new species from the late Trempealeauan part of the Rabbitkettle Formation. *Euptychaspis frontalis* Longacre, 1970 from the early Trempealeauan part of the Wilberns Formation, central Texas and the Signal Mountain Limestone, Oklahoma (Stitt, 1977) differs from the type species of *Euptychaspis*, *E. typicalis* Ulrich, in possessing a rectangular glabella with straight lateral glabellar furrows that do not join, a distinct preglabellar field in many specimens, a deep anterior border furrow, and anteriorly placed eyes. All of these features ally *E. frontalis* to *Kathleenella subula* sp. nov. and Longacre's species is therefore assigned to *Kathleenella*.

Kathleenella is similar in some respects to the eastern Asian and Australian genus Asioptychaspis Kobayashi, 1933. The similarity is well seen by a direct comparison of the pygidium of A. delta Shergold (1975, pl. 29, figs. 2–4) from early Payntonian of Queensland with that of K. subula (Fig. 59M, 60H). Both of these species possess triangular pygidia bearing high axes with few rings and inflated and broadly sloping pygidial borders that are crossed by transverse ribs and that bear terrace lines which run parallel to the margins. The cranidium of A. delta, however, is of the Ptychaspis type and differs considerably from that of K. subula in lacking an anterior border furrow and an occipital spine. The cranidia of both Ptychaspis and Asioptychaspis are sufficiently similar to that of Kathleenella to support a derivation of this euptychaspidine genus from the ptychaspidines in the late Franconian.

Kathleenella subula gen. et sp. nov. Figs. 31, 59, 60A-K

Diagnosis

A species of *Kathleenella* with anteriorly expanding axial furrows on the cephalon, three pairs of lateral glabellar furrows, a short preglabellar field lacking a longitudinal furrow, a high occipital spine, and long slender genal spines.

Occurrences

Rabbitkettle Formation, Broken Skull River (13 collections between 77 m and 148 m below top of formation), *Bowmania americana* Fauna and *Yukonaspis kindlei* Fauna. Road River Formation, Bonnet Plume map area, GSC loc. C-7562 (collection at Geological Survey of Canada, Ottawa), *Yukonaspis kindlei* Fauna.

Holotype

A complete cranidium (ROM 37429) from KK 177 (114 m below top of Rabbitkettle Formation) illustrated on Fig. 59A–C.

Name

From subula—awl (Latin) in reference to the long pointed genal spines.

Description

Cephalon (exclusive of genal spines and anterior prow) is semicircular in outline and strongly convex. Deep axial furrows widen (tr.) towards front and define arched and rectangular glabella. Preglabellar furrow has median posterior deflection. Three pairs of lateral glabellar furrows extend part way, and occasionally full way, across glabella. Occipital ring is long (sag.) and lenticular in outline. A high curved spine occupies central position. Small, knoblike and high palpebral lobe is located far out on cheek; opposite 3p lobe. Palpebral lobe is constricted at base by deep, curved palpebral furrow. Anterior border furrow is deep and, in anterior view, is slightly arched. It defines posterior edge of an inflated triangular prow which constitutes anterior border. Preglabellar field is short (sag.) and steeply inclined; its central part is flat to slightly concave. Cheek is inflated; anteriorly it swells into rounded ridge which defines forward terminus of axial furrow. Lateral border furrows are narrow (tr.) and not noticably impressed, except near the base of genal spines. Anteriorly, they are continuous with deep anterior border furrow. Facial suture follows subangular path from posterior border forward and slightly inward to eye and then across cheek to anterior prow. Genal spines are long (at least twice sagittal length of cephalon), slender, and directed backwardly and gently inwardly. Base of genal spine carries short carina between parallel extensions of lateral and posterior border furrows. Entire cephalon, exclusive of cephalic furrows, is covered by prosopon of densely distributed and coarse granules.

Because the hypostome is unique among Trilobita, it is difficult to identify homologous features and, indeed, to decide on its orientation. The "lower" concave



Fig. 31 Kathleenella subula gen. et sp. nov. Reconstruction of cephalon and pygidium in dorsal view and hypostome in oblique view (prosopon omitted). Bar represents 1 mm.

surface is herein called the ventral surface and the two prominent knobs are assumed to occupy posterior positions. Ventral face of hypostome is smooth, broadly oval in outline, wider than long, and gently concave. A broad tonguelike projection, extending for the entire width of hypostome, is directed obliquely downward. From the recurved inner portion of this tongue, rises the posterior part of the hypostome which carries a pair of large knobs on margin. The knobs are separated by a V-shaped indentation of the inner margin.

Pygidium is broadly triangular and inflated with steeply curving flanks. Convex axis consists of two arched rings and a small terminal piece which carries a pair of minute spines. Axis is well defined by deep axial furrows; it extends for slightly more than half length of pygidium. Flanking the axis is a depressed triangular area that is bounded by faint ridges which parallel pygidial borders. Outside these ridges, the broad pygidial border slopes gradually to margin. The border is crossed by a few transversely directed undulations and is covered by anastomosing terrace lines which run parallel to pygidial margin.

Remarks

Kathleenella subula gen. et sp. nov. differs from *K*. *frontalis* (Longacre) from the *Saukiella pyrene* Subzone in central Texas in possessing both anteriorly expanding axial furrows and a prominent anterior prow on the cephalon. In addition, the species from Texas has only two pairs of lateral glabellar furrows and more posteriorly placed palpebral lobes which are located closer to the glabella.

Kathleenella hamulata gen. et sp. nov. Figs. 32, 550-T

Diagnosis

A species of *Kathleenella* with a median longitudinal furrow crossing the preglabellar field, two pairs of lateral glabellar furrows, short and hooked genal spines, and a short occipital spine.

Occurrences

Rabbitkettle Formation, Broken Skull River (four collections between 152 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A complete cranidium (ROM 374559) from K 510 (177 m below top of Rabbitkettle Formation) illustrated on Fig. 550, P.

Name

From *hamulate*—hooked (Latin) in reference to the inward twist of the tip of the genal spine.

Remarks

Kathleenella hamulata sp. nov. occurs stratigraphically below K. subula sp. nov. and is obviously related to that species. K. hamulata is distinguished by the presence of a distinct median longitudinal furrow crossing the preglabellar field, by possessing a proportionately shorter (sag.) glabella with only two pairs of lateral furrows, and by having shorter genal spines.

Genus Liostracinoides Raymond, 1937

Type Species

Liostracinoides vermontanus Raymond, 1937 from Zone 1 (Hungaia Assemblage) of the Gorge Formation, Highgate Falls, Vermont (by original designation).

Remarks

Liostracinoides vermontanus is similar to *Kathleenella hamulata* sp. nov. (compare Fig. 32 and Fig. 33). This similarity is seen in the general form of the glabella and palpebral lobes and, particularly, in the form of the furrows on the frontal area of the cranidium. *L. vermontanus*, however, is readily distinguished by its conical glabella,



Fig. 32 Kathleenella hamulata gen. et sp. nov. Reconstruction of cephalon (prosopon omitted). Bar represents 1 mm.

wider (tr.) anterior border on the cranidium, strongly divergent posterior branches of the facial suture, and by lacking an occipital spine.

Few species have been assigned to *Liostracinoides*. I have not been able to verify Raymond's (1937: 1093) assignment of *Conocephalites winona* Hall to *Liostracinoides*. *Liostracinoides*? *yukonensis* Palmer, 1968 from the Trempealeauan of the Alaska-Yukon border has a bullet-shaped glabella which lacks furrows, eyes located close to the axial furrows, divergent anterior facial sutures, and a medially interrupted anterior border furrow. These features are unlike those of the type species and Palmer's species should not be assigned to *Liostracinoides*.

Liostracinoides? sp. from the Mindyallan of Queensland (Öpik, 1967: 386, pl. 10, fig. 9) has a glabella of pentagonal outline, forwardly convex anterior border furrow, and a vague longitudinal preglabellar furrow. It does not appear to be congeneric with *Liostracinoides vermontanus*.

As Longacre (1970: 58) pointed out, *Westonaspis? texana* Longacre differs from *Westonaspis* Rasetti in having an anterior border furrow, wider fixed cheeks, and a faint longitudinal furrow crossing the preglabellar field. This species is better accommodated in *Liostracinoides*.

Liostracinoides vermontanus Raymond, 1937

Figs. 33, 53A-D, 70P

Liostracinoides vermontanus Raymond, 1937: 1092, pl. 1, fig. 20. Phylacterus saylesi Raymond—Gilman Clark and Shaw, 1968: 1022, pl. 127, figs. 24–26.

Occurrences

Gorge Formation, Highgate Falls, Vermont, *Hungaia* Assemblage (Raymond, 1937; Gilman Clark and Shaw, 1968). Rabbitkettle Formation, Broken Skull River (single collection 86.5 m below top of formation), *Bowmania americana* Fauna.

Holotype

An internal mould of an incomplete cranidium from the Gorge Formation, Highgate Falls, Vermont illustrated on Fig. 70P.

Description

Glabella is inflated, conical in outline and delimited by deep axial furrows that converge along nearly straight paths towards short (tr.), somewhat rounded preglabellar furrow. Three pairs of lateral glabellar furrows are short (tr.); only 1s is clearly evident. Occipital furrow is straight and firmly impressed; occipital ring lacks spine. Fixed cheek is as wide as glabella at mid-length and is inflated. Palpebral lobe is located in line with half-length of glabella. An extremely faint palpebral ridge joins axial furrow at level of 3s furrow. Anterior branches of facial suture converge forwardly on to anterior border where they are parallel with anterior border furrow. Posterior branches diverge widely. Anterior border furrow is firmly impressed and has slight backward curvature medially. A deep longitudinal furrow crosses the inflated preglabellar field. Cranidium is covered by densely distributed and fine granules.

Remarks

The *Liostracinoides* material from Vermont and the District of Mackenzie differs somewhat in the courses of the sutures and degrees of inflation of the cranidia. Only a few incomplete cranidia are available from either area and a conservative taxonomic approach has been adopted in considering these specimens conspecific.

Liostracinoides texana (Longacre, 1970) from the Corbinia apopsis Subzone of central Texas differs from L. vermontanus in possessing a narrower and less conical glabella, more distinct palpebral ridges, a shallower longitudinal furrow on the preglabellar field, and a nearly transverse anterior border furrow that has only very slight backward curvature medially.

Subfamily Eurekiinae Hupé, 1953

Diagnosis

Ptychaspididae with an inflated glabella that is subrectangular or forwardly narrowing and that bears two pairs of oblique lateral furrows (or faint traces of such furrows). Semicircular or elliptical palpebral lobes are located close to glabella near cephalic mid-length. Preglabellar field is short (sag.) or absent; anterior border is variably upturned. Genal corner is either a sharp angle or it carries a genal spine of variable dimensions. Oblong hypostome is longer than wide, with a central body completely



Fig. 33 Liostracinoides vermontanus Raymond, 1937. Reconstruction of cranidium (prosopon omitted). Bar represents 1 mm.

circumscribed by border furrows. Pygidium is wider than long; axis is well defined and inflated, it reaches or nearly reaches posterior margin; axial ring furrows and interpleural furrows each number one to three. Four or five pairs of blunt or pointed marginal spines project downward and backward. Dorsal surface is either smooth or it is covered by dense granulate or tuberculate prosopon.

Assigned Genera

Eurekia Walcott, 1916; *Bayfieldia* Clark, 1924; *Corbinia* Walcott, 1924; *Yukonaspis* Kobayashi, 1936a, *Magnacephalus* Stitt, 1971; and, questionably, *Maladia* Walcott, 1924.

Remarks

The diagnosis of the Eurekiinae, above, has been modified to accommodate two partially effaced genera, *Yukonaspis* and *Magnacephalus*, whose previous classification was unsatisfactory.

Yukonaspis has previously been known only from cranidia. Kobayashi (1936a) did not assign this genus to a family, but noted similarities with both illaenurids and leiostegiids. Hupé (1953) assigned Yokunaspis [sic] to the Illaenuridae. Lochman (1953; in Moore, 1959) considered both Tatonaspis Kobayashi, 1935 and Yukonaspis to be junior subjective synonyms of Macelloura Resser. Palmer (1968) demonstrated that Tatonaspis and Yukonaspis have separate generic status and that neither is congeneric with Macelloura. He assigned Tatonaspis to the Nileidae and left Yukonaspis unclassified as to family.

Magnacephalus was established by Stitt (1971b) for a new species based on both cranidia and pygidia from the *Saukia* Zone in Oklahoma. Stitt did not assign this genus to a family and, curiously, did not comment upon the pronounced similarity of the *Magnacephalus* pygidium to those of eurekiine genera.

Effaced trilobites are difficult to classify. The cranidia of both Yukonaspis and Magnacephalus are similar to those of Eurekia and Corbinia. The pygidium of Yukonaspis has now been identified and it is becoming clear that this pygidium, and that of Magnacephalus, can barely be distinguished from those of Bayfieldia and Eurekia. The large curving genal spine of Yukonaspis lends a unique aspect to the cephalon, but this spine can be viewed as an extreme development of the small triangular genal spine seen in Eurekia. In spite of the effacement of some cephalic furrows, the available evidence suggests that Yukonaspis and Magnacephalus should be classified with Eurekia, Bayfieldia, and Corbinia in the subfamily Eurekinae.

The eurekiines are typical trilobites of the Middle Carbonate Belt during the Trempealeauan. The earliest known eurekiine (if the poorly known Maladia Walcott is excluded) is Yukonaspis from the late Franconian of Oklahoma. Eurekia and Bayfieldia first appear near the base of the Trempealeauan; Corbinia and Magnacephalus first appear somewhat higher in the Trempealeauan. Eurekia, Corbinia, and Yukonaspis persist into the late Trempealeauan (Corbinia apopsis Subzone and Elkanaspis corrugata Fauna).

Genus Eurekia Walcott, 1916

Type Species

Ptychoparia (Euloma?) dissimilis Walcott, 1884 from the Windfall Formation of Late Cambrian age, Eureka District, Nevada (by original designation; see Taylor, 1978).

Remarks

Taylor (1978) has recently provided convincing evidence that Walcott's (1924) designation of *Eurekia granulosa* Walcott, 1924 as type species of *Eurekia* is invalid. The type species is *Ptychoparia (Euloma?) dissimilis* Walcott and *E. granulosa* is a junior subjective synonym of *E. eos* (Hall, 1863). Taylor's redescription and illustration of both *E. dissimilis* and *E. eos* now provide a firm foundation for evaluating other members of this common taxon of Late Cambrian trilobites. Taylor also demonstrated that the drawings of the *Eurekia* cephalon by Walcott (1924, pl. 12, fig. 1) and by Lochman-Balk (*in* Moore, 1959, fig. 240–3) are highly inaccurate in showing both the course of the facial suture and the size of the genal spine. Unfortunately, Taylor's own reconstruction of *E. eos* is also inaccurate in underrepresenting the width (tr.) of the palpebral lobes, and in not showing the deep palpebral furrows of this species (compare Taylor's reconstruction in text-fig. 2 with the photograph on pl. 1, fig. 11).

Eurekia ulrichi (Rasetti, 1945)

Figs. 34, 61

Bayfieldia ulrichi Rasetti, 1945: 465, pl. 60, figs. 17–19. Corbinia ulrichi—Winston and Nicholls, 1967: 85. Bayfieldia sp. 2, Palmer, 1968: 64, pl. 15, figs. 8, 11.

Occurrences

Levis Formation, North Ridge, Levis, Quebec, *Hungaia* Assemblage (Rasetti, 1945). Jones Ridge Limestone, Jones Ridge area, Alaska-Yukon border, Trempealeauan-2 Fauna (Palmer, 1968). Rabbitkettle Formation, Broken Skull River (three collections between 145 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A cranidium from an Upper Cambrian boulder, Levis Formation, Levis, Quebec illustrated by Rasetti (1945, pl. 60, figs. 17, 18).

Description

Cephalon is subrectangular in outline; length is five-sevenths width; anterolateral corners are rounded; it is strongly (tr.) and moderately (sag.) convex. Glabella is subrectangular in outline and moderately inflated. Two pairs of short (exsag.) and backwardly curving lateral glabellar furrows are present at mid-length. Occipital furrow is sharply incised and nearly straight; it turns forward adjacent to axial furrow. Occipital ring is rather flat; it carries a small median node on its forward flank. Deep axial furrows diverge very slightly to mid-length of glabella, then converge slightly along gentle curve to meet deep and transverse anterior border furrow. Lateral and anterior border furrows are confluent; they define convex and tubelike cephalic borders. Small spine is located at genal corner. In anterior view, anterior border rises in gentle arch towards sagittal line. Posterior border furrows are transverse and deep. Palpebral furrow defines wide (tr.), large (as long as one-half sagittal length of cephalon) and crescentic palpebral lobe. Base of eye marked by convex and longitudinally striated eye socle. Anterior branch of facial suture proceeds straight forward to anterior border furrow, then turns inwardly along anterior border to median connective suture. Posterior branch swings outward along path subparallel with posterior border furrow; just in front of genal corner, it angles straight back.

Cephalon is densely covered by small tubercles which, on the borders, merge with coarse terrace lines that run parallel to margin. On the free cheek, each tubercle is irregularly stellate in shape.

Hypostome is oblong, longer than wide; with rounded posterolateral corners and triangular wings located on either side of a forwardly rounded and ventrally turned anterior margin. Central body is completely circumscribed by border furrows that are deepest laterally. A pair of oblique middle furrows is present on back portion of central body. Ventral surface of hypostome is smooth, with the exception of terrace lines on the lateral borders.

Pygidium is semielliptical in outline; twice as wide as long. Convex axis stands well above moderately inflated pleural portions. Articulating furrow is deep behind



Fig. 34 *Eurekia ulrichi* (Rasetti, 1945). Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

prominent articulating half ring. One axial ring furrow is complete, a second is incomplete. First interpleural furrow is deep, proceeds on to base of first marginal spine; two or three pleural furrows are only faintly defined. Five pairs of blunt, digitate marginal spines extend backward and downward. First four spine pairs are equal in size; fifth pair is slightly smaller. Cephalic micro-ornament is duplicated on pygidium. On spine tips, tubercles merge with coarse terrace lines that run parallel to pygidial margin and across spines.

Remarks

The only differences between *Eurekia ulrichi* Rasetti from the Rabbitkettle Formation and the type material from the Levis Formation are the slightly shorter (exsag.) palpebral areas and a slightly wider and more inflated glabella of the Quebec cranidium. Rasetti's figured cranidium is considerably larger than any available from the Rabbitkettle and these differences are probably the result of the size discrepancy.

The exfoliated cranidium and pygidium from the Trempealeauan of the Jones Ridge Limestone of east-central Alaska (Palmer, 1968, pl. 15, figs. 8, 11) are larger than both the Levis and Rabbitkettle material. These specimens are similar to, and in all likelihood conspecific with, E. ulrichi.

Eurekia ulrichi differs from all other species of *Eurekia* in possessing a relatively long and only moderately inflated glabella with faint lateral glabellar furrows, large and semicircular palpebral areas, and a pygidium with digitate and bluntly rounded marginal spines. In addition, the pervasive tubercles of *E. ulrichi* are finer than those in most other species of *Eurekia*.

Eurekia bacata sp. nov. Figs. 35, 62A–J

Diagnosis

A species of *Eurekia* possessing a moderately inflated glabella with maximum width between eyes. Occipital ring is long (sag.). Anterior cephalic border is sharply upturned. Cephalic furrows are deep and trenchlike. A row of large tubercles surrounds base of eye. Wide pygidial axis is undercut by axial furrows; it overhangs posterior margin. Five pairs of marginal spines hang below posterior border. Anterior spine pairs are paddle-shaped with concave outer faces.

Occurrences

Rabbitkettle Formation, Broken Skull River (three collections between 152 m and 172 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A large pygidium (ROM 37708) from K 525 (172 m below top of Rabbitkettle Formation) illustrated on Fig. 62F, G.

Name

From *bacatus*—adorned with pearls (Latin) in reference to the string of circular tubercles which surrounds the base of the eye.

Remarks

The shape of the marginal pygidial spines, the row of tubercles below the eye, and the narrow fixed cheek in front of the eye of *Eurekia bacata* sp. nov. clearly differentiate this species from all other species of *Eurekia*.

Eurekia spp. Fig. 62K–Q

Occurrences

Rabbitkettle Formation, Broken Skull River (12 collections between 61 m and 148 m below top of formation), *Elkanaspis corrugata* Fauna, *Bowmania americana* Fauna, and *Yukonaspis kindlei* Fauna.



Fig. 35 Eurekia bacata sp. nov. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Eurekia is moderately rare in the upper part of the Cambrian succession in Section KK. The genus is represented by small, fragmentary, and often tectonically deformed specimens which are difficult to classify. These specimens are probably assignable to more than one species.

A few of the better specimens are illustrated on Fig. 62K-Q. Some of the cranidia (Fig. 62K, P, Q) are rather similar to that of *Eurekia ulrichi*, but the palpebral areas tend to be larger. Likewise, some pygidia (Fig. 62M) are similar to that of *E. ulrichi* whilst others (Fig. 62L, O) with pointed marginal spines approach the morphology of pygidia assigned to *Corbinia*. Association of cranidia and pygidia cannot be made at the present time.

This fragmentary material does establish the presence of *Eurekia* in the *Elkanaspis* corrugata Fauna of the Northwest Territories. According to Winston and Nicholls (1967), *Eurekia* occurs rarely in the *Corbinia apopsis* Subzone of central Texas—an interval correlative to the *Elkanaspis corrugata* Fauna.

Genus Yukonaspis Kobayashi, 1936a

Type Species

Yukonaspis kindlei Kobayashi, 1936a from Upper Cambrian rocks (Trempealeauan, Palmer, 1968) on Squaw Mountain, Alaska-Yukon border (by original designation).

Remarks

Yukonaspis differs from Magnacephalus Stitt, 1971b in possessing deeper axial furrows, a more inflated glabella, a pronounced upturned anterior border, and a narrower (tr.) and shorter (sag.) pygidial axis.

During the Trempealeauan, Yukonaspis was a characteristic shelf-edge taxon in North America. It occupied outer shelf sites on the Alaska-Yukon border, in the District of Mackenzie, in Utah (Taylor, 1977, table 3), in western Newfoundland (undescribed material in C.H. Kindle Collection, Geological Survey of Canada, Ottawa), and in Vermont (undescribed material in C.H. Kindle Collection).

> Yukonaspis kindlei Kobayashi, 1936a Figs. 36, 63A–N, 69F–I, 70A–C

Yukonaspis kindlei Kobayashi, 1936a: 164, pl. 21, figs. 3-6. Yukonaspis kindlei—Palmer, 1968: 100, pl. 15, figs. 15, 19.
Occurrences

Jones Ridge Limestone, east-central Alaska, Trempealeauan-2 Fauna (Kobayashi, 1936a; Palmer, 1968). Cow Head Group, Cow Head, western Newfoundland, *Hungaia* Assemblage (C.H. Kindle Collection at the Geological Survey of Canada, Ottawa). Rabbitkettle Formation, Broken Skull River (eight collections between 112 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

An incomplete cranidium from Squaw Mountain, north of Tatonduk River, Alaska-Yukon border illustrated by Kobayashi (1936a, pl. 21, figs. 3, 4) and herein (Fig. 70A-C).

Description

Little can be added to Palmer's (1968: 100) description of *Yukonaspis kindlei* cranidia from east-central Alaska. As Palmer noted, lateral glabellar furrows are absent in this



Fig. 36 Yukonaspis kindlei Kobayashi, 1936a. Reconstruction of cephalon and pygidium. Bar represents 1 mm.

species. Muscle insertion areas may be represented by two pairs of oblique, oval areas of thin shell material whose presence is often indicated by ragged holes on the glabellar flanks of the silicified specimens (Fig. 63J, K). The anterior course of the facial suture cannot be clearly determined in Kobayashi's and Palmer's illustrated material. The specimens from the Rabbitkettle Formation show this suture to proceed forward from the palpebral lobe with faint outward curvature until it passes on to the narrow arched anterior border. It then proceeds inward along the highest part of the border to the mid-line where it meets the median connective suture.

Description of the free cheek and pygidium of Y. kindlei can now augment Palmer's description of the cranidium.

Interior portion of free cheek, below convex visual surface of eye, curves steeply to lateral border furrow which is narrow and deep anteriorly and little more than an abrupt change in slope posteriorly. Lateral border is very narrow and sharp anteriorly; it becomes a broad flat field below eye. This field merges with the base of long genal spine which curves outward and backward for a distance equal to sagittal length of cephalon. Genal spine is tapering and is oval in cross-section. In lateral view, border of free cheek descends steeply and curves backward and inward, beneath genal spine, to join posterior cephalic margin. In lateral view, genal spine is seen to rise gently. Borders contain fine, ledgelike terrace lines. Similar lines occur on genal spine where they are largely exsagittally directed.

Pygidium is semielliptical in outline, nearly three times as wide (tr.) as long (sag.), and gently arched (tr.). Axis is moderately convex; it comprises two axial rings outlined by sharply incised furrows and a long (sag.) terminal piece. Axis is outlined by moderately deep axial furrows; it extends to posterior margin. Pleural field is triangular in outline and crossed by a single deep interpleural furrow. Two other interpleural furrows are faintly defined. Five pairs of marginal spines project backward and slightly downward. Each spine is triangular in outline. Fifth pair is small and well separated. Prosopon consists of low granules.

Remarks

Palmer's (1968) cranidium of *Yukonaspis kindlei* has somewhat larger palpebral areas than are present on either the holotype cranidium or the cranidia from the Mackenzie Mountains. This difference, however, is not considered to be sufficient basis for species separation.

The association of the Y. kindlei cranidium and the peculiar free cheek suggested in this paper has been substantiated by a spectacular cephalon in the C.H. Kindle Collection from western Newfoundland at the Geological Survey of Canada, Ottawa. This specimen shows an identical free cheek attached to a Y. kindlei cranidium.

The only other species assigned to Yukonaspis is Stigmacephaloides verticalis Stitt (1977, pl. 2, figs. 7–9; see also Stitt, 1971b, pl. 3, figs. 16, 17) from the late Franconian of Oklahoma. Yukonaspis verticalis differs from Y. kindlei in possessing a more inflated glabella, wider (tr.) fixed cheeks in front of the eyes, smaller palpebral areas, and a very narrow (sag.) preglabellar field. The similarity in the cranidia and free cheeks of the two species is considerable and Stitt's species is confidently assigned to Yukonaspis.

Occurrence

Rabbitkettle Formation, Broken Skull River (eight collections between 61 m and 96 m below top of formation), *Elkanaspis corrugata* Fauna and *Bowmania americana* Fauna.

Remarks

Tectonically deformed and fragmentary material of at least one other species of *Yukonaspis* occurs in the Rabbitkettle Formation above the collections with *Y. kindlei*. These are best characterized by the free cheeks (Fig. 67M, N) which differ from those of *Y. kindlei* in having a deep curved lateral border furrow that, apparently, is continuous with the anterior and posterior border furrows of the cranidium. The genal spines are shorter than those of *Y. kindlei*. The associated cranidia are generally so deformed that they yield little critical information. These specimens are assigned to *Yukonaspis* sp.

Superfamily Remopleuridacea Family Kainellidae Ulrich and Resser, 1930 (= Apatokephalopsidae Zhou and Zhang, 1978)

Assigned Genera

Kainella Walcott, 1925; Richardsonella Raymond, 1924; Apatokephaloides Raymond, 1924; Pseudokainella Harrington, 1938; Sigmakainella Shergold, 1971; Apatokephalops Lu, 1975; Jiia Zhou and Zhang, 1978; Aristokainella Zhou and Zhang, 1978; Naustia gen. nov.; and Elkanaspis gen. nov.

Remarks

The name *Richardsonella* has served as a catch-all for a number of Franconian to Tremadocian remopleuridacean species that are certainly not all congeneric (Palmer, 1968: 78; Shergold, 1971: 37). The type species of *Richardsonella*, *R. megalops* (Billings), is represented by only two incomplete cranidia (Rasetti, 1944, pl. 39, figs. 48, 49). The pygidium attributed to this species by Whittington (*in* Moore, 1959, fig. 242–3b) actually belongs to *Elkanaspis unisulcata* (Rasetti) (Hupé, 1955, fig. 147–6). The uncertainty about attribution of exoskeletal elements other than cranidia to the type species of *Richardsonella* suggests that the Richardsonellinae Raymond,

1924 is poorly suited as a suprageneric taxon of remopleuridacean trilobites. Shergold (1975: 159) suggested that the Kainellidae Ulrich and Resser is better because *Kainella* is known from complete specimens.

Zhou and Zhang (1978) established the Apatokephalopsidae for Apatokephalops Lu, Jiia Zhou and Zhang, and Wanliangtingia Lu; all from Tremadocian strata of China. As Lu (1975: 304) noted, Apatokephalops and Pseudokainella have similar eyes, free cheeks, anterior facial sutures, and preglabellar fields. Apatokephalops differs by lacking an intraocular fixed cheek and by possessing a longer (sag.) anterior cephalic border. A pygidium is not known for Apatokephalops, but that of Jiia (Zhou and Zhang, 1978, pl. 3, figs. 16, 17) is very similar to those herein assigned to Elkanaspis gen. nov. The cranidial differences between Apatokephalops and Pseudokainella are certainly valid on a generic level, but hardly justifiable on a familial level. I conclude that the Apatokephalopsidae Zhou and Zhang should be synonymized with the Kainellidae Ulrich and Resser.

Genus Naustia gen. nov.

Type Species

Naustia papilio sp. nov. from the Upper Cambrian part of the Rabbitkettle Formation, District of Mackenzie.

Diagnosis

A genus of kainellid trilobite possessing a parallel-sided glabella with two or more lateral furrows. Preglabellar field is long (sag.); anterior border furrow is distinct. Large, semicircular palpebral lobe is located close to axial furrow; its length (exsag.) is half that of glabella (sag.). Palpebral furrow is distinct. Facial sutures are transverse behind eye and markedly divergent in front of eye. Pygidium is large and semicircular. Slender, convex axis consists of seven well-defined rings and a terminal piece with a postaxial ridge that reaches posterior margin. Six or seven pairs of interpleural furrows cross flat pleural regions. Pleural furrows are faint or absent. Seven or eight pairs of slender, backwardly directed spines fringe pygidium.

Name

Acronym for North America and Australia, the two continents where the genus occurs. Feminine.

Other Species

Richardsonella? kainelliformis Shergold, 1971 (= "Tostonia" sp. of Shergold,

1971) from the Gola Beds (Franconian) of western Queensland.

- Richardsonella tyboensis Taylor, 1976 (= Genus and species undet. A of Taylor, 1976) from the Franconian part of the Hales Limestone of Nevada.
- Richardsonella? sp. 2 of Palmer, 1968 from the Trempealeauan-1 Fauna of east-central Alaska.
- Pygidia assigned to *Tostonia iole* (Walcott) by Walcott (1925, pl. 18, figs. 13, 14) from the Upper Cambrian of the Eureka District, Nevada.
- Pygidium assigned to *Dikelocephalus* sp. by Billings (1865, fig. 384) from the Levis Formation near Quebec City.

Remarks

A number of authors have documented the presence of large, semicircular and ribbed kainellid pygidia in Franconian and Trempealeauan rocks of North America and in correlative rocks of Australia and have noted the similarity of these pygidia to those erroneously attributed to *Tostonia iole* by Walcott (1925). Palmer (1968: 78) noted the association of a "*Tostonia*" pygidium and a *Richardsonella* cranidium in Nevada. Shergold (1971: 42) and Taylor (1976: 698) both described such pygidia from collections that also included cranidia similar to that of *Richardsonella megalops*, the type species of *Richardsonella*. Shergold and Taylor each considered the possibility that the "*Tostonia*" pygidium should be associated with the *Richardsonella* cranidium and each stated that if such an association could be demonstrated, it would define a new genus of Richardsonellinae. They concluded, however, that the establishment of a new genus was premature.

"Tostonia"-type pygidia and Richardsonella-type cranidia also co-occur in separate collections from the Rabbitkettle Formation of the District of Mackenzieone from Section KK described below and one from the Bonnet Plume map area, some 200 km north-northwest of Section KK, to be described later. The size of these sclerites and elimination of other cranidium-pygidium associations leave little doubt that the "Tostonia"-type pygidia belong with the Richardsonella-type cranidia.

The association of these unique kainellid pygidia and *Richardsonella*-type cranidia in collections from five localities on two continents is additional evidence that these elements were parts of the same trilobite. A new genus, *Naustia*, is established to receive the Franconian and Trempealeauan species listed above.

> Naustia papilio gen. et sp. nov. Figs. 37, 64Q–U

Diagnosis

A species of *Naustia* with two pairs of deep and curving lateral glabellar furrows, seven pairs of interpleural furrows on the pygidium, and eight pairs of marginal spines on the pygidium.

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 165 m below top of formation), Yukonaspis kindlei Fauna.

Holotype

A nearly complete pygidium (ROM 37628) from K 550 (165 m below top of Rabbitkettle Formation) illustrated on Fig. 64Q.

Name

From papilio-butterfly (Latin) in reference to the shape of the pygidium.

Description

Gently inflated glabella is bounded by deep parallel axial furrows which diverge slightly around occipital ring. Glabella is nearly twice as long (sag.) as wide. Two pairs of distinct lateral furrows extend one-third the way across glabella; 1s curves inward and backward; 2s curves backward, asymptotically to a transverse line. Occipital furrow is well incised medially; laterally it bifurcates. Preglabellar furrow is deep and gently bowed forwardly. Preglabellar field is one-third the length (sag.) of glabella (including occipital ring). Its inner portion is slightly inflated; forwardly it declines gently towards anterior border furrow. Anterior border is relatively long (sag.) Palpebral area is semicircular; palpebral lobe is crescentic and slightly raised; it is defined by firmly impressed palpebral furrow which just touches axial furrow. Posterior portion of facial suture is transversely directed; anterior portion curves widely outward, nearly to the exsagittal level of the edge of palpebral lobe, and then inward across anterior border.

Pygidium is large, flat, and semicircular in outline; slightly wider (tr.) than long. Convex axis is slender, one-fifth the width (tr.) of pygidium, and only slightly tapering. It consists of seven well-defined axial rings and a triangular terminal piece that extends axis to posterior margin. Pleural region is crossed by seven distinct interpleural furrows that become deeper and progressively backwardly swept toward rear. These furrows terminate in a shallow border furrow. Pleural furrows are extremely faint. Eight pairs of backwardly directed marginal spines fringe pygidium. Posterior pairs are slender; anterior pairs are apparently stouter.

Remarks

Naustia papilio gen. et sp. nov. differs from N. kainelliformis (Shergold, 1971) in having less divergent anterior branches of the facial suture, two pairs of deep lateral

glabellar furrows, and a pygidium with eight pairs of marginal spines. *N. papilio* differs from *N. tyboensis* (Taylor, 1976) in having a less inflated glabella, deeper axial furrows, somewhat larger palpebral areas, and an inflated posterior portion of the preglabellar field. The immature pygidia of *N. tyboensis* (Taylor, 1976, pl. 3, figs. 9, 11) appear to be identical to immature pygidia of *N. papilio* (Fig. 64R, S).

Genus Elkanaspis gen. nov.

Type Species

Elkanaspis futile sp. nov. from the Upper Cambrian part of the Rabbitkettle Formation, District of Mackenzie.

Diagnosis

A genus of kainellid trilobite possessing a glabella which has slightly outwardly bowed sides and is constricted near front. Palpebral lobes are long (exsag.) and crescentic; anterior and posterior ends of palpebral furrow merge with axial furrow, thus isolating a narrow (tr.) intraocular fixed cheek. Free cheek is broad (tr.). Preglabellar field is short; equal in sagittal length to convex anterior border. Genal corner is a right angle or obtuse angle; genal spine is slender. Pygidium is elliptical to quadrate in outline. Pygidial axis consists of two to four arched rings and a terminal piece. Axis is well defined by furrows; it tapers slightly and is sharply raised over pleural regions; it terminates before reaching posterior margin. Three or four pleural



Fig. 37 Naustia papilio gen. et sp. nov. Reconstruction of cranidium and pygidium. Bar represents 1 mm.

furrows cross flat to slightly inflated pleural region. Interpleural furrows and border furrows are faint. Three or four pairs of flattened and pointed marginal spines curve backward and inward; they decrease in size posteriorly.

Name

Patronym for Elkanah Billings, Canada's first palaeontologist, plus aspis-shield (Greek). Feminine.

Other Species

Richardsonella unisulcata Rasetti, 1944 from the Levis Formation of Quebec.

Richardsonella quadrispinosa Palmer, 1968 from the Franconian-2 Fauna of east-central Alaska.

Richardsonella variagranula Robison and Pantoja-Alor, 1968 from the Tiñu Formation of Mexico.

Elkanaspis corrugata sp. nov.

Remarks

Shergold (1971: 37) suggested that Richardsonella unisulcata Rasetti, R. quadrispinosa Palmer, and four other species of Richardsonella from North America could be accommodated in Pseudokainella Harrington, 1938. Taylor (1976: 696) suggested the same generic assignment for R. variagranula Robison and Pantoja-Alor from Mexico. There is little doubt that these North American kainellid trilobites are related to Pseudokainella; but its type species, P. keideli Harrington (see Harrington and Leanza, 1957, figs. 51, 52), displays a number of differences which suggest that it is not congeneric with the three species of Richardsonella mentioned above. These include:

- a. An extremely narrow preglabellar field. Harrington and Leanza's (1957, fig. 52-5, 7, 10) photographs show the glabella to terminate in the anterior border furrow and a preglabellar field cannot be distinguished.
- b. Widely divergent anterior branches of the facial suture.
- c. The glabella is not constricted anteriorly.
- d. The posterior end of the palpebral furrow does not merge with the axial furrow.
- e. The anterior pygidial spine pair is very long.

A new genus, *Elkanaspis*, is established for some of the species from Quebec, Alaska, and Mexico that Shergold and Taylor suggested might be assigned to *Pseudokainella* and for two new species from the Rabbitkettle Formation. Only those species with known pygidia are definitely assigned to the new genus.

Whether the other Argentinian and British species of Pseudokainella (that is, P.

lata [Kobayashi], P. pustulosa Harrington and Leanza, and P. impar [Salter] [see Whitworth, 1969]) should be assigned to Elkanaspis is unresolved. Each of these Tremadocian species has a narrow preglabellar field which is somewhat longer (sag.) than that of P. keideli, but still shorter than that of Elkanaspis, and each lacks an anterior glabellar constriction. The pygidia, however, are very close to that of Elkanaspis. These species are, for the present, retained in Pseudokainella. Kobayashi (1953) chose Pseudokainella lata as the type for a new subgenus, Parakainella, which was subsequently synonymized with Pseudokainella by Harrington and Leanza (1957).

Kainella, Richardsonella, Sigmakainella, and Naustia differ from Elkanaspis in having longer preglabellar fields and parallel-sided or forwardly narrowing glabellae lacking anterior constrictions. If Rasetti's (1944: 255) synonymy of Proapatokephaloides with Richardsonella is correct, then these five kainellid genera bear distinctive pygidia: Kainella (Walcott, 1925, pl. 22, fig. 4), Richardsonella (Fig. 700; Shergold, 1971, fig. 9b), Sigmakainella (Shergold, 1971, fig. 12b), Naustia (Fig. 37), and Elkanaspis (Figs. 38, 39).

Elkanaspis differs from *Apatokephalops* Lu, 1975 in having an intraocular fixed cheek, deeper lateral glabellar furrows, larger eyes, and a shorter preglabellar field. Both the cranidium and pygidium of *Jiia* Zhou and Zhang, 1978 are reminiscent of those of *Elkanaspis* (particularly *E. corrugata* sp. nov.). The cranidium of *Jiia* is distinguished by the broad (tr.) occipital ring, the forwardly narrowing glabella which lacks an anterior constriction, the forwardly located palpebral lobes, and the short (sag.) and depressed preglabellar field.

Elkanaspis futile gen. et sp. nov. Figs. 38, 64A-P

Diagnosis

A species of *Elkanaspis* with either extremely faint or effaced axial furrows, advanced genal spines that are long and curving, an elliptical pygidium with a goblet-shaped axis comprising two rings and a terminal piece, and short pygidial spines.

Occurrences

Rabbitkettle Formation, Broken Skull River (six collections between 125 m and 177 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A pygidium (ROM 37532) from K 510 (177 m below top of Rabbitkettle Formation) illustrated on Fig. 64G, H.

Name

From *futile*—a vessel broad above and pointed below (Latin) in reference to the shape of the pygidial axis.

Description

Cephalon is elliptical in outline, one and a half times as wide (tr.) as long, and only slightly inflated. Posterolateral corner is defined by 120 degree angle located on transverse line which passes through one-third sagittal length of cephalon. Barrel-shaped glabella is modified anteriorly by a rounded notch where it is constricted by palpebral lobe. Axial furrows are deep opposite moderately arched and simple occipital ring. In front of occipital furrow, axial furrow is reduced to a thin groove which connects anterior and posterior ends of much deeper and more strongly curved palpebral furrow. In some specimens, the axial furrow cannot be seen; its position is indicated by a faint change in slope. Three pairs of lateral glabellar furrows curve inward and backward; 1s is firmly impressed and does not extend to axial furrow; 2s and 3s are thin grooves extending inward from axial furrow. Front part of glabella is moderately inflated over distinct preglabellar furrow which has slight forward curvature. Preglabellar field is flat and depressed between subparallel courses of preglabellar furrow and anterior border furrow; it widens and merges laterally with equally flat and depressed genal field on free cheek. In sagittal length, preglabellar field is equal to that of anterior border. Anterior border furrow and anterior border maintain their character as they follow evenly curved path to become lateral border furrow and lateral border. The border is extended posteriorly as long, gradually tapering genal spine that has slight inward curvature and is one and a half times sagittal length of cephalon. Crescentic palpebral lobe is wide (tr.) and long



Fig. 38 *Elkanaspis futile* gen. et sp. nov. Reconstruction of cephalon and pygidium. Bar represents 1 mm.

(equal to half sagittal cephalic length). It stands as high as glabella. Deep palpebral furrow merges front and back with axial furrow to isolate a small semielliptical and depressed fixed cheek. Posterior branch of facial suture curves outward and forward before turning back across posterior border furrow and border to bisect posterior margin. Anterior branch of facial suture swings outward at about 30 degrees to sagittal line to a point half-way across anterior border and then cuts abruptly inward along border to meet connective suture on mid-line. Front portion of cranidium is about as wide (tr.) as distance between palpebral furrows.

Cephalon has prosopon of fine and irregularly disposed terrace lines on posterior part of cranidium and on genal spines; remainder is apparently finely granulose.

Pygidium is transverse, twice as wide as long (sag.) and very gently arched (tr.). Axis is high and consists of two short (sag.) rings and a terminal piece. A short postaxial ridge extends nearly to posterior margin and provides axis with a goblet shape. Axial furrows are deep; they undercut axial flanks. Pleural field is crossed by three pleural furrows that are little more than transverse depressions. A faint border furrow extends in even arc from anterolateral corner to tip of postaxial ridge. Four pairs of compressed marginal spines that decrease gradually in size posteriorly curve backward and inward. Each spine is broad-based and terminates in a point.

Remarks

Elkanaspis futile sp. nov. is most similar to E. unisulcata (Rasetti, 1944) from the Levis Formation of Quebec. It differs from the Levis species in having shallower axial furrows, three pairs of lateral glabellar furrows, less divergent anterior branches of the facial suture, and a pygidium with only three pairs of marginal spines. The cranidium of *Elkanaspis* cf. *quadrispinosa* (Palmer, 1968) from east-central Alaska is similar to that of E. futile, but that species lacks a median connective suture and, apparently, has a straight posterior cephalic margin (Palmer, 1968, pl. 14, figs. 7, 8).

Elkanaspis corrugata gen. et sp. nov. Figs. 39, 60L–V

Diagnosis

A species of *Elkanaspis* with a long glabella that is waisted anteriorly by indentation of front part of palpebral furrows. It has straight preglabellar furrow, large palpebral lobes, straight posterior cephalic margin, short and straight genal spines, and a subrectangular pygidium with a long axis composed of three rings and a terminal piece, and four pairs of deep pleural furrows that continue on to four pairs of pointed bladelike marginal spines that curve slightly inward (with the exception of the fourth pair which is hooked outwards).

Occurrences

Rabbitkettle Formation, Broken Skull River (three collections between 64 m and 70 m below top of formation), *Elkanaspis corrugata* Fauna.

Holotype

A pygidium (ROM 37555) from KK 64 (64 m below top of Rabbitkettle Formation) illustrated on Fig. 60T.

Name

For *corrugatus*—wrinkled (Latin) in reference to the state of preservation of these thin-shelled silicified trilobites.

Remarks

Elkanaspis corrugata sp. nov. is so similar to E. quadrispinosa (Palmer, 1968) from the Franconian-2 Fauna of east-central Alaska that a comparison with this well-described species will suffice as a description. E. corrugata differs from the Alaska species in the following features:



Fig. 39 *Elkanaspis corrugata* gen. et sp. nov. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

- a. The glabella is narrower across the occipital ring. It has three pairs of lateral furrows and is bounded in front by a straight preglabellar furrow.
- b. The preglabellar field is slightly narrower (tr.)
- c. The genal spines are shorter.
- d. The pygidial axis includes only three rings and a terminal piece. The pleural regions are less inflated and the marginal spines are flatter, broader, and more inwardly turned. The fourth spine pair is located much closer together and has a distinct outward twist. In addition, the pleural furrows continue along the marginal spines, but this feature could well have been accentuated by compression.

Small cranidia of *Richardsonella arctostriata* (Raymond, 1937) from the Upper Cambrian of Vermont are very similar to those of *Elkanaspis corrugata*. The pygidium attributed to *R. arctostriata* (Fig. 700) has a short (sag.) axis and a scalloped posterior margin of five pairs of spines. These features preclude an assignment to *Elkanaspis*. The holotype cranidium of *R. arctostriata* (Fig. 70N) possesses a relatively wide glabella that is bounded anteriorly by a gently curved preglabellar furrow and a long (sag.) preglabellar field.

The type species of *Apatokephaloides* Raymond, *A. clivosus* Raymond, 1924, has a long glabella that is constricted anteriorly in a manner similar to *Elkanaspis* corrugata. *A. clivosus*, however, has a long (sag.) occipital ring, small posteriorly placed eyes, two pairs of slotlike lateral glabellar furrows, and long (exsag.) posterior limbs on the cranidium.

Elkanaspis? sp. Figs. 40, 630–5

Occurrences

Rabbitkettle Formation, Broken Skull River (two collections 86.5 m and 94 m below top of formation), *Bowmania americana* Fauna.

Remarks

Elkanaspis? sp. has a short (sag.) preglabellar field and a forwardly constricted glabella. These features suggest an assignment to *Elkanaspis*, but the assignment is queried because a pygidium has not been recovered. The great sagittal convexity of the cranidium and the nearly vertical frontal lobe of the glabella are, apparently, unique among kainellid trilobites. The cranidial fragment identified as *Richardsonella arctostriata* (Raymond) by Gilman Clark and Shaw (1968, pl. 127, fig. 33) is similar to *Elkanaspis*? sp. and could be conspecific. Gilman Clark and Shaw (1968: 1020) described both a flat brim and an elevated border on this specimen. Their photograph shows neither.

Superfamily Leiostegiacea Bradley, 1925 Family Leiostegiidae Bradley, 1925 Subfamily Pagodiinae Kobayashi, 1935

Genus Ptychopleurites Kobayashi, 1936b

Type Species

Ptychopleura brevifrons Kobayashi, 1936a from lowermost Ordovician rocks, Jones Ridge, east-central Alaska (by original designation).

Remarks

Kobayashi (1936a) did not assign *Ptychopleurites* to a family, but indicated that he thought it was related to the solenopleurid *Solenopleurella*. *Ptychopleurites* was relegated to "unrecognizable genus" status by Lochman-Balk (*in* Moore, 1959: 525) and Stitt (1977) chose not to assign this genus to a family. The recovery of pygidia of *P. brevifrons* from the Rabbitkettle Formation indicates that this genus belongs in the subfamily Pagodiinae and that it shows particular affinity for *Pagodia* (*Oreadella*) Shergold, 1975 from the Late Cambrian of Australia and China.

The pygidia of *Ptychopleurites brevifrons*, *Pagodia* (*Oreadella*) *buda* Resser and Endo, and *P*. (*O*.) cf. *buda* share a similar outline and trilobed shape, a highly convex axis with few axial rings, inflated and unfurrowed pleurae, and steep flanks above a narrow, convex border (compare Fig. 66Q, R, T, U with Endo and Resser, 1937, pl. 53 fig. 14, pl. 72, fig. 3 and with Shergold, 1975, pl. 36, fig. 2). The cranidia of *P*. (*Oreadella*) differ only slightly from those of *Ptychopleurites* in having wider fixed



Fig. 40 Elkanaspis? sp. Reconstruction of cephalon. Bar represents 1 mm.

cheeks, somewhat constricted glabellar flanks, and more posteriorly placed palpebral lobes (compare Fig. 66K with Endo and Resser, 1937, pl. 53, fig. 10 and with Shergold 1975, pl. 36, fig. 1). The free cheek of *P*. (*Oreadella*) differs from that of *Ptychopleurites* in having a narrower border and slim and short genal spine (compare Fig. 66S with Endo and Resser, 1937, pl. 53, fig. 13).

According to the correlation chart in Jones, Shergold and Druce (1971), the Chinese and Australian occurrences of *Pagodia* (*Oreadella*) would correlate with the late Franconian and Trempeauleauan of North America. Thus, this taxon is somewhat older than *Ptychopleurites*.

Punctularia Raymond, based on *P. ornata* Raymond, 1937 from Zone 1 (*Hungaia* Assemblage) of the Gorge Formation at Highgate Falls, Vermont, is a possible junior subjective synonym of *Ptychopleurites* Kobayashi. Aside from a somewhat greater convexity in *Ptychopleurites*, the cranidia assigned to these genera are indistinguishable (compare Gilman Clark and Shaw, 1968, pl. 127, fig. 1 with Stitt, 1977, pl. 4, fig. 6). A pygidium is not known for *Punctularia*.

Ptychopleurites brevifrons (Kobayashi, 1936a) Figs. 41, 66H–U

Ptychopleura brevifrons Kobayashi, 1936a: 165, pl. 21, figs. 7, 8. Ptychopleurites brevifrons—Kobayashi, 1936b: 922. Ptychopleurites brevifrons—Stitt, 1977: 46, pl. 4, figs. 6, 7, pl. 5, fig. 10.

Occurrences

Jones Ridge Limestone, Jones Ridge, Yukon River at Alaska-Yukon boundary, *Ptychopleurites* Fauna (Kobayashi, 1936a; Palmer, 1968: 104). Signal Mountain Limestone, Wichita and Arbuckle mountains, Oklahoma, *Missisquoia depressa* Subzone (Stitt, 1977). Rabbitkettle Formation, Broken Skull River (six collections between 50 m and 57 m below top of formation), *Missisquoia depressa* Subzone.

Holotype

An incomplete cranidium from Lower Ordovician rocks, Jones Ridge, east-central Alaska illustrated by Kobayashi (1936a, pl. 21, fig. 7) and Stitt (1977, pl. 5, fig. 10).

Description

Cephalon is semicircular in outline and strongly convex (tr.). Posterolateral corner is a sharp angle. Glabella is moderately inflated, barrel-shaped in outline; narrowing slightly toward front. Axial furrows are deep. Three faint and short lateral glabellar furrows are directed obliquely backward; these shorten towards front. Occipital ring is broadly rectangular; it occupies highest portion of cephalon. Preglabellar furrow is short (sag.) and sharply incised; it has slight forward curvature. Deep border furrows define convex and broad cephalic borders. In front view, anterior border furrow rises towards, but does not reach, preglabellar furrow; a short (sag.) and nearly flat preglabellar field is thus defined. Eye is located half-way out on cheek, anteriorly of mid-length of glabella. Semielliptical palpebral lobe is well defined by straight palpebral furrow; it stands somewhat lower than inflated fixed cheek. Below eye, genal field descends at about 45 degrees to lateral border furrow. Anterior branch of facial suture curves forward and inward across anterior border. Rostral suture on free cheek (Fig. 660) suggests presence of lenticular rostral plate. Posterior branch of facial suture curves widely outward and backward to cut posterior margin well inside genal corner. Dorsal surface of cephalon covered by fine granules.

Pygidium is strongly convex (tr.) and subtriangular in outline. Inflated axis continues to posterior margin and consists of four rings that are separated by deep axial ring furrows and a blunt terminal piece. Pleural field is inflated and, anteriorly, it is the same width as axis, giving a pronounced trilobed aspect to the pygidium. Four deep interpleural furrows are present. Laterally, pygidial flank descends steeply to lateral border furrow. Inflated and narrow (tr.) border is covered by closely spaced and parallel terrace lines.

Remarks

Ptychopleurites brevifrons appears to be confined to Lower Tremadocian rocks of Alaska, Oklahoma, and the District of Mackenzie. The genus has also been reported from rocks of similar age in central Nevada (M.E. Taylor, *in* Stitt, 1977: 47).



Fig. 41 Ptychopleurites brevifrons (Kobayashi, 1936a). Reconstruction of cranidium and pygidium. Bar represents 1 mm.

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Family Missisquoiidae Hupé, 1955

Remarks

Only two genera are assigned to this family—*Missisquoia* Shaw from the *Missisquoia* and *Parabolinella* zones in North America and from the *Mictosaukia orientalis* Assemblage in China, and *Parakoldinoides* Endo from the Upper Cambrian of China and from Australia (late Franconian; Jones et al., 1971).

I follow Shergold (1975) in assigning the Missisquoiidae to the Leiostegiacea. It should be noted, however, that *Missisquoia* bears close resemblance to some genera that are firmly assigned to the illaenacean family Styginidae. Such similarity is perhaps best seen in a comparison of *Missisquoia depressa* (Fig. 42) and *Perischoclonus capitalis* Raymond (Whittington, 1963, pl. 22, figs. 4, 13) from the Middle Ordovician of western Newfoundland. It is possible that the Styginidae, which appears to be the ancestor to the Illaenidae and the Scutelluidae (Ludvigsen and Chatterton, 1980), was derived from the Missisquoiidae in the latest Cambrian or earliest Ordovician.

Genus Missisquoia Shaw, 1951

Type Species

Missisquoia typicalis Shaw, 1951 from the Lower Ordovician part of the Gorge Formation (Missisquoia Zone), Highgate Falls, Vermont (by original designation).

Subjective Synonyms

Lunacrania Kobayashi, 1955; Macroculites Kobayashi, 1955; Rhamphopyge Kobayashi, 1955 (see Dean, 1977); Tangshanaspis Zhou and Zhang, 1978; Paranumia Hu, 1973.

Assigned Species

Missisquoia typicallis Shaw, 1951 (? = M. graphica Hu, 1973)
Missisquoia enigmatica (Kobayashi, 1955) (= M. nasuta Winston and Nicholls, 1967 and Paranumia triangularia Hu, 1973; also see Dean, 1977: 4)
Missisquoia inflata Winston and Nicholls, 1967
Missisquoia depressa Stitt, 1971b (= Tangshanaspis zhaogezhuangensis Zhou and Zhang, 1978)

Missisquoia cyclochila Hu, 1971

Missisquoia manchuriensis (Resser and Endo, in Endo and Resser, 1937) Missisquoia mackenziensis sp. nov.

Remarks

From the recent assessment of *Missisquoia* by Dean (1977), it is clear that the genus now includes species that display a remarkably wide range of morphologies, particularly in pygidial and glabellar shapes and in degrees of inflation.

Missisquoia has a wide geographic range in North America. The genus occurs in Newfoundland (Fortey and Skevington, 1980), Vermont (Shaw, 1951), New York (Taylor and Halley, 1974), Oklahoma (Stitt, 1971b, 1977), South Dakota (Hu, 1973), Texas (Winston and Nicholls, 1967), Utah (Hintze et al., 1980), Nevada (Cook and Taylor, 1977), Wyoming (Hu, 1971), Alberta and British Columbia (Dean, 1977), and now the District of Mackenzie.

The generic synonymy of *Missisquoia* above extends the geographic range of the genus to Hopeh and Liaoning Provinces, China. *Tangshanaspis zhaogezhuangenis* Zhou and Zhang, 1978 from Hopeh Province is assigned to *Missisquoia depressa* Stitt because the differences between *Tangshanaspis* and *Missisquoia* listed by Zhou and Zhang (1978: 25) are, in essence, those that distinguish *M. depressa* from *M. typicalis*. The single pygidium from the Wanwan Formation of Liaoning Province that was illustrated by Endo and Resser (1937, pl. 73, fig. 11) as *Encrinurus* (?) *manchuriensis* Resser and Endo is assigned to *Missisquoia*.

The genus *Paranumia* Hu, 1973 was based on small, but well-preserved cranidia and pygidia of *P. triangularia* Hu from the Deadwood Formation of South Dakota. Hu (1973: 86) did not attempt comparisons with *Missisquoia*, but he did state (p. 89) in his discussion of ontogeny that the earliest instars of *P. triangularia* are closely similar to those of *Missisquoia cyclochila* which he had described earlier (Hu, 1971). He claimed that later meraspid stages of *P. triangularia* could be differentiated from *M. cyclochila* on pygidial and glabellar shapes and absence of a preglabellar field. Hu's arguments are not convincing. *P. triangularia* does not have a preglabellar field, and neither does *Missisquoia*. Both cranidia and pygidia of *P. triangularia* are highly similar to those assigned to *Missisquoia enigmatica* by Dean (1977). I



Fig. 42 Missisquoia depressa Stitt, 1971b. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

conclude that *Paranumia* is a junior synonym of *Missisquoia* and that *Paranumia* triangularia is probably a junior synonym of *Missisquoia enigmatica* (Kobayashi).

Missisquoia depressa Stitt, 1971b Figs. 42, 43, 65, 66A–G

Missisquoia depressa Stitt, 1971b: 25, pl. 8, figs. 5-8. Tangshanaspis zhaogezhuangensis Zhou and Zhang, 1978: 17, pl. 1, figs. 22, 23.

Occurrences

Signal Mountain Limestone, Arbuckle and Wichita mountains, Oklahoma, *Missis-quoia depressa* Subzone (Stitt, 1971b, 1977). Notch Peak Formation, Utah, *Missisquoia depressa* Subzone (Hintze et al., 1980). Fengshan Formation, Hopeh Province, China, *Mictosaukia orientalis* Assemblage (Zhou and Zhang, 1978). Rabbitkettle Formation, Broken Skull River (seven collections between 46 m and 57 m below top of formation), *Missisquoia depressa* Zone.

Holotype

An incomplete cranidium from the Signal Mountain Limestone, Joins Ranch Section, Arbuckle Mountains, Oklahoma illustrated by Stitt (1971b, pl. 8, fig. 5).



Fig. 43 Missisquoia depressa Stitt, 1971b. Olbique view of reconstructed cephalon.

Description

The cranidium and pygidium of *Missisquoia depressa* have been described by Stitt (1971b: 25). The material from the Rabbitkettle Formation includes both free cheeks and hypostomes and these are described below. Minor differences between the type material of *M. depressa* and that illustrated here include the variable developments of the anterior border furrow on the cranidium. These vary from deep furrows with a well-developed median notch (Fig. 65B, K, R), to nearly straight furrows (Fig. 65P), to effaced or nearly effaced furrows (Fig. 65A, N). The silicified pygidia of *M. depressa* have as many as six axial ring furrows in front of the terminal piece and the pleurae can be seen to terminate as short, blunt spines. On interior, the convex doublure narrows forwardly from behind axis where it is one-quarter the sagittal length of the pygidium.

Free cheek has evenly curved lateral margins. Weak lateral border furrow defines wide and slightly inflated border. Posterolateral corner carries long and tapering genal spine which diverges at about 30 degrees to sagittal line. On interior, genal spine encased by doublure which, anteriorly, becomes tubelike and extends inwardly as far as lateral border furrow.

Rostral plate has not been recovered, but judging from the shape of rostral suture seen in Fig. 65M, it must have been transverse with posteriorly convergent sides.

Hypostome is subrectangular in outline, longer than wide, with small anterior wings. Posterolateral corner is rounded; a small specimen (Fig. 66B) carries a short spine at this corner. Median body is only slightly inflated, it is delineated anteriorly by median ovate depression and laterally by moderately deep border furrows which tend to converge posteriorly. Median body is unequally divided by middle furrows which nearly meet on sagittal line.

Remarks

Missisquoia depressa Stitt differs from both M. typicalis Shaw and M. enigmatica (Kobayashi) (see Dean, 1977: 4, for synonomy) by its slightly inflated glabella and its semicircular pygidium of low convexity. The free cheek of M. typicalis illustrated by Taylor and Halley (1974, pl. 3, figs. 5, 6) has a deeper lateral border furrow and a genal spine that projects posteriorly in an even curve.

Despite minor differences, the two specimens from the Fanshang Formation of Hopeh Province assigned to *Tangshanaspis zhaogezhuangensis* by Zhou and Zhang (1978) are considered conspecific with M. *depressa*. The Chinese cranidium appears to have the palpebral lobe located slightly further forward than M. *depressa* and the pygidium has slightly larger marginal spines.

The single pygidium of *Missisquoia manchuriensis* (Resser and Endo, *in* Endo and Resser, 1937, pl. 73, fig. 11) from the Wanwan Formation of Liaoning Province is closely similar to *M. depressa*, but may be distinguished by the size of the marginal spines which are longer and slimmer than those of *M. depressa*.

Missisquoia mackenziensis sp. nov. Figs. 44, 67A–K

Diagnosis

A species of *Missisquoia* possessing a moderately inflated glabella with an evenly rounded anterior portion and three pairs of lateral furrows. Prominent palpebral ridge runs immediately inside cephalic border furrow. Genal spines are short. Pygidium is semicircular in outline and moderate in convexity. It bears an annulate axis, six furrowed pleurae, and a narrow convex border.

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 60 m below top of formation). *Missisquoia mackenziensis* Fauna.

Holotype

A complete cranidium (ROM 37563) from KK 123 (60 m below top of Rabbitkettle Formation) illustrated on Fig. 67A–C.



Fig. 44 Missisquoia mackenziensis sp. nov. Reconstruction of cephalon and pygidium (prosopon omitted). Bar represents 1 mm.

Name

From the Mackenzie Mountains.

Remarks

Missisquoia mackenziensis sp. nov. is best differentiated from other species of *Missisquoia* by the course of the palpebral ridge and the anterior cephalic border furrow. In *M. mackenziensis*, the lateral border furrow crosses the facial suture immediately in front of the eye and, on the fixed cheek, defines the front edge of the palpebral ridge (Fig. 67A, D). In other species of *Missisquoia*, the lateral border furrow crosses the facial suture well in front of the eye and the palpebral ridge, if present, is distinctly separated from the anterior border furrow. Such a pattern is well shown on the front part of the fixed cheek of *M. typicalis* Shaw, *M. cyclochila* Hu, *M. inflata* Winston and Nicholls, and *M. depressa* Stitt (see Taylor and Halley, 1974, pl. 3, figs. 1, 3; Hu, 1971, pl. 20, fig. 19; Winston and Nicholls, 1967, pl. 13, fig. 7; Fig. 65K, O).

The pygidium of M. mackenziensis differs from those of similar size of M. typicalis, M. depressa, and M. manchuriensis in possessing a narrow convex border and by lacking marginal spines. The pygidium of M. enigmatica (Kobayashi) also lacks marginal spines, but this pygidium (Dean, 1977, pl. 1, fig. 3; Hu, 1973, pl. 1, fig. 23) is arched (tr.) and carries a highly inflated axis with only a few ring furrows.

Missisquoia sp. Fig. 69J

Occurrence

Rabbitkettle Formation, Broken Skull River (single collection 70 m below top of formation), *Elkanaspis corrugata* Fauna.

Remarks

Were it not for its co-occurrence with acknowledged Cambrian trilobite genera such as *Idiomesus*, *Eurekia*, and *Yukonaspis* in the lower part of the *Elkanaspis corrugata* Fauna of the *Yukonaspis* Zone, these small, immature cranidia of *Missisquoia* would not deserve mention. These specimens now demonstrate that the first occurrence of *Missisquoia* in the Rabbitkettle Formation is 10 m below the base of the *Parabolinella* Zone. The size of the cranidium precludes identification to species level, but it is similar to *M. depressa* cranidia of the same size.

Superfamily Asaphacea Family Asaphidae Burmeister, 1843 Subfamily Symphysurininae Kobayashi, 1955

Genus Symphysurina Ulrich, in Walcott, 1924

Type Species

Symphysurina woosteri Ulrich, in Walcott, 1924 from the Oneota Dolomite, Trempealeau, Wisconsin (by original designation).

Symphysurina cf. brevispicata Hintze, 1953 Figs. 45, 57T

Symphysurina brevispicata—Stitt, 1971: 15, pl. 8, figs. 19–21 (see for synonymy). Symphysurina brevispicata—Hu, 1973: 94, pl. 2, figs. 21–28. Symphysurina brevispicata—Stitt, 1977: 37, pl. 4, fig. 10.

Occurrences

Summarized by Stitt (1977: 32-36) in his discussion of the Symphysurina brevispicata Subzone. Rabbitkettle Formation, Broken Skull River (single collection 25 m below top of formation), Symphysurina brevispicata Subzone.



Fig. 45 Symphysurina cf. brevispicata Hintze, 1953. Drawing of interior of fragmentary free cheek. Bar represents 1 mm.

Remarks

The single, fragmentary free cheek recovered during the present study is generally similar to those of *Symphysurina brevispicata* Hintze, 1953; *S. woosteri* Ulrich, *in* Walcott, 1924; and *S. bulbosa* Lochman, 1964b. The size of the genal spine suggests an affinity with *S. brevispicata*, a species that occurs in Utah (Hintze, 1953), Montana (Lochman, 1964b), Texas (Winston and Nicholls, 1967), South Dakota (Hu, 1973), and Oklahoma (Stitt, 1971b, 1977).

Family Nileidae Angelin, 1854

Genus Tatonaspis Kobayashi, 1935

Type Species

Tatonaspis alaskensis Kobayashi, 1935 from the Trempealeauan-1 Fauna (Palmer, 1968) of east-central Alaska (by original designation).

Remarks

Lochman-Balk's (1953, and *in* Moore, 1959) proposal to synonymize *Tatonaspis* with *Macelloura* Resser, 1935 was rejected by Palmer (1968: 67) who noted that persistent differences separate the two taxa. Palmer's argument is accepted.

Four species are now assigned to *Tatonaspis*: *T. alaskensis* Kobayashi; *T. levisensis* Rasetti, 1944; *T. breviceps* (Raymond, 1924); and *T. diorbita* sp. nov. Rasetti (1944: 257) considered *Illaenurus punctatus* Raymond, 1937 to be a species of *Tatonaspis*. Because this species was not illustrated, it is difficult to evaluate. Raymond (1937: 1091) stated that *I. punctatus* differs from *I. breviceps* only in the presence of large punctae.

The new species of *Tatonaspis* is somewhat closer to *Macelloura* than either of T. *alaskensis* or T. *levisensis* in possessing a well-defined glabella, a deep anterior border furrow along the front margin, and a rimlike anterior border. The assignment of T. *diorbita* to *Tatonaspis* instead of *Macelloura* is based on the size and position of the palpebral lobe, the absence of palpebral or occipital furrows, the direction of the anterior facial sutures, and the presence of a doublure that is identical to that of T. *alaskensis*.

Tatonaspis is confined to Trempealeauan rocks in North America. It occurs at shelf-edge sites in Quebec (Rasetti, 1944), Vermont (Raymond, 1924), Nevada (Taylor, 1976), Alaska (Palmer, 1968), and now the District of Mackenzie.

Palmer (1968) placed *Tatonaspis* in the family Nileidae without commenting on this assignment. The general cephalic form of *Tatonaspis* as well as the shape, orientation, and prosopon of the cephalic and pygidial doublures are similar to those

of many nileids (see Schrank, 1972; Fortey, 1975). Possible phyletic relationships between the Trempealeauan *Tatonaspis* and the Tremadocian *Symphysurus* and *Nileus* have yet to be discovered.

Tatonaspis diorbita sp. nov. Figs. 46, 68A–N, 69R–T

Diagnosis

A species of *Tatonaspis* with deep axial furrows outlining narrow and parallel-sided glabella; palpebral lobes are large and semicircular; genal corners are rounded. Pygidium is semielliptical in outline with a convex, U-shaped axis and a faint border furrow defining flat border.

Occurrence

Rabbitkettle Formation, Broken Skull River (two collections 165 m and 172 m below top of formation), *Yukonaspis kindlei* Fauna.

Holotype

A cranidium (ROM 37619) from K 550 (165 m below top of Rabbitkettle Formation) illustrated on Fig. 68A, B.





Name

From *diorbita*—a two-wheeled track (Latin) in reference to the deep parallel axial furrows.

Description

Cephalon is arched (tr.), semicircular in outline, and slightly wider than long (sag.). Glabella is rectangular (length is twice width), moderately convex; it lacks any trace of lateral or occipital furrows. Anterior border furrow is short (sag.), deep, and transverse. Anterior border is a very short (sag.) rim which extends on to free cheeks; in anterior view it arches up towards mid-line. Palpebral lobe is a large, semicircular flap that droops slightly outward; its length is nearly half sagittal length of cephalon and its mid-point is located opposite mid-length of cephalon. Posterior border furrow is not developed. Cheek slopes steeply to margin below eye. A very narrow lateral border is present on anterolateral flank of cephalon. Genal angle is bluntly rounded. Anterior branch of facial suture swings forward and inward to anterior border and then across anterior margin. Median path of suture is ventral-intramarginal. The cheeks are yoked. Posterior branch of facial suture follows sigmoid path to posterior border. A broad, upturned doublure with a wide median notch is evident in anterior view. Doublure is longest medially where it plunges under cephalon at about 70 degrees; it narrows and becomes flatly convex posteriorly until, near genal angle, it is oriented parallel with cephalic flank. Prosopon on cephalon consists of fine pits. Doublure carries fine terrace lines.

Pygidium is twice as wide as long; it has evenly curved posterior margin between nearly exsagittally directed lateral margins. Convex axis extends for two-thirds pygidial length and is outlined by firmly impressed and U-shaped axial furrows. Only an articulating furrow crosses axis. Pleural region is faintly inflated inside very shallow border furrow which follows a path subparallel with posterior margin. Posterior border is rather broad and flat. Doublure is wide and flat; it extends inward beyond border furrow and its median part is tucked into posterior part of axis.

Remarks

Tatonaspis diorbita sp. nov. is readily distinguished from T. alaskensis Kobayashi, T. levisensis Rasetti, and T. breviceps (Raymond) by its narrow, well-defined glabella, large eyes, rounded genal corners, and the absence of both occipital and posterior border furrows.

Superfamily Ceratopygacea Family Ceratopygidae Linnarsson, 1869

ceratopygid indet. Fig. 53E-J

Occurrence

Rabbitkettle Formation, Broken Skull River (six collections between 78 m and 165 m below top of formation), *Bowmania americana* Fauna and *Yukonaspis kindlei* Fauna.

Remarks

Small and coarsely silicified cranidia and free cheeks from the Rabbitkettle Formation probably belong to this family. In having a glabella that expands towards a short (sag.) anterior border and rather large posteriorly placed palpebral lobes, the cranidia are similar to some species of *Onychopyge* Harrington, 1938. They differ markedly from *Onychopyge*, however, in having greater convexity, and in lacking palpebral and slotlike lateral glabellar furrows. Pygidia that are similar to the characteristic ceratopygid pygidium do not occur in the single collection that contained the illustrated cranidia and free cheeks.

Acknowledgements

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Peter Fenton assisted in the field in 1977. Christine Dudar provided curatorial assistance. The trilobite reconstructions were prepared by David Sargent under my supervision. The drafting is by Subhash Shanbhag. Brian O'Donovan printed the trilobite photographs from my negatives. My wife, Kathleen MacKinnon, assisted in picking and sorting many of these samples of silicified trilobites.

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Fig. 47 Geragnostus (Micragnostus) subobesus (Kobayashi, 1936a).

- A Cephalon, dorsal view, \times 9, ROM 37485, KK 113.
- B Pygidium, dorsal view, \times 9, ROM 37486, KK 113.
- c Cephalon, dorsal view, \times 9, ROM 37487, KK 113.
- D Pygidium, dorsal view, \times 8, ROM 37484, KK 113.
- E,F Cephalon, dorsal and posterior views, \times 9, ROM 37617, KK 113.
- $_{\rm G,H}~$ Pygidium, dorsal and posterior views, \times 8, Rom 37614, KK 113.
- I,J Cephalon, dorsal and anterior views, \times 9, ROM 37615, KK 113.
- K,L Pygidium, dorsal and lateral views, × 9, ROM 37613, KK 113.
- M,N Cephalon, dorsal and lateral views, \times 9, ROM 37616, KK 116.

O,P Anterior thoracic segment, dorsal and anterior views, \times 13, ROM 37618, KK 113. *Pseudagnostus (Pseudagnostina)* sp.

- Q Pygidium, dorsal view, \times 11, ROM 37632, K 550.
- R Complete specimen, dorsal view, \times 11, ROM 37631, K 550.



Fig. 48 Parabolinella cf. prolata Robison and Pantoja-Alor, 1968.

- A-D Cranidium, dorsal, anterior and lateral views, \times 5.5, oblique anterior view, \times 9, ROM 37473, KK 113.
 - E Cranidium, ventral view, \times 5.5, ROM 37474, KK 113.
 - F Cranidium, dorsal view, \times 6, ROM 37475, KK 113.
- G-I Cephalon, dorsal, anterior and oblique views, × 13, ROM 37609, KK 113.
 - J Pygidium, dorsal view, \times 9, ROM 37476, KK 113.
- K,L Cranidium, dorsal and oblique views, \times 7, ROM 37608, KK 113.
- M-0 Yoked cheeks, anterior, oblique and dorsal views, \times 5.5, ROM 37610, KK 113.
- P,Q Pygidium, dorsal and posterior views, \times 9, ROM 37490, KK 116.
 - R Pygidium, ventral view, \times 9, ROM 37491, KK 116.
 - s Cephalon, dorsal view, \times 11, ROM 37478, KK 113.
 - T Pygidium and partial thorax, dorsal view, \times 11, ROM 37477, KK 113.
 - U Hypostome, ventral view, \times 18, ROM 37492, KK 116.



Fig. 49 Parabolinella cf. prolata Robison and Pantoja-Alor, 1968.

- A-C Cranidium, dorsal, anterior and oblique views, \times 6, ROM 37488, KK 116.
- D,E Cranidium, dorsal and oblique views, \times 8, ROM 37489, KK 116.
- F,G Hypostome, ventral and posterior views, \times 13, ROM 37525, KK 119.5.
- H,1 Thoracic segment, posterior and dorsal views, \times 6, ROM 37510, KK 119.5.
- J Yoked cheeks, dorsal view, \times 9, ROM 37513, KK 119.5.
- K.L Yoked cheeks, dorsal and anterior views, \times 6, ROM 37514, KK 119.5.
- M Cranidium, dorsal view, \times 8, ROM 37512, KK 119.5.
- N Pygidium, dorsal view, \times 9, ROM 37516, KK 119.5.
- o Pygidium and partial thorax, ventral view, \times 9, ROM 37515, KK 119.5.
- P Pygidium and partial thorax, dorsal view, \times 11, ROM 37654, KK 119.5.
- Q Partial thorax, ventral view, \times 8, ROM 37653, KK 119.5.
- R Thoracic segment, dorsal view, \times 6, ROM 37511, KK 119.5.
- s Partial thorax, dorsal view, \times 8, ROM 37652, KK 119.5.



- Fig. 50 Parabolinella panosa sp. nov.
 - A Protaspid, dorsal view, \times 27, ROM 37735, KK 122.5.
 - B Meraspid cephalon, dorsal view, \times 27, ROM 37733, KK 122.5.
 - c Enrolled meraspid specimen, oblique view, \times 27, ROM 37730, KK 122.5.
 - D,E Meraspid specimen (M.2), dorsal and lateral views, \times 27, ROM 37729, KK 122.5.
 - F Meraspid specimen (M.3), dorsal view, \times 27, ROM 37734, KK 122.5.
 - G Meraspid specimen (M.3 or M.4), dorsal view, \times 27, ROM 37732, KK 122.5.
 - H Meraspid specimen (M.7), ventral view, \times 18, ROM 37728, KK 122.5.
 - 1,J Meraspid specimen lacking free cheeks (M.9), lateral and dorsal views, \times 18, ROM 37590, KK 123.
 - K Yoked cheeks, dorsal view, \times 11, ROM 37727, KK 122.5.
 - L Pygidium, dorsal view, \times 13, ROM 37592, KK 123.
 - O Cranidium, dorsal view, \times 11, ROM 37596, KK 123.

Q.R Holotype cranidium, dorsal and oblique lateral views, \times 11, ROM 37731, KK 122.5. *Parabolinella* cf. *prolata* Robison and Pantoja-Alor, 1968.

M.N Cranidium, oblique lateral and dorsal views, \times 13, ROM 37591, KK 123.

Parabolinites cf. williamsoni (Belt, 1868).

- P Cranidium, dorsal view, \times 13, specimen lost, KK 133.
- s Cranidium, dorsal view, \times 8, ROM 37597, KK 133.



Fig. 51 Parabolinites cf. williamsoni (Belt, 1868).

- A,B Cranidium, dorsal and lateral views, \times 8, ROM 37691, K 845.
 - c Cranidium, dorsal view, \times 7, ROM 37560, KK 64.
 - D Cranidium, dorsal view, \times 8, ROM 37690, K 845.
 - E Cranidium, dorsal view, \times 11, ROM 37561, KK 64.
- F,G Hypostome, ventral and oblique views, \times 11, ROM 37693, K 845.
 - H Free cheek, dorsal view, \times 9, ROM 37699, KK 64.
- I,J Pygidium, dorsal and lateral views, \times 11, ROM 37692, K 845.
- K Pygidium, dorsal view, \times 8, ROM 37700, KK 64.

Trilobite indet. (not described).

L Pygidium, dorsal view, \times 13, ROM 37562, KK 64.

Apoplanias rejectus Lochman, 1964a.

- M,N Cephalon, dorsal and oblique views, \times 13, ROM 37680, KK 25.
 - 0 Cranidium, dorsal view, \times 9, ROM 37684, KK 43.
 - P Cranidium, ventral view, \times 8, ROM 37688, KK 43.
 - $\rm Q$ $\,$ Cranidium, dorsal view, \times 13, Rom 37682, KK 25.
- R Cranidium, dorsal view, \times 13, ROM 37681, KK 25.
- S,T Cranidium, oblique and dorsal views, \times 11, ROM 37679, KK 25.


Fig. 52 Parabolinella hecuba (Walcott, 1924).

- A,B Cranidium, dorsal and lateral views, \times 5.5, ROM 37703, KK 50.
 - c Cranidium, dorsal view, \times 11, ROM 37706, KK 50.
 - D Cranidium, dorsal view, \times 7, ROM 37705, KK 50.
- E-G Cranidium, oblique view, \times 11, dorsal and lateral views, \times 6, ROM 37702, KK 50.
- H,I Cranidium, dorsal and oblique views, \times 7, ROM 37704, KK 50. *Parabolinella* sp.
- J,K Cranidium, dorsal and anterior views, \times 8, ROM 37683, KK 43.
 - L Cranidium, dorsal view, \times 9, ROM 37686, KK 43.
- M Cranidium, dorsal view, \times 8, ROM 37685, KK 43.

N Free cheek, dorsal view, \times 11, ROM 37687, KK 43.

Rhaptagnostus clarki (Kobayashi, 1935).

- 0 Cephalon, dorsal view, \times 11, ROM 37604, K 510.
- P Pygidium, dorsal view, \times 7, ROM 37601, K 510.
- Q Pygidium, dorsal view, \times 11, ROM 37602, K 510.
- R Cephalon, ventral view, \times 9, ROM 37600, K 510.
- s Pygidium, ventral view, \times 11, ROM 37603, K 510.



Fig. 53 Liostracinoides vermontanus Raymond, 1937.

A,B Cranidium, dorsal and anterior views, \times 13, ROM 37745, KK 86.5. C,D Cranidium, oblique and dorsal views, \times 18, ROM 37746, KK 86.5. Ceratopygid indet.

- E Free cheek, dorsal view, \times 13, ROM 37751, KK 211.
- F Cranidium, dorsal view, \times 13, ROM 37747, KK 211.
- G Cranidium, dorsal view, \times 13, ROM 37749, KK 211.
- H,I Cranidium, dorsal and anterior views, \times 13, ROM 37748, KK 211.

J Cranidium, dorsal view, \times 13, ROM 37750, KK 211.

Bowmania americana (Walcott, 1884).

- κ Pygidium, dorsal view, \times 13, ROM 37744, KK 141.
- L Cranidium, dorsal view, \times 7, ROM 37737, KK 77.
- M Genal spine, dorsal view, \times 8, ROM 37743, KK 141.
- N Cranidium, dorsal view, \times 11, ROM 37739, KK 141.
- O Cranidium, dorsal view, \times 11, ROM 37741, KK 141.
- P Yoked cheeks, dorsal view, \times 8, ROM 37742, KK 141.
- Q Cranidium, lateral view, \times 9, ROM 37738, KK 77.
- R,S Cranidium, oblique and dorsal views, \times 11, ROM 37740, KK 141.



Fig. 54 Bowmania americana (Walcott, 1884).

- A-C Cranidium, dorsal, anterior and lateral views, \times 8, ROM 37663, KK 156.
 - D Cranidium, dorsal view, \times 11, ROM 37664, KK 156.
 - E Cranidium, dorsal view, \times 11, ROM 37665, KK 156.
- F,G Yoked cheeks, ventral and anterior views, \times 7, ROM 37662, KK 156.
- H,1 Pygidium, dorsal and posterior views, \times 11, ROM 37666, KK 156.
- J Pygidium, dorsal view, \times 11, ROM 37668, KK 156.
- K,L Pygidium, posterior and dorsal views, \times 11, ROM 37667, KK 156.
 - M Yoked cheeks, dorsal view, \times 13, ROM 37671, KK 156.
 - N Genal spine, dorsal view, \times 11, ROM 37670, KK 156.
 - O Genal spine, dorsal view, \times 11, ROM 37669, KK 156.

Idiomesus tantillus Raymond, 1924.

- P-R Cephalon, dorsal, anterior, and oblique views, \times 13, ROM 37645, K 550.
 - s Cranidium, dorsal view, \times 18, ROM 37644, K 550.
- T,U Cranidium, dorsal and anterior views, \times 13, ROM 37646, K 550.



Fig. 55 Heterocaryon tuberculatum Rasetti, 1944.

A-C Cranidium, dorsal anterior and oblique views, \times 9, ROM 37464, K 510.

D-F Cranidium, dorsal, lateral and anterior views, \times 9, ROM 37453, KK 177.

G Free cheek, exterior view, \times 11, ROM 37538, K 510.

- H Cranidium, dorsal view, \times 11, ROM 37454, KK 177.
- 1-K Pygidium, posterior, dorsal and oblique views, \times 11, ROM 37461, K 510.
 - L Cranidium, dorsal view, \times 11, ROM 37650, K 550.
- M Pygidium, dorsal view, \times 13, ROM 37462, K 510.

N Pygidium, ventral view, \times 13, ROM 37463, K 510.

Kathleenella hamulata gen. et sp. nov.

O,P Holotype cranidium, dorsal and oblique views, \times 11, ROM 37459, K 510.

- Q Free cheek, exterior view, \times 11, ROM 37537, K 510.
- R Cranidium, dorsal view, \times 11, ROM 37460, K 510.
- S,T Cranidium, dorsal and oblique views, × 18, ROM 37649, K 550.



Fig. 56. Larifugula triangulata gen. et sp. nov.

- A-C Holotype cranidium, dorsal, anterior and oblique views, × 13, ROM 37643, K 550.
 - D Cranidium, dorsal view, \times 13, ROM 37574, KK 180.
 - E Cranidium, dorsal view, \times 13, ROM 37651, K 550.
- F,G Cranidium, anterior and dorsal views, \times 13, ROM 37566, KK 64.
 - H Cranidium, dorsal view, \times 13, ROM 37565, KK 64.
 - 1 Pygidium, dorsal view, \times 18, specimen lost, KK 133.
 - J Cranidium, dorsal view, \times 11, ROM 37586, KK 133.
 - κ Cranidium, dorsal view, \times 13, ROM 37587, KK 133.
 - L Pygidium, dorsal view, \times 18, ROM 37568, KK 64.
- M Free cheek, exterior view, \times 11, ROM 37567, KK 64.
- N Free cheek, exterior view, \times 11, ROM 37593, KK 133.
- o Cranidium, dorsal view, × 13, specimen lost, KK 133.
- Q Pygidium, dorsal view, \times 18, specimen lost, KK 133.
- R Cranidium, dorsal view, \times 13, ROM 37696, K 845.
- s Free cheek, exterior view, \times 11, ROM 37594, KK 133.

Larifugula leonensis (Winston and Nicholls, 1967).

P Cranidium, dorsal view, \times 18, specimen lost, KK 133.

- Plethometopus obtusus Rasetti, 1945.
- T-U Cranidium, anterior, lateral and dorsal views, \times 8, ROM 37518, KK 119.5.



Fig. 57 Leiocoryphe spp.

A,B Cranidium, dorsal and anterior views, \times 13, ROM 37675, KK 156.

c Cranidium, dorsal view, \times 13, rom 37446, KK 177.

D Pygidium, dorsal view, \times 13, ROM 37447, KK 177.

E,F Pygidium, anterior and dorsal views, \times 13, ROM 37676, KK 156. *Idiomesus intermedius* Rasetti, 1959.

G,H Cranidium, dorsal and anterior views, \times 13, ROM 37442, KK 177.

1 Pygidium, dorsal view, \times 13, ROM 37444, KK 177.

J Pygidium, dorsal view, \times 13, ROM 37445, KK 177.

K Cranidium, dorsal view, \times 18, ROM 37443, KK 177.

L Cranidium, dorsal view, \times 13, ROM 37583, KK 180.

M Pygidium, dorsal view, \times 13, ROM 37580, KK 180.

Idiomesus levisensis (Rasetti, 1944).

N Cranidium, dorsal view, \times 13, ROM 37599, KK 133.

o Cranidium, dorsal view, \times 18, specimen lost, KK 133. Saukiid indet.

P Pygidium, dorsal view, \times 6, ROM 37633, K 550.

Q,R Cranidium, anterior and dorsal views, \times 11, ROM 37640, K 550. *Bienvillia* cf. *corax* (Billings, 1865).

s Cranidium, dorsal view, \times 13, ROM 37564, KK 64. Symphysurina cf. brevispicata Hintze, 1953.

T Free cheek, interior view, \times 11, ROM 37678, KK 25. *Triarthropsis limbata* Rasetti, 1959.

U Cranidium, dorsal view, \times 11, ROM 37636, K 550. Euloma (Plecteuloma) sp.

v Cranidium, dorsal view, \times 11, ROM 37634, K 550.



- Fig. 58 "Calvinella" palpebra sp. nov.
 - A,B Cranidium, dorsal and anterior views, \times 11, ROM 37465, K 510.
 - C,D Holotype cranidium, oblique and anterior views, \times 9, ROM 37466, K 510.
 - E Cranidium, ventral view, \times 9, ROM 37467, K 510.
 - F Free cheek, dorsal view, \times 8, ROM 37469, K 510 (specimen is stretched in a transverse direction).
 - G Pygidium, dorsal view, \times 13, ROM 37471, K 510.
 - H Pygidium, dorsal view, \times 13, ROM 37472, K 510.
 - 1 Cranidium, dorsal view, \times 13, ROM 37468, K 510.
 - J Pygidium, ventral view, \times 11, ROM 37470, K 510.

Euptychaspis typicalis Ulrich, in Bridge, 1931.

- к-м Cranidium, dorsal, oblique anterior and oblique views, × 9, ROM 37456, K 510.
 - N Free cheek, dorsal view, \times 11, ROM 37536, K 510.
- O,P Free cheek, dorsal and lateral views, \times 9, ROM 37535, K 510.
 - Q Cranidium, dorsal view, \times 11, ROM 37458, K 510.
- R Cranidium, ventral view, \times 11, ROM 37455, K 510.
- s-u Pygidium, posterior, dorsal and lateral views, \times 13, ROM 37714, K 595.
- v,w Cranidium, dorsal and oblique anterior views, \times 11, Rom 37457, K 510.



Fig. 59 Kathleenella subula gen. et sp. nov.

- A-C Holotype cranidium, dorsal, anterior and oblique views, \times 11, ROM 37429, KK 177.
 - D Cranidium, oblique anterior view, \times 11, Rom 37427, KK 177.
- E,F Cranidium, dorsal and oblique anterior views, \times 13, ROM 37428, KK 177.
 - G Cranidium, dorsal view, \times 13, ROM 37430, KK 177.
 - H Cranidium, dorsal view, \times 11, ROM 37431, KK 177.
 - I Cranidium, ventral view, \times 11, ROM 37432, KK 177.
- J,K Pygidium, posterior and dorsal views, \times 13, ROM 37434, KK 177.
 - L Cranidium, dorsal view, \times 9, ROM 37426, KK 177.
- M Pygidium, dorsal view, \times 13, ROM 37435, KK 177.
- N Pygidium, dorsal view, \times 13, ROM 37436, KK 177.
- O-Q Hypostome, dorsal, posterior and oblique views, \times 18, ROM 37437, KK 177.
 - R Hypostome, dorsal view, \times 18, ROM 37438, KK 177.
 - s Free cheek, dorsal view, \times 8, ROM 37440, KK 177.
 - T Free cheek, dorsal view, \times 8, ROM 37441, KK 177.
 - U Cranidium, dorsal view, \times 13, ROM 37433, KK 177.



Fig. 60 Kathleenella subula gen. et sp. nov.

- A Cranidium, dorsal view, \times 11, ROM 37572, KK 180.
- B Cranidium, ventral view, \times 9, ROM 37573, KK 180.
- c Cranidium, dorsal view, \times 11, ROM 37569, KK 180.
- D,E Hypostome, posterior and oblique views, \times 18, ROM 37585, KK 180.
 - F Free cheek, dorsal view, \times 7, ROM 37576, KK 180.
 - G Pygidium, dorsal view, \times ,11, ROM 37577, KK 180.
- H,1 Pygidium, dorsal and posterior views, \times 13, ROM 37579, KK 180.

J,K Free cheek, dorsal and lateral views, \times 8, ROM 37575, KK 180.

Elkanaspis corrugata gen. et sp. nov.

- L Cranidium, dorsal view, \times 9, ROM 37694, K 845.
- M Cranidium, dorsal view, \times 7, ROM 37552, KK 64.
- N Cranidium, dorsal view, \times 11, ROM 37558, KK 64.
- 0 Free cheek, dorsal view, \times 7, ROM 37698, KK 64.
- P Cranidium, dorsal view, \times 11, ROM 37695, K 845.
- Q Pygidium, dorsal view, \times 8, ROM 37553, KK 64.
- R Free cheek, dorsal view, \times 8, ROM 37556, KK 64.
- s Cranidium, dorsal view, \times 13, ROM 37557, KK 64.
- T Holotype pygidium, dorsal view, \times 11, ROM 37555, KK 64.
- U Pygidium, dorsal view, \times 8, ROM 37554, KK 64.
- v Pygidium, dorsal view, \times 7, ROM 37697, KK 64.



- Fig. 61 Eurekia ulrichi (Rasetti, 1945).
 - A,B Cranidium, oblique and dorsal views, \times 9, ROM 37539, K 510.
 - C Cranidium, ventral view, \times 8, ROM 37540, K 510.
 - D Cranidium, dorsal view, \times 11, ROM 37541, K 510.
 - E,F Cranidium, dorsal and oblique views, \times 9, ROM 37542, K 510.
 - G Free cheek, interior view, \times 9, ROM 37545, K 510.
 - H Free cheek, exterior view, \times 9, ROM 37543, K 510.
 - 1 Free cheek, exterior view, \times 9, ROM 37544, K 510.
 - J-L Pygidium, dorsal, posterior, and lateral views, \times 7, ROM 37546, K 510.
 - M Pygidium, dorsal view, \times 9, ROM 37548, K 510.
 - N Pygidium, ventral view, \times 8, ROM 37547, K 510.
 - 0 Hypostome, dorsal view, \times 9, ROM 37551, K 510.
 - P Hypostome, ventral view, \times 11, ROM 37550, K 510.
 - Q Hypostome, ventral view, \times 9, ROM 37549, K 510.



Fig. 62 Eurekia bacata sp. nov.

- A-C Cranidium, dorsal, lateral and anterior views, \times 5.5, ROM 37709, K 525.
- D,E Pygidium, dorsal and posterior views, \times 9, ROM 37711, K 525.
- F,G Holotype pygidium, posterior and dorsal views, \times 5.5, ROM 37708, K 525.
 - H Cranidium, dorsal view, \times 5.5, ROM 37712, K 550.
 - 1 Free cheek, exterior view, \times 5.5, ROM 37710, K 525.
 - J Free cheek, exterior view, \times 5.5, Rom 37713, K 550.

Eurekia spp.

- κ Cranidium, dorsal view, \times 11, ROM 37450, KK 177.
- L Pygidium, dorsal view, \times 9, ROM 37582, KK 180.
- M Pygidium, dorsal view, \times 13, ROM 37581, KK 177.
- N Hypostome, ventral view, \times 11, ROM 37452, KK 177.
- O Pygidium, dorsal view, \times 11, ROM 37451, KK 177.
- P,Q Cranidium, dorsal and oblique views, \times 8, ROM 37449, KK 177.



Fig. 63 Yukonaspis kindlei Kobayashi, 1936a.

- A,B Cranidium, dorsal and oblique views, \times 9, ROM 37715, K 595.
- C Pygidium, dorsal view, \times 11, ROM 37717, K 595.
- D,E Cranidium, dorsal and anterior views, \times 9, ROM 37502, K 510.
- F,G Pygidium, posterior and dorsal views, \times 11, ROM 37716, K 510.
- H,I Free cheek, dorsal and lateral views, \times 8, ROM 37505, K 510.
- J Cranidium, dorsal view, \times 9, ROM 37504, K 510.
- K,L Cranidium, dorsal and oblique views, \times 9, ROM 37503, K 510.
- M Free cheek, dorsal view, \times 8, ROM 37506, K 510.
- N Cranidium, dorsal view, \times 9, ROM 37718, K 510.

Elkanaspis? sp.

- 0 Free cheek, exterior view, \times 11, ROM 37674, KK 156.
- P Free cheek, exterior view, \times 18, ROM 37673, KK 156.
- Q-S Cranidium, dorsal, anterior and lateral views, \times 13, ROM 37672, KK 156.



Fig. 64 Elkanaspis futile gen. et sp. nov.

- A,B Cranidium, dorsal and oblique views, \times 8, ROM 37528, K 510.
 - c Cranidium, dorsal view, \times 9, ROM 37527, K 510.
 - D Free cheek, dorsal view, \times 7, ROM 37533, K 510.
 - E Cranidium, dorsal view, \times 11, ROM 37529, K 510.
 - F Free cheek, dorsal view, \times 9, ROM 37534, K 510.
- G,H Holotype pygidium, posterior and dorsal views, × 11, ROM 37532, K 510.
 - 1 Pygidium, dorsal view, \times 11, ROM 37530, K 510.
 - J Pygidium, dorsal view, \times 11, ROM 37531, K 510.
 - K Pygidium, dorsal view, \times 11, ROM 37639, K 550.
- L,M Cranidium, dorsal and oblique views, \times 11, ROM 37637, K 550.
 - N Free cheek, dorsal view, \times 7, ROM 37642, K 550.
 - 0 Free cheek, dorsal view, \times 7, ROM 37641, K 550.
 - P Cranidium, dorsal view, \times 11, ROM 37638, K 550.

Naustia papilio gen. et sp. nov.

- Q Holotype pygidium, dorsal view, \times 5.5, ROM 37628, K 550.
- R Pygidium, dorsal view, \times 9, ROM 37629, K 550.
- s Pygidium, dorsal view, \times 9, ROM 37630, K 550.
- T Cranidium, dorsal view, \times 11, ROM 37635, K 550.
- U Cranidium, dorsal view, \times 13, ROM 37648, K 550.



Fig. 65 Missisquoia depressa Stitt, 1971b.

- A Cranidium, dorsal view, \times 13, ROM 37479, KK 113.
- B Cranidium, dorsal view, \times 8, ROM 37493, KK 116.
- C Cranidium, dorsal view, \times 11, ROM 37501, KK 116.
- D Pygidium, dorsal view, \times 13, ROM 37480, KK 113.
- E Pygidium, ventral view, \times 11, ROM 37495, KK 116.
- F.G Pygidium, dorsal and lateral views, \times 11, ROM 37494, KK 116.
 - H Cranidium, ventral view, \times 11, ROM 37499, KK 116.
 - 1 Pygidium and incomplete thorax, ventral view, \times 11, ROM 37500, KK 116.
 - J Free cheek, ventral view, \times 11, ROM 37497, KK 116.
- K,L Cranidium, dorsal and oblique views, \times 11, ROM 37498, KK 116.
 - M Free cheek, oblique view, \times 11, ROM 37496, KK 116.
 - N Cranidium, dorsal view, \times 11, ROM 37519, KK 119.5.
 - O Cranidium, dorsal view, \times 11, ROM 37521, KK 119.5.
 - P Cranidium, dorsal view, \times 11, ROM 37520, KK 119.5.
 - Q Pygidium, dorsal view, \times 11, ROM 37523, KK 119.5.
 - R Cranidium, dorsal view, \times 11, ROM 37522, KK 119.5.
 - s Pygidium, dorsal view, \times 11, ROM 37524, KK 119.5.



Fig. 66 Missisquoia depressa Stitt, 1971b.

- A Hypostome, ventral view, \times 18, ROM 37655, KK 119.5.
- B Hypostome, ventral view, \times 18, ROM 37656, KK 119.5.
- c Hypostome, ventral view, \times 18, ROM 37661, KK 116.
- D Free cheek, dorsal view, \times 13, ROM 37658, KK 119.5.
- E Free cheek, dorsal view, \times 11, ROM 37526, KK 119.5.
- F Cranidium, dorsal view, \times 13, ROM 37659, KK 116.
- G Meraspid specimen, dorsal view, \times 18 (specimen lost), KK 116.

Ptychopleurites brevifrons (Kobayashi, 1936a).

- H-J Cranidium, dorsal, anterior and oblique views, \times 11, ROM 37481, KK 113.
- K-M Cranidium, dorsal, anterior and lateral views, × 11, ROM 37517, KK 119.5.
- N-P Cranidium, dorsal, anterior and oblique views, \times 9, ROM 37707, KK 50.
- Q,R Pygidium, dorsal and posterior views, × 13, ROM 37611, KK 113.
- s Free cheek, oblique view, \times 13, ROM 37483, KK 113.
- T,U Pygidium, dorsal and lateral views, \times 13, ROM 37482, KK 113.



Fig. 67 Missisquoia mackenziensis sp. nov.

- A-C Holotype cranidium, dorsal, anterior and oblique views, \times 13, ROM 37563, KK 123.
 - D Free cheek, dorsal view, \times 18, ROM 37589, KK 123.
- E,F Pygidium, dorsal and posterior views, \times 13, ROM 37588, KK 123.
- G Pygidium, dorsal view, \times 18, ROM 37677, KK 123.
- H Cranidium, dorsal view, \times 18, ROM 37719, KK 123.
- I Cranidium, dorsal view, \times 18, ROM 37720, KK 123.
- J Pygidium, dorsal view, \times 18, ROM 37721, KK 123.
- K Hypostome, ventral view, \times 18, ROM 37660, KK 123.

Yukonaspis sp.

- L Cranidium, dorsal view, \times 13, ROM 37725, KK 124.
- M,N Free cheek, dorsal and lateral views, \times 11, ROM 37726, KK 124. Larifugula leonensis (Winston and Nicholls, 1967).
- O Partial thorax, dorsal view, \times 13, ROM 37722, KK 124.
- P,Q Cranidium, dorsal and oblique views, \times 11, ROM 37723, KK 124.
- R Pygidium, dorsal view, \times 13, ROM 37724, KK 124.



Fig. 68 Tatonaspis diorbita sp. nov.

- A,B Holotype cranidium, dorsal and anterior views, \times 6, ROM 37619, K 550.
 - c Cranidium, dorsal view, \times 6, ROM 37620, K 550.
 - D Cranidium, dorsal view, \times 7, ROM 37621, K 550.
 - E Cranidium, dorsal view, \times 13, ROM 37627, K 550.
- F-H Yoked cheeks, oblique, anterior and dorsal views, \times 9, ROM 37626, K 550. 1 Pygidium, dorsal view, \times 9, ROM 37622, K 550.
- J-L Pygidium, posterior, dorsal and lateral views, \times 8, ROM 37623, K 550.
- M Pygidium, ventral view, \times 8, ROM 37625, K 550.

N Pygidium, ventral view, \times 11, ROM 37624, K 550.

Levisaspis glabrus (Shaw). O-Q Cranidium, dorsal, oblique and anterior views, \times 13, ROM 37612, KK 113. Meteoraspis? sp.

- R Cranidium, dorsal view, \times 18, ROM 37507, K 510.
- s Cranidium, dorsal view, \times 18, ROM 37508, K 510.
- T Cranidium, ventral view, \times 18, ROM 37509, K 510.



Fig. 69 Geragnostus sp.

- A Pygidium, dorsal view, \times 13, ROM 37605, K 510.
- B Pygidium, dorsal view, \times 13, ROM 37607, K 510.
- C Cephalon, dorsal view, \times 13, ROM 37606, K 510.
- "Calvinella" palpebra sp. nov.
 - D Cranidium, dorsal view, \times 11, ROM 37753, K 510.
 - E Cranidium, dorsal view, \times 6, ROM 37752, K 510.
- Yukonaspis kindlei Kobayashi, 1936a.
- F-H Pygidium, posterior, lateral and dorsal views, \times 5.5, ROM 37754, K 510.
 - 1 Free cheek, ventral view, \times 9, ROM 37755, K 510.
- Missisquoia sp.
 - J Cranidium, dorsal view, \times 13, ROM 37756, KK 133.
- Apoplanias rejectus Lochman, 1964a.
- K,L Cranidium, dorsal and lateral views, \times 13, ROM 37757, KK 43.
- M-O Pygidium, dorsal, posterior and lateral views, × 11, ROM 37759, KK 43.
- P,Q $\,$ Cranidium, oblique and dorsal views, \times 11, ROM 37758, KK 43.
- Tatonaspis diorbita sp. nov.
 - R Cranidium, dorsal view, \times 11, ROM 37760, K 525.
 - s Pygidium, dorsal view, \times 13, ROM 37761, K 525.
 - T Cranidium, dorsal view, \times 7, ROM 37762, K 525.


Fig. 70 Yukonaspis kindlei Kobayashi, 1936a.

A-C Holotype cranidium, dorsal, oblique, and anterior views, × 9, GSC 8718, Upper Cambrian limestone, Squaw Mountain, north of Tatonduk River, Alaska-Yukon boundary.
Geragnostus reductus (Winston and Nicholls, 1967).

Both from Missisquoia typicalis Subzone, Wilberns Formation, central Texas.

D,E Pygidium, dorsal and posterior views, \times 9, USNM I185940.

F,G Holotype cephalon, dorsal and anterior views, \times 9, USNM I185941.

Larifugula leonensis (Winston and Nicholls, 1967).

All from Corbinia apopsis Subzone, Wilberns Formation, Leon Creek, Mason County, central Texas.

- H-J Holotype cranidium, dorsal, anterior and oblique views, \times 13, USNM I185888.
- K Pygidium, dorsal view, \times 13, USNM I185887.

L Cranidium, dorsal view, \times 13, USNM I185889.

Geragnostus (Micragnostus) subobesus (Kobayashi, 1936a).

M Lectotype cephalon, dorsal view, × 9, GSC 8717, Lower Ordovician limestone, Jones Ridge, north of Tatonduk River, Alaska-Yukon boundary.

Richardsonella arctostriata (Raymond, 1937).

Both from Zone 1, Gorge Formation, Highgate Falls, Vermont.

N Holotype cranidium, dorsal view, \times 5.5, YPM 14701A.

0 Pygidium, dorsal view, \times 5.5, YPM 14701C.

Liostracinoides vermontanus Raymond, 1937.

P Holotype cranidium, dorsal view, × 13, YPM 14710, Zone 1, Gorge Formation, Highgate Falls, Vermont.

Richardsonella spiculata (Raymond, 1937).

Q Holotype pygidium, dorsal view, \times 9, YPM 14704, Zone 1, Gorge Formation, Highgate Falls, Vermont.



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