CONODONT PALEONTOLOGY OF THE PERMIAN

SABINE BAY, ASSISTANCE AND TROLD FIORD FORMATIONS, NORTHERN ELLESMERE ISLAND, CANADIAN ARCTIC ARCHIPELAGO

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ABSTRACT

A succession of late Early through Medial Permian conodont faunas is documented for the first time from the calcareous, fine grained, quartzose sandstones of the Assistance and Trold Fiord Formations on northern Ellesmere Island, Northwest Territories. Of the taxa identified and described, one species and three subspecies are proposed as new. The taxa include, in chronological order: Neogondolella idahoensis subsp. indet., Neostreptognathodus prayi, Neogondolella idahoensis n.subsp. A, Anchignathodus minutus, Neogondolella serrata(?), N. n.sp. B, N. postserrata(?), N. bitteri n.subsp. <u>C</u>, and <u>N</u>. rosenkrantzi n.subsp. <u>D</u>. Numerous ramiform elements are also associated with <u>Neogondolella</u> <u>idahoensis</u> n.subsp. <u>A</u>. These elements may comprise part of a multielement Neogondolella apparatus or they may represent separate form species. In observation of their questionable status, a somewhat unsatisfactory dual taxonomy is proposed for these elements and includes the following taxa: N. idahoensis n.subsp. A - Xaniognathus tortilis, N. idahoensis n.subsp. A - Ellisonia excavata, N. idahoensis n.subsp. <u>A</u> - <u>Ellisonia</u> tribulosa, and <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> - <u>Pri</u>oniodella decrescens.

Statistical work on the abundant platform elements of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> provides evidence for minor evolutionary trends of increasing size and increasing number of denticles upsection. Comparison of these conodonts with <u>N</u>. <u>serrata</u> and <u>N</u>. <u>postserrata</u> from the Great Basin of SW USA suggests that the phylogenetic development of Permian <u>Neogondolella</u> followed and evolutionary path more appropriate to punctuated equilibria than to phyletic gradualism.

The conodont taxa indicate that the Assistance Formation is Upper

Leonardian to Uppermost Roadian in age whereas the Trold Fiord Formation includes most of the Wordian stage. These two formations have been separated into five subdivisions on the basis of both lithology and the presence or absence of various biota. A sixth subdivision is described for the Sabine Bay Formation which underlies the Assistance and where conodonts are apparently absent.

Lithologic and biotic evidence (including trace fossils and mega- and microbiota) point to shallow, offshore marine conditions well within the photic zone and characterized by low energy and slow depositional rates, for most of the conodont bearing strata. A much thicker correlative section to the south represents, in large part, a delta front sequence. The Sabine Bay Formation, on the other hand, is composed of shoreface sandstones, possibly in a barrier island setting.

The results of this research indicate that conodonts may be very promising for correlation of Permian strata in the Canadian Arctic Archipelago and for worldwide comparison. More work within the Sverdrup Basin, including both marginal and basinal sections , is necessary to provide a good biozonation of these marine Permian strata. The use of the abundant brachiopods in combination with the conodonts is probably the best way to resolve this zonation. The taxonomic descriptions and subdivisions proposed herein should provide a foundation for future work.

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INTRODUCTION

This thesis records the results of a study of the conodont biostratigraphy of the Permian Sabine Bay, Assistance and Trold Fiord Formations of northern Ellesmere Island, N.W.T. To a lesser extent brachiopods and lithofacies were utilized to establish correlations.

Location and Scope of the Study

Ellesmere Island, the most northerly island of the Canadian Arctic Archipelago, is located between 76° and 83° North latitude. The study is based primarily on seven sections from four different areas including two from Hamilton Peninsula (80°10' N, 081°45' W), two from McKinley Bay (81°10' N, 079°10'W), two from the head of Tanquary Fiord (81°25' N, 076°30' W) and one from the Sawtooth Range (79°30' N, 083°20' W) (sections A, B, C, and D respectively on Fig. 1). Other sections have been studied in minor detail (Fig. 1) and are only referred to where they proved valuable as support for any interpretations.

The lithology studied in the above mentioned sections represent the marginal facies for the Permián part of the Sverdrup Basin; a basin of deposition from early Carboniferous to Tertiary. Despite the descriptive and reconnaissance studies by previous workers (Thorsteinsson, 1974; Christie, 1964; Nassichuk and Christie, 1969; and Mayr, 1976) the Permian part of the basin remains the poorest understood of the Phanerozoic systems. Fossil collections and age determinations have been previously reported from the Sabine Bay, Assistance and Trold Fiord Formations by Nassichuk et al. (1965), Harker and Thorsteinsson (1960), Nassichuk (1970), Nassichuk and Spinosa (1970) and by J.B. Waterhouse and R.E. Grant in Thorsteinsson (1974). The material reported on herein constitutes the first systematic collections through the



Figure 1. Map of northern Ellesmere Island, showing location of the sections studied.

complete sections: the previous reports were largely of isolated occurrences. These previous studies emphasized ammonoids and brachiopods to facilitate correlation. Both of these groups have their own peculiar problems associated with them (see p. 25) that hinder correlation schemes. This report emphasizes the use of conodonts, a group whose once many problems hindering correlation have been largely ironed out by intensive research over the past five years (Clark and Behnken, 1979; Clark et al., 1979 and Wardlaw and Collinson, 1979b).

It is because of the correlation problems for certain fossil groups, the abrupt lithologic changes over short distances, and the presence of disconformities and transgressive units that the correlation and environmental relationships of the formations pertaining to this report are poorly understood. The original intention for the research was to better define the age and correlation of these formations. This seems to have been accomplished through the use of conodonts although the results should only be regarded as a beginning, but a start that at least justifies optimism. Field Work

Access to the study area is by Twin Otter or DC-3 aircraft from Resolute Bay, Cornwallis Island, to Eureka or Tanquary Fiord airstrips. From these bases access to the section localities was accomplished through the use of Jet Ranger helicopters.

The field work was completed during three weeks between June 16 and August 11, 1979. The section description was completed with the aid of an assistant from fly camps consisting of a logan and a pyramid tent at each of the localities. Radio contact was maintained at regular times with the main base at Eureka or Tanquary Fiord to report weather, and to indicate move dates and supplies required.

The weather through the period indicated above was a mixture of sun and cloud and included only two weather related down-days. This fiftyseven day period saw three days with snow flurries and nine days of showers or rain. During this entire period the sections studied were free of ice and snow with the exception of the minor flurries. Otherwise sunshine was the order of the day with temperatures reaching as high as 19%C (July 30) but more typically averaged 3 to 10°C. Daytime temperature fluctuations were minor as at this latitude the sun remains above the horizon from April 15 to August 29 (Thorsteinsson, 1974). Part of the camp remained at Tanquary Fiord after the 11th of August but snow began to fall on the 12th and camp was folded for the season by the 16th when no break was in sight. <u>Previous Work</u>

The summary of previous work in the area as presented herein, and especially of the early history, is largely taken from R.L. Christie's Geological Survey of Canada (GSC) Memoir 331 (1964) and to whom the credit is due.

The history of exploration and geological investigation of northern Ellesmere Island is a very auspicious and colourful one. The first geological studies were by a British explorer, Captain Sir George Nares, on a 1875-76 Royal Navy expedition to Lady Franklin Bay. Captain H.W. Feilden, a naturalist on Nares' expedition, and others made extensive collections of rocks and fossils in the region between Discovery Harbour and Feilden Peninsula. Lieutenant Adolphus W. Greely of the U.S. Army established Fort Conger in Discovery Harbour in 1881. Expeditions went to Lake Hazen and Greely Fiord during 1882-83 where geological and archaeological specimens were collected and copious notes made. This success was tainted by the tragic end of the expedition where all but seven men died of starvation because a planned rendesvous with a return vessel was late.

The area was explored by a number of others over the next seventy years including Commander R.E. Peary (1898-1909), a geologist W. Elmer Ekblaw (1913-17) who collected Permian fusulinids from near the mouth of Tanquary Fiord, and a geologist Dr. J.C. Troelsen (1939-40).

The first appearance of the GSC was in 1948 by V.K. Prest along the northeast shore of Ellesmere. G. Hattersley-Smith (Defence Research Board) and R.G. Blackadar (GSC) later conducted geological reconnaissance in the Lake Hazen area. R.L. Christie of the GSC conducted field work in 1954, 1957, and 1958 in northeast Ellesmere producing a map in his GSC Memoir In 1956 and 1957 R. Thorsteinsson and E.T. Tozer investigated western 331. Ellesmere Island. This work and much of the previous work was conducted by means of dog teams and canoe over extended field seasons. In 1961 and 1962 Operation Eureka, under the direction of R. Thorsteinsson of the GSC, included J. Wm. Kerr, E.T. Tozer, and H.P. Trettin. During this period transportation included Piper Super Cub aircraft and a G2A helicopter. In 1963 R. Thorsteinsson and P. Harker conducted further stratigraphic studies and mapping of Ellesmere. These five field seasons are the foundation dtion for Thorsteinsson's GSC Bulletin 224 (1974) which remains today as the major work on Carboniferous and Permian stratigraphy in the area.

Previous fossil work was largely on brachiopods and ammonoids as indicated in the first part of this chapter. However, late Lower Permian through Middle Permian conodonts from the area have only been reported once previously (Kozur and Nassichuk, 1977) and this was of just two collections (see p. 28 for details).

The designation of the three formations of this report date between 1960 and 1974. The Sabine Bay Formation was named by Tozer and Thorsteins-

son (1964) for a section on Sabine Peninsula, Melville Island. The Assistance Formation was named and defined by Harker and Thorsteinsson (1960) for a succession on Grinnell Peninsula, Devon Island. Finally, the Trold Fiord Formation was defined by Thorsteinsson (1974) and includes a type section on a small, unnamed tributary of the East Cape River that issues into the northeast side of Canon Fiord on the west coast of Ellesmere (very near the Hamilton Peninsula sections of this report).

The most precise way to summarize the previous work in the area on Carboniferous and Permian rocks is to say that the reconnaissance has been completed but that detailed studies are merely beginning.

Laboratory and Analytical Methods

Laboratory work was conducted from the fall of 1979 to the spring of 1981. A standard technique of acetic acid dissolution, wet sieving, and heavy liquid separation (tetrabromoethane) was used to concentrate the conodonts from their host rocks.

The bulk samples that were processed were of two types. The first consisted of large single blocks or a number of moderate sized slabs that weighed up to 25 kg (55 lbs.) but more typically averaged 10 kg (22 lbs.). These blocks were collected for their finely silicified brachiopod content which were to have been the major emphasis of the research (the emphasis switched to conodonts about half-way through the processing). The second type consisted of 2 to 3 cm diameter chips collected from single horizons specifically for conodonts and weighing between 3.2 and 4.2 kg (7 to 9 lbs.) in total.

The large blocks were broken into two fractions. Small fragments were broken off the blocks and retained for conodonts while the remainder (1/2 to 3/4 of the total) was placed in hydrochloric acid baths (diluted, but not to specific percent as the only criterion to be met was that bubbling was not to be so strong as to cause further breakage of the silicified fossils) to separate the silicified brachiopods. The conodont samples were placed in plastic buckets which were subsequently filled with a solution of 60% glacial acetic acid at a dilution of 1 part acid to 6 to 9 parts water (to keep the acid at or below 10% - stronger acetic acid tends to etch the conodonts while any strength of hydrochloric will dissolve the conodonts). The samples were left in a fume hood for up to two months but more typically for two to three weeks with the acid being changed weekly. The longer than normal dissolution period for such work was required because the rocks, being calcareous quartzose sandstones, were slow to dissolve and contained a high percentage of insolubles (as opposed to pure carbonates which are more commonly sampled for conodonts). Even after these long periods, the samples were rarely entirely dissolved and dissolution was usually discontinued after it was felt sufficient insoluble residue had been separated. As a result, it is impossible to report the actual percentage of insoluble residue. It was necessary to use a modified procedure for isolating the conodonts due to the large insoluble fractions. After the samples were dissolved, they were wet sieved and washed through a four sieve stack consisting of 20 (.841 mm), 35 (.500 mm), 100 (.150 mm) and 200 mesh (.075) mm) standard 21 cm diameter sieves. On top of this stack was a 1.2 mm nylon screen to retain the coarsest particles and undissolved The two coarsest sieves were used to separate any coarse sand or chunks. small undissolved fragments from the fine sand and, hopefully, conodonts which would be trapped in the finest two sieves. This stack was necessary because of the high percentage of insoluble material. Normally, a single

150 or 200 mesh sieve with a nylon screen on top is sufficient for the insolubles of relatively pure carbonates. All of the insoluble residue was retained and left to air dry in porcelain crucibles. The silt and clay fraction that filtered through the finest sieve was also collected in plastic buckets and allowed to settle. After the sediment had settled most of the excess water was poured off and the wet sediment stored in covered plastic containers. Some of these samples were later analyzed for their palynomorph content in conjunction with a graduate course with G.E. Rouse at UBC.

After drying, the 100 and 200 mesh insoluble fractions were placed in separatory funnels filled with tetrabromoethane (specific gravity = 2.89). The remaining coarser insolubles were placed in a container and stored in cabinets. The insolubles in the separatory funnels divided into two fractions: a light fraction floating on top and consisting of quartz, chert, glauconite and silicified or siliceous microfossils and a heavy fraction sinking to the bottom and consisting of opaques, iron coated grains, fish debris (teeth, plates...) and conodonts (specific gravity = 2.84 to 3.10: Ellison, 1944). These heavy fractions were then allowed to run out of the funnel onto a filter paper. Similarly, the light fraction was filtered onto a separate paper. The tetrabromoethane was constantly reused owing to the high cost of the material. These fractions were then thoroughly washed with acetone and left to dry. The acetone with its dissolved tetrabromoethane in solution was placed in an open beaker and allowed to evaporate in a fume hood until the tetrabromoethane was concentrated (acetone evaporates more rapidly). This procedure allowed only minimal loss of heavy liquid with each separation. After drying, the conodonts were picked from the heavy fractions with the

aid of a binocular microscope and a wét, very fine paint brush. However, if the heavy fraction was large and contained abundant iron minerals, the sample was passed through a magnetic separator where the conodonts are further concentrated in the non-magnetic heavy fraction. This procedure saves unnecessary time spent picking non-productive residues.

The condonts having been concentrated from their rock in abundances, when present, ranging from one to as many as 150 per kg (F49), were thus available for detailed study. The analysis of these faunas first consisted of simple observation under the binocular microscope and description. Secondly, the samples were measured for various parameters with a micrometer mounted on a binocular microscope. These measurements were used to enhance descriptions and subjected to various statistical procedures as outlined in a later chapter. Thirdly, the samples were putrion Scanning Electron Microscope (SEM) stubs, coated with gold-palladium, and photographed with the SEM. These photos besides providing the illustrations for the plates facilitated even more detailed description. Indeed, adequate description would be impossible without the SEM. The identification and comparison. to other similar conodonts to determine the age relationships and correlation of the studied sections concluded the analysis of the conodonts.

The sections were also analyzed in terms of their lithology and other biota. Descriptions of the lithology were restricted to the field notes and a close inspection of hand specimens. Although a few thin sections were prepared it was decided that time was insufficient to do an adequate study, nor did it seem necessary in a paleontological thesis. The remaining biota were identified at high taxonomic levels and used as a rough guide to changing biofacies. Some brachiopod genera were identified as they aided, to a lesser degree, the age determinations of the strata herein described.

STRATIGRAPHY AND PALEOENVIRONMENT - GENERAL STATEMENT

A discussion of the stratigraphy for the marginal facies of the youngest Permian on Ellesmere Island follows. This chapter is based on the megascopic description of the strata and sediments, and on the megabiota and trace fossils present. The paleoenvironmental interpretations recorded herein are not meant to be definitive as they are founded on rough data. The expected characteristics for various environments as described in Brenner and Davies (1974), Davies et al. (1971), Dickinson et al. (1972), Goldring and Bridges (1973), Harms et al. (1975), Howard (1972) and Miall (1978) are summarized in Figure 2.

Sabine Bay Formation

A. Hamilton Peninsula area

Here the Sabine Bay Formation, which overlies the Belcher Channel Formation and overlain by the Assistance, is characterized by cyclic sedimentary environments (Fig. 3 shows features mentioned in this chapter).

The formation consists of 180 metres of medium, clean, well sorted, friable quartzose sandstones with some fine and coarse sand and sparse granules and pebbles. The sandstones are porous (10 to 15% estimated) and usually uncemented although local calcite cement is present. Fresh surfaces are generally white to light beige in colour while weathered surfaces are dominantly yellowish brown to brownish orange but may also be medium brown and pale red or creamy pink. The sandstones are generally thick bedded to massive but exhibit faint internal laminae upon closer examination. Crossbedding is not common but locally conspicuous. The sequence is cut by a couple of dykes (up to 3 m thick), the delineation of which would be important in terms of hydrocarbon preservation as Thorsteinsson (1974) reports

	<u>}</u>			<u> </u>				
shallow offshore	transition	lower shoreface	upper shoreface	transition	foreshore			
thin beds few sedi- mentary structures- siltstone extensive bioturba- tion low energy organic rich conodonts abundant neogondol- ellids occur in deeper, lower en- ergy, less nutrient rich enviro idiognathod	-increasin -increasin shore fine, and clean sand- stone fine sand beds thick- en upwards siltstone inter- bedded ripple laminae cross bedding mega ripples	g depth g distance from -fine to medium dirty sand- stone -30 to 45 cm thick beds -parallel laminae -lens like crossbedding -abundant large distinct trace fossils	-fine to medium, clean sandstone -well sorted -trough crossbedding -minor amount of burrowing -beds trunca- ted -ripple laminae	-fine to medium, clean sandstone -well sort- ed -trough cross- bedding -minor amount of bur- rowing	-very clean, well sorted, fine to medium sandstone -low dipping, parallel to sub- parallel bedding -some convolute laminae -no trace fossils			
deposit and feeders -burrows mor tal and dev branches -higher dive	sediment e horizon- elop ersity	-low diversity of burrows, suspension feeders -unbranched, vertical to steeply inclined burrows						

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Figure 2. Generalized list of characteristics for various shallow marine environments.

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Figure 3. Lithologic and biologic characteristics and correlation of the formations and sections pertinent to this report.

bituminous residues in an outcrop on Hamilton Peninsula.

A coquinoid unit of rugosochonetid brachiopods outcrops 30 metres from the top of the formation. Coarse ribbed <u>Spirophyton</u> is present in this unit and in the overlying 30 m, but absent below.

The type of ribbing or laminae present on Spirophyton seems to be very useful for paleoenvironmental interpretation for the Permian rocks of Ellesmere. Marintsch and Finks (1978) in a study of Devonian Zoophycus (a trace fossil similar to Spirophyton) demonstrated environmental significance for the mean and maximum diameter of the trace and for the meniscus height (related to ribbing diameter of the trace and maximum body diameter of the organism creating the burrow). They found that the animal is largest near the centre of its environmental range (quiet, relatively deep offshore marine), smallest near the margins (shallower, higher energy) and absent in the shallowest water beds within their sequence. Observations for the Permián of Ellesmere suggest that the coarse ribbed, smaller diameter (10 to 20 cm) Spirophyton are found in shallow shoreface environments while the fine ribbed, larger diameter (20 to 35 cm) are found in deeper, quieter offshore marine conditions. Any environments interpreted as foreshore or transitional between foreshore and shoreface do not contain any Spirophyton. Apparently, Spirophyton is also absent from the Van Hauen and Degerbols Formations which are the basinal equivalents of the Assistance and Trold Fiord Formations. Brachiopods were never found in abundance in beds containing Spirophyton although a few may be present near by.

Two other features are noteworthy with regards to the Sabine Bay Formation. The first is an unusual unidentified helical burrow (5 to 12 cm diameter) found on bedding surfaces with large scale ripples (wavelength = 0.9 to 1.15 m, Amplitude = 20 to 30 cm) and probably representing an upper

shoreface environment. These burrows are fairly evenly spaced (0.3 m apart) suggesting high competition for resources. These burrows have been found at Hamilton Peninsula and McKinley Bay within the Sabine Bay Formation and at Henrietta-Nesmith (Fig. 1) in possible shallow water equivalents of the Trold Fiord Formation. Secondly, no conodonts or any other microbiota other than palynomorphs are present in this formation.

B. McKinley Bay area

Here 33 metres of Sabine Bay Formation unconformably overlie the Nansen and are overlain in turn by a thin section of the Assistance Formation. The Sabine Bay begins with dirty, fine to very fine quartzose sandstone with coarse ribbed <u>Spirophyton</u> and carbonaceous material to clean, very fine arenite with a coquina of rugosochonetid brachiopods all of which is interpreted as a lower shoreface environment. This unit apparently progrades into an upper shoreface environment (fine to medium grained, clean quartzose arenites), which in turn transgresses into a lower shoreface environment (brachiopod and bivalve coquinoid quartzose sandstone), and finally progrades into a foreshore environment (fine grained, very clean quartzose arenite).

C. Tanquary Fiord area

The formation ranges in thickness from 36 to 70 metres, thinning towards the north and onlapping the Tanquary structural high. The Sabine Bay Formation unconformably overlies the Canyon Fiord Formation and is in turn overlain unconformably by the Triassic Bjorne Formation as no Assistance or Trold Fiord equivalents are present. The Sabine Bay can be divided into three units including upper and lower units of clean, fine tomedium grained quartzose arenites representing shallow shoreface to fore-

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shore environments, and a middle unit of poorly sorted, very fine sandstone to siltstone and minor shale with a distinct root zone (with coalified roots or other plant fragments) suggesting a backbarrier lagoon or marsh environment at least partly emergent. Except for roots no other megafossils or traces were observed.

Assistance Formation

A. Hamilton Peninsula area

The Assistance Formation at Hamilton Peninsula includes between 162 and 178 metres of section depending on the position of the talus-covered boundary with the overlying Trold Fiord Formation. The lowest part of the Assistance consists of a fine grained, poorly sorted, quartzose sandstone with carbonaceous material, trace fossils (coarse ribbed <u>Spirophyton</u> and <u>Skolithos</u>), minor rounded pebbles and fragmented biota at the top of one bed, calcite cement, and glauconite. The Assistance is similar to parts of the Sabine Bay, except for the glauconite. Although the appearance upsection of glauconite is abrupt, the remaining lithology suggests that the boundary between the Assistance and the underlying Sabine Bay may be gradational and continuous. Thorsteinsson (1974) interprets this boundary as a disconformity which, if present, must be of short duration.

The pebbly sandstone unit is followed by strata that typically weather yellowish grey to greyish orange with fresh surfaces being various shades of grey, and composed of very fine quartzose sandstone to siltstone with variable amounts of calcareous cement. These rocks contain abundant carbonaceous material, trace fossils (<u>Asterosoma</u>, fine ribbed <u>Spirophyton</u>, <u>Planolites</u> (3 to 5 mm diameter) and other unidentified types), and abundant megaand microbiota. Glauconite is present in all of these rocks but never as abundant as in the overlying Trold Fiord Formation. A large part of the section is soft and friable and was generally measured as cover or talus while harder more calcareous sandstones stand out prominently. Bedding is generally thin to medium but poorly defined. Few other sedimentary structures were observed although carbonaceous material is often arranged as irregular laminations. All factors point to the prevalence of shallow offshore marine conditions away from shoreface environments although a few fine grained, cleaner quartzose sandstone beds may represent transitional beds between offshore and lower shoreface. The extensive bioturbation and presence of the authigenic-mineral glauconite suggest that rates of deposition were considerably less than for the Sabine Bay.

Conodonts are abundant in the lower half of the formation and include <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> and <u>Anchignathodus minutus</u>. The <u>Neogon-</u> <u>dolella</u> fauna is very abundant and include a significant proportion of complete specimens. A large number of ramiform elements occur in association with <u>Neogondolella</u>. No other assemblage in the Assistance or Trold Fiord Formations has as many ramiforms compared to platforms; in fact, most had none. The colours of these conodonts are brown to dark brown and have an alteration index of 2.0 according to Epstein et al. (1977). This indicates métamorphic temperatures of 60 to 140°_{\circ} C and a fixed carbon range of 55 to 70%, well within the limits for petroleum preservation. Conodonts in the upper half of the formation are fragmented and rare and include <u>N. serrata(?)</u> and a couple of ramiform fragments.

B. McKinley Bay area

The Assistance Formation, which was not previously recognized at Mc Kinley Bay, is defined here as a thin (3 to 4 m) unit of greyish yellow weathering, fine to medium grained quartzose sandstone followed by a unit of matrix supported, dark grey chert-pebble conglomerate. Large brachiopods and bryozoan fragments occur within this unit which is variably cemented by calcite. Recrystallized conodonts (possibly as a result of intense heating by a nearby dyke) were found in one sample (F100) and included Neogondolella idahoensis and Neostreptognathodus prayi. The occurrence of two Neostreptognathodus fragments is unique to this sample. Clark (1974) indicated that gnathodids throve in very shallow nutrient rich water of moderate energy and normal salinity, whereas gondolellids and anchignathodids preferred deeper water, perhaps at the limit of the photic zone. There are no indications from the lithology or associated biota at F100 (dominantly moderate sized productids and small spiriferids), to suggest that the represented environments are shallower than those of other conodont occurrences in the Assistance at Hamilton Peninsula. The most significant difference is the position within the basin to the extent that the McKinley Bay section is closer to the basin margin than the Hamilton Peninsula sections. Despite the obvious cyclicity of environments at Hamilton Peninsula no Neostreptognathodus specimens were found. Those samples with Neogondolella were nearly always associated with 3 to 5 mm diameter Planolites; untransported megafauna intensely bored by an endolithic chlorophyte alga indicate a low energy, shallow marine environment well within the photic zone. These observations and interpretations suggest that either the different environmental conditions controlling the distribution of these two genera are subtle and as yet unrecognized for this area or that Neostreptognathodus was very rare in the Permian of the Sverdrup Basin.

D. Sawtooth Range area

This section of Assistance rocks is very thick (515 to 545 m after removing the 88 m sill) and can be divided into two units. The lower 450 m

thick unit is characterized by yellow-grey weathering, fine grained quartzose sandstone, with variable amounts of carbonaceous material, trace fossils (<u>Skolithos</u> and coarse ribbed <u>Spirophyton</u>), calcareous and/or siliceous cements and practically no megafossils. Pendants within the sill and a few beds above it contain brachiopods (<u>Jakutoproductus(?</u>) - see p.32 for significance) and small pelecypods. As glauconite is not present in any of these rocks relatively rapid deposition is implied. The proposed paleoenvironmental interpretation for this unit is of some sort of a delta complex. The deposition is interpreted as occurring at the delta front in lower shoreface and transitional environments. The thickness of these deposits compared to sections to the northeast, the rapidity of deposition, dominance of deposit feeders, and the abundance of carbonaceous material all confirm a deltaic environment (Weimer, 1970).

The upper 95 m thick unit is characterized by fine to very fine grained, fossiliferous (almost coquinoid), quartzose sandstone with varying amounts of carbonaceous material and glauconite. These sediments are intensely burrowed (fine ribbed <u>Spirophyton</u>, and <u>Asterosoma</u>), have irregular platy bedding and are very similar to the lithology of the Assistance at Hamilton Peninsula. The presence of abundant brachiopods and bryozoans as well as glauconite suggests lower energy conditions and slower deposition. Apparently this unit is transgressive over the lower unit. Transgressions are often initiated when all or part of a delta system is abandoned so that subsidence increases relative to the deposition.

Trold Fiord Formation

A. Hamilton Peninsula area

The Trold Fiord Formation is characterized by glauconite rich, fine

quartzose sandstones but also consists of minor biogenic arenaceous limestone, chert-pebble conglomerate, and chert (major components are sponge spicules). On the basis of regional overstepping by the Trold Fiord on older formations from NW to SE, Thorsteinsson (1974) indicated a disconformity at the boundary between the Assistance and Trold Fiord Formations. However, this author saw no evidence for such an interpretation at Hamilton Peninsula. Unless the seas totally vacated the basin one would expect some sections to show a nearly continuous record while others may show a major hiatus.

The lowest parts of the Trold Fiord (Subdivision D) are characterized by silicified coquinas of brachiopods in a glauconitic, fine quartzose sandstone which contains only minor amounts of carbonaceous material (in distinction to the more carbonaceous Assistance) presumably due to decreased introduction of terrigenous plant material further offshore. The coquinas, which are typically of shallow subtidal origin, are composed of dominantly small, unfragmented, and sometimes articulated productids, and lesser amounts of fragmented large productids and spiriferids. Other biota form only a small fraction of the total biomass while conodonts are apparently absent. This unit weathers dusky yellow with minor red while fresh surfaces are greyish yellow-green and only occasionally red.

The majority of the glauconite formed in the small pores of echinoderm fragments and progressively replaced the structure until a solid bleb of glauconite resulted. Glauconite also formed in the chambers of small forams and in the zooecia of bryozoa. It is generally regarded that glauconite forms by the alteration of kaolinite clays in locally reducing conditions (provided by the small pores of biotic elements, presumably owing to con-

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centrations of decaying organic matter) but in a generally oxidizing environment (provided by action of shallow marine waves). As well as being most common on the outer edge of the shelf and on topographic highs, glauconite is invariably associated with low sedimentation rates because of the low concentration of soluble iron in the ocean and because the glauconitization process stops after burial owing to the loss of the proper chemical environment (Burst, 1958).

A 5½ metre unit of chert granule and pebble conglomerate is a characteristic part of Subdivision E in the middle of the Trold Fiord Formation. The lower five metres are concentrated in lenses or channels and grade laterally into burrowed (8 to 10 mm diameter Planolites), very fine to fine grained glauconitic quartzose sandstone. The upper 0.5 metres is represented by a solid bed of red and yellow chert pebble conglomerate which may represent a transgressive lag deposit. Large unbroken productids (Thamnosia) are present in this interval. Despite their thick shells, the energy of the depositional environment must have been low for the shells to remain unbroken, which seems somewhat anomalous in light of the grain size. The brachiopods are also intensely bored by polychaetes and barnacles suggesting that they were exposed to the marine environment for a significant time The conodonts, which before their incorporation into the conglomerate. are rare and fragmented in this unit, include <u>Neogondolella</u> n.sp. <u>B</u> and <u>N</u>. postserrata(?).

The upper parts of the Trold Fiord (Subdivision F) begin with coquinas of silicified brachiopods similar to those lower in the section. Some beds are dominated by bryozoans where these encrusting sheet-like and cylindrical trepostomes comprise up to 50% of the rock volume. A minor amount of

blue-grey chert also occurs in this interval. Carbonaceous blebs and films are sporadic and usually associated with burrowing. The sandstones throughout this unit are very fine to fine grained and moderately to well sorted. Weathering colours include greyish orange, greyish yellow and greyish yellow -green whereas fresh surfaces are greyish olive to dusky yellow-green.

Abundance of conodonts in this unit is comparable to that of <u>Neogon-</u> <u>dolella</u> n.subsp. <u>A</u> assemblages. Between these two assemblages conodont populations are sparse. The conodonts in this Trold Fiord unit, some of which are complete, include <u>Neogondolella</u> <u>bitteri</u> n.subsp. <u>C</u> and <u>Neogondolella rosenkrantzi</u> n.subsp. <u>D</u>. Only one small fragmented and unidentified ramiform element was found in association. Colours of these conodonts are almost original amber and have a colour alteration index of 1.5 (very pale brown) according to Epstein et al. (1977). This indicates metamorphic temperatures of 50 to 90° C and a fixed carbon range of 55 to 70%, well within the limits for petroleum generation and preservation.

The highest beds of the Trold Fiord are burrowed (medium ribbed <u>Spirophyton</u>), fine grained, quartzose sandstone with small spiriferids and phosphatic nodules containing moderately large inarticulate brachiopods (<u>Lingula</u>) and fish debris. The environments represented by this unit are largely shallow subtidal marine to possibly transitional shoreface at the top. This unit is overlain unconformably by the Triassic Bjorne sandstone. B. McKinley Bay area

Here the Trold Fiord Formation ranges in thickness from 24 to 61 metres over a distance of 1.6 km (1 mile). The base of the formation consists of one metre of red weathering chert granule and pebble conglomerate with large spiriferids and moderate sized productids (<u>Thamnosia</u>?). Above the conglomerate, silicified coquinas of brachiopods (mostly of small size)

occur in a very fine grained sandstone to arenaceous carbonate. At least part of this unit demonstrates features suggesting hardground development; brachiopod coquinas (most are in life position) totally surrounded by encrusting trepostome bryozoans with the zooecia later filled with glauconite. The brachiopods are intensely bored by endolithic algae and acrothoracican barnacles, the density of which may be an indicator of relative exposure time. The remainder of the section consists of fine grained, glauconitic, quartzose sandstones with minor burrowing (<u>Spirophyton</u>) and rare brachiopods and gastropods. Inarticulate brachiopods characterize the highest beds. Only a couple of unidentifiable <u>Neogondolella</u> fragments were found at this locality.

D. Sawtooth Range area

This sequence of Trold Fiord strata is thicker and contains less biota then the Hamilton Peninsula section. The lower parts of the formation are characterized by fine to very fine glauconitic, quartzose sandstones with shaly layers, minor burrowing, and rare brachiopods. The few brachiopod horizons that do occur have been leached of all original shell. The lowest 169 metres are particularly low in bioclastic debris. Most of this interval weathers dark green and has more glauconite than quartz grains, however, two samples (L38 and L46) weathered blue-grey in colour and had far less glauconite. The cements in these sandstones are dominated by silica but minor calcite is also present.

Once again the middle part of the Trold Fiord is characterized by chert granule and pebble conglomerates. The conglomerate interval is 20 metres thick but discontinuous as the granules and pebbles are concentrated in lenses or channels. The majority of this unit is red weathering and has

abundant abraded and bored bioclasts (polychaetes, sponge(?), and barnacle borings) including a few Thamnosia and many large spiriferids. Large Planolites (8 to 10 mm diameter), identical to those at Hamilton Peninsula, are also present. Above the conglomeratic unit are about 40 metres of sandstone, similar to the lowest 169 metres. The next 56 metres of section consist of fine grained, variably glauconitic quartzose sandstones that weather green with occasional purplish layers, lacking in carbonaceous material, and contain a few small Planolites burrows. There appears to be evidence for channeling in these sandstones as coquinas of brachiopods are lens-like in distribution. The next 30 metres consist of fine grained sandstone and minor dark greenish grey chert that would be best described as a spiculite. The section ends with monotonous light green weathering, fine grained quartzose sandstone which, except for one locality with inarticulate brachiopods, is generally devoid of megabiota. It is difficult to distinguish particular environments but the majority of the section is undoubtedly of shallow subtidal shelf origin. It is perplexing why brachiopod localities are so few despite the slow depositional rates denoted by the presence of abundant glauconite.

No samples from this section were processed for conodonts, largely because no silicified faunas were present.

AGE AND CORRELATION

A correlation chart for Permian stages and zones is provided in Figure 4; it includes schemes from Grant and Cooper (1973), Furnish (1973), Wardlaw and Collinson (1979a), Waterhouse (1976), and the scheme adopted for this study which is a combination of the others.

The research conducted for this study has significantly refined the age

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Figure 4. Correlation chart for series, stages and zones of the Permian. L = Lower Permian,M = Middle Permian,U = Upper Permian AA = Waterhouse (1975), BB = Furnish (1973), CC = Moore et al. (1965) 1 = Europe, 2 = North America, DD = Wardlaw and Collinson (1979a,b). EF = This study.

relationships of the Assistance and Trold Fiord Formations through the use of conodonts as the biostratigraphic index. Before discussing the results it seems appropriate to relate the state of the art prior to this research. Relative Value of Various Fossil Biota

Five groups have led the way over all others for the determination of biostratigraphic subdivisions of the Permian. These include brachiopods, ammonoids, fusulinids, palynomorphs and conodonts.

Brachiopods were the predominant marine megafauna of the Permian. It is because of this dominance that they can be used to correlate more rocks and on a wider basis than any other group. It is the opinion of many authors that as brachiopods are latitudinally (climatically) controlled and relatively long ranging, their correlation potential is decreased. However, Waterhouse (1976) states that this is a widely reiterated misapprehension and that brachiopod species and genera, during the Permian, were less latitudinally or facies controlled than fusulinids or ammonoids, and just as short-lived. Even if Waterhouse is proven correct by this statement, the extreme diversity of the group makes worldwide mastery of this group, especially at the specific level, very difficult indeed. Waterhouse (1976) also indicates that certain correlation problems will not be solved until paleontologists in the USSR reexamine brachiopod faunules in the Permian type or standard sections of the Urals. In the formations pertinent to this study brachiopods (productids and spiriferids) are by far the dominant biota but need to be studied at the specific level since many genera range throughout the entire section. Because of the problems at the specific level, age determinations have been of minor value or conflicting to officers of the GSC concerned with the Carboniferous and
Permian of Arctic Canada.

Ammonoids are very short-lived, often even at the generic level, and thus prove of infinite value for correlations (Furnish, 1973). However, their value is quickly diminished when one considers the rarity of their occurrence. According to Waterhouse (1976; <u>fide</u>. R.E. Grant, pers. comm.) detailed studies in West Texas produced only 5,000 ammonoids from 97 localities compared to some 3,000,000 brachiopods from about 800 localities. Waterhouse (1976) also indicated that in over 1500 localities from the Yukon Territory only five yielded ammonoids. Although ammonoids have been found previously in the Sabine Bay, Assistance and Trold Fiord Formations (however, rarely) this author found none in his detailed sections.

Fusulinids are short-lived and often, when present, as abundant as brachiopods. In opposition to these positive aspects is the strong latitudinal or climatic restriction to their distribution. Fusulinids are generally restricted to warm waters and although present in the Carboniferous and Earliest Permian of Ellesmere Island they are absent from the late Lower and Middle Permian sections covered by this report.

Carboniferous and Tertiary systems have long dominated palynological studies although the Permian is becoming increasingly important (Hart, 1965; Jansonius, 1962).

Palynomorphs could prove very valuable for correlation of those parts of sections where other biota are rare or absent. Two samples from the Assistance Formation at Hamilton Peninsula yielded palynomorph assemblages dominated by <u>Vittatina</u> which, according to Hart (1965), is Kungurian in age. This form is similar to <u>V. simplex</u> described by Jansonius (1962) from the Permian Belloy Formation of the Peace River area, Canada. Two samples from the Trold Fiord Formation at Hamilton Peninsula yielded <u>Vittatina</u> cf. <u>V</u>. <u>lata</u> which was first described from the Guadalupian Flowerpot Formation of Oklahoma, USA (Wilson, 1962). These floral differences suggest that these palynomorphs may be useful for discriminating Assistance and Trold Fiord equivalents. These palynomorphs were found in the same samples as those containing conodonts. A correlation scheme combining the distributions of both of these groups would be useful for resolving stratigraphic problems in correlative rocks at Henrietta-Nesmith (Fig. 1) which lack conodonts entirely.

Furthermore, palynomorphs (as well as conodonts) can be used to estimate the temperatures that their host strata were subjected to. The two Assistance samples had an average Thermal Alteration Index (TAI) of between 2.8 and 3.0 (Staplin 1969, 1974) whereas the Trold Fiord samples averaged 2.8. According to Epstein et al. (1977) conodont colour alteration does not begin until late stages of palynomorph diagenesis; explaining the very minimal differences for palynomorph. TAI's upsection. According to Staplin (1969, 1974) TAI's on the order of 2.8 indicate hydrocarbon potential for oil and wet gas and a mature organic metamorphic facies. Temperatures of 100°C are typical for this facies which falls within the range of 50 to 140°C suggested by the conodonts. Conodont colour alteration indexes of 1.5 to 2.0 and palynomorph TAI's of 2.8 to 3.0 are entirely consistent with comparisons presented in Epstein et al. (1977).

Conodonts, compared to these other groups, are still in their infancy in terms of their use as a biostratigraphic index for the Permian. As many problems arose from the early intensive study of Permian conodonts Waterhouse (1976) wassled to express his doubt that they will ever be able

to provide worldwide correlation for the marine Permian. In fact, no conodonts have been found from the cold water Permian of east Australia despite intensive search (Nicol, 1975). However, biostratigraphic schemes based on conodonts have improved substantially during the last five years, largely through the work of Clark, Behnken, Wardlaw and Collinson. This fact in combination with the abundance and excellent preservation of conodonts found in the cold water faunas of the Assistance and Trold Fiord Formations (this study) which are closely allied to warm water faunas of West Texas, Wyoming, Montana, Utah, and Idaho (this cannot be said for the brachiopods from the same areas) justify optimism that conodonts will enjoy a very bright future for worldwide correlation of the Permian.

Previous Conodont Work

The only previous Permian conodont work on Ellesmere Island was based on a single sample from the Assistance Formation on Hamilton Peninsula (near the position of F54) and a single sample from the base of the Degerbols Formation (basinal equivalent of the Trold Fiord Formation) from near Otto Fiord as summarized by Kozur and Nassichuk (1977).

The Assistance sample yielded six conodont specimens, three of which were assigned to <u>N</u>. <u>idahoensis</u> and the remainder to an intermediate position between <u>N</u>. <u>idahoensis</u> and <u>N</u>. <u>serrata</u> or <u>N</u>. <u>nankingensis</u>. These samples seem very much like the population samples defined in this report as <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> which are intermediate between <u>N</u>. <u>serrata</u> (not <u>N</u>. <u>nankingensis</u> since serrations are not present on the posterior parts) and <u>N</u>. <u>idahoensis</u>. The authors (ibid.) placed their fauna in the Upper Roadian (this report places it in the Lower Roadian).

The Degerbols sample yielded several fragmentary conodont specimens

all belonging to single species N. cf. N. gracilis and possibly intermediate between N. idahoensis and N. gracilis to which the authors assigned an Upper Roadian age (younger than type Roadian but older than Wordian sensu stricto). As indicated in this report, forms similar to N. gracilis occur in populations of N. idahoensis n.subsp. A which are assignable to the Lower Roadian. However, as these forms are few in number they are therefore unlikely to be the only forms present in a small sample. As indicated earlier it seemed reasonable to suggest that the varieties within N. idahoensis n.subsp. A, if separated as peripheral isolates could, following speciation, lead to populations of N. gracilis. If this is indeed the case then the Upper Roadian age is entirely consistent. However, there may be some ecological requirements that increase the number of one variety or another in different environments. In other words, it cannot be discounted that the gracilis variety of N. idahoensis n.subsp. A becomes the dominant member in the more basinal environment of the Degerbols Formation (as opposed to a subordinate member on the margins) leading to an age assignment for Kozur and Nassichuk's N. cf. N. gracilis of Lower Roadian. More work is indeed necessary to clarify this problem. However, the Upper Roadian age more closely fits the stratigraphic framework for the area as it is understood at present.

Earlier Age Assignments for Arctic Permian Formations

Sabine Bay Formation (Thorsteinsson, 1974)

In 1974 no fossils had been observed in the Sabine Bay on Ellesmere Island but its age was given early Artinskian because of its position above the Belcher Channel Formation and below the Assistance. Artinskian ammonoids identified as <u>Sverdrupites</u> were reported from basal beds of the Sabine Bay Formation on Melville Island.

Assistance Formation (Thorsteinsson, 1974)

On the Bjorne Peninsula the Assistance Formation is dated as early Artinskian or Aktastinian in age on the basis of ammonoids (Nassichuk et al., 1965) and brachiopods (identified by J.B. Waterhouse as brachiopod fauna "E" of the N. Yukon and probably to the <u>Jakutoproductus</u> zone). However, this age assignment is considerably older than the type Assistance (Grinnell Peninsula, Devon Island) and the Assistance in the vicinity of Hamilton Peninsula. Harker and Thorsteinsson (1960) suggested an age equivalent to the Baigendzhinian subseries (upper Artinskian) on the basis of brachiopods. Brachiopods from Hamilton Peninsula (identified by J.B. Waterhouse) indicate an age of Ufimian or Kungurian. Ammonoids (Nassichuk, 1970; Nassichuk et al., 1965) indicate both latest Early Permian and latest Artinskian (Baigendzhinian) age.

Trold Fiord Formation (Thorsteinsson, 1974)

Brachiopods (identified by J.B. Waterhouse) from the Trold Fiord Formation indicate a Kazanian age (Wordian substage). A single ammonoid (Nassichuk et al., 1965), <u>Neogeoceras macnari</u>, indicates a Guadalupian age.

Age Assignments Resulting From This Work

The correlations and age assignments resulting from this study are based on conodonts - as opposed to the previous work in the area with abundant brachiopods and rare ammonoids. The results refine, but do not drastically alter, the ages assigned by previous workers.

Six subdivisions are proposed for the late Lower and Middle Permian of Ellesmere Island represented by the Sabine Bay, Assistance and Trold Fiord Formations. The traceability of these subdivisions for the entire Arctic Archipelago is impossible to assess at this time because of the rather infant stage of Permian conodont work in the area and because of the environmental and resulting lithologic changes into the basinal equivalents of the described sections. The six units are referred to as subdivisions rather than zones because they are in part based on lithology and environment and in part on paleontology.

The writer is optimistic that future work will eventually lead to further refinement and synthesis of a good traceable biozonation based primarily on conodonts but also supplemented by brachiopods.

Subdivision A

This subdivision is assigned to the Sabine Bay Formation and regarded as essentially a lithostratigraphic unit. Shallow marine tongues do occur near the top of the formation at both the McKinley Bay and Hamilton Peninsula sections. Brachiopods and a few pelecypods were collected at both of these localities - apparently the first reported fossils in Ellesmere Island exposures of the formation. Marine tongues with ammonoid fossils were reported from the Sabine Bay Formation on Melville Island. The brachiopods are dominated, almost exclusively, by rugosochonetids (Neochonetes or Svalbardia). Although the range is much greater, these brachiopods may be related to Waterhouse's (Bamber and Waterhouse, 1971) brachiopod fauna of Leonardian to Roadian age from the N. Yukon. Because of their position below the Assistance Formation an early Leonardian or Baigendzinian age is assigned. Previous age assignments to the Sabine Bay Formation from Melville Island indicated an Aktastinian age at the base of the formation. Rocks assigned to the basal part of the Assistance Formation on Bjorne Peninsula, Ellesmere Island indicated a correlation with Waterhouse's (ibid)

Jakutoproductus zone of the N. Yukon and an Aktastinian age. Fossil collections from near the base of the Sawtooth Range section (Fig. 3) contain productids unlike any seen at Hamilton Peninsula and tentatively identified as Jakutoprodúctus. These collections are followed by a few hundred metres of largely unfossiliferous section before abundant brachiopod fossils are once again encountered - these faunas being very similar to those assigned a Late Leonardian to Early Roadian age at Hamilton Peninsula. The age for the basal parts of the Bjorne Peninsula and Sawtooth Range sections suggest greater correlation to the Sabine Bay Formation than to the Assistance For-Lithologic differences have resulted in these strata being assigned mation. to the Assistance Formation but they might be better described as a new formation. Furthermore, it would appear that the Sabine Bay Formation on Hamilton Peninsula and at McKinley Bay is younger than that at Bjorne Peninsula or at the Sawtooth Range.

In summary, although the unit is based largely on lithology, the few fossil collections indicate that the unit ranges in age from Aktastinian to Early and possibly Medial Leonardian or Baigendzinian.

Subdivision B

This subdivision is defined as a lithostratigraphic unit at the base and a biostratigraphic range zone at the top. In other words, it includes all that section above the top of the Sabine Bay Formation assignable to the Assistance formation up to the top of the range for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. In the Hamilton Peninsula section this includes the strata from the base of the Assistance Formation to the top of F54 (Fig. 3). At McKinley Bay this subdivision comprises all the strata assigned to the Assistance Formation.

Neogondolella idahoensis has been reported extensively in sections from

the western United States. Similar assemblages to the conodont fauna of subdivision B in the Assistance Formation have been reported from the Meade Peak Phosphatic Shale Member of the Phosphoria Formation of Idaho, Wyoming, and Utah (Youngquist et al., 1951; Clark and Ethington, 1962; Clark and Behnken, 1971; Wardlaw and Collinson(fig. 3), 1979b)and assigned a Roadian age. Other similar faunas occur in the Bone Spring Limestone, Victorio Peak Formation, Guadalupe Mountains, Texas (Leonardian in age according to Behnken (1975) and Upper Leonardian to Lower Roadian by Wardlaw and Collinson (1978)). According to Wardlaw and Collinson (1979a) N. idahoensis certainly ranges through the latest part of the Leonardian and doubtfully into the early part of the Roadian. N. serrata on the other hand has been reported from the Cutoff, Brushy Canyon and Getaway Member of the Cherry Canyon Formation of West Texas and from the Meade Peak Phosphatic shale member of the Phosphoria Formation and assigned a Roadian to Early Wordian age (Clark and Behnken, 1979; Behnken, 1975; and Clark and Ethington, 1962). Neostreptognathodus prayi has been reported from the Kaibab of Nevada and Utah and the Bone Spring Limestone and the Victorio Peak Formation of West Texas where it is apparently restricted to the Late Leonardian.

It appears that subdivision B can be correlated with the Late Leonardian to Early Roadian of the western United States. The assemblage for F100 (Fig. 3) at McKinley Bay which has <u>N. idahoensis</u> subsp. indet. in association with <u>Neostreptognathodus prayi</u> suggests a Late Leonardian age. The faunas quantitatively studied in detail at Hamilton Peninsula (F48 to F54) appear to be morphologically intermediate between <u>Neogondolella idahoensis</u> and <u>N. serrata</u> suggesting that an early Roadian age is more appropriate.

No serrations were noted on samples from F100 and because of the association with <u>Neostreptognathodus prayi</u> these representatives of <u>Neogondolella</u> <u>idahoensis</u> are considered older than those from F48 to F54. However, since the distributions of <u>Neostreptognathodus prayi</u> and <u>Neogondolella</u> <u>idahoensis</u> are facies controlled to the extent that they rarely occur interbedded in a single section, it is difficult to assess the significance of <u>Neostreptognathodus prayi</u> without its presence at Hamilton Peninsula. As well it is impossible to assess whether Lower Roadian strata are present and condensed, were originally present and eroded, or unrecognized, or were never deposited at McKinley Bay.

This subdivision can be correlated in part with the Kapp Starostin Formation of Spitsbergen (Szaniawski and Malkowski, 1979) where the authors report <u>N. idahoensis</u>, <u>N. cf. N. gracilis</u>, and <u>Neostreptognathodus</u> <u>sval</u>bardensis, Sweetocristatus arcticus and several ramiform elements.

This subdivisionis also correlated with Wardlaw and Collinson's (1979a) well defined biozonation for the Great Basin-Rocky Mountain Region USA as including their Zone 1 (<u>Peniculauris ivesi - Neostreptognathodus</u> prayi zone) and the lower part of Zone 2 (<u>Peniculauris bassi - Neostrepto-</u>gnathodus sulcoplicatus zone).

As a result of these age assignments the base of the Assistance Formation at Hamilton Peninsula can be regarded as no older than Late Leonardian.

Subdivision C

This subdivision is very loosely defined and is represented by a couple of sparse conodont collections at F63 and F73 from the Hamilton Peninsula section. The base of the unit is defined by the top of subdivision B while the upper limit is defined as the highest part of the Assistance Formation (although covered by talus). A large part of subdivision C is covered by talus resulting in sparse collections. The low number of collections is also owing to the decreased abundance and possible lower diversity of brachiopods apparent in the rocks. Conodonts show an equal, if not more dramatic, decrease in numbers when they are present at all.

Those conodonts reported are questionably assigned to <u>N. serrata(?</u>) because of their smaller size at apparently similar growth stages to <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>, sharper more compressed posterior denticles, and the lack of four distinctive node-like denticles just anterior of the cusp. As reported in the discussion for subdivision <u>B</u>, <u>N. serrata</u> has a range distribution of Medial Roadian to Early Wordian. Because of the age assignment to the overlying subdivisions, this subdivision C can be assigned a Medial to Late Roadian age.

Subdivision C can be correlated with Wardlaw and Collinson's (1979a) biozonation as including the upper part of Zone 2, Zone 3 (<u>Peniculauris</u> <u>bassi</u> - <u>Neostreptognathodus</u> sp. <u>C</u> zone), and their barren interval at the top of the Roadian. Perhaps this paucity of conodonts seen for the Roadian at Hamilton Peninsula is real and not related to preservational factors since Wardlaw and Collinson (1979a) also report a barren interval in the Upper Roadian to lowermost Wordian. The conodonts may have undergone a crisis Like that ofpre-Wolfcampian conodonts (Clark, 1972) which would in part explain the subsequent increased abundance and diversity in the middle and upper parts of the Trold Fiord Formation (as is often the case after a near-extinction).

The top of the Assistance can therefore be regarded as no younger than Upper Roadian and the full range for the Assistance Formation at Hamilton Peninsula is from the Upper Leonardian to Upper Roadian.

Subdivision D

This subdivision is also lacking in conodonts but dominated by the brachiopod <u>Cancrinelloides</u>. Above unit D the presence of <u>N</u>. <u>postserrata(?</u>), <u>N</u>. <u>bitteri</u> n.subsp. <u>C</u> and <u>N</u>. <u>rosenkrantzi</u> n.subsp. <u>D</u> indicate a Late Wordian or Kazanian age, so that D itself is regarded as Early Wordian or Late Kungurian in age.

Waterhouse, in Bamber and Waterhouse (1971), reports a <u>Cancrinelloides</u> zone in the N. Yukon which he assigns a Kazanian age. He does indicate, however, that <u>Cancrinelloides</u> can occur in slightly lower beds included in his <u>Thamnosia</u> zone; <u>Thamnosia</u> is the dominant genus in this report's subdivision E. Waterhouse assigns a Late Ufimian or Kungurian age to the <u>Thamnosia</u> zone. For this reason it seems reasonable to assign an Early Wordian age to unit D.

Wardlaw and Collinson (1979a) also define a <u>Thamnosia depressa</u> zone which they assign an Early Wordian age. If the overlying subdivision E at Hamilton Peninsula is dominated by <u>Thamnosia</u> and various <u>Neogondolella</u> species then subdivision D cannot be as young as Kazanian. Furthermore, since the base of unit D is defined by the base of the Trold Fiord Formation then at least part of the Trold Fiord is older than Kazanian; unlike previous reports which restricted it to the Kazanian.

The four distinctive features of this unit are the apparent lack of conodonts, the lack of large thick-shelled productids like <u>Thamnosia</u>, the presence of <u>Cancrinelloides</u> and occurrence in the base of the green sandstones of the Trold Fiord Formation. The environmental significance of the distribution of these brachiopods is not well understood (Waterhouse, 1973). Until more sections in the area are studied, encompassing a wide variety

of environments, both marginal and basinal, the biostratigraphic significance of this unit D cannot be established.

Subdivision E

Unit E is the closest to a true range or acme biozone as it is based on the presence and dominance of the brachiopod <u>Thamnosia</u> and the occurrence of reasonably abundant conodonts. Also characteristic of this subdivision is a conglomeratic unit that, except for varying thickness, is identical in the McKinley Bay, Hamilton Peninsula and Sawtooth Range sections. If this conglomerate can be shown to be synchronous then it could prove a very useful marker horizon(Fig. 3) - possibly related to a single tectonic pulse or other short-duration physical phenomenon.

At Hamilton Peninsula subdivision E includes fossil collections F83 to F90 and F35 to F44. F36 and F83 contain specimens of a new species; <u>Neogondolella</u> n.sp. <u>B</u>. Both of these collections occur below the chert-pebble conglomeratic unit. F87 includes conodont fragments questionably referable to <u>N</u>. <u>postserrata(?)</u>. This collection occurs within the conglomeratic unit. <u>N</u>. <u>postserrata</u> has previously been reported from the Southwells Member of the Cherry Canyon Formation to the Lower McCombs Member of the Bell Canyon Formation of Idaho and Texas and assigned a Wordian and Capitanian age (Behnken, 1975; Clark and Behnken, 1979). Wardlaw and Collinson (1979a)describe a <u>Thamnosia depressa</u> zone from the upper part of the Plympton Formation and Rex Chert Member of the Phosphoria Formation in the Great Basin and Rocky Mountain region of the western USA to which they assign an Early to Medial Wordian age. They indicate that this zone is more or less equivalent to the <u>Neospathodus arcucristatus</u> assemblage (Clark and Behnken, 1971; Clark et al., 1979) which Clark et al. assign a Wordian age.

37.

Clark et al. (1979) indicate the equivalence of this zone to the Neogondolella denticulata fauna of West Texas despite giving it a Capitanian to Amarassian age in Clark and Behnken (1979). Wardlaw and Collinson (1979a) and Clark et al. (1979) both describe overlying faunas of N. bitteri and N. rosenkrantzi assigned to a Late Wordian and Capitanian age. For these reasons N. postserrata (which is older than N. denticulata) cannot be any younger than Wordian. Assuming ages assigned to the type N. postserrata and for the Thamnosia depressa zone the collections below and within the conglomerate of subdivision E can be regarded as Medial Wordian or Uppermost Kungurian (Ufimian) in age. Supporting this assignment is another Thamnosia zone described by Waterhouse (Bamber and Waterhouse, 1971) from the N. Yukon. Here Waterhouse assigns a Late Ufimian age stating that the Thamnosia of his zone-Ft are more evolved than those found in the Assistance Formation. Thamnosia is abundant throughout the conglomeratic unit and slightly above it and thus defines the top of unit E, Late Kungurian or Medial Wordian in age.

Subdivision F

Subdivision F occurs above the zone with dominant <u>Thamnosia</u> and includes the fossil collections F91 to F97 and F45 to F47. The conodonts identified from this zone include <u>Neogondolella bitteri</u> n.subsp. <u>C</u> and <u>N. rosenkrantzi</u> n.subsp. <u>D</u>. Brachiopods include various spiriferids and productids in varying degrees of abundance; especially common are species of <u>Yakovlevia</u> and <u>Kuvelousia</u>. However, both of these genera occur in many underlying zones and require specific identification before they could be used for range zone determination.

> The fauna just described compares very well with that present in Wardlaw and Collinson's (1979a)zones 5 and6 (Kuvelousia leptosa zone and

<u>Yakovlevia multistriata</u> - <u>Neogondolella bitteri</u> zone) from the Great Basin -Rocky Mountain region of western USA and assigned a late Wordian age. The conodonts at hand are very similar to faunas figured in Wardlaw and Collinson (1979b) from the Retort Phosphatic Shale Member of the Phosphoria Formation from Montana (in the case of <u>N. rosenkrantzi</u>) and Wyoming (for <u>N. bitteri</u>). Representatives for both species from the Gerster Formation appear more advanced.

<u>N. rosenkrantzi</u> has also been described from East Greenland (where it was named by Bender and Stoppel1965) though the age relationships were not clear at the time. Clark and Behnken (1979) and Clark et al. (1979) assign a Capitanian and Amarassian age to faunas described from the Radar, McCombs, and Lamar Members of the Bell Canyon Formation of Texas and the Gerster Formation of Nevada and Wyoming. The main reason for contradicting age assignments are the differences of opinion for the recognition of <u>N. bitteri</u> and <u>N. rosenkrantzi</u> by Wardlaw and Collinson and Clark et al. Clark et al. (1979) identified specimens of <u>N. rosenkrantzi</u> (according to Wardlaw and Collinson, 1979b) as <u>N. bitteri</u>. Therefore, <u>N. rosenkrantzi</u> can occur down into the Late Wordian (see Clark et al., 1979 for discussion and description).

Having resolved these contrasting age assignments and stated that the conodonts at hand are less advanced than Capitanian specimens from the Gerster limestone, I assign subdivision F to a Late Wordian or Kazanian age.

One other feature that is characteristic of this final subdivision at the Sawtooth Range and Hamilton Peninsula is the dominance of inarticulate brachiopods near the top. Although such a feature is probably environmentally controlled, the horizon could prove to be a useful marker (Fig. 3).

<u> 3</u>9

The absence of inarticulates at McKinley Bay suggests that all or part of this subdivision is missing here: perhaps as a result of regression in the last part of the Trold Fiord Formation.

The top of unit F is coincident with the top of the Trold Fiord Formation, the last Permian strata in the Arctic. The Blind Fiord or Bjorne Formations of Lower Triassic age rest unconformably on the Trold Fiord. Indications are that the Trold Fiord Formation ranges in age from the Lower Wordian or Upper Kungurian to the Uppermost Wordian or Upper Kazanian. Although there is no direct evidence for it, a Capitanian age represented in the upper parts of the Trold Fiord Formation cannot be entirely ruled out since <u>N. bitteri</u> and <u>N. rosenkrantzi</u> can range this high. It is also impossible to say whether younger rocks may have been present and eroded, or never deposited at all. It is fair to say that the time represented by the Trold Fiord/Bjorne unconformity is considerable: $f_{\rm In}$ the order of 10 million years.

Summary

The Sabine Bay, Assistance and Trold Fiord Formations have been separated into six subdivisions which can be collectively referred to as Aktastinian to Latest Wordian or Kazanian age. Although the three formations are separated by unconformities (Thorsteinsson, 1974) this author considers them, if present at all, to be of short duration. Perhaps more basinal sections could indicate continuous sedimentation with the transgressions and regressions only affecting the margins of the basin.

QUANTITATIVE ANALYSIS OF MEASURABLE CHARACTERS FOR <u>NEOGONDOLELLA</u> Introduction

Qualitative observation of the conodont populations in samples F48, F49, F52, F53 and F54 indicated that there are no distinguishable differ-

ences with respect to overall platform shape and denticle configuration. A description based on these observations was sufficient to erect a new subspecies of <u>Neogondolella idahoensis</u> but did nothing to elucidate any evolution in the populations. It also seemed expedient to have more than just my subjective opinion on which to base the new subspecies. As a result, a quantitative analysis was undertaken to determine if there was any demonstrable evolution in the populations and to provide unbiased criteria on which to base the taxonomy (see Appendix I for data).

The measurable parameters analyzed include the overall platform length (L1), the length from the posterior cusp to the fourth denticle anterior of the cusp (L2), the height from the tip of the cusp to the base of the flange (H1), the maximum width (W1), the width at the posterior end of the platform (W2), and the number of denticles (#) on the platform. Some of these parameters have been measured on similar conodont populations by other workers (L1 and # by Behnken, 1975; L1, H1 and # by Dzik and Trammer, 1980). In addition a number of ratios were determined including L1/H1, L1/W1 and L1/#. The final parameter analyzed is a function of area in the posterior end of the platform determined by the equation $L2(W1 + W2)^{1}_{2}$.

These various parameters were analyzed by calculating the mean, standard error for the mean, the standard deviation of the mean and, finally, a comparison using z- and t-tests to determine the statistical significance of any differences between populations. Before listing and discussing the results of these calculations the background, assumptions and implications of such statistical testing should be outlined.

Above all one must remember that in each case we are dealing with a sample of the population and not the population itself. Any two samples

from the same population will vary; however, in samples of sufficient size this difference is minimal. Since the population is the unit of evolution, the samples studied herein can only be regarded as approximating the evolutionary trends. A requirement for a sample to be representative of the population is that it be selected at random. The conodonts selected for this study were all those (large and small) in each fossil collection that were sufficiently preserved to allow for the measurement of the various characters. The only processes in the selection of the specimens were those as a result of the environment of deposition, the diagenetic history and the sample processing. Although these processes can be non-random (preferential breakage or etching of more fragile specimens), the resulting frequency curves (Fig. 5) reasonably approximate a normal distribution, suggesting that the processes were too small to be selective. Having a representative approximation of the population, the sample is now available for statistical analysis. Calculation of the mean of any character involves the simple solving of the equation $M = \frac{\Sigma X}{N}$ (M = mean, ΣX = sum of the values for a character, and N = the number of specimens within the sample). However, Burma (1948) points out that the mean of a sample consisting of a growth series is merely the mean size of half grown specimens, the minimum size is that of the smallest of the youngest specimens and the maximum size is the largest of the oldest specimens. Burma (1948) furthermore states that such a procedure is meaningless and lacking in biological significance: and that if one dictum is established in quantitative paleontology it should be that comparisons of one character, to be valid, must be made at comparable growth stages only. His point is well taken but one difficult to heed in many groups, especially the conodonts. Such a procedure would



Figure 5. Frequency distribution of the number of denticles and platform length for <u>Neogondolella,idahoensis</u> n.subsp. <u>A</u>. Those elements with a given platform length (eg. 350 µm) actually range between 300 µm and 400 µm.

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be easy with a group like the ammonites where features are present that allow one to distinguish an adult conch. However, no such features exist for the conodont platform (Dzik and Trammer, 1980). Are we defeated before even beginning the analysis? Other workers have shown that conodontophores like Neogondolella have a complex ontogeny. Merrill and Powell (1980) demonstrated an ontogeny of Pennsylvanian Gondolella where the apparatus began as ramiform elements only and subsequently developed into platform ("juvenile") and ramiform elements and finally into a platform only ("mature") apparatus. Other workers have also suggested that more than one pair of platforms, each of which are at different developmental stages, comprise the apparatus. In other words, the developmental stage of the platform may bear no relationship to the actual age of the conodont animal. Unless the samples display some unusual mortality rate, it may be valid to compare the entire range of platform sizes as the majority of them probably reached a certain stage in development before death. With these considerations in mind I proceeded with the statistical comparisons of the entire sample but also separated the data into two subsets (those elements with 10 denticles and those with 11) of possible particular growth stages. After calculating the mean of each sample the standard error of the mean was calculated at the 95% confidence level ($\sigma_m = \frac{2\sigma}{N}$ where $\sigma =$ standard deviation or measure of central tendency of variability). Finally, the limits of variability were set at the 75% and 95% levels (M \pm 1.15 σ and M \pm 2.00 respectively). Proper use and full value of these calculations assumes a near normal distribution of the characters. These values were then graphed for visual impact and compared in the cases of length and the ratio length/number of denticles using z- and t-tests to determine the sig-

nificance of the differences. The t-test assumes a normal distribution and equal standard deviations for the two samples being compared (Hodges et al., 1975) and is valuable for samples of low number. The z-test does not depend on the same assumptions but is only useful for samples of approximately 20 or more specimens.

It is generally thought that the quantitative approach in science is the only truly objective approach (Raup and Stanley, 1971; p. 42). Despite this assertion the technique is often met with objection by paleontologists. Many workers state that the method is good for a large number of specimens but not for a few. However, statistical methods are available for study of samples with a very few specimens or with 1000 or more (Burma, 1948). Secondly, anything which a person attempts to do with a small sample, which he could not do by statistical analysis will probably be founded on error (ibid.). Another objection is that misuse of statistics by those who apply them to paleontology is often either owing to lack of knowledge or lack of appreciation of the philosophy behind them (ibid.). So long as one recognizes the limits of interpretation for the derived information this last objection should be minimized. The value of such an analysis to define minute changes in the specimens through time, and to indicate the full range of variation of any species or infraspecific unit far outweighs these objections. All species that are created with the concept of species being an entity of little variation should be viewed with suspicion (ibid.).

Results and Discussion

The measurements for the specimens studied are included in Appendix A. All measurements were completed with a micrometer set in a binocular micro-

scope at 75 power. This method allowed an approximate accuracy of \pm 5 µm for the length of a 1000 µm platform; in other words an accuracy of approximately 1.0% and allowing for at least three significant figures. Except for F54, the samples were measured in terms of all the parameters studied. Only length and the number of denticles were determined for F54 as these specimens were placed on SEM stubs and photographed before it seemed appropriate to proceed with the more detailed analysis.

Overall length of platform (L1)

Perhaps the most obvious reflection of increasing maturity of the platform is an increase in length. More significant is the progressive increase upsection for the mean value of length from 816 μ m to 905 μ m (Table 1). Although the variation in the population samples overlaps for the most part, the increase in the mean value is entirely consistent upsection (Fig. 6) for <u>N. idahoensis</u> n.subsp. <u>A</u>. However, <u>N. rosenkrantzi</u> n.subsp. <u>D</u> represented in F96 has a mean length considerably less than that for F48 to F54 indicating a reversal in the trend. The large variability in length in F96 results in a significance level, at best, of 16% (Table 2) when subjected to the z-test. This is of even less significance than that represented for the change of length from F49 to F54 (11.5%). Despite this lack of significance for the difference, the trend indicated is consistent with the evolution of <u>N. idahoensis</u> to <u>N. rosenkrantzi</u> according to the results of other workers (Behnken, 1975; Clark and Behnken, 1979).

Although the trend from F48 to F54 may possibly be explained by evolutionary processes, it could also be the result of the ontogenetic stages preserved. Merrill and Powell (1980) indicated that the ontogeny of Pennsylvanian <u>Gondolella</u> proceeded from ramiform only to platform only

					1	
Parameter	Sample Data	F48 N = (9-10)	F49 N = (58-60)	F52 N = (24-25)	F53 N = (38-40)	F54 N = (37)
L _{1µm}	M ± 2σ σ ^m 75% range* 95% range**	$816 \pm 134 \\ 212 \\ 572 - 1060 \\ 402 - 1230$	847 ± 48 184 635 - 1059 479 - 1215	847 ± 80 199 618 - 1076 449 - 1245	888 ± 82 259 590 - 1186 370 - 1406	905 ± 84 255 612 - 1198 395 - 1415
^L 2յո	M ± 20 0 75% range* 95% range**	$297 \pm 26 \\ 40 \\ 251 - 343 \\ 217 - 377$	$279 \pm 10 \\ 42 \\ 231 - 327 \\ 195 - 363$	$286 \pm 16 \\ 38 \\ 242 - 330 \\ 210 - 362$	$\begin{array}{r} 303 \pm 16 \\ 53 \\ 242 - 364 \\ 197 - 409 \end{array}$	
W _{lµm}	M ± 2σ σ ^m 75% range* 95% range**	$ \begin{array}{r} 181 \pm 28 \\ 44 \\ 130 - 232 \\ 93 - 269 \end{array} $	$ \begin{array}{r} 183 \pm 16 \\ 61 \\ 113 - 253 \\ 61 - 305 \end{array} $	$200 \pm 18 \\ 44 \\ 149 - 251 \\ 112 - 288 \\ 34 \\ 34 \\ 34 \\ 34 \\ 34 \\ 34 \\ 34 \\ $	209 ± 18 55 146 - 272 99 - 319	
^W 2 µm	M ± 20 σ ^m 75% range* 95% range**	$ \begin{array}{r} 152 \pm 24 \\ 38 \\ 108 - 196 \\ 76 - 228 \end{array} $	163 ± 8 31 127 - 199 101 - 225	174 ± 18 47 120 - 228 80 - 268	180 ± 16 53 119 - 241 74 - 286	
H _{1 µm}	M ± 2σ σ ^m 75% range* 95% range**	$ \begin{array}{r} 149 \pm 20 \\ 29 \\ 116 - 182 \\ 91 - 207 \\ \end{array} $	$ \begin{array}{r} 164 \pm 10 \\ 35 \\ 124 - 204 \\ 94 - 234 \end{array} $	$ \begin{array}{r} 166 \pm 18 \\ 42 \\ 118 - 214 \\ 82 - 250 \\ \end{array} $	$ \begin{array}{r} 172 \pm 14 \\ 44 \\ 121 - 223 \\ 84 - 260 \end{array} $	
#	M ± 2σ σ ^m 75% range* 95% range**	$10.00 \pm 1.02 \\ 1.61 \\ 8.15 - 11.85 \\ 6.78 - 13.22$	10.78 ± .42 1.62 8.92 - 12.64 7.54 - 14.02	10.80 ± .60 1.50 9.07 - 12.53 7.80 - 13.80	11.02 ± .66 2.12 8.58 - 13.46 6.78 - 15.26	10.92 ± .60 1.80 8.85 - 12.99 7.32 - 14.52
L ₁ /# _{µm/#}	M ± 20 0 75% range* 95% range**	80.8 ± 7.0 11.1 68.0 - 93.6 58.6 - 103.0	78.3 ± 3.0 11.7 64.8 - 91.8 54.9 - 101.7	77.6 ± 3.8 9.5 66.7 - 88.5 58.6 - 96.6	79.3 ± 3.6 11.1 66.5 - 92.1 57.1 - 101.5	82.0 ± 5.0 15.3 64.4 - 99.6 51.4 - 112.6
L ₁ /W ₁	M ± 2σ σ 75% range* 95% range**	$\begin{array}{r} 4.51 \pm .22 \\ 0.34 \\ 4.12 - 4.90 \\ 3.83 - 5.19 \end{array}$	$\begin{array}{r} 4.44 \pm .14 \\ 0.54 \\ 3.82 - 5.06 \\ 3.36 - 5.52 \end{array}$	$\begin{array}{r} 4.27 \pm .22 \\ 0.55 \\ 3.64 - 4.90 \\ 3.17 - 5.37 \end{array}$	4.23 ± .12 0.40 3.77 - 4.69 3.43 - 5.03	
L ₁ /H ₁	M ± 2σ σ 75% range* 95% range**	$5.30 \pm .70 \\ 1.05 \\ 4.09 - 6.51 \\ 3.20 - 7.40$	$5.21 \pm .22 \\ 0.81 \\ 4.28 - 6.14 \\ 3.59 - 6.83$	$5.18 \pm .30 \\ 0.73 \\ 4.34 - 6.02 \\ 3.72 - 6.64$	5.14 ± .34 1.05 3.93 - 6.35 3.04 - 7.24	
$\frac{L_2(W_1+W_2)^{l_2}}{10^4}$	M ± 2 ₀ 0 75% range* 95% range**	$\begin{array}{r} 4.99 \pm .88 \\ 1.40 \\ 3.38 - 6.60 \\ 2.19 - 7.79 \end{array}$	$\begin{array}{r} 4.79 \pm .43 \\ 1.67 \\ 3.05 - 6.89 \\ 1.63 - 8.31 \end{array}$	$5.48 \pm .88 \\ 2.18 \\ 2.97 - 7.99 \\ 1.12 - 9.84$	$\begin{array}{c} 6.11 \pm .86 \\ 2.71 \\ 2.99 - 9.23 \\ 0.69 - 11.53 \end{array}$	

. Table 1. Statistics from data given in Appendix I. See page 44 for discussion of statistical values used.

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	z-Test	for L1	z-Tes	t for #	z-Test	for L1/#
	+ ++		Entire Sample			
Samples Compared	z-score'	P-value''	z-score'	P-value''	z-score'	P-value ^{TT}
F49 → F52	0.01	0.496	0.055	0.478	0.29	0.386
F49 → F53	0.87	0.192	0.61	0.271	0.43	0.334
F49 → F54	1.20	0.115	0.39	0.348	1.26	0.104
(F49+F52) → (F53+F54)	1.37	0.085	0.64	0.261	1.30	0.097
F49 → F96	0.51	0.305	1.89	0.029	3.95	0.000
F54 → F96	0.97	0.166	1.70	0.045	4.35	0.000

Table 2. Values derived from z-tests for L1, # and L1/#.

- $\frac{1}{1 M_2} = \text{the z-score of the difference between two independent samples (1, 2) } \\ \sqrt{\frac{\sigma_1^2 + \sigma_2^2}{N_1 N_2}} \qquad M = \text{mean } \sigma = \text{standard deviation} \quad N = \text{number of specimens}$
- $^{++=}$ the area under a normal curve (total area = 1) to the left or right of M $\pm .z\sigma$ which indicates the probability that the difference between samples 1 and 2 could occur by chance alone (a two sided test is equal to the total area to the left and right and indicates the combined chance of getting a deviation in either direction

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apparatuses. If this is true for the <u>Neogondolella</u> apparatus as well, then the increasing degree of platform overrepresentation or, rather, ramiform underrepresentation, could be related to increasing maturity and larger size of the preserved sample. Table 3 lists the data for element representation and demonstrates a fluctuation in the platform to ramiform ratio. Except for the change from F49 to F52 the data show a clear increase in the ramiform underrepresentation comparing well with the increase in length for the same interval. The mean value for length in F52 is equal to that for F49 which, although it should be a decrease, approximates the trend in element representation. Although it seems clear that this concept may be important for explaining some of the change in length nevertheless it is not completely satisfactory.

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Heeding Burma's (1948) plea that only similar growth stages should be statistically compared the data for each sample were divided into two subsets (Table 4): the first with all those elements with 10 denticles and the second with all thes elements with 11 denticles. The number of denticles cannot be considered a perfect indicator of relative age, however, it is true that their number increases during the inferred ontogeny of the element. Furthermore, it is probably the best tool available for distinguishing relative age. The values derived from t-tests of the resulting subsets provide some interesting results. The difference between the samples with 10 denticles is insignificant whereas the difference between elements with 11 denticles in F49 and F54 is significant, even at the 1% level. The graph in Figure 7 illustrates this observation well in that as denticle number increases the data points for the two samples plot progressively further apart. Early stages cannot be distinguished at the subspecific or

	Element Representation								
Sample	Number of Platforms	Number of Complete Platforms	Percentage of Complete Platforms	Number of Ramiforms	Number of Platforms: Number of Ramiforms				
F48	28	10	36%	12	2.33 : 1				
F49	705	60	9%	175	4.03 : 1				
F52	95	25	26%	48	1.98 : 1				
F53	174	40.	23%	32	5.44 : 1				
F54	190	37	19%	25	7.60 : 1				
Total	1192	172	14%	292	4.08 : 1				

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Table 3. Counts and percentages of platforms and ramiforms of Neogondolella in F48 - F54.

Statistical Lata Derived from Sample Subsets								
	Sample	F48	F4 9.	F52	F53	F54		
Parameter	Data	N = 1, 2	N = 12, 12	N = 6, 5	N = 11, 7	N = 7, 9		
L	м	630	772	733	752	811		
10 denticles	σ	-	75	44.	75	88		
-	$\sigma^{\perp} = 78.1$							
L	м	1060	863	816	923	984		
11 denticles	σ	-	108	46	105	102		
	σ ¹ = 105.3							
L1/#	М	63.0	77.2	73.3	75.2	81.1		
10 denticles	$\sigma^1 = 7.81$	-	7.5	4.4	7.5	8.8		
L1/#	М	96.4	78.5	74.2	83.9	89.5		
11 denticles	$\sigma^{1} = 9.53$	-	9.6	4.2	9.6	9.4		

Table 4. Statistics from sample subsets (elements with 10 and 11 denticles).

t-Test for L_1 and $L_1/#$

	10 Den	ticles	11 Denticles		
Samples Compared	t-score*	P-value**	t-score*	P-value**	
F49 → F52	1.00	0.17	0.84	0.21	
F49 → F53	0.61	0.27	1.20	0.13	
F49 → F54	1.05	0.15	2.60	0.009	
(F49+F52) → (F53+F54)	0.58	0.28	2.75	0.005	

Table 5. Values derived from t-tests on sample subsets.

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$$= \frac{M_1 - M_2}{s\sqrt{1/N_1 + 1/N_2}} \qquad s = \sqrt{\frac{N_1 \cdot \sigma_1^2 + N_2 \cdot \sigma_2^2}{N_1 + N_2 - 2}} \qquad \sigma = \sqrt{\frac{N_1 \cdot \sigma_1^2 + N_2 \cdot \sigma_2^2}{N_1 + N_2 - 2}} \qquad s = \sqrt{\frac{N_1 \cdot \sigma_1^2 + N_2 \cdot \sigma_2^2}{N_1 + N_2 - 2}}$$

 $= \frac{\text{standard}}{\sqrt{\frac{\Sigma f x^2}{N} - M^2}} \text{deviation}$

 Σfx^2 sum of the squares of values for a character

**= the probability that the difference between two sample means could occur by chance (i.e. if Z-score = 1.2, then P-value = .115, thus there is a 11.5% chance that the difference occurred by chance alone).



specific level. A second interesting observation is the increase in mean length from 10 to 11 denticles for each sample. This increase is approximately 85 μ m for F49 and F52 and about 170 μ m for F53 and F54 (Table 4). The importance of this observation will be discussed in the section for length/number of denticles.

Number of Denticles per Element (#)

The mean number of denticles increases from F48 to F53 but decreases marginally for F54. If the number of denticles can be used as a "rough" guide to relative stages of development and if platform overrepresentation is directly related to ontogenetic stages, then the trends for these two parameters should roughly coincide. This is not the case, however (Table 3, Fig. 6). This indicates that either length is a more sensitive indicator of relative maturity or that platform overrepresentation does not explain the observations suggesting that the changes are related to evolution... The differences recorded in the number of denticles upsection are insignificant (significance is considered at 5%) according to z-scores (Table 2).

Ratio of length to number of denticles (L1/#)

The comparison of two parameters together tends to produce some interesting results with regards to possible evolutionary implications that could not be deciphered through analysis of the two parameters alone. This is not surprising as animals or their skeletal remains are not differentiated from one another by this or that character but rather by the sum of many characters (Burma, 1948). The results indicate a decrease in the ratio of length to number of denticles for F48 through F52 followed by an increase in samples F53 and F54 (Fig. 6). Z-tests for the entire sample indicate a fail-

ure of significance even at the 10% level (Table 2). As a result, the possibility that this variation could be related to a process of random sampling cannot be discounted. Further evidence suggests, however, that the observed trend may be significant. The t-test for L1/# indicates that the data are significant at the 5% level for those elements with 11 denticles from F49 to F54. Further upsection to F96, a very sharp decrease in the L1/# ratio occurs which has a very high statistical significance (Table 5). Obviously, to proceed from F54 to F96, at least one more point of inflection is required to obtain this decrease. What starts to become apparent is a fluctuating mode of evolution for this particular ratio. Combining data from Behnken (1975) with my data for length versus number of denticles, these trends may be made graphically visible (Fig. 8). The evolution of <u>Neogondolella</u> idahoensis (F54) to N. serrata and finally to N. postserrata-N. rosenkrantzi (F96) produces and initially large decrease in the length for an element of given denticle number followed by a slight increase. These major inflection points are thus significant at the specific level. Perhaps similarly shaped but smaller points of inflection like that seen for F48 to F54 are significant at the subspecific level.

Another factor that becomes apparent from an analysis of the data is that the more mature the element is (ie. the larger and more denticles it has) the greater one's ability to distinguish between the population samples. In support of this statement are t-tests for L1/# for 11 denticles (Table 5). As was pointed out earlier, F49 to F52 increases in length by 85 µm between 10 and 11 denticles whereas F53 and F54 increase by 170 µm. Grouping these variations together and testing for the significance between F49 plus F52 and F53 and F54 provided the closest results to significance for z-tests



Figure 8.

Graph showing the relationship of the platform length to the number of denticles per element of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>, <u>N</u>. <u>serrata</u>, and <u>N</u>. <u>postserrata</u> (in chronological order). A fluctuating mode of evolution is indicated by the decrease in length for given denticle number from <u>N</u>. <u>idahoensis</u> n.subsp. <u>A to N</u>. <u>serrata</u>, followed by an increase in length from <u>N</u>. <u>serrata</u> to <u>N</u>. <u>postserrata</u>.

<u>N. idahoensis</u> n.subsp. <u>A</u> region defined by F49 to F54 from Ellesmere Island whereas <u>N. serrata</u> and <u>N. postserrata</u> are based on data presented in Behnken, 1975. for this interval (however, the only significant tests at the 5% level were the t-tests for 11 denticles). It should be obvious from Figure 7 that the increase in mean L1/# from 11 to 12 denticles is even more significant than that for 10 to 11 between F49 and F54 as the fields represented by the data points become even more divergent.

Length from tip of cusp to fourth denticle anterior of the cusp (L2)

The first four denticles anterior of the cusp tend to be more closely spaced and more circular in cross section than the remaining laterally compressed denticles. The maximum width of the element often occurs at about this same point on the platform. Consequently, it seemed appropriate to analyze this parameter as it could be valuable even for fragmental specimens. Except for F48 (based on the smallest sample) the trend is one of increasing length upsection similar to the increase for L1 (Fig. 9). This similarity of trends points to the value of this parameter for samples where only fragmental specimens are available.

Maximum width (W1)

The data here indicate a consistent increase in mean width upsection (Fig. 9). More discussion will follow in the section for Ll/Wl.

Width at posterior end (W2)

This parameter shows a consistent increase upsection similar to that for W1 (Fig. 9). The main reason for taking the two width measurements was for the determination of an area function in the posterior 1/3 to 1/2 of the denticle.

Height from tip of cusp to base of flange (H1)

Dzik and Trammer (1980) found that this parameter was very useful for discriminating Triassic <u>Gondolella</u> species. The height increases upsection



Figure 9. Graphical representation of part of Table 1. Lines in full black show range of $M \pm 2\sigma_M$. Stippled pattern = $M \pm 1.15\sigma$ (i.e. 75% variation). White = $M \pm 2\sigma$ (i.e. 95% variation).

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very consistently. So far it has been established that the two lengths, the two widths and the height measurements all increase, with some minor fluctuations, from F48 to F54. What is interesting , however, is the trend in the ratios of these values as they all decrease upsection.

Ll/Wl Ratio

Despite the increases in both length and width the L1/W1 ratio de+ creases consistently upsection (Fig. 9). Obviously, this results from a greater increase in width relative to the increase in length. This would be reflected in a platform becoming more "square" in shape rather than elongated and narrow. Z-test scores for this trend indicate that the changes from F48 to F53 and from F49 to F53 are significant at the 5% level (even for a two-sided test). It is impossible to tell whether this trend fluctuates like that for L1/# or whether this decrease is translated through the entire section of Permian rocks discussed in this study. Two fragments of N. serrata(?) suggest a Ll/Wl ratio of about 4 while the ratio for N. rosenkrantzi varied between 4.0 and 4.7, averaging 4.3. A look at illustrations of specimens from the Great Basin of the USA suggests a similar pattern of L1/W1 ratios for N. idahoensis (3.9), N. serrata (3.3), N. postserrata (3.6), N. bitteri (3.6) and N. rosenkrantzi (4.0) (Clark and Behnken, 1979; Clark et al., 1979; Wardlaw and Collinson, 1979b). Admittedly, such comparisons, stand on shaky ground as the measurements are based on a few specimens preselected by the above authors and which do not take into account the variation of L1/W1 during ontogeny (although I did try to select similar intermediate to mature specimens from the figured specimens). Furthermore, samples from Texas (Behnken, 1975) suggested a continuous decrease from 4.3 to 3.05 for N. idahoensis to N. rosenkrantzi. These

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<u>N. rosenkrantzi</u> are more elongate than those from Ellesmere Island or the Great Basin. Probably the trends vary with environment and/or geography. Nevertheless there seems to be some merit in suggesting a fluctuating trend at the specific level for Ll/Wl similar to that for Ll/# in the Ellesmere Island samples of Neogondolella.

L1/H1 Ratio

Here again although both Ll and Hl increase from F48 to F53 the ratio L1/Hl decreases for the same interval. However, z-test scores indicate that the difference between F48 to F53 is insignificant and could be the result of random sampling. Despite this, the trend is strikingly consistent. Once again it is impossible to tell if this trend continues for the remainder of the section, nor are there data to make inferences from. Intuitively, how-ever, the shorter length of N. serrata(?) and the high, robust cusps of N. n.sp. <u>B</u> would indicate decreased L1/Hl ratios while the short cusps of N. <u>bitteri</u> n.subsp. <u>C</u> and <u>N. rosenkrantzi</u> n.subsp. <u>D</u> would indicate a subsequent increase in the L1/Hl value.

 $\frac{L2(W1 + W2)^{\frac{1}{2}}}{10^4} \xrightarrow{Posterior area}$

Data for this parameter indicates an increase in this area value for F48 to F53. Z-scores indicate that the difference between F48 and F53 is significant only at the 7% level whereas the difference between F49 and F53 is significant at the 2% level, even for a two sided test. Measurements suggest that this area value would be much less for <u>N</u>. <u>serrata(?)</u> but greater again for <u>N</u>. n.sp. <u>B</u> to <u>N</u>. <u>rosenkrantzi</u> n.subsp. <u>D</u> in the Trold Fiord Formation. Once again a fluctuating mode is suggested for this parameter as well.

Discussion of Evolutionary Trends and Concepts

Evidence for the L1/# ratio from population samples of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> from Ellesmere Island compared to data from population samples of <u>N</u>. <u>serrata</u> and <u>N</u>. <u>postserrata</u> (Behnken, 1975) from western USA indicate a fluctuating mode in the evolution of these platform elements with respect to this parameter. Furthermore, the results for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> suggest that this fluctuating mode may be important at the subspecific level. Although not backed up by statistical data from large samples, conodonts upsection to <u>N</u>. <u>idahoensis</u> which are closely allied to <u>N</u>. <u>serrata</u>, <u>N</u>. <u>post-</u> <u>serrata</u> and <u>N</u>. <u>rosenkrantzi</u> indicate a similar trend to that seen for the comparison with Behnken's samples (1975) from western USA. In addition similar fluctuating trends seem apparent for several other parameters measured from the Ellesmere Išland samples. It therefore seems reasonable, with all this supporting documentation to suggest that this fluctuating tendency is the rule rather than the exception for the evolution of Permian neogondolellids.

Having proposed a mode for the evolution of these conodonts I have opened myself to the argument of interpretation of this trend and, in particular, amobhiged to face the question of phyletic gradualism (of which many authors are proponents) versus punctuated equilibria (Eldredge and Gould, 1972; Gould and Eldredge, 1977). As I pondered over this problem I tried to take heed of Eldredge and Gould's warning (1972) that all observation is coloured by theory and expectation. My original intention for the statistical analysis was to see if there was any quantitative difference between five population samples that I could not differentiate qualitatively (especially because of the high degree of variability) and then determine
if any differences were significant for the determination of subspecies. It was not until well into the analysis that I saw the possibility of purporting an evolutionary scheme. I did not then, and I do not now wish to get into a deep philosophical discussion of the merits of one or the other scheme. Rather I would like to indicate my data and suggest an interpretation and leave this interpretation open to critical analysis by other workers as part of the continuing process of evolutionary model synthesis for this group of biota. I certainly cannot claim that my data would ever solve the problem of phyletic gradualism versus punctuated mode of organic evolution.

The concept of phyletic gradualism states that new species evolve by the slow and continuous transformation of entire populations resulting in an unbroken gradation of fossil forms (Eldredge and Gould, 1972). These unbroken gradational series are rarely (if ever) found because of the "supposed" imperfections in the geologic record. The theory of "punctuated equilibria" states that new species evolve rapidly from small, peripherally isolated local populations (allopatric speciation) resulting in many breaks in the fossil record since the new species evolve in an area remote from its ancestors (Eldredge and Gould, 1972). The history of evolution is, therefore, not one of stately unfolding, but a story of homeostatic equilibria, disturbed only rarely by rapid and episodic events of speciation (ibid.).

Since 1972 when Eldredge and Gould first published their "punctuated equilibria" interpretation of evolution a few workers have come out to support it while many have come out in opposition and contend that their research data indicates phyletic gradualism. This prompted Gould and Eldredge to write a second paper in 1977 to refute these claims and indicate the success of their model. In order to refute their punctuated equilibria model a researcher must show gradational species level lineages well preserved over the full span of an extensive geographic and temporal range. As Gould and Eldredge (1977) adequately point out most of the claims for phyletic gradualism are based on local sections(not their full geographic range) and short duration (too small a scale) and are therefore invalid as the data are insufficient for a test. In defence of their openmindedness Gould and Eldredge (1977) do accept one case of gradualism as being very impressive. This case illustrated the increase in prolocular diameter of a verbeekinoid foraminifer in 34 relatively large samples spanning the Middle to Upper Permian from southeast Asia, southern China and Japan. As Gould and Eldredge (1977) state, "We are delighted with these results as we expect some countercases, especially among predominantly asexual forms". Their discussion of another gradualistic case, that of Gingerich (1976) for Early Eocene mammals in northern Wyoming, is of particular interest to this work. Gingerich (1976) claimed that species of the Eocene mammal Hyopsodus evolved in a manner conforming to Cope's rule (increasing size through time) based on the increase upsection of the logarithm of length times width of the first lower molar. However, this overall increase was achieved only after a number of fluctuations (of nine descendant species, five evolve toward smaller size and only four to larger). Gould and Eldredge (1977) counter that Gingerich's splitting of lineages fits their model of punctuated equilibria better. They found long segments of apparent stasis within his supposedly gradualistic sequences. Furthermore, they state the fluctuating pattern towards increase in tooth size confirms the most important implication of punctuated equilibria, that speciation is essentially random with

respect to the direction of a macroevolutionary trend (Wright's rule, Wright, 1967). Stanley (1975) wrote that macroevolutionary trends are not a result of gradualistic orthoselection, but arise from a "higher level selection" of certain morphologies from a random pool of speciation events produced by punctuated equilibria. According to Gould and Eldredge (1977) the phylogeny of Hyopsodus affirms Wright's rule where size increase in the entire clade arose from the differential success of larger species in a random subset of cladistic events. It is my opinion that the phylogeny of Neogondolella idahoensis n.subsp. A to N. rosenkrantzi n.subsp. D equally supports the model of punctuated equilibria and affirms Wright's rule. The data displayed on Figure 8 is based on N. serrata and N. postserrata from West Texas (from Behnken, 1975) and on N. idahoensis n.subsp. A from northern Ellesmere Island. The material thus covers a large geographic area and a significant portion of the temporal range of the Neogondolella serrata complex, that of the late Lower Permian through Middle Permian (about 15 million years), both necessary prerequisites for an adequate test. The data indicates an overall increase in number of denticles per unit length upsection but only after a fluctuating path where N. serrata has more denticles percunit length than the resulting descendent N. postserrata. N. rosenkrantzi n.subsp. D from Ellesmere Island falls within the same field represented by data points for N. postserrata from West Texas. However, all of these members of the clade have a larger value for denticle number per unit length than that for the ancestral form, N. idahoensis n. subsp. A. Having accepted a punctuated equilibria mode of evolution to explain the fluctuating pattern of denticle number per unit length I must also accept some of the other features of the model; namely, that between these speciation events the forms did not change, that is they underwent a

period of stasis. However, at first glance I cannot do this, as some consistent trends were apparent in the samples F48 to F54 studied quantitatively in detail (Table 1).

Gould and Eldredge (1977) indicate that the norm for a species during the heyday of its existence as a large population is morphological stasis, minor non-directional fluctuation in form, or minor directional change bearing no relationship to pathways of alteration in subsequent daughter The nature or degree of this minor change can be best understood species. by realizing that the rapidity of speciation in such a model does not require the intermediate stage of a recognizable subspecies (Stebbins, 1977). My naming the studied populations represented by F48 to F54 as a new subspecies of Neogondolella idahoensis indicates that I feel recognizable changes do occur between the rapid speciation events and that these are significant at the subspecific level. The time represented from F48 to F54 (15 m of a 200 m section) may represent as much as one million years but is probably more on the order of 500,000 years (assuming continuous sedimentation and time scales for the Permian). Clark and Behnken (1979) indicate that the average species duration for Permian neogondolellids is 3.3 million years but that this may vary from 2 to 10 million years (the latter figure for N. idahoensis - considered high by this author). Even if we assume the average duration of 3.3 million years for N. idahoensis, the time represented between F48 and F54 is only a small fraction of this temporal range. In other words even if the change from F48 to F54 is insignificant, it could, if extended to the presumed full range of the species, become significant.

Z-tests for the parameters Ll, #, and Ll/# indicated that differences between samples were insignificant. However, when the samples were separated into just those elements with ll denticles a t-test indicated that

differences between F49 and F54 were very significant. This significance alone could not be used to differentiate between subspecies but may indicate that differences between entire samples, if extended through greater temporal range, could become significant. Although Gould and Eldredge (1977) do allow for some minor changes it is with the amount that many authors seem to be at odds with them. I would prefer to believe that between these rapid speciation events some gradualism does occur. However, Newell (1956) indicated that spurious "phyletic change" may arise in local sections by successive immigration of normal geographic variants responding to changing local environments. If the environment was changing in a progressive manner (eg. shallowing during regression) then samples upsection would change in one direction with respect to a parameter. Given the genetic and physiological complexity of any population of organisms, many different ways of adjusting to a new factor of the environment are possible (Stebbins, 1977), suggesting that any change in a local section with respect to environment need not be accompanied by a similar consistent gradual change in biotic response. If the immigrants (normal geographic variants) respond in many ways to environmental change then the results are unlikely to be consistent upsection and unidirectional. A form of selection different from non-directional (stabilizing) or directional is that of diversifying selection where, if environmental heterogeneity is increasing over time, the response of the population will be to become more heterogeneous with respect to various parameters resulting in a once homogenéous population breaking up into several differently adapted subunits (Stebbins, 1977). The variability of those populations from F48 to F54 seems to be increasing as evidenced by the almost consistently increasing standard deviation of the samples upsection. How these two types of selection, directional and diversifying, interact

and whether the resulting gradation upsection can still be regarded as spurious rather than real, is difficult to say unequivocally. There are many complicating factors, obviously. Perhaps easier to demonstrate would be whether or not the minor change in form bears a relationship to the evolution of subsequent daughter species.

If one considers the interval represented between <u>N</u>. <u>idahoensis</u> and <u>N</u>. <u>serrata</u> the expected trends would be towards overall decreasing size and increasing denticle number. The results for F48 to F54, which represents part of this just mentioned interval, depict increasing length, width, height and posterior area upsection (exactly opposite the expectation) and overall increase but fluctuating denticle number (approximates the expected trends). These between-speciation trends could be regarded as random or chance events in the developmental pathway because only one of the two trends bears any relationship to the speciation trends.

It seems appropriate at this time to compare the results of a study by Dzik and Trammer (1980) which in many respects is similar to this one. Their analysis is the result of study of 25 samples over about 23 metres of section from the Holy Cross Mountains of Poland which contain Triassic neogondolellids (gondolellids to them). Their results indicate a general decrease in denticle number and length but along a fluctuating path. They interpret their results as the result of phyletic gradualism and not of punctuated equilibria. However, these results fail in providing an adequate test since they represent a local section of short duration. In such a section one would not expect to see trends that are the result of punctuated equilibria. Furthermore, the fluctuating path (if it were over a larger time frame) could be better interpreted in a punctuated equilibria

model. These results could be interpreted as "spurious" directional phyletic change because they are from a local section. Furthermore, a complicating factor previously discussed, that of increasing variability, does not seem to be the case here. They indicate, however, that platform conodonts in the uppermost Muschelkalk of Germany (slightly younger than the Holy Cross Mountain specimens) represent in morphology a progress along the trend direction recognized in the conodonts from the Holy Cross Mountains suggesting that their trends were not "spurious" and that the populations of Gondolella inhabiting the Central European basin were evolving simultaneously and regardless of local facies changes. Despite the fact that the time frame represents a large fraction of the Middle Triassic, the demonstrated evolution is of three temporal subspecies. Two of these subspecies are represented in the local Holy Cross Mountain section - in the uppermost and lowermost samples. As indicated earlier the trends at this taxonomic level should be more gradual. These results give me some reason to accept my bias that the changes from F48 to F54 are real at the subspecific rank and that gradual changes should be expected at this taxonomic level.

In summary, the results for the <u>Neogondolella</u> species described from the Assistance and Trold Fiord Formations of northern Ellesmere Island, Arctic Canada compared to species from the Great Basin of the western USA, are best interpreted as the result of evolution consistent with a punctuated equilibria model. The results for a small fraction of this interval seem to indicate that directional and/or diversifying selection result in gradual changes at the subspecific level. This should not be considered in opposition to the punctuated equilibria model but regarded as a feature that en-

hances the resultant changes during the rapid but punctuated speciation events. Just as Gould and Eldredge (1977) regard stasis as real so should gradual change between punctuated speciation events be regarded as a reality at the subspecific level. This does not seem to be an unreasonable statement when one considers the many varying evolutionary styles demonstrated by different biotic forms.

SYSTEMATIC PALEONTOLOGY

Introduction

There are a number of problems with the designation of the genus <u>Neogondolella</u> that make its concept unclear. It was originally erected for forms that developed from the genus <u>Spathognathodus</u> (now <u>Neospathodus</u>) in the Lower Triassic. Subsequently, Upper Carboniferous, Permián and Lower Triassic species have been assigned to <u>Neogondolella</u> by many authors including all American authors. Kozur (1968) retains the genus <u>Gondolella</u> for all of these forms. The present controversy over the designation is one of the opposing views between the European and North American "schools".

The revised diagnosis (Sweet, 1970; fide. Ziegler, 1973) includes conodont species in which the skeletal apparatus comprises elements of a single morphologic type. "These elements, which are elongate, paired, and individually asymmetrical, have a terminal or subterminal posterior cusp; a median nodose or denticulate carina; and finely to coarsely pitted, largely unornamented, platformlike lateral extensions, which are joined posteriorly in most species by a more or less well developed brim that encloses the posterior end of the carina. Underside of elements marked by a longitudinally grooved keel that widens posteriorly to enclose a pit beneath the cusp (Ziegler, 1973, p. 127-128)." Kovacs and Kozur (1980)

suggest that this diagnosis of Neogondolella Bender and Stoppel, 1965 is insufficient to separate this genus from Gondolella Stauffer and Plummer, 1932. It appears that many of these features (posterior brim, ornamentation) are variable within the phylogeny of this group and ontogeny of its members (eg. smooth and pitted platform of <u>N. idahoensis</u> versus serrated and pitted platform of N. serrata and lack of serration in early ontogeny of N. postserrata). Kovacs and Kozur (1980) indicate that the main argument for separation of the two genera is the assumption that Neogondolella has a single element apparatus (platform only) whereas Gondolella has a multielement apparatus (platform plus ramiforms). Because of the conflicting opinion of a number of senior workers it is not clear which argument has greater merit. Von Bitter and Merrill's (1977) suggestion that a Pennsylvanian Neogondolella had a multielement apparatus was rejected by Clark and Behnken (1979). One of the reasons for this conflicting opinion is the phenomenon of platform overrepresentation; although the frequency varies in any local section, it generally increases from Carboniferous to Triassic. Merrill and Powell (1980) have shown that this platform overrepresentation in Missourian Gondolella is probably the result of an ontogenetic series of only ramiform apparatuses, to ramiform plus platform, to apparatuses comprising platform only. In other words, they suggest a mechanism for this low index of mutual occurrence which indicates that a pure statistical analysis could lead to serious mistakes in the combination of conodont apparatuses. They agree with Kovacs and Kozur's (1980) opinion of a multielement apparatus for both of these genera but at the same time retain the designation of Neogondolella. Von Bitter (1976) suggests that the reticulated microstructure is distinctive; covering much more of the oral surface

in <u>Neogondolella</u>. Sweet (1970) indicated that if <u>Neogondolella</u> contained elements of a single type then <u>Neogondolella</u> was fundamentally different from <u>Gondolella</u>. Evidence seems to indicate that the two genera are not fundamentally different but that minor differences do exist (reticulation, variable but much less ribbed or serrated ornament) to the extent that many authors (if not most: Kozur the notable exception) retain the genus <u>Neogon</u>dolella.

Furthermore, the origin and phylogeny of the genus remains clouded. The original Neogondolella was erected as a form derived from Neospathodus but Mosher (1968) indicates that N. mombergensis (the type species) is not related to Neospathodus making the original diagnosis impractical. Szaniawski and Malkowski (1979) indicate that the evolutionary development of the Permian neogondolellids shows clearly that they represent one phylogenetic branch and that the recognized ontogeny bears no relationship to Neospatho-Clark and Behnken (1979) indicate that N. bisselli, the ancestor of dus. all Permian and younger species, occurs several hundred feet above Gondolella bella with which it bears little morphologic similarity. Movshovich et al. (1979, fide. Kovacs and Kozur, 1980) indicate that "G". praebisselli is intermediate between G. bella and "G". bissélli. There appears at present no clear solution for a student attempting to decipher these reports in terms of an adequate phylogeny. It does seem clear that more work is necessary from an unbiased point of view to determine the significance of differences between Neogondolella and Gondolella. Only at this point could the evolution of these forms be deciphered.

Until a revised diagnosis is presented that is widely acknowledged and refutes the genus Neogondolella, this author refers his gondolelliform ele-

ments to species of Neogondolella as diagnosed in Ziegler (1973). Using this diagnosis indicates that descriptions for the species at hand assume a single element-type apparatus. For this reason the platform elements of Neogondolella will be discussed separately from the ramiforms. Recognizing that the ramiform elements could belong to multielement "Neogondolella" apparatus a dual taxonomic nomenclature is adopted for these elements as Multielement species - Form species. This method of description follows: is somewhat unsatisfactory but it does reflect the present controversy and the desire by the author that the question be resolved in the near future. Should the genus be found to have a multielement apparatus then the form species name should be placed in synonymy while if the genus is found to have a single element apparatus then the multielement species name should be dropped. Description of these ramiform elements will follow that of the platforms of Neogondolella.

As the platform elements evolved rapidly and are consequently stratigraphically very important they are described in detail, whereas the ramiform elements evolved slowly and are, as a result, of little value stratigraphically and thus are not described in detail.

The platform elements of <u>Neogondolella</u> species are described in chronological order. Two other genera, including <u>Anchignathodus minutus</u> and <u>Neostreptognathodus prayi</u> are discussed first because of their association with the oldest <u>Neogondolella</u> platform species (<u>N. idahoensis</u>). These two genera are only briefly described as they are unimportant in the area owing to their slow evolutionary rates and very rare occurrence, respectively.

In summary, the order of appearance will be <u>Anchignathodus minutus</u>, <u>Neostreptognathodus prayi</u>, platform elements of various <u>Neogondolella</u> species, and finally the ramiform elements .

Systematics

Genus ANCHIGNATHODUS Sweet, 1971

Type species Anchignathodus minutus (Ellison), 1941

ANCHIGNATHODUS MINUTUS (Ellison), 1941

Pl. 1, figs. 3-6.

Spathodus minutus Ellison, 1941

Occurrence: Lower Assistance Formation, Hamilton Peninsula section (F48, F49, F52, F53, F54, F63 and F75).

Description: This element possesses a short, thin, laterally straight to slightly curved blade about three times as long as wide and with six to nine laterally compressed, subequal, partly fused denticles posterior to the cusp and zero to three short denticles anterior to the cusp. The denticles are offset abruptly to the cusp which is large and triangular in outline. The basal cavity of the blade is broadly flared in the mid region, especially under the denticles posterior to the cusp. The cavity reduces to a narrow groove at both the anterior and posterior ends of the aboral surface. The deepest point of this basal cavity is below the first or second denticle posterior to the main cusp.

Discussion: Representatives of this species range from Chesterian (Late Mississippian) to Roadian (early Medial Permian) in age (Behnken, 1975; Ziegler, 1973). They are differentiated from the younger <u>A. typicalis</u> by the abrupt offset in lateral profile posterior to the cusp as opposed to a gradual diminution of the lateral profile.

Genus NEOSTREPTOGNATHODUS Clark, 1972

Type species <u>Streptognathodus</u> sulcoplicatus (Youngquist, Hawley and Miller, 1951)

NEOSTREPTOGNATHODUS PRAYI Behnken, 1975

P1. 1, figs. 1,2.

<u>Occurrence</u>: Assistance Formation, McKinley Bay section (F100). <u>Description</u>: This element consists of a subsymmetrical, posteriorly pointed platform with closely spaced, subparallel, transverse ridges on the oral surface which extend almost to completely across the medial groove. <u>Discussion</u>: No anterior free blades were observed. The two fragments appear to represent forms intermediate in ontogeny, following descriptions by Behnken (1975). According to Wardlaw and Collinson (1979à) and Clark et al. (1979) the youngest occurrence of this species is Latest Leonardian. Genus <u>NEQGONDOLELLA</u> Bender and Stoppel, 1965

Type species <u>Gondolella</u> <u>mombergensis</u> (Tatge)

NEOGONDOLELLA IDAHOENSIS (Youngquist, Hawley and Miller, 1951) subsp. indet. Pl. 1, figs. 7-13.

Gondolella idahoensis Youngquist, Hawley and Miller, 1951

<u>Gondolella phosphoriensis</u> Youngquist, Hawley and Miller, 1951 Occurrence: Assistance Formation, McKinley Bay section (F100). Discussion: These specimens are very similar to <u>N</u>. <u>idahoensis</u> n.subšp. <u>A</u> except that no serrations or distinct varieties were recognized. This is partly owing to the low number of specimens and poor preservation (recrystallized). For these reasons and because of its occurrence with <u>Neostreptognathodus prayi</u> (suggesting a slightly older age from <u>Neogondolella idahoensis</u> n.subsp. <u>A</u>) a subspecific determination was not made. Their description is similar to that of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> (except for the varie ties) which follows.

NEOGONDOLELLA IDAHOENSIS n.subsp. A

Pl. 2, figs. 9-19; Pl. 3; Pl. 4; Pl. 5.

Occurrence: Lower Assistance Formation, Hamilton Peninsula section (F48, F49, F52, F53, F54).

<u>Diagnosis</u>: This subsymmetrical unit has a carina composed of 6 to 16 denticles (average 10 to 11) which are discrete in early growth stages, becoming partially fused and finally completely fused in gerontic forms. The platform elements are very variable, ranging from long and slender forms to robust and serrated. The maximum width typically occurs at some point in the posterior half, after which the element tapers gradually and finally rapidly in the anterior half. Except for the anterior tip the platform margin is reticulated in all examples. This reticulation although generally absent from the well developed furrows and carina, is present on these in some mature robust forms. During ontogeny the keel on the aboral side changes from narrow and high, terminating in an oval loop to wide and low with a terminal triangular loop.

The cusp is large, erect and inclined posteriorly while the four denticles anterior to it are low, node-like, and closely spaced. The remainder of the denticles increase in height and are progressively compressed anteriorly.

<u>Description</u>: A. Juvenile - The element is small (length = 350 to 800 μ m; maximum width = 100 to 180 μ m), subsymmetrical, and slightly arched. The thin platform has its lateral margins upturned more in the central portions of the element than at either end. The position of the maximum width, though variable, is generally slightly anterior of the posterior tip. The lateral margins are subparallel to only slightly tapering anteriorly for much of

their length corresponding to the position of the reticulated micro-orna-The remaining 1/3 of the length bears little or no reticulate patment. tern and tapers much more rapidly than the posterior 2/3. The reticulate ornament is restricted to the oral surface on the edges of the platform and is absent on both the carina and the furrows lateral to it. The carina generally consists of 6 to 9 laterally compressed triangular and nodose denticles. The posterior cusp is higher than all other denticles, circular but more commonly slightly oval in crosssection, inclined posteriorly but with a slight anteriorly directed curvature, and situated variably behind the posterior margin of the platform. The cusp thus extends as a posterior free blade in the earliest recognized stages but this feature is quickly lost as the platform extends to the posterior edge of the cusp and finally forms a brim posterior to the cusp in later ontogenetic stages. The next three or four denticles anterior to the cusp are small and slightly compressed but are more generally nodose compared to the rest of the carina. This feature remains in all ontogenetic stages and would seem to be of major genetic significance and important to the diagnosis. The remaining denticles increase in size rapidly and become compressed, inclined posteriorly and triangular in outline as the anterior tip is approached. In the earliest stages the platform does not reach the anterior portion where the carina extends as a free blade, but in later stages it lengthens to encompass this free blade. The aboral surface bears a narrow and very high keel terminating posteriorly as an elevated oval loop. The basal groove is very narrow, extends the entire length of the keel and terminates posteriorly as an elongated, narrow and curved pit. The crimp is very wide, about 3/4 of the platform width, and smooth in contrast to the ornamented oral surface.

B. Intermediate - As the element increases in length the platform becomes thicker and wider. As is the rule rather than the exception for these conodonts the values and ratios for the measured parameters are extremely This variability is especially large for L1/H1 and L1/W1 ratios. variable. In general, however, the length of the intermediate element ranges between 800 and 1100 μ m and the width between 180 and 220 μ m. The position of maximum width is generally 1/3 to 1/4 the length from the cusp to the anterior. The platform extends from the posterior edge of the cusp to the anterior tip: no free blades exist at this stage. It is at this stage that varieties start to become apparent but their differentiation becomes even more clear in mature forms where it will be discussed in detail. Generally, taper of the platform is gentle towards the anterior for much of the length but increases for the anterior 1/3 to 1/4. The reticulate pattern extends to the anterior tip but is still restricted to the thickened margins of the platform. The carina consists of 10 to 11 laterally compressed, triangular, nodose denticles. The posterior cusp (is similar to that described for the juvenile stage except that it is larger. The next 3 to 5 denticles anterior to the cusp (in most specimens it is 4 denticles) are low, roughly circular in cross section and node-like. The remaining denticles increase in height and are progressively compressed anteriorly. All denticles are entirely discrete at this stage. The aboral surface bears a wider and lower keel (as compared to juvenile stages) which terminates posteriorly as an elevated oval to slightly square shaped loop. The basal groove is similar to that in juvenile stages, but a little less narrow. The crimp is narrower, 2/3 to 3/4 of the platform width, and smooth.

C. Mature - The variability of form for these conodonts is very high, as was mentioned above, and becomes accentuated in the mature stages. It is at

these stages that different varieties can be distinguished. Some of the varieties are so distinctive that, if found alone, they might well be described as different species, however, it seems that the variability is actually that within a single subspecies. The graphical evidence (Figs. 10- 1^4) fails in all cases to isolate these varieties from each other. Those graphical plots that to a certain degree separate the two extreme varieties, namely the posterior area versus length/denticle number ratio and the posterior area versus length (Figs. 12-14), do so with some overlap between themselves and a large number of intermediate forms. It seems apparent that such a feature is the result of the normal distribution of variability in a single gene pool. An anisometric type of growth, indicated by the graph of area versus length (Fig. 12), demonstrates quantitatively that shape of the element changes during ontogeny: a fact alluded to throughout the description of this species.

The two very different varieties present for this subspecies will be described as the <u>gracilis</u> variety and the <u>robustus</u> variety. A number of forms that cannot qualitatively be separated into one or another of these varieties will be referred to as the <u>intermediatus</u> variety. The <u>gracilis</u> variety, so-named because of its very long and slender platform, is very similar to the species <u>Neogondolella gracilis</u> Clark and Ethington, 1962. The variety <u>robustus</u> resembles the species <u>Neogondolella serrata</u> Clark and Ethington, 1962 except for the much larger length per denticle number and the lack of ridges associated with the serrate margin. The <u>intermediatus</u> variety most resembles the species <u>Neogondolella idahoensis</u> Youngquist, Hawley and Miller, 1951 leading to the new subspecies being referred to <u>N</u>. <u>idahoensis</u> rather than <u>N</u>. <u>gracilis</u> or <u>N</u>. <u>serrata</u>. It was considered that referring the populations in question to a new specific rank required unsub-



Figure 10. Graph showing the relationship of Length/Height to Length of the platform for F49. r= var. robustus g= var. gracilis, the remainder are var. intermediatus



Figure 11. Graph showing the relationship of Length/Width to Length of the platform for F49. r= var. robustus g= var. gracilis, the remainder are var. intermediatus.

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Figure 12....Graph showing the relationship of Posterior Area to Length of the platform for F53. r=-var. <u>robustus</u> g= var. <u>gracilis</u>, the remainder are var. intermediatus



Figure 13. Graph showing the relationship of Posterior Area to Length of the platform for F49. r= var. robustus g= var. gracilis, the remainder are var. intermediatus.



Figure 14. Graph showing the relationship of Posterior Area to Length/number of denticles for F49. r= var. robustus g= var. gracilis, the remainder are var. intermediatus.

stantiated taxonomic splitting. If quantitative methods indicated a separation of this form from older <u>N</u>. <u>idahoensis</u> similar to the separation for <u>N</u>. <u>serrata</u> and <u>N</u>. <u>postserrata</u> (Behnken, 1975 - he referred to <u>N</u>. <u>postserrata</u> as <u>N</u>. <u>serrata</u> postserrata which was subsequently elevated to specific rank) then perhaps this new subspecies could be later elevated to specific rank. It is possible that these varieties if separated as peripheral isolates could, following speciation and migration, lead to populations more reliably described as <u>N</u>. <u>gracilis</u> or <u>N</u>. <u>serrata</u>.

As well as these three named morphologies a number of "experiments" or unusual forms are mentioned below. Perhaps, as these unusual forms are few in number, they could be considered as mutations that were not particularly advantageous; at least one, however, has a platform shape similar to that of the Triassic species <u>N</u>. <u>constricta</u>.

N. idahoensis n.subsp. <u>A</u> var. gracilis

The platforms are typically long and slender (Ll = 850 to 1200 μ m; Wl = 160 to 220 μ m), subsymmetrical, and gently arched. The platform extends the full length of the element and is flush with the posterior edge of the cusp. The lateral edges of the platform are upturned, especially in the central regions. The lateral margins of the posterior half of the platform are subparallel to parallel and taper gently in the anterior half. The posterior margin is gently rounded and with the reticulated portion tapering to the cusp. The reticulation ornament tapers on the lateral margins in the same fashion as the platform itself tapers but is absent in the most anterior portions. The reticulate pattern is absent on both the denticles and furrows. Some faint ridges were observed on the cusp of a couple of specimens - these may represent the very early formation of reti-

culae. The carina typically comprises 12 or 13 discrete denticles, the anterior four of which are low and nodiform, all of which are connected by a noticeable crease or mid-line. No anterior serrations have been noted on this variety.

N. idahoensis n.subsp. <u>A var. robustus</u>

As the name indicates this variety is thicker, wider and generally more stout or robust compared to var. gracilis. The length of the element is generally between 800 and 1250 μ m and the width between 200 and 270 μ m. This results in posterior areas averaging 6.2 units ($\mu m^2 \times 10^4$), considerably more than the 4.4 unit average for the gracilis variety. The platform extends the full length of the element, in some cases forming a minor posterior brim but normally flush with the rear edge of the cusp. The margins of the platform are subparallel for the posterior 3/10, increase in width over the next 2/10, and finally taper over the anterior half: slowly at first and more rapidly close to the tip. The posterior margins are quite square as opposed to the rounded gracilis variety. The reticulated pattern parallels the platform margin and is missing on the anterior -most edges where the margin tapers most rapidly. The reticulate pattern migrates onto the furrows and the denticle tips in many specimens. This feature seems to be related to early fusion of the denticles - a feature representative of gerontic individuals. The ridges that constitute the meshes of the reticulation are typically sharp in the middle of its range, flattened but distinct on the outer edge, and fading and elongate towards the furrows (P1. 5, fig. 1). Denticles (generally 11 to 13) except for some fusion of the posterior ones, conform to earlier descriptions. A number of specimens exhibit a serrate platform margin in the anterior 1/3. The serrations are variably developed but generally weaker than those described

by Clark and Behnken (1979) for <u>N</u>. <u>serrata</u> and younger Permian conodonts and without the ridges accompanying the serrations as in <u>N</u>. <u>serrata</u>. The keel is wide and low and terminates in an extensive triangular loop. The basal groove is wider than in more juvenile forms and terminates in the basal pit. The smooth crimp typically covers 6/10 to 2/3 of the aboral surface.

N. idahoensis n.subsp. A var. intermediatus

The form of the carina, position of the reticulae, and development of the aboral surface are similar to those described for the other varieties. The platform shape is intermediate between that for the gracilis and <u>robustus</u> varieties with the maximum width generally corresponding to the position of the fourth denticle anterior to the cusp. Areas in the posterior region average about 5.0 units. The platform tapers more or less gradually from the maximum width to the anterior tip. Anterior serrations are present but less common than in the robustus variety.

The main differences in platform shape are the average maximum width, and the manner, position, and degree of taper. These features have been described in detail for the extreme varieties, whereas it seems adequate to state that the representatives of var. <u>intermediatus</u> form the central part of a continuous gradation and typify the population means. Introduction to the unusual varieties of <u>N. idahoensis n.subsp. A</u>

Those forms that are unusual in terms of their platform shape are generally recognized at the mature to gerontic stages of development and do not show observable ontogeny. These forms comprise only a small fraction of any population sample.

N. idahoensis n.subsp. A var. constrictus

This variety has a constricted platform margin in the posterior of the

element. The platform is rounded in the posterior and tapers slightly anteriorly for about 1/4 of its length where it widens rapidly to its widest point about 3/8 of it length. From this point the platform tapers normally for the subspecies. The illustrated specimen is a gerontic form and has fused posterior denticles (Pl. 4, fig. 7). Var. <u>constrictus</u> has also been recognized in specimens with all denticles discrete. This platform shape is characteristic of <u>N. constricta</u> from the Triassic in terms of the constricted posterior margin.

N. idahoensis n.subsp. A var. lobátus

This form has a very wide and thick platform overall that is similar, except for the posterior end, to <u>N</u>. <u>rosenkrantzi</u>. The posterior margin of the platform is tri-lobed: one lobe surrounding the cusp and separated by furrows from the two lobes forming the postero-lateral margins of the element. The furrows are wider and slightly deeper than those in similar <u>N. rosenkrantzi</u> n.subsp. <u>D</u> and are not directed postero-laterally as well. The denticles increase only slightly in height anteriorly and are not distinct and node-like as is generally characteristic for the subspecies. The cusp is also more compressed then normal and not directed posteriorly but rather straight upwards.

<u>Discussion</u>: Juvenile forms of <u>N</u>. <u>idahoensis</u> were described for the first time by Szaniawski and Malkowski (1979) from the Kapp Starostin Formation of Spitsbergen. The ontogeny described by these authors is very similar to that for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>, except that the juvenile carina has 6 to 9 denticles rather than 8 to 10 for the Kapp Starostin specimens. Szaniawski and Malkowski (1979) stated that the ontogeny for <u>N</u>. <u>idahoensis</u> was very similar to that of <u>N</u>. <u>bitteri</u> (Kozur) as described by Clark and Behnken (1971) and concluded that these two species bore a close relation-

ship. The juvenile forms of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> are very similar to those of <u>N</u>. <u>rosenkrantzi</u> n.subsp. <u>D</u>...Furthermore juvenile forms of <u>N</u>. <u>post-</u> <u>serrata</u> as illustrated in Behnken (1975) are also very similar to those of the other species just mentioned. There seems to be good reason to believe that the close similarity of the juvenile forms described above is the result of close phylogenetic affinity for all those species belonging to the <u>serrata</u> complex (Clark and Behnken, 1979) and including <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. Clearly, species cannot be determined on the basis of juvenile material alone. The differences between members of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> from F49 to F54 are directly proportional to the number of denticles on the element which is more or less directly related to size and ontogenetic development and illustrates the need for intermediate and mature forms before differentiation of subspecies and species can be attempted.

Mature specimens differ little from specimens previously referred to <u>N. idahoensis</u>. Most workers attest to a high variability in shape and in length to width ratio although none have attempted to quantify this. Variability is a characteristic of <u>N. idahoensis</u> n.subsp. <u>A</u> (Figs. 10, 11). Perhaps the most closely comparable specimens that I have seen are those illustrated and described by Szaniawski and Malkowski (1979) from Spitsbergen. As well as <u>N. idahoensis</u> (137 fragments) these authors described <u>N. cf.</u> <u>N. gracilis</u> (3 fragments) and <u>N. sp. <u>A</u> (1 specimen). In the light of my faunas and their variability all of these fragments would be included in a single species. The <u>N. cf. N. gracilis</u> is similar to the Ellesmere Island var. <u>gracilis</u> whereas the <u>N. sp. A</u> is similar to var. <u>lobatus</u>. These specimens differ from <u>N. idahoensis</u> n.subsp. <u>A</u> in terms of the lack of anterior serrations, the number of denticles (8 to 13 denticles compared to 6 to 16), and in the manner of tapering (widest point closer to posterior tip).</u> Their specimens appear closer to the type specimens for the species and are probably slightly older than N. idahoensis n.subsp. A.

Clark and Mosher (1966) regarded <u>N</u>. <u>phosphoriensis</u> Youngquist, Hawley and Miller with its posterior ridge-like carina, as a later growth stage of <u>N</u>. <u>idahoensis</u> where the posterior carina has become fused. In the Ellesmere collections that form is restricted to mature and gerontic forms only. As well, the fusion of the carina is shown to be gradational (Pl. 4, figs. 5, 6, 10). These observations most certainly lend further support to Clark and Mosher's conclusion that <u>N</u>. <u>phosphoriensis</u> be placed in synonymy with N. idahoensis.

The basal loop shows a development from a high elongate oval to rounded shape in juvenile and intermediate forms to a low, large, triangular shape in mature and gerontic forms. Observation of the growth lamellae in a few specimens (P1. 5, figs. 9, 10) shows that some of the lateral traces of the lamellae are truncated at the posterior of the loop. The truncation is apparently caused by resorption as described by Muller and Nogami (1972) which, according to these authors, is a common phenomenon for the Conodontiformes. It resulted in squaring-"off the posterior of the loop such that subsequent regeneration of the loop led to a triangular shape. Resorption, then, seems to be an important phenomenon within the ontogeny of this conodont. Muller and Nogami (1972) conclude that the conodont element, besides having the function to support a tissue, may also have served as an organ for the temporary deposition of phosphatic substance, which might later be utilized to form another element in the same animal. One cannot help but speculate whether this resorption phenomenon observed in the platform element of Neogondolella also occurred in the ramiforms (if a multielement

apparatus indeed existed) resulting in a platform-only apparatus (as suggested by Merrill and Powell, 1980): the excess phosphate being used to form the large, thick-margined mature and gerontic platform elements.

NEOGONDOLELLA SERRATA(?) (Clark and Ethington, 1962)

Pl. 6, figs. 7-9.

<u>Gondolella serrata</u> Clark and Ethington Gondolella nankingensis Ching, 1960

Occurrence: Upper Assistance Formation, Hamilton Peninsula section (F63, F73).

This designation is based only on fragmental specimens. Description: Estimates of length were made by taking into consideration the gentle taper. Specimens that would be regarded as intermediate in ontogeny have an estimated length of 400 to 580 μm and a maximum width of 100 μm . Although the anterior denticles were not observed, the total number of denticles for these intermediate forms is on the order of 11. The four denticles anterior to the cusp are sharp, fused at their bases, laterally compressed and not distinct from the other denticles as in N. idahoensis n.subsp. A. The cusp is high and laterally compressed, especially the anterior half. The platform is gently tapering, laterally upturned, arched and rounded at the posterior end. The lower surface of the plätform is smooth and bears a high and relatively narrow keel. The reticulate pattern on the upper surface is sharp, irregular in shape and restricted to the lateral margins as it fades quickly towards the carina, reaching the latter only at the position of the cusp.

<u>Discussion</u>: These specimens differ from the older specimens of <u>N</u>. <u>idahoen</u><u>sis</u> n.subsp. <u>A</u> in their smaller size and they do not have the four nodiform denticles distinct from the others anterior to the cusp. Reduction in size

at comparable growth stages has been observed in the evolution of $\underline{\mathbb{N}}$. <u>ida-hoensis</u> to $\underline{\mathbb{N}}$. <u>serrata</u> in other regions. Another characteristic of $\underline{\mathbb{N}}$. <u>ser-rata</u> that is present in these specimens is the fusion of denticles in intermediate rather than gerontic stages of growth. Since anterior fragments of the platform were not observed it is impossible to assess whether the anterior serrations, diagnostic of the species and providing the derivation of the name, are present.

According to the figures mentioned above, the values for L1 and W1 individually average about two standard deviations smaller than the mean for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. The ratio L1/number of denticles is more than two standard deviations less than the means for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> and almost two standard deviations less than that for <u>N</u>. <u>rosenkrantzi</u> n. subsp. <u>D</u>. Despite the fact that these figures are based on only very few specimens their significant departure from the means for specimens lower in the section suggest that they are indeed a different species. Furthermore, since they share some of the features of <u>N</u>. <u>serrata</u> they are assigned to that taxon but are more probably intermediate between <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> and <u>N</u>. <u>serrata</u>. The specimens also plot in or near the field of data points for L1 versus number of denticles of <u>N</u>. <u>serrata</u> as defined by Behnken (1975). The assignment is listed as indefinite because of the poor preservation and paucity of specimens.

The irregular reticulate pattern on the upper platform sufface also seems worthy of further discussion. Behnken (1975, Pl. 2, figs. 35, 36) illustrates the reticulate microstructure of an intermediate and a mature <u>N. postserrata</u>. The microstructure is very regularly shaped and arranged in linear rows (ordered) in the intermediate form whereas microstructure of

the mature form is irregular and arranged in a roughly sinuous manner (disordered). Similar ontogenetic variation, although not as marked, was observed in specimens of <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. Perhaps the feature is indicative of relative maturity. This would suggest that the small specimens referred here to <u>N</u>. <u>serrata(?</u>) are approaching maturity since they exhibit disordered reticulation.

A purely qualitative observation of the platforms referred to <u>N</u>. <u>ser-</u> <u>rata(?)</u> is their general degenerate appearance, lacking the robustness of the older faunas. There appears to be evidence that the lack of conodonts for a significant part of the section above <u>N</u>. <u>serrata(?)</u> is the result of a biologic crisis. Perhaps the degenerate appearance of these specimens of <u>N</u>. <u>serrata(?)</u> reflect the initiation of this crisis. The faunas above the barren interval are equally sparse a feature common to any crisis or near extinction. <u>N</u>. <u>rosenkrantzi</u> marks the reappearance of robust and abundant specimens.

NEOGONDOLELLA n.sp. B

P1. 6, figs: 1-4.

Occurrence: Lower part of the Trold Fiord Formation, Hamilton Peninsula section (F36, F83).

<u>Diagnosis</u>: This very symmetrical platform element is distinguished by its very large cusp which is round in cross section and directed straight upwards. Other diagnostic features include a well developed, faintly trilobed brim posterior to the cusp in mature elements. This brim bears a coarsely striate to faintly reticulate ornament on the oral surface. Furthermore, the reticulation on the platform margin ends very abruptly at the furrow margin.

Description: This new species is based only on the posterior regions of the platform owing to fragmentation of the elements. Nevertheless the features present on the posterior half are very distinctive. In the intermédiate form the platform margins are subparallel (how they taper in the anterior region is unknown) and rounded on the posterior end where it meets the cusp. The cusp is large, rounded in cross section, directed almost straight upward, and shows little to no lateral compression. The denticles are all low, laterally compressed, and fused at their bases. The platform margins are reticulated in a regular fashion. The reticulation does not reach the rounded parts of the posterior of the platform margin. The furrows and denticles are smooth up to the point where the reticulation begins abruptly.

In mature forms a platform margin forms posterior to the cusp. This posterior margin is faintly tri-lobed in outline on most specimens but in others can be very narrow. The cusp is generally very large, circular in cross section, and directed straight upwards. The reticulate ornament is similar to that in the intermediate form except that the reticulation reaches the posterior margin and the cusp. The reticulation generally gives way to a coarse striated ornament on the brim posterior to the cusp. The denticles are smooth, laterally compressed (some can be node-like), and fused up to half of their height. The aboral surface is smooth and bears a low, wide keel which terminates into an equally low, rounded basal loop. The narrow basal groove terminates in a slightly curved, elongated oval pit The crimp occupies about 2/3 of the aboral width.

<u>Discussion</u>: Superficially, the intermediate form looks similar to <u>N</u>. <u>ida-</u> <u>hoensis</u> n.subsp. <u>A</u>. However, <u>N</u>. n.sp. <u>B</u> has a larger, less compressed cusp that is directed upwards unlike that for the older species. The reticulate

ornament fades towards the furrows ending in faint linear ridges perpendicular to the length in <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> whereas the same ornament ends abruptly and lacks any linear ridges in <u>N</u>. n.sp. <u>B</u>. Other differentiating features are the partial fusion of denticles at their base and the lack of reticulation on the posterior "shoulders" of the platform. Furthermore, the element of <u>N</u>. n.sp. <u>B</u> is much more symmetrical than in older species owing to the position of the cusp and the parallel margin in the posterior of the platform. These forms look very similar to a younger species identified by Clark and Behnken (1979) as <u>N</u>. <u>wilcoxi</u> although the cusp in N. n.sp. B is generally larger.

Mature forms are distinguished from <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> in terms of the well developed posterior brim surrounding the cusp that is ornamented with coarse striations. This posterior brim is present in younger species (<u>N</u>. <u>babcocki</u> and <u>N</u>. <u>wilcoxi</u> in particular; see Clark and Behnken, 1979, Pl. 2, figs. 14, 21), however, the ornament is reticulated rather than of coarse striations. <u>N</u>. n.sp. <u>B</u> differs from <u>N</u>. <u>bitteri</u> n.subsp. <u>C</u> in being much more symmetrical.

The aboral surface is similar to that in younger and older species. The measurements for L2 which range between 240 and 310 μ m are similar to that for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> whereas the measurements for maximum width which range between 140 and 280 μ m, tend to be a little wider on average.

NEOGONDOLELLA POSTSERRATA(?) (Behnken, 1975) Pl. 6, figs. 5, 6.

Neogondolella serrata postserrata Behnken, 1975

<u>Occurrence</u>: Middle Trold Fiord Formation, Hamilton Peninsula section (F87). <u>Description</u>: This identification is based on only a very few fragments that are distinctly unlike any others seen through the entire sequence.

The gently arched to almost flat platform possesses subparallel margins and an abruptly squared-off posterior. The denticles in the mature form are large, circular in cross section and distinct. In a small midplatform fragment the denticles are laterally compressed and almost entirely fused suggesting this may be a gerontic form. The cusp is actually a rectangular shaped node projecting to one side of the platform. A small ridge marks the posterior border on the side opposite to the cusp. A fairly regularly arranged reticulate ornament on the margins of the platform reaches the posterior margin and ends abruptly where the furrows lateral to the carina begin. Very faint ridges perpendicular to the length can be seen on the otherwise smooth furrows of the mid-platform fragment but there are no serrations on the platform margins.

Measurements for W1 (mean = 200 μ m) and L2 (mean = 260 μ m) are very similar to those for <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. <u>Discussion</u>: These specimens are referred to <u>N</u>. <u>postserrata(?)</u> because of their stratigraphic position, their uniqueness compared to other species in the same section and because of their similarity to some of the squareended specimens figured by Clark and Behnken (1979, Pl. 1, fig. 17).

The shape of the cusp and the squared posterior end are the main distinguishing features. However, Behnken (1975) indicates that <u>N</u>. postserrata can have both rounded and squared posterior margins, so that the above distinguishing features should not be considered exclusive to the species.

NEOGONDOLELLA BITTERI n.subsp. C

Pl. 7, figs. 1-8.

<u>Occurrence</u>: Upper Trold Fiord Formation, Hamilton Peninsula section (F96). <u>Diagnosis</u>: A species characterized by a thick platform with a low, wide cusp of circular cross section surrounded by a brim with reticulate orna-

ment and low denticles on the carina. The subspecies is characterized by a distinct asymmetry resulting from the off-centre position of the larger posterior lobe.

<u>Description</u>: This designation is based on a number of posterior end fragments which have very distinctive features.

The postero-lateral margins are parallel to sub-parallel while the posterior end is lobed and distinctly asymmetrical. The posterior margin extends beyond the cusp as a well developed brim. The posterior asymmetry is formed by a large lobe occupying one side or the other of the platform The cusp is positioned near the median but may be to one side or centre. the other as well. The low, wide cusp has a circular cross section. The denticles on the carina are low and rounded, forming nodes that are partially fused at their bases. Longitudinal furrows adjacent to the carina are relatively deep, narrow and smooth. The thick and laterally upturned platforms are reticulated on the margin. The reticulate ornament extends very close to the carina fading into linear ridges as the ornament approach-The reticulation extends around the entire posterior brim es the carina. as well.

Measurements for the width of the platform range between 180 and 220 μ m whereas those for L2 range from 260 to 300 μ m. The aboral surface has a straight oval shaped pit surrounded by a roughly triangular shaped loop which roughly follows the outline of the posterior end. The pit extends anteriorly as a narrow groove bordered by a low, wide keel. The crimp is smooth and occupies 6/10 of the aboral surface width in the posterior region and 7/10 in the medial to anterior parts.

Discussion: According to Wardlaw and Collinson (1979b) N. bitteri is char-

acterized by a platform that abruptly narrows in the anterior third or fourth of its length, a low cusp of circular cross section, and low denticles on the carina. They distinguish this species from <u>N. rosenkrantzi</u> which is characterized by a wide platform that has a blunt posterior end and that commonly gradually tapers anteriorly and by a large cusp of elongate-oval cross section. Unfortunately, other authors differ in their determinations for the same material. Clark and Behnken (1971) and Clark et al. (1979) include forms Wardlaw and Collinson (1979b) refer to <u>N. bitteri</u> within N. rosenkrantzi and N. babcocki.

Designation of any species is a subjective and arbitrary procedure by the paleontologist. He justifies this procedure by separating his species on comparable morphologic variability exhibited by different but related extant species. This is impossible to accomplish with conodonts. Furthermore, with the lack of a functional model for conodonts (Bengtson, 1980), it is difficult to interpret taxonomic problems by comparison to other biotic forms. This leaves the interpretation of importance of various morphologic features for differentiating species open to subjective and arbitrary procedure without means of resolution. However, the success and validity of any morphological model is determined by the ease with which another student of these conodonts can apply the model to his material. Wardlaw and Collinson's diagnoses seem more appropriately to fit the material from Ellesmere Island.

The specimens here referred to <u>N</u>. <u>bitteri</u> are identified as such because of their very thick platforms, their cusp of circular cross section, and their low nodiform denticles on the carina. Wardlaw and Collinson(1979b) figure specimens of <u>N</u>. <u>bitteri</u> from the Gerster Limestone in Nevada and Utah
and from the Retort Phosphatic shale Member of the Phosphoria Formation, Wyoming. There seem to be minor differences between these two collections which may be of significance at the subspecific level. The specimens from the Retort Member appear to have slightly rounder posterior margins and taper more gradually then those from the Gerster Limestone. The Retort Member includes asymmetric forms owing to the off-centre position of the larger lobe (Wardlaw and Collinson (1979b) Pl. 1, figs. 11, 12). These specimens are very similar, indeed almost identical to those from Ellesmere Island.

These specimens differ from \underline{N} . n.sp. \underline{B} in terms of their different symmetry, generally smaller cusp, and reticulate microornament on the platform brim as opposed to striations.

The measurements for L2 and W1 are similar to those for N. idahoensis n.subsp. A but the other features make the separation clear.

The Ellesmere samples do not exhibit any postero-lateral denticles that can be present in N. bitteri, but Wardlaw and Collinson (1979b) indicate that those that do are rare variants.

NEOGONDOLELLA ROSENKRANTZI n.subsp. D

Pl. 7, figs. 9-12; Pl. 8.

Occurrence: Upper Trold Fiord Formation, Hamilton Peninsula section (F96). Diagnosis: This species is characterized by a thick, wide platform with almost blunt to slightly rounded posterior which gradually tapers anteriorly, by a prominent, often modified, cusp of oval cross section surrounded by a well developed brim, and by a narrow but shallow furrow lateral to the carina and directed postero-laterally towards the corners of the posterior margin. The subspecies is based on the enlarged postero-lateral platform margins, the gradual taper throughout the entire length, and by the slightly rounded posterior as opposed to a straight and blunt margin. <u>Description: A. Juvenile</u> - The element is small, subsymmetrical, slightly arched and upturned on its margins. The degree of upturning is greatest in the anterior half whereas the posterior half is barely upturned at all. The carina has at least 9 denticles including the cusp which, äs the platform extends only to the anterior tip of the cusp forms a free blade posteriorly. The cusp is high, élongate oval in cross section, triangular in outline, laterally compressed, and directed slightly posteriorly. The denticles anterior to the cusp are pointed, distinct, laterally compressed and increase slightly in height anteriorly.

The platform tapers gradually towards the anterior and bears a reticulate ornament restricted to the margins over the entire length of the The aboral surface is smooth and bears a high narrow keel which platform. terminates posteriorly in a high elongate oval basal loop or flange. B. Intermediate - The element is subsymmetrical, slightly arched, and scarcely upturned on its margins. This slight upturning is greatest in the anterior 1/3 and the posterior 1/3 whereas the middle part is flat. The platform margins are subparallel to gradually tapering over the posterior 2/3 whereas the anterior 1/3 tapers a little more rapidly. The platform extends the entire length of the element and is adjacent to, or forms a small brim behind, the cusp. The posterior margin is rounded in outline. The reticulate microornament, which is restricted to the margins, occurs throughout the entire length of the element. The aboral surface is smooth and bears a relatively high, wide keel which terminates in a rounded to slightly squared-off basal loop.

The cusp is high, oval in cross section, pointed, and directed straight upwards if not barely anteriorly. The denticles anterior to the cusp of which there are 11 or 12, increase in height and compression anteriorly and are fused at their bases. The first four denticles are barely perceptibly more closely spaced, of equal height and slightly distinct from the others on the carina. The tips of the denticles are flat to slightly pointed in the posterior half and pointed in the anterior half.

C. <u>Mature to Gerontic</u> - It is at this stage that the many diagnostic features tures of the species and subspecies become apparent. Only minor differences exist even between this species and <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> at the intermediate and especially at the juvenile growth stage.

The platform element has a roughly elongated triangular outline and a very robust appearance owing to its width (W1 = 200 to 260 μ m) and very thick margins. Arching of the element is greater than that observed for the intermediate forms whereas the degree of upturning is imperceptible. Some specimens actually show a degree of downturning. The posterior margin is straight to slightly rounded and sometimes lobed but not with the same asymmetry as N. bitteri n.subsp. C. The postero-lateral margins are enlarged to the anterior end of the cusp, where the lateral margins remain subparallel until they begin to taper more rapidly \pm in the anterior 1/3. Whereas an extensive brim is formed about the cusp on the posterior of the platform it is absent from the anterior tip, where the last 2 to 3 almost totally fused denticles form a free blade. The margins of the platform bear a reticulate microornament which is widest near the mid-length and extends over the entire length. The interior border of the reticulation does not end abruptly but rather fades into faint ridges directed towards

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On some specimens this reticulation can be found on the dentithe carina. cles and cusp but even in these specimens at least part of the furrow is a smooth. The reticulation extends around the brim in most specimens. Tn some, this reticulation is faint and almost striated in appearance. The smooth furrows are shallow and narrow and parallel the carina up to the position of the cusp where they diverge towards the postero-lateral corners. The cusp is generally low, elongate oval in outline and positioned at about the median of the platform and directed straight upwards. In some specimens the cusp is directed either dextral or sinistral to the midline whereas in a few of the specimensit is fused with a couple of adjacent denticles forming an elongate ridge directed towards a postero-lateral corner. The majority of the denticles anterior to the cusp (as many as 10) are flat-topped, laterally compressed, fused to about 1/2 to 2/3 of their height and of equal height. From this point, which roughly coincides with the more rapidly tapering of the platform, the denticles first increase in height and then de-The smallest anterior denticles are almost totally fused, crease again. forming a characteristic blade which is in part free of the platform. In other specimens the denticles are more node-like. Rare specimens have the first four denticles anterior to the cusp smaller and more closely spaced than the others.

The aboral surface is smooth and bears a low, wide keel which terminates in a higher and roughly triangular basal loop. The shape of this basal loop is quite variable. The narrow basal groove terminates posteriorly in a straight elongate oval pit. The keel increases in height and narrows in a blade-like ridge which connects with the oral free blade at the anterior tip. The crimp covers roughly 6/10 of the width in the posterior parts of the platform.

<u>Discussion</u>: The early growth stages are very similar even to <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u>. Szaniawski and Malkowski (1979) pointed out the similarity of early growth stages between <u>Nr. idahoensis</u> and <u>Nr. bitteri</u>. This similarity of early growth stages throughout the phylogeny of <u>Neogondolella</u> points to the close relationship of all the species. Some mature forms of <u>Nr. idahoensis</u> n.subsp. <u>A</u> actually mimic <u>Nr. rosenkrantzi</u>, Mature specimens of <u>Nr. rosenkrantzi</u> n.subsp. <u>D</u> differ in terms of a more triangular outline, larger number of denticles, shape and arrangement of the denticles including the anterior blade (a feature not seen in <u>Nr. idahoensis</u>), shallower furrows, and thicker platform margins. However, for reliable identification this mimicry points to the need, not only for mature forms, but also for enough representatives to include all of the wide variability of form so characteristic of these species.

As pointed out in the discussion for <u>N</u>. <u>bitteri</u> n.subsp. <u>C</u> the main features distinguishing <u>N</u>. <u>rosenkrantzi</u> from <u>N</u>. <u>bitteri</u> are the slightly straight to almost blunt posterior ends, and a large cusp of elongateoval cross section. As well the enlarged postero-lateral margins and different symmetry distinguish <u>N</u>. <u>rosenkrantzi</u> n.subsp. <u>D</u> from <u>N</u>. <u>bitteri</u> n.subsp. <u>C</u>.

Wardlaw and Collinson (1979b) figure specimens of <u>N</u>. <u>rosenkrantzi</u> from the Retort Phosphatic Shale Member of the Phosphoria Formation and from the Gerster Limestone. The latter have a very blunt posterior end and appear more "advanced" than the Ellesmere specimens, which more closely resemble the Retort Member specimens in posterior outline and manner and degree of tapering. There seem to be grounds for suggesting that these differences are significant at the infraspecific level (subspecies). To call attention to some of these differences, therefore, I have referred these

specimens to a distinct subspecies.

The specimens differ from other species in the Trold Fiord Formation in their denticle shape and configuration, the shape and position of the cusp, the greater thickness of the platform margins and the position and configuration of reticulate ornament.

Ramiform Elements

NEOGONDOLELLA IDAHOENSIS n.subsp. A - XANIOGNATHUS TORTILIS (Tatge)

P1. 2, figs. 1-4.

Ozarkodina tortilis Tatge, 1956

Occurrence: Lower Assistance Formation, Hamilton Peninsula section. Description: This blade-shaped element has a long anterior process with as many as 8 sharp, pointed, subequal and laterally compressed denticles, all inclined posteriorly. The cusp is high, sharp and laterally compressed. At least three denticles are present on the short posterior process, which is twisted to one side or the other. The undersurface of both processes is grooved and terminates in a pronounced basal pit directly below the main cusp. The denticles all bear a very fine striate microornament. Discussion: This species is distinguished from the older X. abstractus by the less robust blade and the twisted (as opposed to straight) posterior process. According to Behnken (1975) the range of X. tortilis begins at about the end of that of N. serrata. This would indicate a Late Roadian age but this species occurs withNeogondolella platforms of Early Roadian age. These specimens may be intermediate between X. tortilis and the older X. abstractus as the base of the denticles appear more robust than specimens of X. tortilis figured by Behnken (1975), nevertheless they do appear closer to X. tortilis in most respects.

<u>NEOGONDOLELLA IDAHOENSIS</u> n.subsp. <u>A</u> - <u>ELLISONIA</u> <u>EXCAVATA</u> Behnken, 1975

Pl. 1, fig. 15.

Occurrence: Lower Assistance Formation, Hamilton Peninsula section. Description: The specimens have a variable hindeodelliform morphology with, beneath the cusp, a small conical basal pit which is laterally compressed and inclined posteriorly. The posterior bar is long and bears at least 10 to 12 discrete pointed denticles that are of variable size along the bar. 3 denticles are present on the downward projecting short anterior bar.

<u>Discussion:</u> The figured speciment probably represents the LB element of a multielement species which includes U, LA, and LF elements which were not observed. Behnken (1975) indicates that this species occurs with <u>N. idaho-ensis</u> in West Texas, and would thus have a Leonardian age.

<u>NEOGONDOLELLA IDAHOENSIS</u> n.subsp. <u>A</u> - <u>ELLISONIA TRIBULOSA</u> (Clark and Ethington, 1962)

Pl. 2, figs. 5-8 <u>Apatognathus tribulosus</u> Clark and Ethington, 1962 <u>Occurrence</u>: Lower Assistance Formation, Hamilton Peninsula <u>Description</u>: Of the U, LA1, LA2 and LC elements LA1 (figs. 6, 7) and LC (figs. 5, 8) elements are present and described.

LA1 - This is a slightly asymmetrical lonchodiniform element with a high, laterally compressed and posteriorly inclined cusp. The posterior bar bears 3 to 4 denticles whereas the short anterior bar bears 2 pointed but larger denticles. The basal pit below the cusp is formed by very slight expansion of a groove which is present over the entire length of the aboral surface.

LC - This is an enantiognathiform element with a long posterior bar projecting downward from the main cusp and bearing 5 denticles that are discrete and subparallel for much of their length. The main cusp is triangular in cross section and the corners are extended into sharp ridges. The short downward projecting anterior bar bears one to two denticles and projects at an angle of about 60 degrees to the posterior bar. Below the cusp is a large triangular basal pit.

<u>Discussion</u>: This species occurs through the range of <u>N</u>. <u>serrata</u> and <u>N</u>. <u>postserrata</u> indicating <u>a</u> Roadian to Early Wordian age. Perhaps the presence of both <u>E</u>. <u>excavata</u> and <u>E</u>. <u>tribulosa</u> together indicates overlap of their ranges in the Early Roadian which fits in well with the Early Roadian age assigned to <u>N</u>. <u>idahoensis</u> n.subsp. <u>A</u> because of its intermediate position between <u>N</u>. <u>idahoensis</u> and <u>N</u>. <u>serrata</u>.

NEOGONDOLELLA IDAHOENSIS n.subsp. A - PRIONIODELLA DECRESCENS Tatge, 1956

Pl. 1, fig. 14.

Occurrence: Lower Assistance Formation, Hamilton Peninsula section. Description: This specimen is a short, straight and denticulate element without a main cusp. The six discrete and pointed denticles are subequal in height.

<u>Discussion</u>: Behnken (1975) includes this species within the range of \underline{N} . <u>postserrata</u>, in other words, Early Wordian. However, similar forms have much greater ranges. Other elements which may be assigned to <u>Prioniodella</u> species are fragmental and unidentified.

Addendum: A paper in preparation by the author describes <u>Neogondolella</u> <u>idahoensis</u> n.subsp. <u>A</u>, <u>N</u>. nsp. <u>B</u>, <u>N</u>. <u>bitteri</u> n.subsp. <u>C</u> and <u>N</u>. <u>rosenkrantzi</u> n.subsp. <u>D</u> as <u>N</u>. <u>idahoensis</u> praeserrata n.subsp., <u>N</u>. <u>perryi</u> n.sp., <u>N</u>. <u>bitteri</u> <u>arctica</u> n.subsp. and <u>N</u>. <u>rosenkrantzi</u> ellesmerensis n.subsp., respectively.

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All figures are Scanning Electron Micrographs.

Figs. 1, 2 Neostreptognathodus prayi

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1. Oblique lateral to oral view. Note the recrystallized texture. loc. F100. (X250).

Oblique lateral to oral view of platform posterior.F100.(X125).
Figs. 3-6 <u>Anchignathodus minutus</u> Page 73

3. Lateral view. Note dentition anterior to cusp. F49: (X100).

4. Oral view.F49.(X100).

5. Lateral view. Note lack of dentition anterior to cusp. F49. (X100).

6. Close-up of dentition on Fig. 5. Note the smooth surface free of ornament.F49.(X400).

Figs. 7-13 Neogondolella idahoensis subsp. indet. Page 74

7. Oral view of intermediate to mature form. F100. (X125).

8. Lateral view of anterior part of element showing discrete denticles. F100. (X125).

9. Lateral view of posterior of intermediate form.F100.(X125).

10. Oral view of intermédiate form. F100. (X125).

11. Oral view of mature form. F100. (X250).

12. Close-up of recrystallized (apatite) texture.F100.(X500).

13. Aboral view of posterior of intermediate form. F100. (X125).

Fig. 14 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> - <u>Prioniodella decrescens</u> 14. Lateral view.F49. (X100). Page 105

Fig. 15 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> - <u>Ellisonia excavata</u> 15. Lateral view.F49.(X100). Page 104



All figures are Scanning Electron Micrographs.

Figs. 1-4 Neogondolella idahoensis n.subsp. A - Xaniognathus tortilis

1. Close-up of denticle. Note the fine striated surface texture.F49. (X400). Page 103

2. Close-up of denticle.F49.(X400).

3. Lateral view. F49. (X100).

4. Lateral view.F49.(X100).

Figs. 5-8 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> - <u>Ellisonia tribulosa</u>

5. LC element. Note ridge or keel on main cusp. F49. (X100). Page 104

6. LA1 element.F49. (X100).

7. LA1 element.F54. (X150).

8. LC element. F49. (X100).

Figs. 9-19 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> Page 75

9. Oral view of var. gracilis. Main cusp and posterior end pointing to the bottom of the page.F49.(X100). Page 84

10. Oral view of var. intermediatus. F49. (X100). Page 86

11. Oral view of var. intermediatus.F54.(X90).

12. Oral view of var. gracilis. Note the distinct four denticles anterior to the cusp.F49.(X100).

13. Oral view of var. intermediatus. F49. (X75).

14. Oral view of var. robustus. Note the servations on anterior 1/3. F49.(X100). Page 85

15. Lateral view of posterior showing large cusp and lack of brim posterior to cusp: intermediate to mature.F49.(X100).

16. Lateral view of juvenile. Note the lack of platform on laterally compressed, triangular outlined cusp. F49. (X150).

17. Oblique lateral view of juvenile.F49.(X150).

18. Oblique lateral view of intermediate.F49.(X100).

19. Oblique lateral view of juvenile. Note the gradual increase in denticle height anteriorly and the upturning on the platform margin. F49. (X100).



All figures are Scanning Electron Micrographs.

Figs. 1-17 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u>

 Oral view var. <u>intermediatus</u>. Note four distinct denticles anterior to cusp. F49. (X80).

2.	Oral	view var.	intermediatus. F49. (X100).	Page 86
<i>4</i> •	orar	ATCM AGT .	THEELMEGIACUS, 149, (MI 00).	rage o

3. Oral view var. gracilis. F49. (X75).

4. Oral view var. gracilis. F49. (X75).

5. Oral view var. gracilis. F49. (X100).

6. Oral view var. gracilis. F49.(X100).

7. Oral view var. robustus.F49.(X100).

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8. Oral view showing high, discrete denticles at anterior end.F54.(X150).

9. Oral view var. robustus.F49.(X100).

10. Aboral view.F54 (X125).

11. Aboral view. Note different outline of posterior margin from that in Fig. 10.F54.(X125).

12. Oral view of thick platform margins of mature form.F54.(X85).

13. Lateral view of intermediate form. F49. (X100).

14. Lateral view of intermediate to mature form.F49.(X80).

15. Lateral view of mature form. Note that the platform reaches the posterior of the cusp (unlike that in Figs. 13, 14). F54.(X80).

16. Lateral view of var. gracilis. F49. (X100).

17. Lateral view of var. gracilis.F49.(X100).



All figures are Scanning Electron Micrographs.

Figs. 1-10 <u>Neogondolella idahoensis</u> n.subsp. <u>A</u> Page 75

1. Oral view of mature to gerontic form of var. <u>lobatus</u> that mimics <u>N. rosenkrantzi</u> in shape. Note discrete anterior denticles.F49.(X75).

2. Oral view of var. <u>intermediatus.F49.(X100)</u>. Page 86

3. Oral view of var. <u>intermediatus</u> with anterior serrations. Note the lack of reticulated ornament on the anterior-most margins of platform. F54.(X75).

4. Close-up of anterior part of Fig. 3.F54.(X150).

5. Oral view of mature to gerontic form. F54. (X125).

6. Oral view of mature to gerontic form showing partial fusion of posterior denticles. F54.(X150).

7. Oral view of var. constrictus. F49. (X100). Page 86

8. Oral view of var. <u>lobatus</u>. Note the thick platform margin and discrete, very laterally compressed denticles.F54. (X150). Page 87

9. Oral view of intermediate to mature var. <u>intermediatus</u>. Note the lack of reticulated ornament at the anterior end of the platform.F54.(X150).

10. Oral view of gerontic form with complete fusion of posterior denticles. Note the gradual and progressive fusion of posterior denticles displayed by Figs. 5, 6 and 10. This demonstrates the synonymy of <u>N</u>. <u>phosphoriensis</u> with N. <u>idahoensis.F54.(X180)</u>.



All figures are Scanning Electron Micrographs.

Figs. 1-10 Neogondolella idahoensis n.subsp. A

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1. Close-up of reticulated ornament. Note the distinct but rounded edges of ridges on the outside margin (left), the distinct and sharp ridges on the mid-part of the platform margin, and fading and elongate ridges near the furrow (right). F49.(X1500).

2. Close-up of Pl. 2, Fig. 14 showing the presence of reticulated ornament on the denticle tip.F49.(X400).

3. Close-up of Pl. 2, Fig. 14 showing the presence of reticulated ornament on the cusp and fused posterior denticles but absence on the furrows.F49.(X400).

4. Aboral view of juvenile form showing the high, narrow keel and elongate-oval loop. F49.(X100).

5. Aboral view. F49. (X100).

6. Aboral view of intermediate form.F49.(X100).

7. Aboral view of intermediate to mature form showing low, wide keel and slightly triangular loop.F49.(X100).

8. Aboral view of mature form showing very low and wide keel and triangular loop. Note the progressive changes of aboral features from Fig. 5 (juvenile) to Fig. 8 (mature). F49.(X100).

9. Aboral view of posterior end of mature form.F49.(X150).

10. Close-up of loop in Fig. 9. Note the truncation of growth lamellae at posterior of loop (especially evident on right hand side) which accompanies the transition from elongate oval to triangular shape of loop.F49. (X600).



All figures are Scanning Electron Micrographs.

Figs. 1-4 <u>Neogondolella</u> n.sp. <u>B</u>

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Oral view of intermediate form. Note the very symmetric shape.
F83.(X250).

2. Oral view of mature form showing large circular cusp directed straight upwards and with coarse striate ornament on brim.F83.(X300).

3. Oral view of symmetric mature form.F36.(X250).

4. Oral view of gerontic form with large, circular (in cross section)
cusp with narrow posterior platform margins and fused denticles.F36.(X250).
Figs. 5, 6 <u>Neogondolella postserrata(?)</u> Page 94

5. Oral view.F87.(X125).

6. Close-up of Fig. 5 showing blunt posterior margin and rectangular nodiform cusp. F87. (X250).

Figs. 7-9Neogondolellaserrata(?)Page90

7. Oral view of intermediate to mature form. Note the degenerate overall appearance. F73. (X300).

8. Close-up of posterior end of Fig. 7. F73.(X600).

9. Oblique-lateral to oral view of intermediate form. Note the sharpness of all the denticles. F63.(X300).



All figures are Scanning Electron Micrographs.

Figs. 1-8 Neogondolella bitteri n.subsp. C

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1. Aboral view of mid-platform fragment. F47. (X125).

2. Aboral view of posterior end.F47.(X125).

3. Oral view of mature form with asymmetric posterior end and large brim.F47. (X250).

4. Oral view of mature form with asymmetric posterior end and large brim.F47.(X250).

5. Oral view. Note the large, circular cusp similar to \underline{N} . n.sp. \underline{B} but also the distinct asymmetry. F47. (X250).

6. Oral view.F96.(X100).

7. Oral view showing partial fusion of cusp and posterior-most denticle and reticulate ornament on the carina. F96. (X100).

8. Oral view of mature form showing a slightly rounded and asymmetric posterior end that is similar to the more blunt ended <u>N. rosenkrantzi.F96.(X150).</u> Figs. 9-12 <u>Neogondolella rosenkrantzi n.subsp. D</u> Page 98

9. Oral view of mature form showing the straight, less distinctly asymmetric posterior end as compared to <u>N</u>. <u>bitteri</u>. Note the reticulated ornament on the carina.F96.(X100).

10. Oral view of mature form with a very thick platform, elongateoval cusp directed postero-laterally and with furrows and carina that are almost entirely covered with reticulate microornament.F96.(X100).

11. Aboral view of platform showing a wide triangular, and asymmetric loop.F96.(X85).

12. Oral view of mature to gerontic form showing the postero-laterally directed furrows and swollen posterior platform margins.F96.(X140).



All figures are Scanning Electron Micrographs.

Figs. 1-13 <u>Neogondolella rosenkrantzi</u> n.subsp. <u>D</u> Page 98

1. Oral view of intermediate form that looks very similar to N. idahoensis.F96.(X85).

2. Lateral view of posterior end of a mature to gerontic form showing large brim, fused carina and downturned lateral margins.F96.(X100).

3. Oral view of mature form showing the postero-laterally directed furrows and a slight twist of the platform at the anterior end.F96.(X85).

4. Oral view of mature form with narrow brim and wide but shallow furrows.F96.(X100).

5. Lateral view of intermediate form.F96.(X85).

6. Lateral view of anterior end showing the keel-like carina (owing to fusion of denticles) and lack of platform at anterior-most end: both features are characteristic for mature to gerontic individuals of this subspecies.F96.(X85).

7. Lateral view of intermediate form.F96.(X85).

8. Lateral view of Fig. 3 showing keel-like anterior carina.F96.(X75).

9. Oblique lateral view of juvenile form. Note the similarity to juveniles of N. idahoensis n. subsp. A (Pl. 2, Fig. 16).F96.(X225).

10. Oral view of gerontic individual with cusp and posterior-most denticle(s) fused and directed postero-laterally.F96.(X85).

11. Close-up of ordered reticulated microornament and flat-topped, smooth denticle.F96.(X900).

12. Close-up of gerontic oral surface showing the almost complete lack of furrows. Reticulated microornament covers almost the entire oral surface. Note the elongate form of reticulated ornament where the furrows are normally positioned.F96.(X200).

13. Aboral surface of intermediate form.F96.(X100).

Plate S



APPENDIX I

Schematic of morphological terminology and measured parameters for <u>Neogondolella</u> and measurements (L_1 , L_2 , H_1 , W_1 , W_2 : all in μ m) of specimens from F48 - F54.



Parameter Measurements for Sample F48.

Specimen	L	^L 2	н	L_1/H	#	L ₁ /#	L ₁ /W ₁	W ₁	^w 2	$\frac{1}{2}L_{2}(W_{1}+W_{2})$
										104
1	1060	28Q	170	6.24	12	88.33	4.42	240	180	5.88
2	690	380	150	4.60	8	86.25	4.31	160	140	5.70
3	1020	320	140	7.29	11	92.73	5.10	200	170	5.92
4	1100	300	22Q	5.00	11	100.00	4.58	240	220	6.90
5	630	260	110	5.73	10	63.00	4.85	130	120	3.25
6	600	240	140	4.29	8	75.00	4.62	130	110	2.88
7	720	330	120	6.00	ð	80.00	4.80	150	130	4.62
8	580	250	150	3.87	9	64.44	4.14	140	100	3.00
9	1100	300	160	6.88	13	84.62	4.58	240	200	6.60
10	660	310	140	4.71	9	73.33	3.67	180	150	5.12

Specimen	L 1	^L 2	Н	L_1/H_1	#	L ₁ /#	L_1/W_1	W ₁	^W 2 ¹ 2 ^L	(W ₁ +W ₂)
										104
- 1	800	24 Q	140	5.71	11	72.73	4.00	200	150	4.20
2	1400	380	280	5.00	13	107.69)	4.83	290	280	10.83
3	780	250	170	4.59	12	65.00	3.90	200	200	5.00
4	700	240	160	4.38	10	70.00	4.12	170	130	3.60
5	1040	340	160	6.50	9	115.56	4.00	260	200	7.82
6	700	240	140	5.00	9	77.78	3.89	180	140	3.84
7	860	280	180	4.78	12	71.67	4.53	190	190	5.32
8	600	230	150	4.00	9	66.67	4.00	150	110	2.99
9	760	260	190	4.00	10	76.00	4.47	170	140	4.03
10	740	310	190	3.89	10	74.00	4.63	160	150	4.81
11	1020	310	180	5.67	9	113.33	4.43	230	220	6.98
12	1220	340	240	5.08	15	81.33	4.57	270	240	8.67
13	840	240	160	5.25	11	76.36	5.25	160	130	3.48
14	460	220	120	3.83	8	47.40	3.29	140	120	2.86
15	900	240	160	5.63	12	75.00	4.74	190	170	4.32
16	760	260	160	4.75	. 9	84.44	4.22	180	160	4.42
17	760	240.	160	4.75	12	63.33	4.00	190	150	4.08
18	800	230	140	5.71	11	72.73	4.00	200	180	4.37
19	1000	340	200	5.00	12	83.33	4.76	210	160/	6.29
20	860	320	200	4.30	10	86.00	4.53	190	160	5.60
21	860	210	100	.8.60	13	66.15	5.06	170	140	3.26
22	820	320	170	4.82	10	82.00	4.10	200	180	6.08
23	640	300	140	4.57	9	71.11	4.QO	160	140	4.50
24	1060	360	220	4.82	. 12	88.33	4.42	240	210	8.10
25	1020	320	140	7.29	12	84.00	4.25	240	220 6	7.36
26	1180	280	19Q	6.21	13	90.77	5.36	220	180	5.60
27	980	3 50	230	4.26	11	89.09	4.45	220	200	7.35
28	1100	290	200.	5.50	13	84.62	5.00	220	200	6.09
29	800	330	220	3.64	10	80.00	4.00	200	170	6.11
30	600	280	140	4.29	9	66.67	4.29	140	120	3.64

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Parameter Measurements for Sample F49 (cont.)

Specimen	L_1	L ₂	Н	L ₁ /H	#	L ₁ /#	L_1/W_1	W ₁	W-2	$^{1}_{2}L_{1}(W_{1}+W_{2})$
										104
31	980	340	190	5.16	12	81.67	5.44	180	170	5.95
32	820	280	180	4.56	10	82.00	4.32	190	170	5.04
33	960	270	160	6.00	12	80.00	4.36	220	170	5.27
34	1060	300	190	5.58	12	388.33	4.42	240	190	6.45
35	720	240	160	4.50	10	72.00	5.14	140	120	3.12
36	820	310	150	5.45	10	82.00	4.10	200	160	5.58
37	780	280.	160	4.88	12	65.00	4.88	160	150	4.34
38	900	270	140	6.43	10	90.00	5.00	180	160	4.59
39	920	240	160	5.75	13	70.77	5.11	180	170	4.20
40	1000	260	180	5.56	12	83.33	5.56	180	160	4.42
41	880	260	170	5.18	11	80.00	4.63	190	180	4.81
42	<u>9</u> 40	240	190	4.95	12	78.33	4.70	200	170	4.44
43	760	240	120	6.33	11	69.09	4.00	190	160	4.20
44	880	280	190	4.63	12	73.33	4.40	200	180	5.32
45	520	250	140	3.71	8	65.00	3:47	150	120	3.38
46	680	280	140	4.86	8	85.00	4.25	160	130	4.06
47	980	260	170	5.76	12	81.67	3.92	250	200	5.85
48	660	230	140	4.71	9	73.33	4.40	150	140	3.34
49 .	600	240	120	5.00	10	60.00	4.62	130	110	2.88
50	520	220	70	7.43	9	57.78	3.47	150	120	2.97
51	720	280	120	6.00	10	72.00	4.24	170	140	4.34
52	900	300	150	6.00	11	81.82	4.50	200	160.	5.40
53	720	260	130	5.54	11	65.45	4.50	160	140	3.90
54	460	290	100	4.60	7	65.71	3.29	140	100	3.48
55	820	250	140	5.86	. 11	74.55	4.82	170	140	3.88
56	780	260	120	6.50	11	70.91	4.33	180	140	4.16
57	1100	34 0	180	6.11	11	100.00	5.24	210	180	6.63
58	280	320	100	9.80	. 11	89.09	5.16	·190	160	5.60
59	7 60.	300	140	5.43	9	84.44	4.22	180	130	4.65
60	1120	320	180	6.22	14	80.00	5.09	220	1 <u>9</u> 0	6.56

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Specimen	$^{L}1$	L ₂	H	L ₁ /H	#	L ₁ /#	L_1/W_1	W ₁	W ₂	$^{1}_{2}L_{1}(W_{1}+W_{2})$
										104
1	1120	280	190	5.89	12	93.33	4.31	260	230	6.86
2	1190	300	190	6.26	12	99.17	5.95	200	180	5.70
3	860	2 <u>9</u> 0	160	5.38	11	78.18	4.10	210	180	5.66
4	600	240	110	5.45	9	66.67	3.75	160	140	3.60
5	720	260	170	4.24	10	72.00	3.79	190	180	4.81
6	760	220	100	7.60	11	69.09	4.00	190	170	3.96
7	690	280	150	4.60	10	69.00	4.93	140	130	3.78
8	570	270	140	4.07	8	71.25	4.07	140	110	3.38
9	700	280	150	4.67	9	77.78	4.38	160	120	3.92
10	880	300	200	4.40	11	80.00	4.19	210	170	5.70
11	800	240	150	5.33	11	72.73	5.71	140	120	3.12
12	740	290	140	5.29	10	74.00	4.11	180	160	4.93
13	700	270	150	4.67	10	70.00	3.68	190	160	4.73
14	1000	270	140	7.14	12	83.33	4.55	220)	180	5.40
15	1100	380	240	4.58	13	84.62	3.93	280	240	9.88
16	610	260	120	5.08	9	67.78	3.59	170	150 6	4.16
17	800	290	140	5.71	10	80.00	4.21	190	140	4.79
18	780	280	140	5.57	11	70.91	4.59	170	140	4.34
19	960	260	160	6.00	13	73.85	4.57	210	190	5.20
20	820	250	160	5.13	12	68.33	4.32	190	170	4.50
21	560	270	110	5.09	8	70.00	3.73	150	130	3.78
22	750	230	150	5.00	10	75.00	3.95	190	180	5.18
23	1200	410	300	4.00	13	92.31	4.00	300	290	12.10
24	1100	340	200	5.50	12	91.67	3.79	290	260	9.35
25	1170	330	220	5.32	13	90.00	4.50	260	240.	8.25

	т	т	77	т /тт	л	т / 4	т /тт	.,	T T.	1
specimen	^L 1	^L 2	n.	L ₁ /H	11	^L 1 ^{/ #}	¹ 1 ^{/w} 1	^w 1	^w 2	$\frac{1}{2} \frac{1}{1} \frac{1}{1} \frac{1}{2}$
										104
1	760	220	160	4.75	11	69.09	4.22	180	1.50	3.63
2	1180	340	250	4.72	13	90.77	4.07	290	280	9.69
3	1160	320	220.	5.27	. 15	77.33	4.46	260	220	7.69
4 .	1270	300	210	6.05	16	79.38	5.29	240	200	6.60
5	1310	320	1 <u>9</u> 0	6.89	14	93.57	5.04	260	260	8.32
6	1120	320	180	6.22	13	86.15	4.31	260	240	8.00
7	<u>9</u> 80	340.	190	5.16	11	89.09	4.45	220	180	6.80
8	580	280	130	4.46	<u>9</u>	64.44	3.63	160	130	4.06
9	720	320	180	4.00	10	72.00	4.00	180	160	5.44
10	700	300	160	4.38	<u>9</u>	77.78	3.68	190	180	5,55
11	980	280	140	7.00	13	75.38	4.45	220	180	5.60
12	1500	380	170	8.82	16	93.75	3.95	380	310	13.11
13	960	290	180	5.33	11	87.27	4.00	240	200	6.38
14	860	320	160	5.38	10	86.00	4.30	200	160	5.76
15	640	260	130	4.92	9	71.11	3.56	180	140	4.16
16	1100	400	170	6.47	11	100.00	4.23	260	200	9.20
17	920	350	180	5.11	10	92.00	4.18	220	180	7.00
18	620	280	140	4.43	9	68.89	3.65	170	140	4.34
19	670	280	160	4.19	9	74.44	4.47	150	130	3.92
20	740	240.	150	4.93	10	74.00	4.63	160	140	3.60
21	700	240	130	5.38	10	70.00	4.38	160	140	3.60
22	500	260	120	4.17	8	62.50	3.57	140	120	3.38
23	800	300	200	4.00	10	80.00	3.64	220	200	6.30
24	1200	400	190	6.32	12	100.00	4.14	290	280	11.40
25	840	290	160	5.25	11	76.36	4.67	180	140	4.64
26	700	280	130	5.38	10	70.00	4.12	17Q	120	4.06
27	660	280	. 120 .,	5.50	10	66.00	3.67	180	160	4.76
28	980	360	180	5.44	11	89.09	4.45	220	180	7.20
29	580	240	120	4.83	. 9_	64.44	4.14	140	120	3.12
30	760	340	150	5.07	9	84.44	4.75	160	120	4.76

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Parameter Measurements for Sample F53 (cont.)

Specimen	L ₁	^L 2	H.	L_1/H	#	L ₁ /#	L_1/W_1	W ₁	W2	$^{1}2L_{1}(W_{1}+W_{2})$
										104
31	840	260	120	7.00	11	76.36	4.20	200	180	4.94
32	780	300	160	4.88	10	78.00	4.33	180	160	5.10
33	1020	260.	220	4.64	12	85.00	5.10	200	180	4.94
34	950	320	230	2.97	12	79.17	4.32	220	180	6.40
35	7 0.0	2 60,	140	5.00	10	70.00	4.38	160	120	3.64
36	1010	280	180	5.61	13	77.69	4.81	210	180	5.46
37	1160	400	250	4.64	12	96.67	4.14	280	250	10.60
38	380	220	100.	3.80	7	54.29	3.45	110	80	2.09
39	690	260	160	4.31	10	69.00	3.83	180	170	4.55
40.	1500	440	320	4.69	15	100.00	4.41	340	320	14.52

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Specimen	: L 1		L ₁ /#	Specimen	L	#	L ₁ /#
1	600	. 9	66.67	20	580	9	64 44
2	1000	15	66, 67	21	740	10	7/ 00
3	720		80.00	22	780	10	79.00
4	1080	11	98 18	22	700	10	70.00
5	1120	11	101.82	25	700	10	70.00
<u> </u>	1000	**	101.02	24	. 740	9	82.22
Ø	T0.60	ΤT	96.36	25	900	11	81.82
7	1000	12-	83.33	26	1000	13	76.92
8	1220	13	93.85	27	54 0	8	67.50
9	1460	13	112.31	28	1220	14	87.14
10	<u>9</u> 00	10	90.00	29	360	6	60.00
11	84 O .	11	76.36	30	900	13	69.23
12	960	11	87.27	31	1300	13	100.00
13	800.	10	80.00	32	1360	12	112.50
14	560	11	50.91	33	560	12	46.67
15	840	11	76.36	34	1020	11	92.73
16	720	9	80.00	35	1200	13	92.31
17	960	10	96.00	36	1280	13	98.46
18	1040	11	94.55	37	800	10	80.00
19	640	9	71.11				

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Parameter Measurements for Sample F54