

**LATE CARNIAN (LATE TRIASSIC) CONODONT AND AMMONOID
PALEONTOLOGY OF WRANGELLIA**

by

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Abstract

The development of conodont biochronology for the Triassic Period is hindered by the lack of understanding of the genus *Metapolygnathus* Hayashi, 1968a and, to a lesser extent, *Carniepigondolella* Kozur, 2003. Specimens of these genera collected at Klaskino Inlet, British Columbia are described as species populations of *M. polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* and variations within these species populations are identified. The morphological variations on platform shape, relative strength of anterior platform nodes, the “*communisti* trend,” fused carinal nodes and an extra carinal node are shared between all species populations. Although it is beneficial to fully document the generic variability within *Metapolygnathus*, these variations should not be included in the genus description. Not all variations occur in all species of the genus and only three species were looked at in this thesis.

The secondary focus of this thesis addresses the uncertain position of the allochthonous terrane Wrangellia in the Late Carnian. Using paleobiogeographic techniques, data on ammonoid genera occurrences were compiled for cratonic North America, Wrangellia, and the western Pacific, and then compared using the Dice coefficient. It is concluded that ammonoid similarity levels are too low to assess significance levels. Based on the collected data, however, it appears that the Wrangellian fauna is most similar to the fauna of the middle paleolatitude of the North American craton. This means that Wrangellia was probably in the eastern Pacific and at a mid-paleolatitude in the Late Carnian.

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Chapter 1: Introduction

The Triassic Period was a time of transition. Among other taxa, conodonts and ammonoids were recovering from the end-Permian mass extinction and would experience another mass extinction at the end of the Triassic. The conodonts would not survive the end Triassic mass extinction, but the ammonoids survived to flourish in the Jurassic.

Triassic rocks in British Columbia are widespread, with occurrences on Vancouver Island, the Queen Charlotte Islands, the Coast Mountains, northern, southern and central British Columbia, as well as the eastern part of the province along the craton margin. The majority of the Triassic rocks in British Columbia are of Late Triassic, Carnian and Norian age (Figure 1.1). These rocks have varying depositional histories, from allochthonous volcanic terranes to sedimentary deposits on the continental shelf. My field area at Klaskino Inlet on the northwestern coast of Vancouver Island shows basalt flows (Karmutsen Formation) with overlying carbonate and siliciclastic deposition (Quatsino and Parson Bay formations, respectively).

The Carnian age in the Late Triassic is an important time period for the study paleontology, particularly conodonts. An understanding of Carnian conodonts is necessary because they provide the stock for the Norian and Rhaetian species later in the Triassic, and they are useful fossils for refining the Triassic biochronology. Conodonts of the Carnian are predominantly of the genera *Metapolygnathus* and *Carniepigondolella*. *Metapolygnathus* in particular is poorly understood which is a serious problem considering its species are very useful in creating a conodont biochronology which can be integrated into the ammonoid time scale that is the global standard for the Triassic. The ammonoid time scale needs integration with conodont data so that future workers can base their studies on more precise time zones and

Figure 1.1 **Triassic Time Scale**

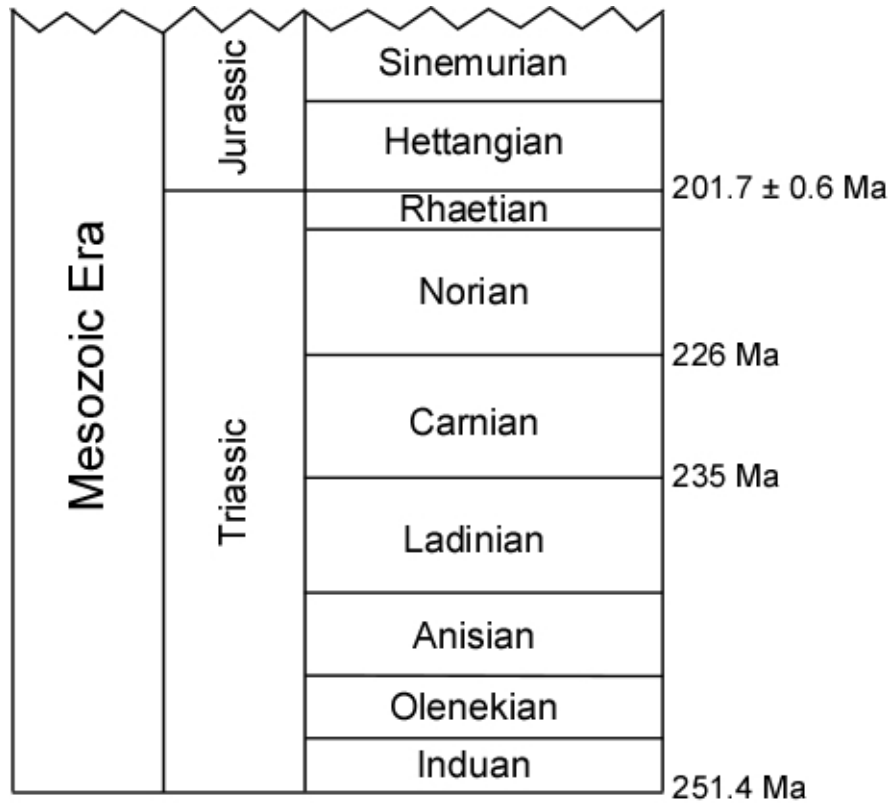


Figure 1.1: The stages of the Triassic Period. The date for the base of the Induan Stage was determined by Mundil *et al.* (2004). The dates for the base of the Carnian and Norian stages are suggested by Brack *et al.* (2005). The date for the base of the Hettangian Stage was determined by Friedman, *et al.* (2008).

because ammonoids are not always present or preserved well enough in an outcrop to determine age. For these reasons it is important to understand the characteristics of the genus *Metapolygnathus* which is the main purpose of this thesis.

Late Triassic conodont biochronology in North America has been worked on for many decades, but is still in a state of revision as new data are considered. Mosher (1968a, 1970) used occurrences of Late Triassic age conodonts in western North America to propose a zonal scheme which used among other species, *Metapolygnathus polygnathiformis* (Budurov and Stefanov, 1965). Conodont zones for the Upper Carnian were revised more recently by Orchard (1991a) and resulted in the conodont zonation scheme recognized today in North America (Figure 1.2).

The conodont genus *Metapolygnathus* was first described by Hayashi (1968a) from the Adoyama Formation of Japan. Since that time, several species, both new and previously described, have been assigned to this genus from North America (e.g., Orchard, 1991c) and Europe (e.g., Krystyn, 1980). Recently, the species of *Metapolygnathus* from the Ladinian-Carnian boundary have been re-evaluated systematically (Orchard, 2007; Orchard and Balini, 2007). *Carniepigondolella* was introduced by Kozur (2003) as a new genus for some of the younger metapolygnathids described previously by Orchard (1991c).

The goal of the first part of my thesis is to clarify the understanding of the species of *Metapolygnathus* and *Carniepigondolella* found at Klaskino Inlet by describing the variety of morphologies present within each species.

The second question addressed in this thesis addresses the Late Carnian position of the allochthonous terrane Wrangellia which, along with many other terranes, makes up parts of western North America. As the second topic is spatial in nature, a spatial approach is necessary to attempt to solve the problem.

Wrangellia's past movement has been studied for many time periods but its position in the Late Triassic is still uncertain. Determining the paleolatitude of Wrangellia is important

Figure 1.2 Ammonoid and Conodont Zones of the Carnian Stage

Series	Stage	Substage	Ammonoid Zone	Conodont Fauna/Zone	
Upper Triassic	Carnian	Upper	Macrolobatus		
				M. communisti	
			Welleri	M. nodosus	M. samueli
					M. zoeae
					M. lindae
			Dilleri	M. polygnathiformis	
		Lower	Nanseni		
			Obesum		
			Desatoyense		



 omitted for clarity
 no zone recognized

Figure 1.2: Integrated ammonoid and conodont zones for the Carnian Stage. The conodont genera *Metapolygnathus* and *Carniepigondolella* are abbreviated to “M.” and “C.” respectively (Modified from Orchard and Tozer, 1997).

because it is a piece to understanding how the tectonic plates have moved in the geologic past. Paleobiogeography can provide valuable constraints on plate reconstruction especially when one considers the ambiguity inherent in paleomagnetic studies. Due to the symmetry of the Earth's magnetic field, hemispheric distinctions cannot be made conclusively with paleomagnetic data.

Triassic ammonoid superfamilies reached peak diversity in the Ladinian and maintained this diversity into the Carnian (Page, 1996) making Carnian ammonoids quite useful fossils for paleobiogeography. Paleobiogeographic studies using ammonoids have the potential to indicate the past position of Wrangellia by comparing the similarity of ammonoid faunas found on the North American craton with those of Wrangellia. Paleobiogeographic patterns in the Triassic have been recognized by several workers (e.g., Nichols and Silberling, 1979; Tozer, 1981, 1982; Page, 1996), illustrating that it is possible to constrain the paleolatitude of a terrane given a suitable distribution of ammonoids.

The goal of this part of the thesis was to determine the paleolatitude of Wrangellia and its relative longitudinal position in the Pacific in the Late Carnian using ammonoid biogeography. However, as a result of this study I found that our current knowledge of the distribution of Upper Carnian ammonoids is not sufficient to determine the paleolatitude of Wrangellia using paleobiogeographic methods. In this section I will detail the paleobiogeographic methods utilized and identify paleobiogeographic trends observed in my data. If new ammonoid collections are discovered from the Upper Carnian, future paleobiogeographic studies can be pursued.

Chapter 2: Geology and Stratigraphy

2.1 Regional Geology and Stratigraphy

The field area studied is located on the Wrangellia terrane which, along with the Alexander terrane, makes up the Insular Belt. This belt is one of several that form the western margin of British Columbia. Muller *et al.* (1974) noted the presence of ten major fault blocks on northern Vancouver Island in the Cape Scott – Alert Bay map areas. Klaskino Inlet is located within the Cape Scott Block.

Karmutsen Formation

The Karmutsen Formation is composed of tholeiitic basalt and ranges from approximately 3,100 to 3,500 meters in thickness in northern Vancouver Island depending on the location. This formation was erupted sometime during the Late Ladinian to the Dilleri Zone of the Late Carnian based on ammonoids found in the intervolcanic limestone lenses at the top of the Karmutsen and the Ladinian age bivalve *Daonella* found below the Karmutsen (Muller *et al.*, 1974).

Many forms of the Karmutsen basalts have been described in the literature (e.g. Muller *et al.*, 1974; Carlisle, 1972) but most recently Greene *et al.* (2009) have described the Karmutsen Formation as consisting of a basal sediment-sill complex, both massive and pillowed submarine flows, pillow breccia, and massive subaerial flows.

Quatsino Formation

The Quatsino Formation is composed of light to medium gray colored limestone with varying degrees of purity and is locally interlayered with tuffs, igneous sills and dikes. The limestone beds range from thickly bedded at the formation's base to thinly bedded near the top,

and some authors have informally subdivided the Quatsino Formation based on this bedding change. These subdivisions were not observed at the Klaskino Inlet section studied here.

This unit thins from a thickness of approximately 300 meters on eastern Vancouver Island to approximately 30 meters on the western shore. The drastic change in thickness of the Quatsino Formation highlights the nature of its diachronous contact with the Parson Bay Formation.

The Quatsino Formation ranges in age from Late Carnian at the contact with the Karmutsen Formation to Middle Norian at the contact with the Parson Bay Formation on the eastern side of Vancouver Island (Nixon *et al.*, 1993). On the western side, the Quatsino Formation ranges from Late Carnian, possibly Upper Dilleri Zone, to approximately the middle of the Late Carnian Welleri Zone (Nixon *et al.*, 1993).

The Quatsino Formation is fossiliferous in certain localities and contains ammonoids, conodonts, bivalves, brachiopods, nautiloids, and gastropods. The Quatsino Formation is the best source of Late Carnian, Dilleri Zone fossils in western Canada.

Parson Bay Formation

The Parson Bay Formation encompasses a variety of lithologies, including calcareous siltstone, shaly limestone, feldspathic greywacke, and limestone breccia (Muller *et al.*, 1974). This unit ranges from 300 to 400 meters thick, and is best exposed at the opening of Klaskino Inlet at a locality examined by Muller *et al.* (1974), Nixon *et al.* (1995) and Tozer (1994).

The base of the Parson Bay Formation varies in age from Late Carnian to Middle Norian due to the diachronous nature of its contact with the Quatsino Formation. The top of this unit marks the end of Late Triassic sedimentation in the area and is overlain by the Lower Jurassic Harbledown Formation of the Bonanza Group. Fossils found in the Parson Bay Formation

include ammonoids, bivalves, and in some areas corals of indeterminate or Norian age (Muller *et al.*, 1974).

2.2 Geology and Stratigraphy of Klaskino Inlet

Klaskino Inlet is on the northwestern coast of Vancouver Island, due south of Quatsino Sound (Figure 2.1). There are at least two sections of strata at Klaskino Inlet that show a fairly complete sequence of the Karmutsen, Quatsino, and Parson Bay formations (Figure 2.2). One occurrence is recorded by Nixon *et al.* (1993) on the northern side of the inlet near its mouth. Tozer (1994) reports on the ammonoid faunas found at this locality (GSC loc. 86284 and 86293) and confirms a Late Carnian age of Dilleri and Welleri Zone.

I studied approximately 44 m of discontinuous section that are exposed at the second occurrence of strata at Klaskino Inlet. The locality referred to herein as Klaskino Inlet is geographically close to, but not the same as, the “Klaskino section” of Muller *et al.* (1974). The Klaskino section as per Muller *et al.* (1974) is located northwest of Mocino Point along the coastline of the inlet. Tozer (1994) also collected ammonoids from the inlet at GSC loc. 86284 and 86293 which are located 1.5 km northeast of Mocino Point along the northern coast of the inlet. The locality I studied is located further east in the inlet, 7.95 km east of Mocino Point on the northern shore of the inlet.

Karmutsen Formation

Measurement of the section started at the base of the first carbonate mudstone lens found within the upper Karmutsen Formation (Figure 2.3). With the base defined as such, the uppermost 10.1 m of the Karmutsen Formation were measured. The youngest part of the Karmutsen Formation is composed of basalt, which is black in color and exhibits weak pillow

Figure 2.1 **Locality Map of Klaskino Inlet**

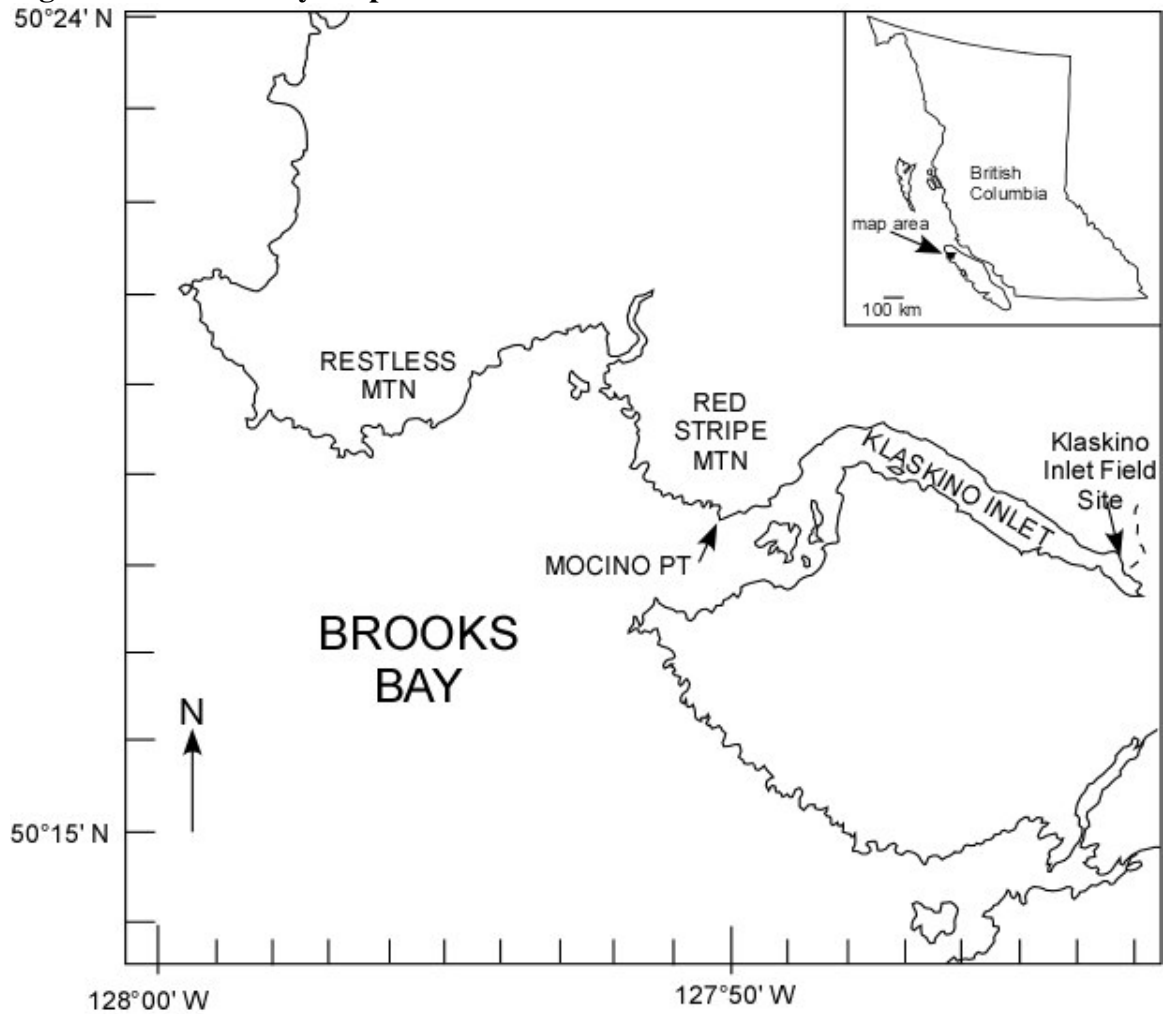


Figure 2.1: Map showing the location of the studied Klaskino Inlet site. (Modified from Map 1733G, Neroutsos Inlet, Sheet 92 L/5, Geological Survey of Canada).

Figure 2.2 Geologic Map of Klaskino Inlet

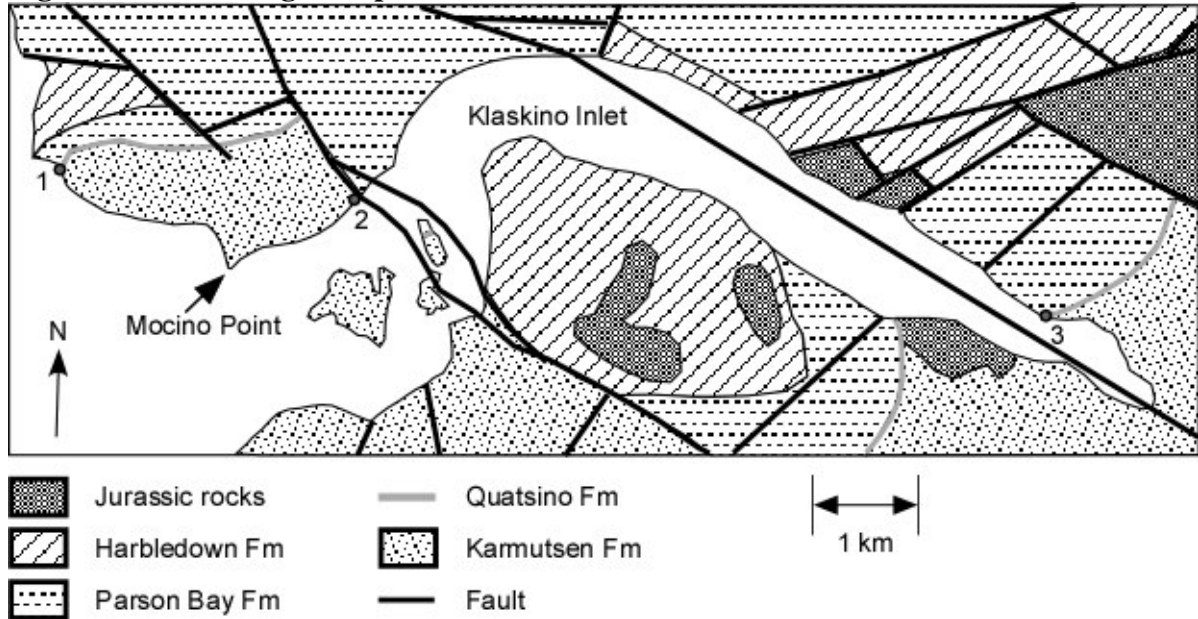


Figure 2.2: Geologic map of the field site and surrounding area (Modified from Nixon, *et al.*, 1997).

1: Locality of Muller *et al.* (1974) and Nixon *et al.* (1993).

2: Locality of Tozer (1994).

3: Locality of field area studied for this thesis.

Figure 2.3 Stratigraphy of Klaskino Inlet Section

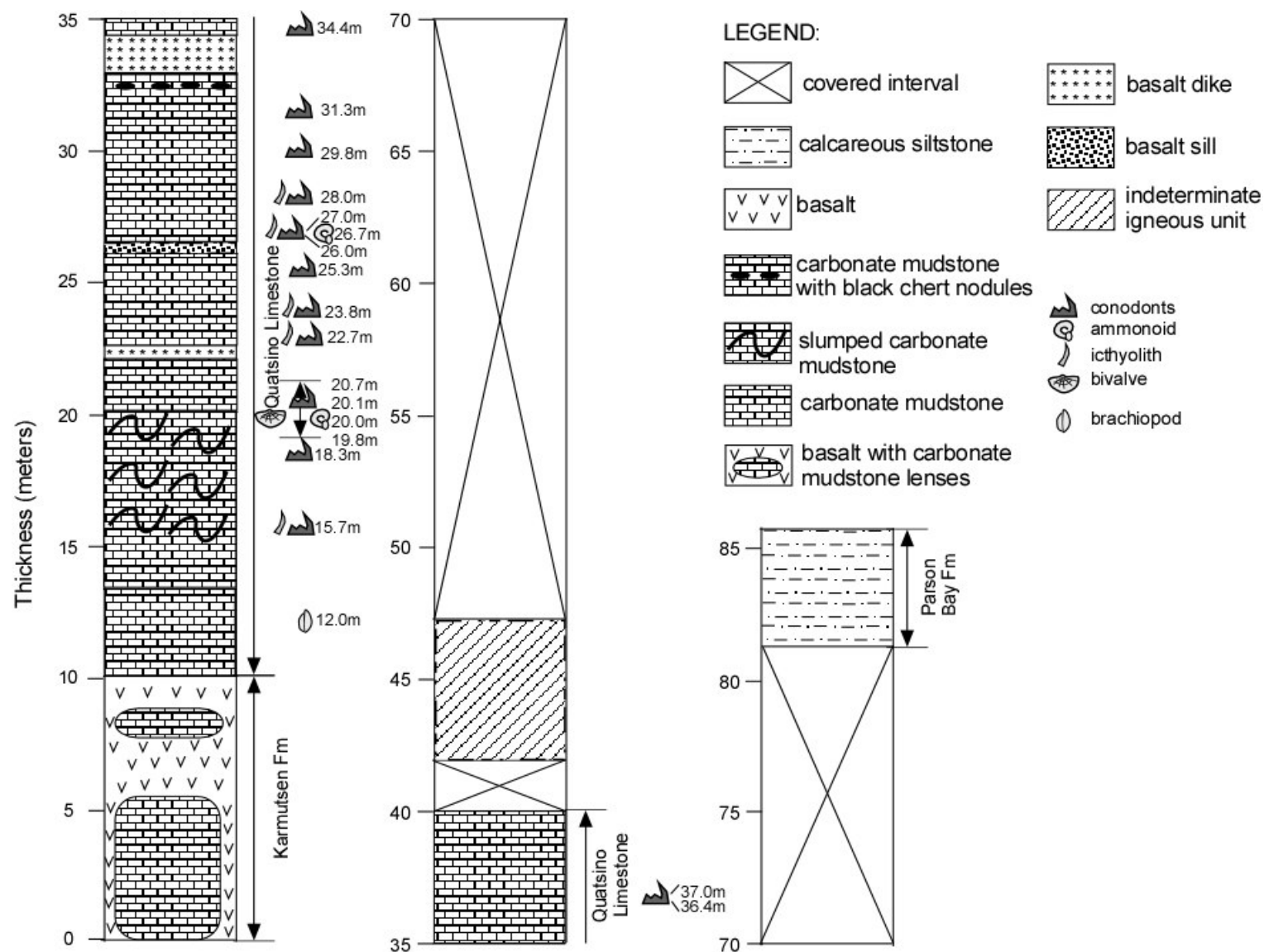


Figure 2.3: The stratigraphy and fossil content of the Klaskino Inlet section is presented.

structures around the first measured limestone lens; otherwise, there are no obvious structures in the volcanics.

The first carbonate mudstone lens is 5.5 meters thick. The thinly bedded layers appear to be fractured at 0.6 meters from the base of the section. There is a sharp, irregular contact between the volcanic rocks and the carbonate lens. The second carbonate mudstone lens has a wavy, irregular contact with the volcanics and is only 2.2 meters thick. The carbonate mudstone lens is further overlain by 1.2 meters of basalt. A wavy, irregular contact separates the Karmutsen Formation and the Quatsino Formation.

The carbonate limestone lenses of the Karmutsen Formation were sampled for conodonts and radiolarians. No microfossils were recovered, and no macrofossils were found within the lenses.

Quatsino Formation

The Quatsino Formation consists of 30 meters of carbonate mudstone which changes in color from light gray to medium gray throughout the section. Bedding is highly variable, ranging from thinly bedded to massively bedded. Based on acid residues, it is clear that there are different constituents floating in the carbonate mudstone that change as often as once every meter or two meters. The more common constituents include unidentified lithic fragments, silica, and pyrite.

Thin layers of reddish-brown chert, black chert nodules, and volcanic tuffs, sills, and dikes are also found within the Quatsino limestone. Soft sediment deformation, in the form of chevron-shaped slump folds, occurs from approximately 13 to 20 meters in the stratigraphy. More minor slump folding is present further up the section at approximately 32 and 37 meters.

Ammonoids, bivalves, brachiopods, and conodonts were collected from the Quatsino Formation. The brachiopods collected are silicified and appear to be indeterminate terebratulids

and spiriferids. The ammonoids are mostly recrystallized and are unidentifiable. At certain horizons within the Quatsino Formation there are concentrated layers of silicified ammonoids but, again, preservation is a problem. Among the better preserved specimens are indeterminate trochitid and arceid ammonoids. A few fragments of what appear to be halobid bivalves are preserved in the shaly limestone at approximately 20 meters in the section.

Parson Bay Formation

At Klaskino Inlet only the very base of the Parson Bay Formation was measured and included in the stratigraphic section. The Parson Bay Formation is separated from the Quatsino Formation by an estimated 36 meters of cover and one igneous intrusion of unknown origin. The exposed portion is 4.5 meters thick and consists of calcareous siltstone/shale, which displays thin to medium bedding. Neither micro- nor macrofossils were found.

2.3 Depositional Setting of Quatsino Formation

Muller *et al.* (1974) hypothesized that the Quatsino Formation was deposited in the open ocean and built upon the older Karmutsen lava flows. Desrochers and Orchard (1991) reach a similar conclusion for the depositional setting of a Quatsino Formation equivalent, the Sadler Formation, on the Queen Charlotte Islands.

Laminated carbonate mudstones in the Klaskino Inlet section have been interpreted to represent a dysoxic, slope to basin facies with limited water circulation. This interpretation was based partly on intercalated slump folded units, limited winnowing action, and locally abundant pyrite (Sano, personal communication, 2005). There is little evidence of wave action in the beds, only evidence of a weak current that produced minor winnowing of fossil tests.

Chapter 3: Conodont Population Morphologies and Systematic Species Descriptions

3.1 Purpose

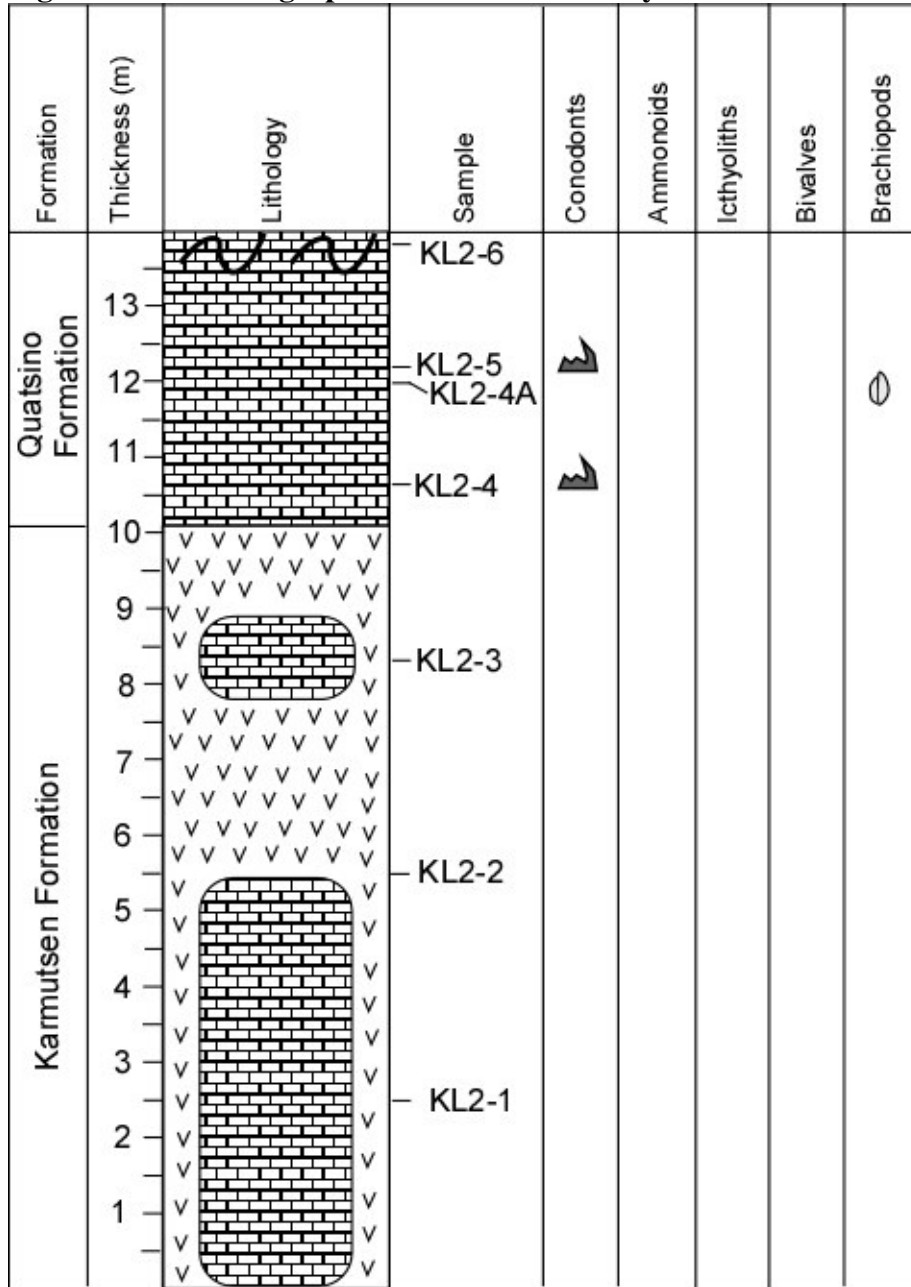
The conodont genus *Metapolygnathus* is useful in Triassic biochronology because its global distribution and quickly evolving species provide a basis for subdividing the Carnian Stage, which has traditionally been subdivided based on ammonoids. *Metapolygnathus* is a problematic genus, however, because there is a poor understanding of the value of morphological characteristics in speciation and of the intraspecific variation within species. In addition, there is little agreement among conodont workers in regards to which species should be assigned to the genus. I think that a better understanding of *Metapolygnathus* can aid the definition of the Triassic biochronology.

The purpose of this chapter is to describe the variability of species of *Metapolygnathus* from the Welleri Zone of Western Canada. To accomplish this goal, both species populations and systematic descriptions of species and their morphotypes are provided for all the specimens of *Metapolygnathus* found at Klaskino Inlet, and of select specimens from the Queen Charlotte Islands and northeastern British Columbia. One species of *Carniepigondolella* will also be described in this manner because it has similar biochronologic value for the Late Carnian.

3.2 Methods

Conodont elements of the genera *Metapolygnathus* and *Carniepigondolella* collected from Klaskino Inlet during this study, as well as others collected by the Geological Survey of Canada (Pacific Division) from the Queen Charlotte Islands and northeastern British Columbia, were examined for morphological variability within a particular species. Populations of species were identified within these collections. I consider the holotypes of common Late Carnian species and place them in what are considered as a spectrum of morphological variants within a species population. Growth stages reflecting the holotype morphology were identified and

Figure 3.1 Stratigraphic Levels and Locality Information for Klaskino Inlet



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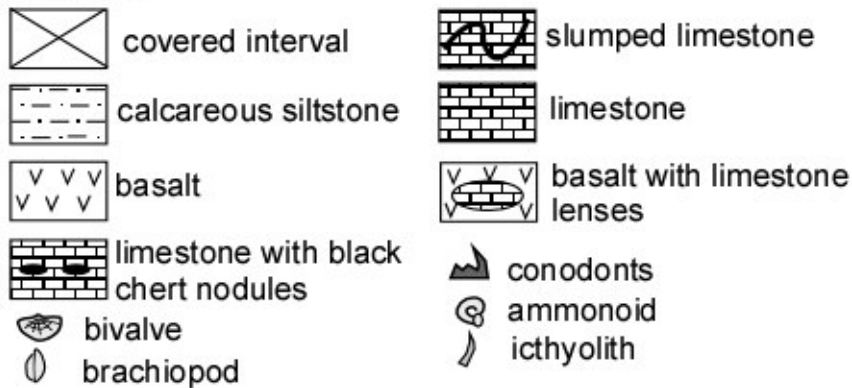


Figure 3.1 continued

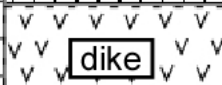

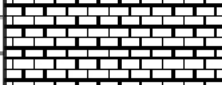









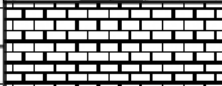






















Formation	Thickness (m)	Lithology	Sample	Conodonts	Ammonoids	Ichthyoliths	Bivalves	Brachiopods
Quatsino Formation	34	 dike	KL2-25					
	33							
	32							
	31	 sill	KL2-24					
	30		KL2-23					
	29							
	28	 sill	KL2-22					
	27		KL2-21					
	26		KL2-20		@			
	25	 sill	KL2-19					
	24		KL2-18					
	23		KL2-17					
	22	 dike	KL2-16					
	21		KL2-15					
	20		KL2-14					
	19	 sill	KL2-13		@			
	18		KL2-12					
	17		KL2-11					
	16	 sill	KL2-10					
	15		KL2-9					
	14		KL2-8					
	13	 sill	KL2-7					
	12							
	11							

Figure 3.1 continued

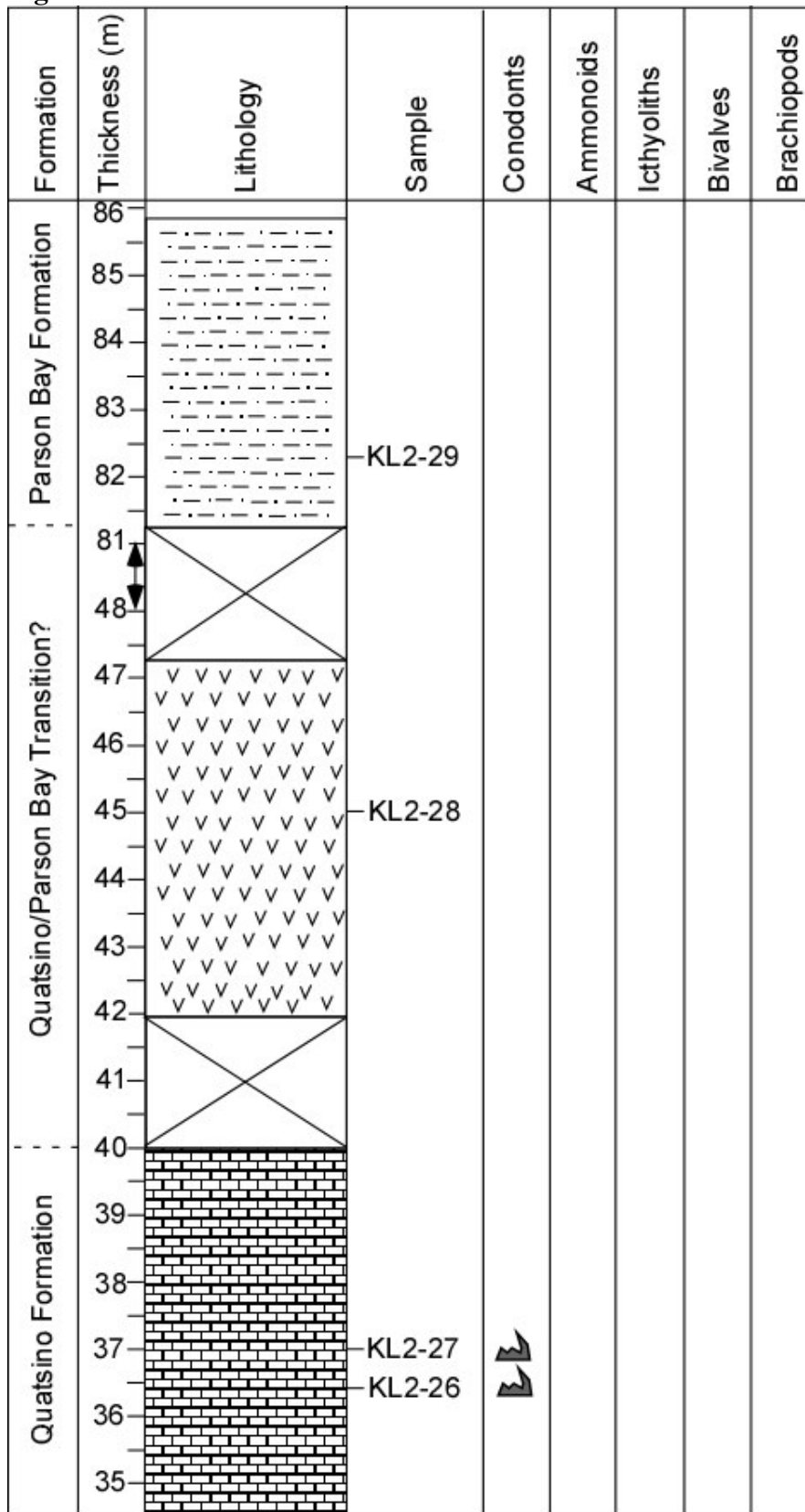


Figure 3.1: Stratigraphic information for the occurrences of conodonts and various macrofossils found at Klaskino Inlet, BC. Interval between 48 and 81 m is covered and is not to scale.

Figure 3.2 Microfossils Present in Samples from Klaskino Inlet

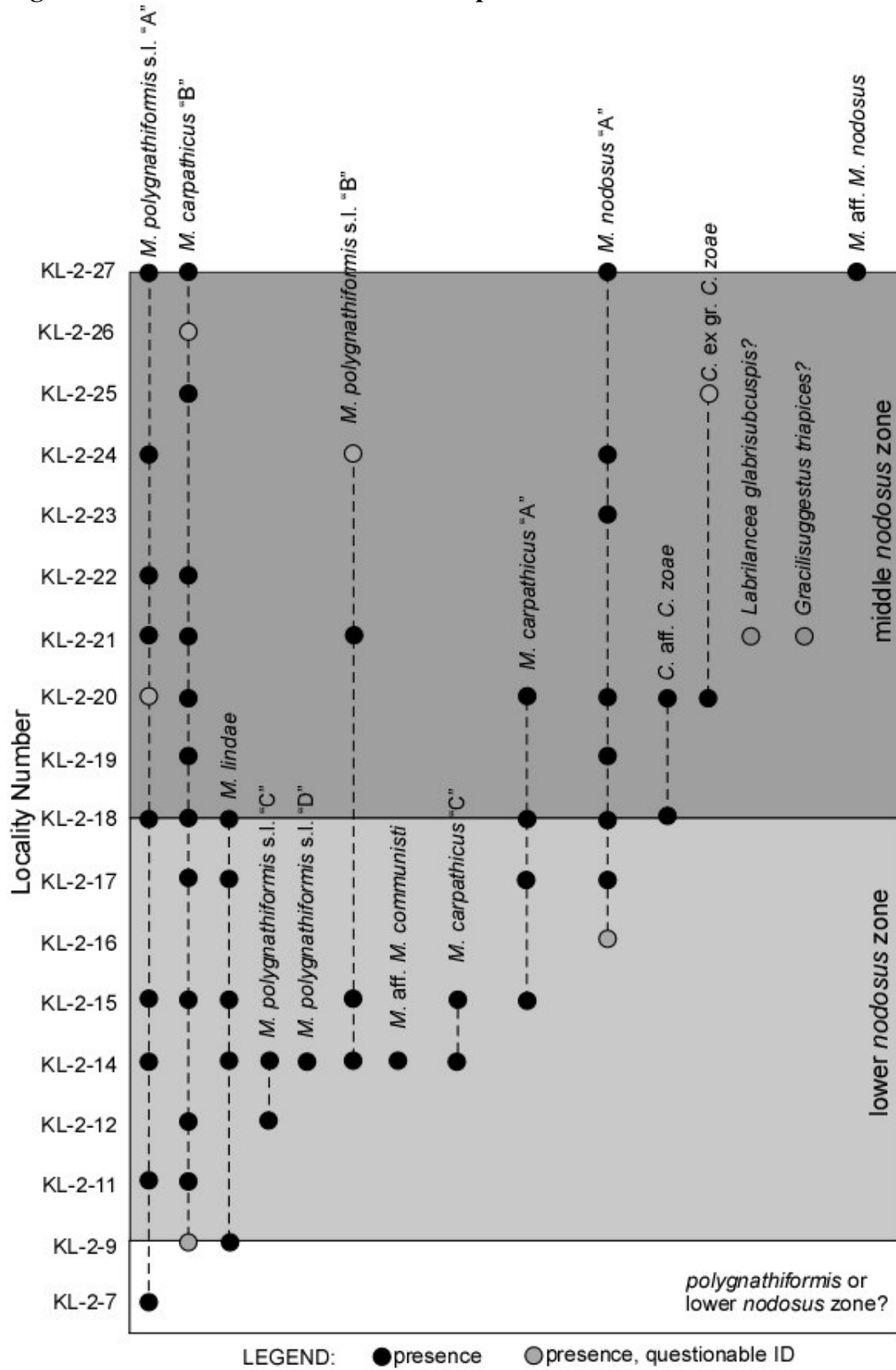
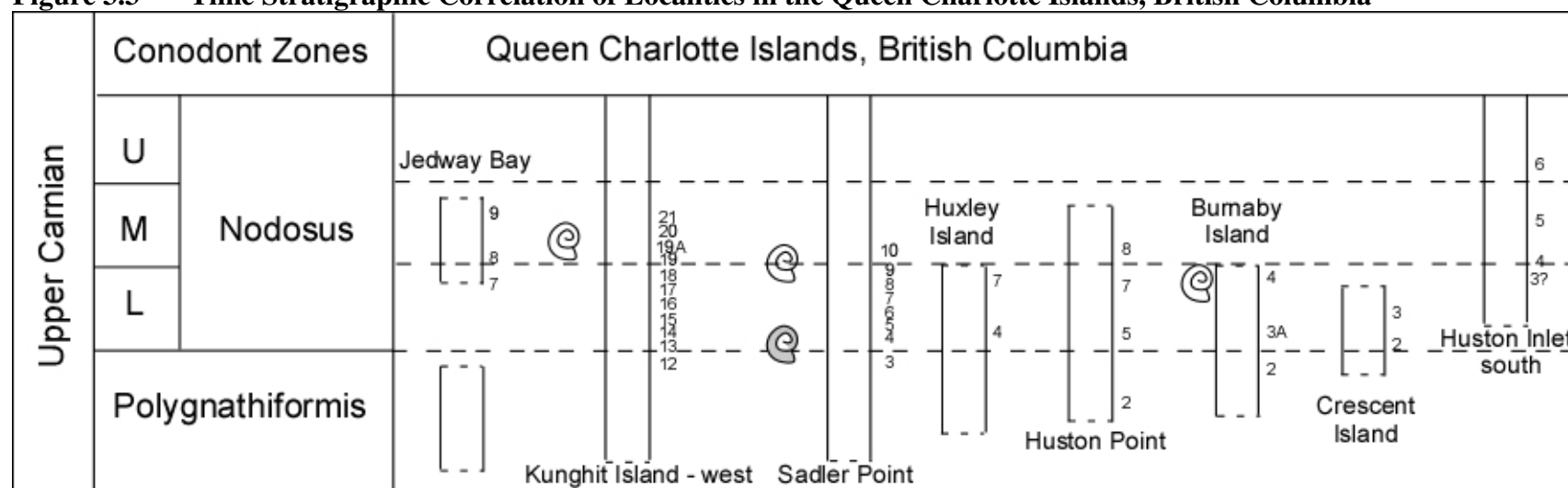


Figure 3.2: Samples containing specimens of *Metapolygnathus* as well as the ichthyoliths found at Klaskino Inlet are shown. Samples that were barren of microfossils are not included on this figure. No scale is intended.

Figure 3.3 Time Stratigraphic Correlation of Localities in the Queen Charlotte Islands, British Columbia



⊙ Dilleri Zone ammonoid found

⊙ Welleri Zone ammonoid found

Figure 3.3: Time stratigraphic relationships between the conodonts discussed from the Queen Charlotte Islands, BC. The vertical axis is relative and not scaled. In chapter 3 figure captions, the following abbreviations match up with these localities: KT-A, Kunghit Island – west; SHU, Huston Inlet South; HP, Huston Point; JED, Jedway Bay; SP, Sadler Point. Modified from Orchard (1991a).

Figure 3.4 Time Stratigraphic Correlation of Localities from Northeastern British Columbia

	Conodont Zones		Northeastern British Columbia				
Upper Camian	U	Nodosus			GB4 GB3		?59
	M				GB2 ?GK-2-35		
	L			Pardonet Hill		62 BH-B1	⊙ 42306
	Polygnathiformis					Brown Hill	BH-B5

@ Welleri Zone ammonoid present

Figure 3.4: Time stratigraphic relationships between the conodonts discussed from Williston Lake, northeastern British Columbia. Vertical axis is relative and not scaled. GK-2-35 is given a questionable time stratigraphic placement, as this unit could also be placed in the lower *nodosus* zone, pending new conodont data. Information for this figure was gathered from Zonneveld and Orchard (2002). The figure is modified from Orchard (1991a).

described where possible. Stratigraphic levels and locality information for the conodont elements I discuss can be found in Figures 3.1, 3.2, 3.3, and 3.4.

The population groups of three key Late Carnian species are considered below. These species are *Metapolygnathus polygnathiformis* (Budorov and Stefanov, 1965) sensu lato, *M. carpathicus* (Mock, 1979), and *M. nodosus* (Hayashi, 1968a). These species are primarily differentiated by the presence and distribution of platform nodes and the lateral profile of the platform margin. There is however variation of these features within each species and also in the characteristics of platform shape, carinal nodes and cusp, lower surface features of the basal pit and keel, and in blade characteristics. The Klaskino specimens often are missing the blade due to breakage. These variations are described and comparisons to other species made.

After I detail each species population, a full description of some individual species morphotypes within each population is given. These descriptions provide more detailed information about the various morphotypes of potential biostratigraphic value.

Following the description of the common species populations, I will describe the other remaining species of *Metapolygnathus* and *Carniepigondolella* that were recovered from the Quatsino Limestone. These specimens were found in low abundance so a full species population description is not possible but they most likely correspond to the species *Metapolygnathus* aff. *M. communisti* Hayashi, 1968a, *M. lindae* Orchard, 1991c, *C. zoeae* (Orchard, 1991c), or an intermediate form between the latter two species.

3.3 Descriptions

In this thesis, all conodont elements of the *polygnathiformis* s.l., *carpathicus*, and *nodosus* species populations are placed under a single genus, *Metapolygnathus* (Figure 3.5), which was first described by Hayashi (1968a) from the Adoyama Formation in Japan. At its conception, Hayashi (1968a) included three species in the genus (*M. communisti*, *M.*

linguiformis, and *M. noah*), but none of the three key species listed above were included within it. The debate as to which species should be included in *Metapolygnathus* is ongoing. While many conodont workers agree on the validity of the species discussed herein, their generic assignments are sometimes contentious.

Assignments to *Epigondolella* Mosher (1968a) and *Paragondolella* Mosher (1968a) are common (e.g., Channel *et al.*, 2003) but both are weak choices.

Mosher (1968a) defines *Epigondolella* as having an anteriorly positioned pit and lacking a platform during early ontogenetic development, among other characteristics. Most species here assigned to *Metapolygnathus* have a basal pit that is very close to the posterior end of the platform. However, the type species of *Metapolygnathus*, *M. communisti*, has the basal pit in a more anterior position and anterior migration of the pit does occur in several lineages presently combined in *Metapolygnathus* (Figure 3.6) but separation of them into other genera would be quite arbitrary. The juvenile specimens from Klaskino Inlet show the presence of a small, wing-like platform, and there are no juvenile specimens which lack a platform altogether, as is described for *Epigondolella* by Mosher (1968a). Micro-reticulation is also a feature of *Metapolygnathus*, which is observed on the studied specimens, but it is not a consistent feature of *Epigondolella*. Based on these characteristics, *Epigondolella* does not appear to be an appropriate genus for the conodont species described in this thesis.

Paragondolella resembles *Metapolygnathus* more closely in regards to morphology than does *Epigondolella*. Mosher (1968a) described the genus *Paragondolella* as being elongate and boat shaped, often with fused carinal nodes on the platform. As with *Epigondolella*, juvenile forms of *Paragondolella* show no platform. Juveniles of *Metapolygnathus* from Klaskino Inlet, the Queen Charlotte Islands, and northeastern British Columbia show the presence of a small platform.

Figure 3.5 Generalized *Metapolygnathus* Morphological Terms

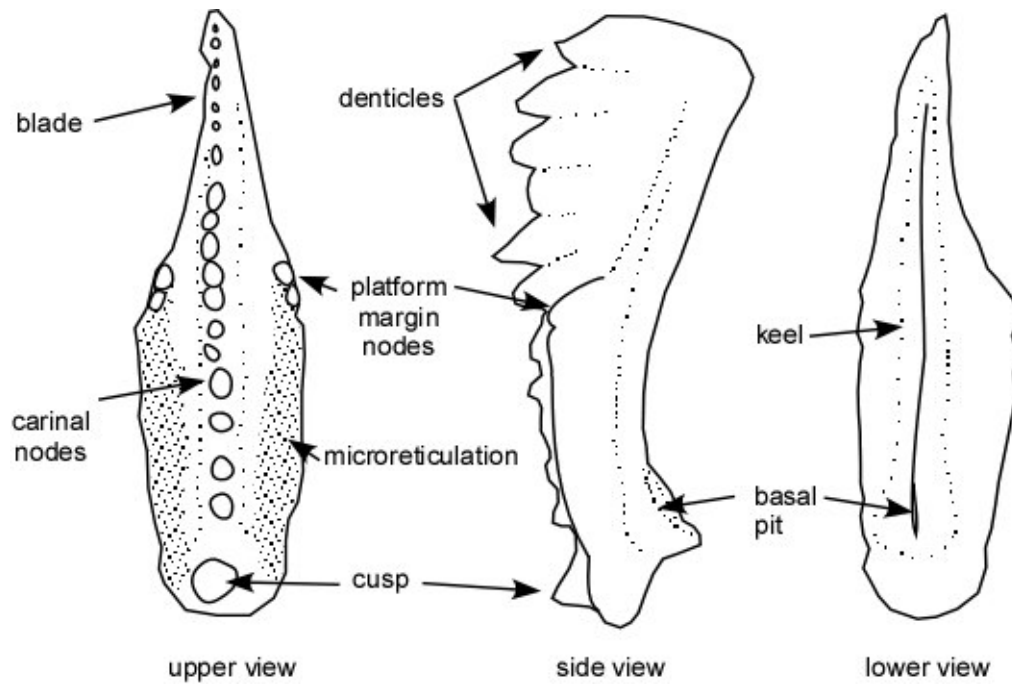


Figure 3.5: Some common morphological terms are illustrated for a generalized *Metapolygnathus* conodont element. These terms also apply to elements of the genus *Carniepigondolella*.

Figure 3.6 Variations in the Placement of the Basal Pit in *Metapolygnathus*

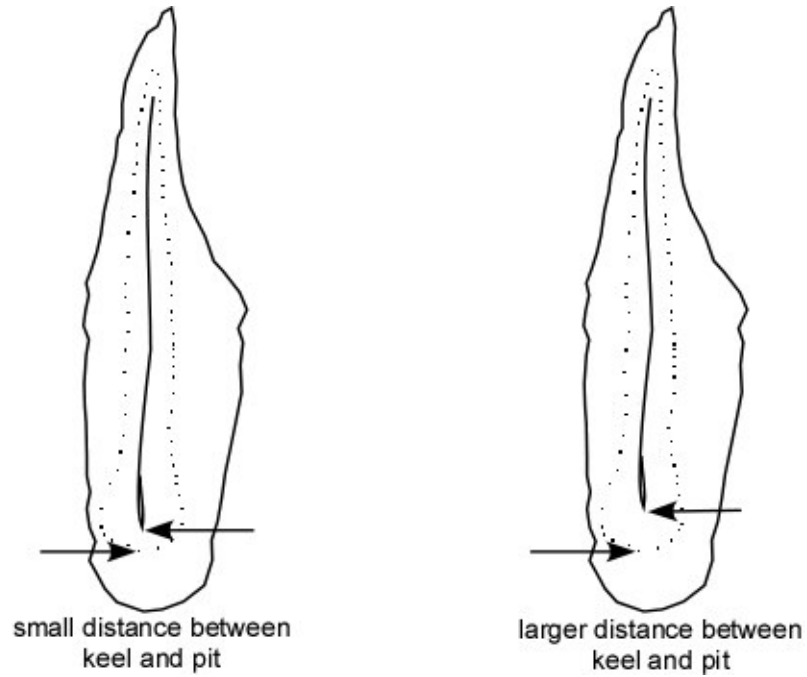


Figure 3.6: The element to the left illustrates the most common keel-to-pit distance found in *Metapolygnathus*, which is 50 microns or less. The element to the right illustrates the notable feature of a larger keel-to-pit distance of greater than 50 microns.

The specimens described in this thesis are not as elongate or as flat-platformed as those species contained in *Paragondolella*, nor do they have fused and high carinal nodes on the platform in the same frequency as paragondolellids. Furthermore, Orchard (2006) has reconstructed multielement *Paragondolella* and shown how it differs from both of these Upper Triassic genera.

3.3.1 *Metapolygnathus* Genus Description

Phylum Conodonta Eichenberg, 1930

Class Conodonta Eichenberg, 1930

Order Conodontiphorida Eichenberg, 1930

Superfamily Gondolellacea Lindström, 1970

Family Gondolellidae Lindström, 1970

Subfamily Neogondolellinae Hirsch, 1994

Genus *Metapolygnathus* Hayashi, 1968a

Type Species: *Metapolygnathus communisti* Hayashi, 1968a

Remarks: This genus is characterized by several morphological features (Figure 3.5).

Representatives of this genus typically have micro-reticulation that covers the entire upper platform, although it is not always preserved due to breakage. Platforms are longer than they are wide. The presence of nodes covers the spectrum in this genus from a total absence (e.g., *Metapolygnathus polygnathiformis* s.l.) to nodes bordering most of the platform margin (e.g., *M. nodosus*). The blade is well developed and is usually composed of five to eight denticles.

Posterior to the blade, denticles become separated as carinal nodes, which continue as a straight row down the platform and end with a pronounced posterior cusp, usually in front of the

posterior end. On the lower side of the platform beneath the cusp there is a basal pit, which is often surrounded by a loop-like keel. A basal groove runs the length of the lower side of the platform from the basal pit to just before the anterior tip of the blade.

Main Characteristics of Key Species: The three key species in this thesis, *Metapolygnathus polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus*, are primarily differentiated on the characteristics of the lateral profile of the platform, the presence of anterior platform nodes, and to a lesser extent blade length. *Metapolygnathus polygnathiformis* s.l. has no anterior platform nodes and short to no free blade. *Metapolygnathus carpathicus* has some anterior platform nodes, a smooth sloping platform profile, and a free blade that is approximately one-third the total length of the element. *Metapolygnathus nodosus* has anterior nodes on the platform, a bi-leveled lateral profile margin, and a free blade approximately the length of one-half the total length of the element. As mentioned, there is variation within these and other characteristics of these three species which is described subsequently. Some specimens within the species are separated into morphotypes when variations are frequently present.

Age and Distribution: Carnian – Early Norian. This genus has been recorded from around the globe. For the discussion in this thesis, the most notable occurrences are in central Japan (Hayashi, 1968a, b) and western Canada (Orchard, 1991a,c).

3.3.2 *Metapolygnathus polygnathiformis* s.l. Population

Metapolygnathus polygnathiformis (Budurov and Stefanov, 1965)

1965 *Gondolella polygnathiformis* n. sp. – BUDUROV and STEFANOV, p. 118, Pl. 3, figs. 3a,b – 7a,b.

1968 *Paragondolella polygnathiformis* (BUDUROV and STEFANOV) – MOSHER, p. 939, Pl. 118, figs. 9-17, 19.

1991a *Metapolygnathus polygnathiformis* (BUDUROV and STEFANOV) – ORCHARD, p. 176, Pl. 4, figs. 1, 3, 4.

2007 *Metapolygnathus polygnathiformis* (BUDUROV and STEFANOV) – ORCHARD and BALINI, p. 334, figs. 6.14-19, 6.46-51.

Diagnosis of *Metapolygnathus polygnathiformis* s.l.

The holotype of *M. polygnathiformis* was originally described from a collection close to the Ladinian-Carnian boundary from Bulgaria (Budurov and Stefanov, 1965). *Metapolygnathus polygnathiformis* s.l. is a metapolygnathid with a slightly triangular to quadrate platform shape, short to no free blade, and discrete carinal nodes. This species also has a posteriorly positioned basal pit and is differentiated from other similar metapolygnathids primarily by the absence of nodes on the anterior platform. Older specimens of *M. polygnathiformis* sensu stricto from the Ladinian-Carnian boundary are described by Orchard and Balini (2007) as having the additional feature of fused carinal nodes on the platform. While fused carinal nodes are a variation which is present in my younger collection of Late Carnian *M. polygnathiformis* s.l., the most common presentation of the carina is as discrete nodes.

Description of *Metapolygnathus polygnathiformis* holotype and morphology

The posterior end of the platform in the *M. polygnathiformis* holotype has a sub-round shape. Element numbers 1-3 (Figure 3.7) from the Queen Charlotte Islands and Brown Hill seem to most closely match the typical growth series and species description of *M. polygnathiformis* s.l.. These elements have a gently rounded posterior end that becomes increasingly quadrate through growth similar to the quadrate posterior of the holotype. Element number 3 (Figure 3.7) shows the moderately triangular shape of the entire platform including the blade. Another feature of the *M. polygnathiformis* holotype is the slowly tapering nature of the anterior platform, which results in a very short free blade or a complete lack thereof.

Figure 3.7 **Growth Series of *Metapolygnathus polygnathiformis* s.l.**

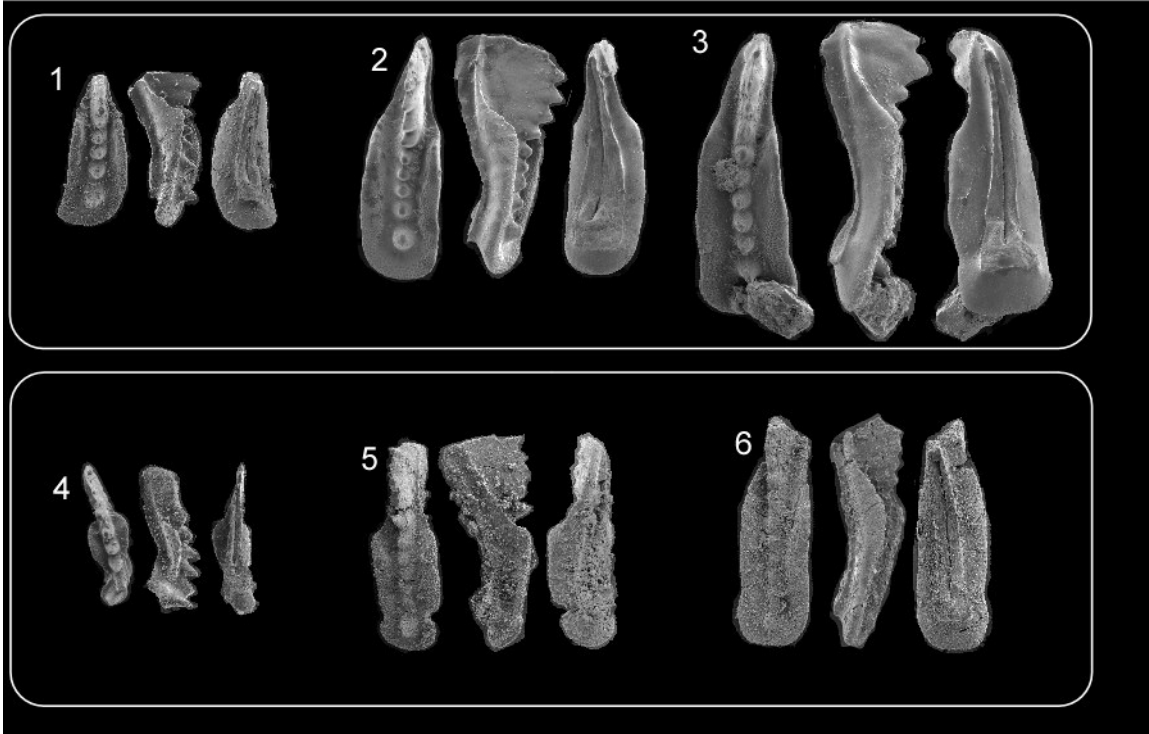


Figure 3.7: All elements are shown in three views: upper, side, and lower. All images are at 50x magnification. *Elements 1-3*: Growth series which most closely matches the typical *Metapolygnathus polygnathiformis* s.l. 1: sample KT-A19, Queen Charlotte Islands (QCI). 2: sample 93-OF-BH-B5, Brown Hill. 3: sample 93-OF-BH-B5, Brown Hill. *Elements 4-6*: Growth series most typical of *M. polygnathiformis* s.l. of Klaskino Inlet. 4: sample KL2-20. 5: sample KL2-18. 6: sample KL2-15.

Figure 3.8 Population of *Metapolygnathus polygnathiformis* s.l.

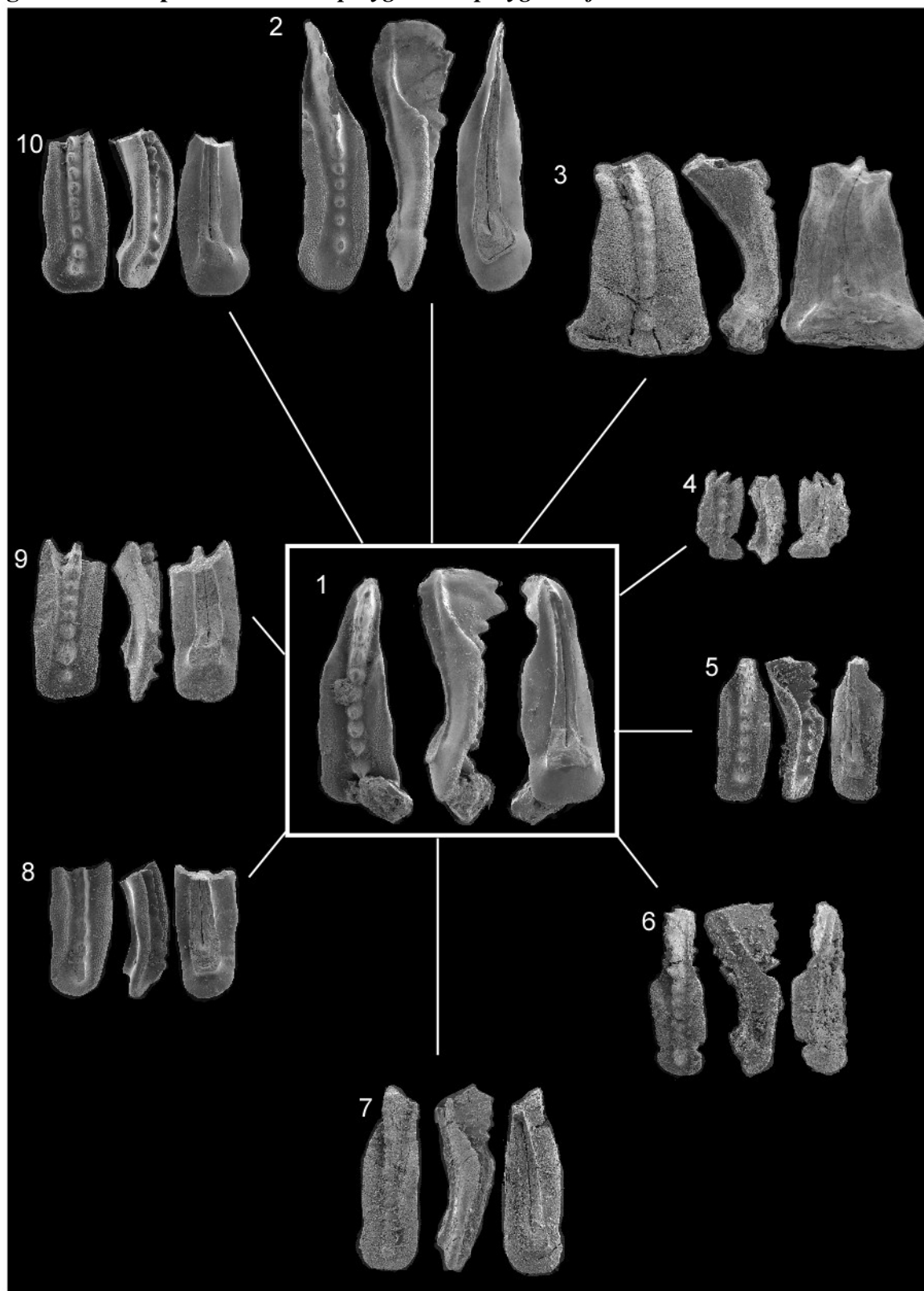


Figure 3.8: Selected elements from the *Metapolygnathus polygnathiformis* s.l. population which display the variations discussed in the text. All elements are shown in three views, upper, side, and lower. All elements are shown at 50x magnification.

Element 1: sample 93-OF-BH-B5, Brown Hill. This element most closely matches the characteristics of the holotype, but also displays the variation of a downturned anterior margin profile.

Element 2: sample 89-GK-2-35, Brown Hill. This element displays the variations of an elongated platform, widely spaced carina, and the "*communisti* trend."

Element 3: sample KL2-14, Klaskino Inlet. This element displays the variations of a triangular shaped platform, and a wide keel.

Element 4: sample KL2-14, Klaskino Inlet. This element displays the variations of an inturning of the posterior platform, and a narrow keel.

Element 5: sample JED-8, QCI. This element displays the variation of a rounded posterior end.

Element 6: sample KL2-18, Klaskino Inlet. This element displays the variation of a steeply sloping anterior margin.

Element 7: sample KL2-15, Klaskino Inlet. This element shows the variation of a gently sloping anterior margin.

Element 8: sample O-42306, mile 428 on Alaska Highway. This element shows the variation of fused carinal nodes.

Element 9: sample KL2-21, Klaskino Inlet. This element displays the variation of an extra carinal node posterior of the cusp which is smaller than the cusp.

Element 10: sample O-42306, mile 428 on Alaska Highway. This element displays the variations of an extra carinal node posterior of the cusp which is equal in size to the cusp, closely spaced carina, and a quadrate keel.

The lateral profile of the platform margin of the holotype is relatively straight and flat from the posterior end to the location where the blade begins to develop. At this point the platform margin curves downward in a gentle slope towards the anterior portion of the element. This shape is well illustrated by element numbers 2 and 5 (Figure 3.8) among others.

The illustrated holotype (Budurov and Stefanov, 1965) is somewhat unclear regarding the nature of the carina and cusp. There appears to be five carinal nodes and a low profile cusp that is of equal size to the nodes of the carina. The holotype has no visible nodes on the anterior platform margin.

A basal keel runs from the anterior of the holotype posteriorly until it wraps around the basal bit forming a small loop. The ratio of the width of the keel to the width of the element is measured from an approximate location midway between the anterior and posterior tips of the platform and is approximately 1:2. The posterior position of the basal pit is unclear on the illustrated holotype, so the distance of the basal pit to the posterior portion of the keel is unknown, but it is assumed to be in a posterior position.

Comparison of *Metapolygnathus polygnathiformis* s.l. to Other Species

Metapolygnathus polygnathiformis s.l. is most commonly confused with *M. carpathicus*. The main difference between these two species is that *M. polygnathiformis* s.l. has no anterior nodes on its platform margin. *Metapolygnathus carpathicus* always has nodes on its anterior platform margin. While the free blade is often not preserved in the elements studied herein, when it is present, the free blade of *M. carpathicus* is longer than that of *M. polygnathiformis* s.l..

In comparison with another common species in the Late Carnian, *M. polygnathiformis* s.l. lacks the developed anterior nodes present on the platform margins of *M. nodosus*.

Metapolygnathus nodosus is also characterized by a bi-leveled platform margin when viewed in

profile; in contrast, *M. polygnathiformis* s.l. usually has a straight platform margin that steps down at the anterior end.

Variations in the *Metapolygnathus polygnathiformis* s.l. Population

1) Platform Shape: Element numbers 4-6 (Figure 3.7) illustrate the most typical growth stages of the Klaskino fauna. One variant to this shape is a marked inturning of the posterior end in which one side of the platform extends laterally further than the other side. This platform shape is usually found in elements with a posterior constriction and is evident in element numbers 4 (Figure 3.8) and 6 (Figure 3.9). Element number 5 (Figure 3.8) illustrates a more rounded posterior end. Element numbers 3 (Figure 3.8) and 7 (Figure 3.9) show a strongly triangular platform shape which was found in this population only from Klaskino Inlet. This could be a size dependent feature as there are no juveniles or small sized adults with this characteristic. Element number 7 (Figure 3.9) is similar in size to many of the other elements in this population that do not bear the triangular platform but element number 3 (Figure 3.8) is one of the largest elements in the collection. The last morphological variation in relation to platform shape for the *M. polygnathiformis* s.l. population is a rather elongate platform length. Element number 2 (Figure 3.8) has a much longer and more slender platform, and is an example of the subspecies *M. polygnathiformis noah* (Hayashi, 1968a).

2) Lateral Profile of the Platform Margin: Elements 3 and 5 (Figure 3.7) deviate from the platform margin morphology of the holotype. While it is the best overall element at matching the holotype, element number 3 (Figure 3.7) shows a platform margin profile that is not straight from the posterior of the blade to the posterior end of the element. At the posterior constriction, the platform margin is downturned. Element number 5 (Figure 3.7) shows the other platform margin variation present in this population: a steeply sloping anterior platform margin. Instead

Figure 3.9 *Metapolygnathus* species illustrations

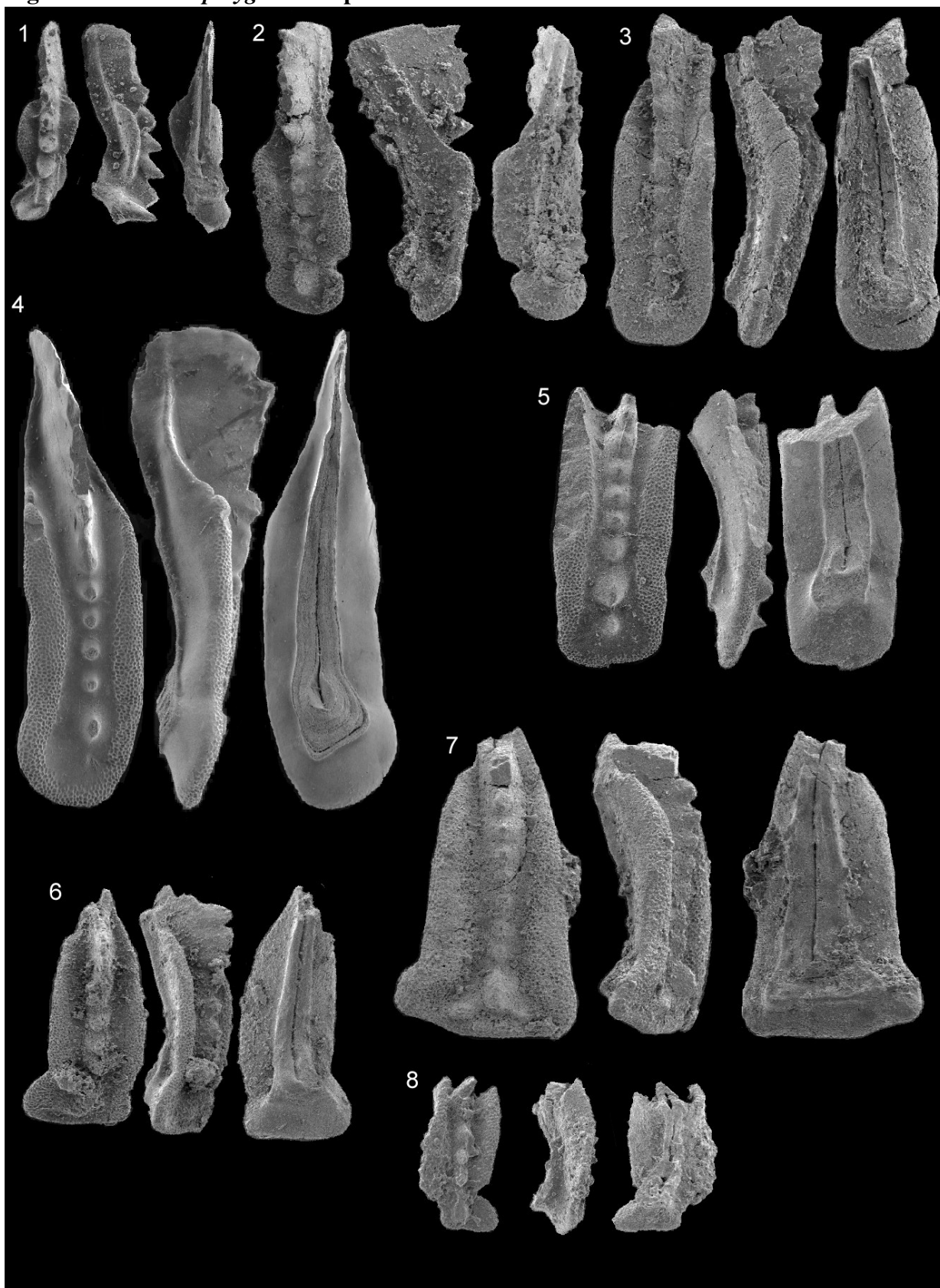


Figure 3.9: Detailed upper, side, and lower views of each morphotype of *Metapolygnathus polygnathiformis* s.l. elements. All images are 95x magnification.

Element 1 – Metapolygnathus polygnathiformis s.l. morphotype A (Budurov and Stefanov). Sample KL2-20, Klaskino Inlet.

Element 2 – Metapolygnathus polygnathiformis s.l. morphotype A (Budurov and Stefanov). Sample KL2-18, Klaskino Inlet.

Element 3 – Metapolygnathus polygnathiformis s.l. morphotype A (Budurov and Stefanov). Sample KL2-15, Klaskino Inlet.

Element 4 – Metapolygnathus polygnathiformis noah (Hayashi). Sample 89-GK-2-35, Brown Hill.

Element 5 – Metapolygnathus polygnathiformis s.l. morphotype B? (Budurov and Stefanov). Due to the missing anterior of this specimen, it is questionably assigned to *M. polygnathiformis* based on its platform shape and straight profile. Sample KL2-21, Klaskino Inlet.

Element 6 – Metapolygnathus polygnathiformis s.l. morphotype C (Budurov and Stefanov). Sample KL2-12, Klaskino Inlet.

Element 7 – Metapolygnathus polygnathiformis s.l. morphotype D (Budurov and Stefanov). Sample KL2-14, Klaskino Inlet.

Element 8 – Metapolygnathus polygnathiformis s.l. morphotype C (Budurov and Stefanov). Sample KL2-14, Klaskino Inlet.

of being a smoothly curving anterior platform margin as is shown in element number 6 (Figure 3.7), this anterior margin is abruptly downturned.

3) Carina and Cusp: The most common forms in this population have a row of five or six closely spaced but separate nodes posterior of the blade. These carinal nodes are usually of equal size and strength and terminate with the presence of a slightly larger cusp. Posterior of the cusp there are no other carinal nodes present. All of these features are present in element numbers 2, 3 (Figure 3.7), and 5 (Figure 3.8), among others.

There is much morphological variability within this population in regard to the number, spacing, and size of an element's carinal nodes and cusp. Some elements have an additional carinal node posterior of the cusp. This extra node is often smaller than the cusp and, in the case of element number 9 (Figure 3.8), it is smaller than the other carinal nodes as well. A second variation on the carinal node-cusp relationship, illustrated by element number 10 (Figure 3.8), occurs when the carinal node either anterior to or posterior to the cusp is of the same size as the cusp, creating the illusion of two cusps.

The number and spacing of carinal nodes also vary within this species population. Element number 2 (Figure 3.8) has only three widely spaced nodes anterior of the cusp. In contrast, the element number 3 (Figure 3.10) has four nodes which are closely spaced but still individual before they begin to fuse together and run into the broken blade. Element number 8 (Figure 3.8) is unique in the population because its carinal nodes are all fused rather than discrete.

4) Presence of Anterior Nodes: These specimens of *M. polygnathiformis* s.l. have no anterior nodes on the platform.

Figure 3.10 *Metapolygnathus* Species Illustrations

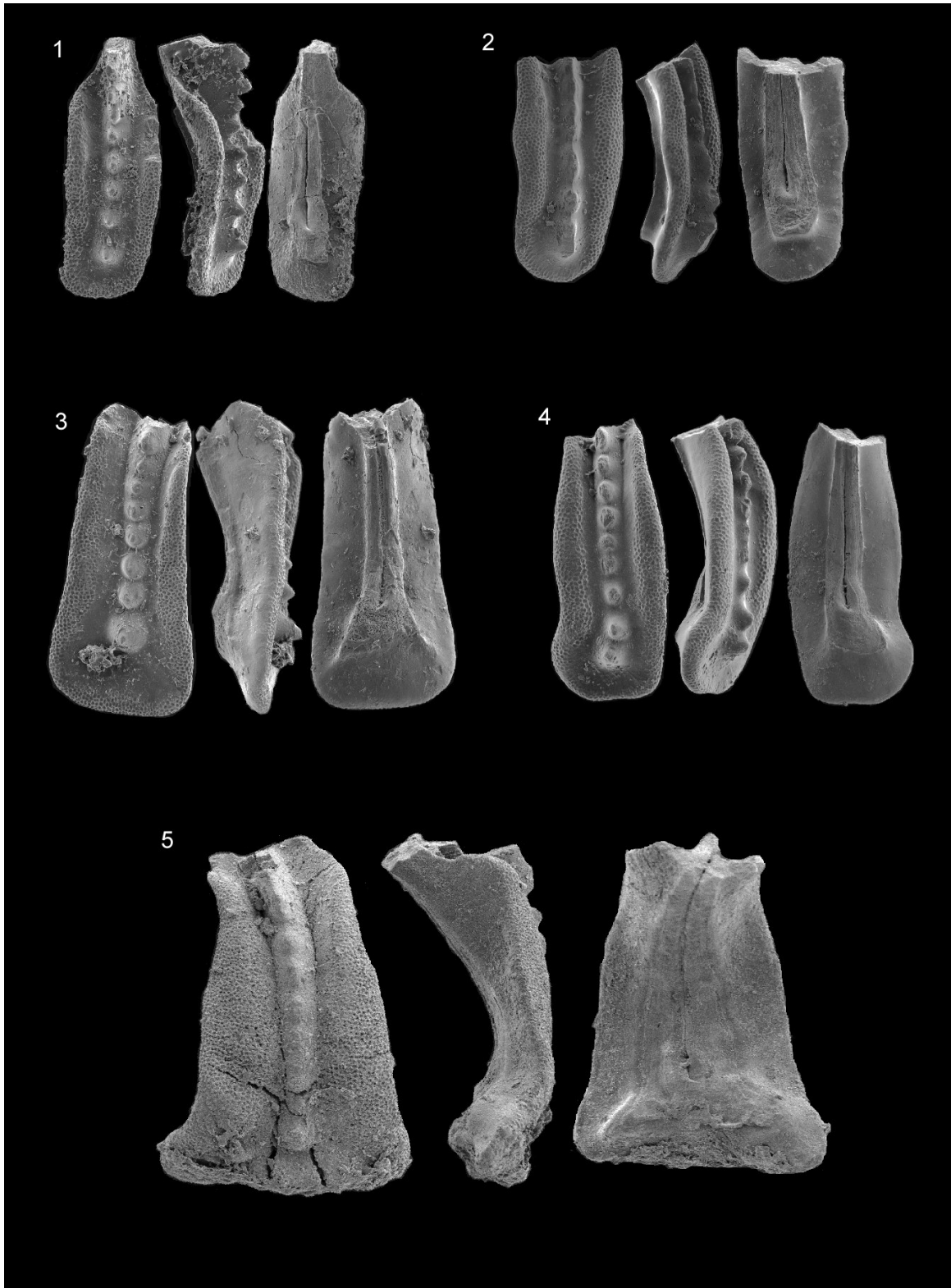


Figure 3.10: Detailed upper, side, and lower views of morphotypes of *Metapolygnathus polygnathiformis* s.l.. All images are 95x magnification.

Element 1 – Metapolygnathus polygnathiformis s.l. morphotype A (Budurov and Stefanov).
Sample JED-8, Queen Charlotte Islands (QCI).

Element 2 – Metapolygnathus polygnathiformis s.l. morphotype B (Budurov and Stefanov).
Sample O-42306, mile 428 on Alaska Highway.

Element 3 – Metapolygnathus polygnathiformis s.l. morphotype B (Budurov and Stefanov).
Sample 80-MJO-BH-62, Brown Hill.

Element 4 – Metapolygnathus polygnathiformis s.l. morphotype E (Budurov and Stefanov).
Sample O-42306, mile 428 on Alaska Highway.

Element 5 – Metapolygnathus polygnathiformis s.l. morphotype D (Budurov and Stefanov).
Sample KL2-14, Klaskino Inlet.

5) Basal Pit and Keel: The width of the keel varies from being fairly narrow (e.g., element number 6 [Figure 3.9]) to broad (e.g., element numbers 3 [Figure 3.8] and 7 [Figure 3.9]), but is most commonly somewhere in between. The ratio of the keel width to the width of the platform ranges from 1:5 to 1:2.

On many variants, the basal keel forms a smooth curve around the basal pit, as is seen on the holotype. But when it does not form a smooth curve, a more quadrate posterior end is seen, as in element numbers 10 (Figure 3.8) and 3 (Plate 3.10). In general, keel shape appears to mirror the shape of the posterior platform.

Some specimens of the *M. polygnathiformis* s.l. population illustrate the “*communisti* trend.” This trend is named after *M. communisti* which has its basal pit located in a central or anterior position on the lower side of the element, and it occurs when the basal pit begins migrating anteriorly to a more central position within the keel than is common in primitive *Metapolygnathus* species. It is difficult to quantify this trend in the present specimens because the majority of elements showing the trend are broken. For specimens that are complete and showing the “*communisti* trend,” the ratio of the distance of the basal pit from the base of the keel to the length of the entire element is 1:6. The ratio for the complete specimens not showing the trend is 1:8 to 1:9. This trend is not as clearly defined in the *M. polygnathiformis* s.l. population as it is in the *M. carpathicus* population.

For the specimens of *M. polygnathiformis* s.l. that appear to show the “*communisti* trend” but are broken, I measured the distance of the pit from the keel. When the specimens were measured, those appearing to display the typical posterior pit position had a pit-keel distance of less than 50 microns, while those appearing to have a more anteriorly positioned pit had a pit-keel distance of more than 50 microns. In this report, if the basal pit is a distance of 50 microns or more from the base of the keel, the specimen is considered to exhibit the “*communisti* trend.”

In the most common specimens, the basal pit is approximately a distance of 50 microns or less from the posterior part of the basal keel (Figure 3.6); however, there are some specimens that show the “*comunisti* trend.” These anterior pits are at a distance of greater than 50 microns from the posterior part of the basal keel. Element number 2 (Figure 3.8) is a good example of the more extreme position of the basal pit in the *M. polygnathiformis* s.l. population. It appears that platform size is not entirely the reason for the anteriorly shifting pit but perhaps growth stage is the controlling factor. In this population adults of small, typical, and large size can have an anteriorly shifting pit, but no juveniles show this feature. Juveniles are differentiated from small adults in this population by a poorly developed, wing-like platform and/or a pronounced posterior constriction.

Metapolygnathus polygnathiformis noah (Hayashi, 1968a)

(Figure 3.9, element 4)

Material: 1 complete specimen contributed to this description.

Description: A subspecies of *Metapolygnathus polygnathiformis* s.l. with sub-round postero-lateral margins and an elongate platform. There are four discrete carinal nodes on this specimen, and the more anterior carinal nodes fuse to form a fixed blade which is about one-third the length of the total platform. The cusp is round and slightly larger than the other carinal nodes. This specimen also displays the “*comunisti* trend.”

Discussion: This subspecies differs from *M. polygnathiformis* s.l. and all the morphotypes primarily by having a more elongated platform. It differs from morphotype "C" by not having a marked inturning of the posterior platform where one side is laterally extended. It differs from morphotype "D" by its elongate, non-triangular platform shape. This subspecies varies from morphotype "E" by having a straight lateral platform profile with no weak bi-leveled shape.

Occurrence and Age: Found at Brown Hill, B.C., Late Carnian.

Metapolygnathus polygnathiformis s.l. morphotype “A”

(Figure 3.9, elements 1, 2, 3; Figure 3.10, element 1)

Material: 2 complete specimens and 4 incomplete specimens have contributed to this description.

Description: A morphotype of *Metapolygnathus polygnathiformis* s.l. with sub-round postero-lateral margins; juvenile specimens have a posterior constriction. No anterior or exterior nodes flank the margin of the platform. The basal pit is in a posterior position on the platform. The free blade is relatively short and comprises just under one-third of the total length of the platform. The cusp is slightly larger than the carinal node preceding it. In juvenile specimens (e.g., Figure 3.9, element 1) the cusp is sharp and tooth-like while in the adult specimens (e.g., Figure 3.9, element 3) it appears more rounded.

Discussion: This morphotype is placed in this species group based on the straight shape of the posterior margin, posteriorly positioned pit, and rounded carinal nodes. It is different from *M. polygnathiformis* s.l. morphotype “B” because of the posteriorly positioned basal pit. The cusp of morphotype “B” also appears to be stronger and less rounded into adulthood than is seen in morphotype “A.” Morphotype “C” has one laterally extended side on the posterior end of the platform, which is not seen in morphotype “A.” The typical squat platform shape of morphotype “A” differentiates it from the strongly triangular platform shape of morphotype “D.” The straight sided lateral platform profile of morphotype “A” differentiates it from the weak bi-leveled profile of morphotype “E.”

Occurrence and Age: Found from KL-2-7, 2-11, 2-14, 2-15, 2-18, 2-20 – 2-22, 2-24, and 2-27 in the Quatsino limestone. Late Carnian, possibly *polygnathiformis* zone, but most likely lower to middle *nodosus* zone (Welleri Zone 1 and possibly Welleri Zone 2).

Metapolygnathus polygnathiformis s.l. morphotype “B”

(Figure 3.9, element 5; Figure 3.10, elements 2, 3)

Material: 4 incomplete specimens have contributed to this description.

Description: A morphotype with sub-rounded postero-lateral margins and a small but prominent posterior cusp. All specimens demonstrate varying degrees of the “*communisti* trend” in terms of pit position.

Discussion: This morphospecies is distinguished from all other *M. polygnathiformis* s.l. morphotypes by exhibiting the “*communisti* trend.” All of these specimens have a basal pit greater than 50 microns from the posterior end of the basal keel.

Occurrence and Age: Found from KL-2-14, 2-15, 2-21, and a questionable occurrence in KL-2-24 from the Quatsino limestone. Also found at Brown Hill and mile 428 of the Alaska Highway. Late Carnian, lower to middle *nodosus* zone (Welleri Zone 1 and possibly Welleri Zone 2).

Metapolygnathus polygnathiformis s.l. morphotype “C”

(Figure 3.9, elements 6, 8)

Material: 2 incomplete specimens have contributed to this description.

Description: *Metapolygnathus polygnathiformis* s.l. morphotype showing a marked inturning of the posterior platform where one side of the posterior end of the platform is extended laterally. A posterior constriction is also present in the specimens.

Discussion: This morphotype is distinguished from all *M. polygnathiformis* s.l. morphotypes by having a posterior constriction that is followed by one end of the posterior margin being extended laterally. In certain specimens of *M. polygnathiformis* s.l. morphotype “D” there can be a similar posterior asymmetry; however, *M. polygnathiformis* s.l. morphotype “C” does not exhibit a triangular platform shape. This morphotype is further distinguished from *M. polygnathiformis* s.l. morphotype “B” by its posteriorly situated basal pit. Morphotype “E”

displays a weak bi-leveled lateral platform profile which differentiates it from the smooth slope of the lateral platform profile in morphotype "C."

Occurrence and Age: Found from KL-2-12, and 2-14 in the Quatsino limestone. Late Carnian, lower *nodosus* zone (Welleri Zone 1).

Metapolygnathus polygnathiformis s.l. morphotype "D"

(Figure 3.9, element 7; Figure 3.10, element 5)

Material: 2 incomplete specimens have contributed to this description.

Description: *Metapolygnathus polygnathiformis* s.l. morphotype with a triangular posterior end.

The basal keel mirrors the triangular shape of the platform, and the pit is in a posterior position.

Discussion: This morphotype is distinguished from other morphotypes by its triangle-shaped posterior end. Both specimens show one side of the platform end extended outwards more than the other side, similar to *M. polygnathiformis* s.l. morphotype "C." However, in *M.*

polygnathiformis s.l. morphotype "D," there is no posterior constriction present.

Occurrence and Age: Found only in KL-2-14 from the Quatsino limestone. Late Carnian, lower *nodosus* zone (Welleri Zone 1).

Metapolygnathus polygnathiformis s.l. morphotype "E"

(Figure 3.10, element 4; Figure 3.8, element 1)

Material: 1 complete and 1 incomplete specimen have contributed to this description.

Description: A morphotype with sub-round postero-lateral margins and no anterior platform nodes. The fixed blade is approximately one-third of the total platform length. This morphotype displays a weakly bi-leveled lateral profile, reminiscent of the bi-leveled profile observed in *M. nodosus*. Also observed is the "*communisiti* trend."

Discussion: This morphotype varies from all the other morphotypes by having a weakly bi-leveled lateral platform profile. It differs from morphotypes "A," "C," and "D" by displaying the "*communisti* trend." This morphotype varies from *M. nodosus* by the absence of anterior nodes on the platform and a fixed blade.

Occurrence and Age: Found at Brown Hill, B.C., and Mile 428 on Alaska Highway. Late Carnian.

3.3.3 *Metapolygnathus carpathicus* Population

Metapolygnathus carpathicus (Mock, 1979)

1979 *Gondolella carpathica* n. sp. – MOCK, p. 172, Pl. 1, figs. 1-5.

Diagnosis of *Metapolygnathus carpathicus*

The holotype of *M. carpathicus* was described from Upper Carnian rocks of Slovakia (Mock, 1979). *Metapolygnathus carpathicus* is a metapolygnathid with a quadrate to triangular platform shape, a free blade about one-third the length of the platform, a smoothly sloping anterior platform profile, and nodes on the anterior platform which are visible in the upper view but can be either easily visible or relatively inconspicuous in profile view.

Comparison of *Metapolygnathus carpathicus* to Other Species

Specimens in the *M. carpathicus* population are most similar to *M. polygnathiformis* s.l. and *M. nodosus*. *Metapolygnathus carpathicus* shares a similar platform shape with *M. polygnathiformis* s.l., but differs in the fact that it has developed anterior nodes on its platform margin. The confusion between these two species is most common when the specimen of *M.*

carpathicus has very weak anterior nodes. The platform of *M. carpathicus* also tends to show less tapering towards the blade in the upper view than is seen in most specimens of *M. polygnathiformis* s.l. which results in *M. carpathicus* having a longer free blade.

When specimens of *M. carpathicus* have strong anterior nodes, they are likely to be confused with *M. nodosus*. These two species vary from each other in several ways. The free blade of *M. carpathicus* is often only one-third of the length of the entire platform element, while the free blade of *M. nodosus* is usually longer, at one-half the length of the total platform element. *Metapolygnathus nodosus* also tends to have more well defined anterior nodes on the platform margin and these nodes often continue in the posterior direction up to one-half the length of the platform. The last major difference between these two species is that *M. carpathicus* does not exhibit the bi-leveled platform margin of *M. nodosus*.

Description of *Metapolygnathus carpathicus* holotype morphology

The holotype has a platform that is squat and triangular in shape. The blade is one-third to one-half the length of the element, and there appears to be no free portion of the blade. The lateral profile of the holotype is a slightly curved margin which rises to its highest point at the last anterior node and gradually declines in elevation towards the posterior end of the element.

The illustration of the holotype is only of moderate quality, so information on the carina and cusp of *M. carpathicus* is somewhat difficult to ascertain. It appears that the holotype has five or six denticles on the blade which continue down the platform as seven distinct carinal nodes. The cusp is smaller than the nodes of the carina and does not project above the lateral platform margin in profile. There are between 3 and 5 nodes on the anterior platform which are defined and appear tooth-like in profile.

The keel reflects the triangular platform shape of the holotype. It appears to be starting to branch on both sides of the posterior platform. The ratio of the width of the keel to the width of the element is approximately 3:10.

Variations in the *Metapolygnathus carpathicus* Population

1) Platform Shape: The growth series which most closely matches the holotype of *M. carpathicus* is illustrated by element numbers 1-4 (Figure 3.11), where element number 3 is the most morphologically similar to the holotype. The juvenile element in this growth series has a slim platform with a rounded posterior end and a weak posterior constriction. The adult elements show a more quadrate posterior end with an overall stout, triangular outline to the platform. The anterior platform tapers somewhat towards the blade. The complete blade is roughly one-third to one-half of the total length of the element but the free portion of the blade is only one-quarter to one-third of the element's length.

More typical forms of the posterior end of the platform are sub-rounded to quadrate (e.g., element 2 [Figure 3.12] and element 2 [Figure 3.13]). Element numbers 5 and 9 (Figure 3.13) are juvenile specimens which show a posterior constriction that is often lost in adulthood. Element number 5 (Figure 3.13) shows the intermediate posterior constriction in between a juvenile and an adult, as well as a tapering anterior platform like that of the holotype. This tapering anterior platform is not common to many of the other specimens of *M. carpathicus* studied here. This specimen is still considered part of *M. carpathicus* because of its common characteristics with the species, including the presence of anterior nodes only on the anterior portion of the platform and the smooth curved platform margin when viewed in profile.

The growth series most commonly found at Klaskino Inlet (e.g., element numbers 5-8 [Figure 3.11]) has a different platform shape than the holotype. The juvenile platform shape in this growth series, represented by element number 5, shows a rounded posterior with a

Figure 3.11 Growth Series of *Metapolygnathus carpathicus*



Figure 3.11: Elements 1-4 are a growth series of *M. carpathicus* that most resembles the holotype, of which element 3 is the best representation of the holotype. 1: sample SP-7, Queen Charlotte Islands (QCI). 2: sample KT-A21, QCI. 3: sample HP-8, QCI. 4: sample KT-A21, QCI. Elements 5-8 are a growth series which is most typical of *M. carpathicus* at Klaskino Inlet. 5: sample KL2-15, Klaskino Inlet. 6: sample KL2-17, Klaskino Inlet. 7: sample KL2-15, Klaskino Inlet. 8: sample KL2-20, Klaskino Inlet. All elements are presented in upper, side, and lower views at 50x magnification.

Figure 3.12 *Metapolygnathus* Species Illustrations

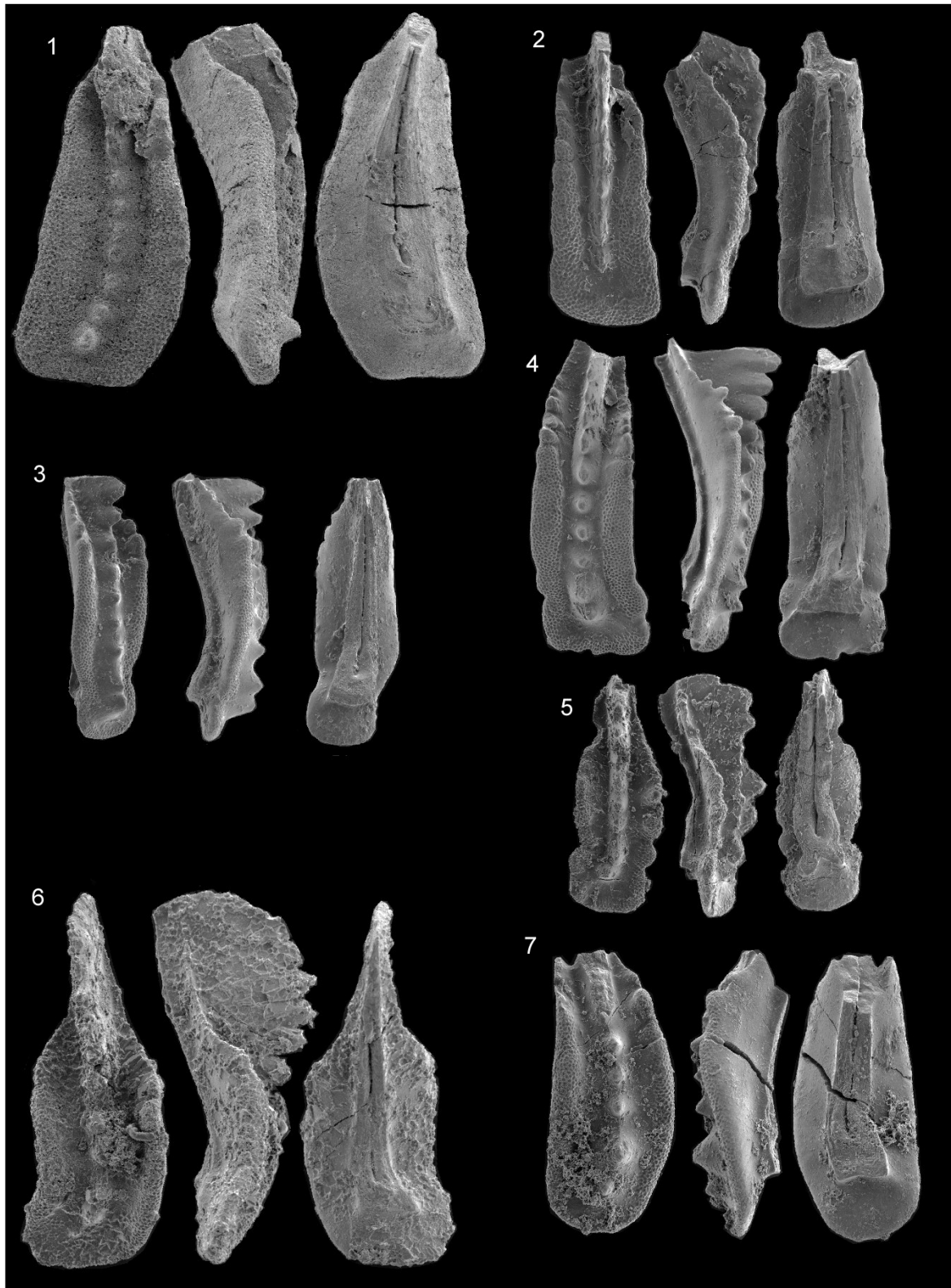


Figure 3.12: Illustrations of *Metapolygnathus carpathicus* morphotypes. All elements are shown in upper, side, and lower view at 95x magnification.

Element 1 – Metapolygnathus carpathicus morphotype A (Mock). Sample KL2-14, Klaskino Inlet.

Element 2 – Metapolygnathus carpathicus morphotype A (Mock). Sample JED-9, Queen Charlotte Islands (QCI).

Element 3 – Metapolygnathus carpathicus (Mock). Sample SP-7, QCI.

Element 4 – Metapolygnathus carpathicus morphotype B (Mock). Sample SP-7, QCI.

Element 5 – Metapolygnathus carpathicus morphotype B (Mock). Sample KT-A19, QCI.

Element 6 – Metapolygnathus carpathicus morphotype B (Mock). Sample SP-5, QCI.

Element 7 – Metapolygnathus carpathicus morphotype A (Mock). Sample SHU-3, QCI.

Figure 3.13 *Metapolygnathus* Species Illustrations

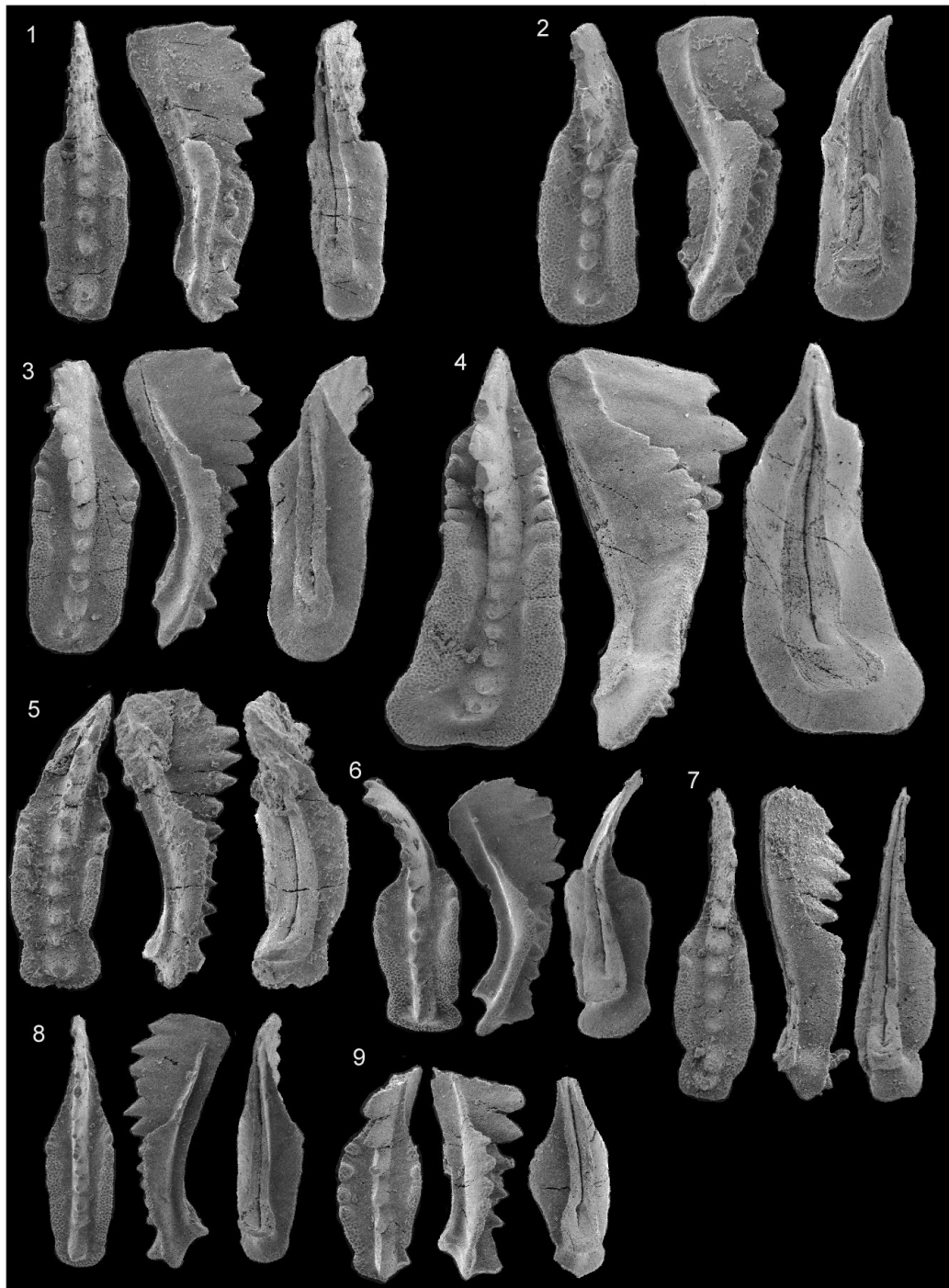


Figure 3.13: Illustrations of *Metapolygnathus carpathicus* morphotypes. All elements are shown in upper, side, and lower views at 95x magnification.

Element 1 – Metapolygnathus carpathicus morphotype A (Mock). Sample KL2-17, Klaskino Inlet.

Element 2 – Metapolygnathus carpathicus morphotype A (Mock). Sample KL2-18, Klaskino Inlet.

Element 3 – Metapolygnathus carpathicus morphotype A (Mock). Sample KL2-15, Klaskino Inlet.

Element 4 – Metapolygnathus carpathicus morphotype A (Mock). This specimen also exhibits an inturned posterior platform. Sample KL2-15, Klaskino Inlet.

Element 5 – Metapolygnathus carpathicus morphotype B (Mock). Sample KL2-18, Klaskino Inlet.

Element 6 – Metapolygnathus carpathicus morphotype B (Mock); Note distorted blade. Sample KL2-20, Klaskino Inlet.

Element 7 – Metapolygnathus carpathicus morphotype B (Mock). Sample KL2-17, Klaskino Inlet.

Element 8 – Metapolygnathus carpathicus morphotype B (Mock). Sample KL2-17, Klaskino Inlet.

Element 9 – Metapolygnathus carpathicus morphotype B (Mock). Due to a broken blade, this specimen could be a *carpathicus-nodosus* transition specimen, but is assigned to *M. carpathicus* due to its platform shape. Sample KL2-17, Klaskino Inlet.

constriction and a slowly tapering anterior platform towards the blade. Element numbers 6-8 (Figure 3.11) illustrate the more rectangular platform shape which is typical of the Klaskino elements. In these three elements, the anterior platform does not taper as slowly towards the blade as in the juvenile specimen. This more rapid tapering produces a small free blade which is preserved on element numbers 6 and 7 (Figure 3.11) from Klaskino Inlet. Another common variation on the platform shape of *M. carpathicus* is a strongly squared posterior end. This is most often seen on elements that are also more elongate, as is illustrated by element numbers 8 (Figure 3.14) and 4 (Figure 3.12).

Differing from the triangular posterior of the holotype, element numbers 4 (Figure 3.14) and 7 (Figure 3.12) have a highly rounded posterior. Element number 9 (Figure 3.14) has a posterior end which is very rounded but also curves towards one side. The last morphological variation on the platform shape of the holotype is illustrated by element number 2 (Figure 3.14). This element shows an extreme triangular platform shape with a marked inturning of the posterior platform.

2) Lateral Profile of the Platform Margin: There appears to be two equally common platform margin shapes observed in profile view within this population. One is a flat, straight margin and the other is a slightly curved margin that lacks significant change in elevation (*i.e.* not the bi-leveled platform margin of *M. nodosus*). The lateral profile most similar to the holotype is element number 3 (Figure 3.11) where the anterior margin gently tapers towards the blade.

A variation on the gently tapering anterior platform of the holotype is visible in element numbers 6 (Figure 3.11), 4 (Figure 3.14), and 2 (Figure 3.13). As the platform tapers anteriorly towards the blade, the platform margin appears to drop abruptly with a steep slope. Element 6 (Figure 3.12) appears to show an asymmetrical development of the anterior platform described in

Figure 3.14 Population of *Metapolygnathus carpathicus*

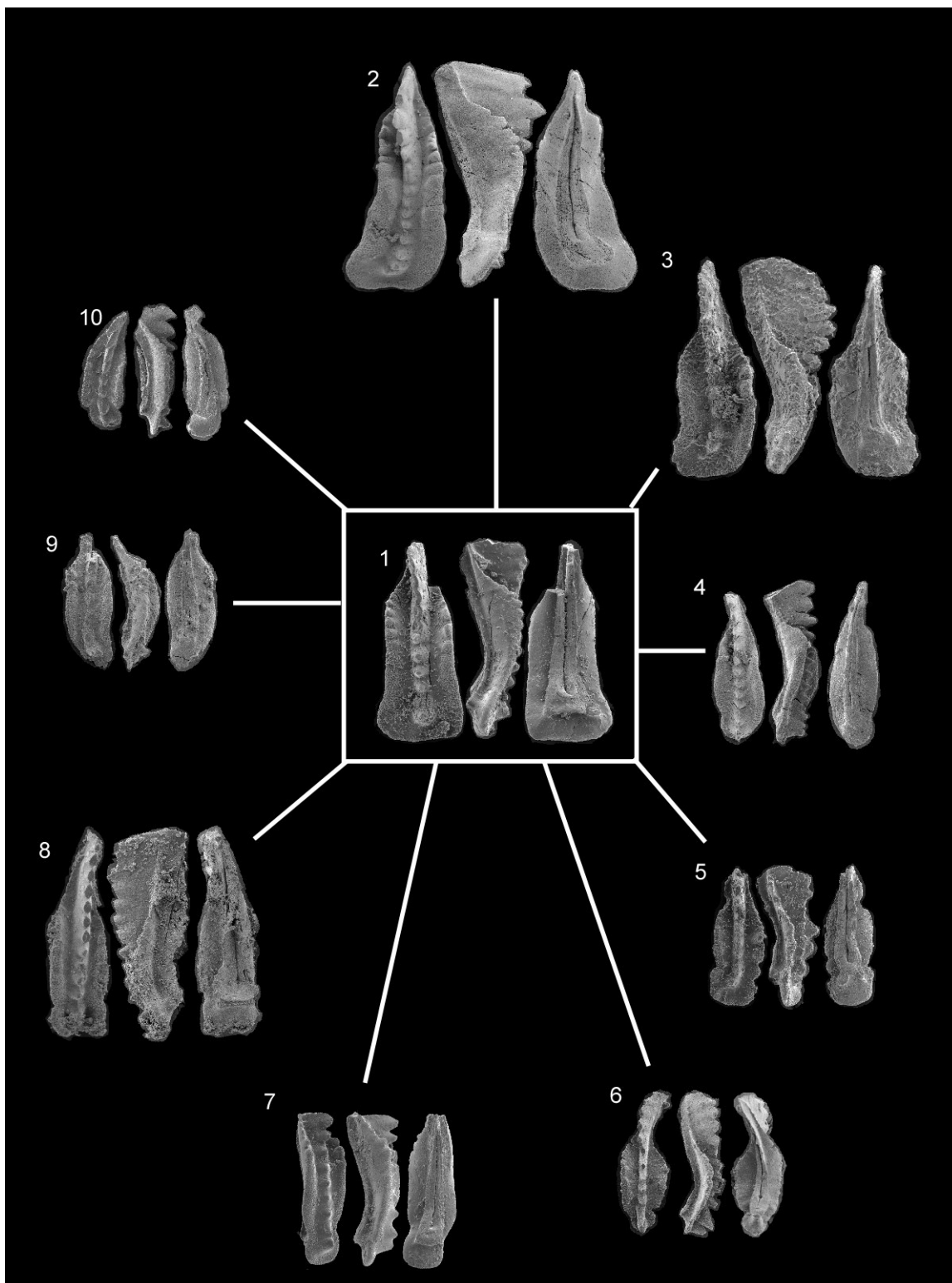


Figure 3.14: Selected elements showing the variations present within the *Metapolygnathus carpathicus* population. All elements are shown in an upper, side, and lower view at 50x magnification.

Element 1: sample HP-8, Queen Charlotte Islands (QCI). Closest in morphology to the holotype.

Element 2: sample KL2-15, Klaskino Inlet. Displays the variations of a triangular platform shape, strong anterior nodes on the platform margin, and a wide keel.

Element 3: sample SP-5, QCI. Illustrates the variations of weak anterior nodes on the platform margin and an asymmetrically developed anterior shoulder.

Element 4: sample KL2-15, Klaskino Inlet. Displays the variations of a horizontal anterior shoulder, the presence of an extra carinal node posterior of the cusp which is equal in size to the cusp, and a narrow keel.

Element 5: sample KT-A19, QCI. Displays the variation of a branched keel.

Element 6: sample KL2-15, Klaskino Inlet. Illustrates the variation of the presence of an extra carinal node posterior of the cusp which is smaller than the cusp.

Element 7: sample SP-7, QCI. Displays the variation of a narrow keel.

Element 8: sample KL2-27, Klaskino Inlet. Displays the variations of a quadrate platform shape, and denticles which are still fused lower on the posterior platform than is typical.

Element 9: sample KL2-14, Klaskino Inlet. Illustrates the variation of a rounded posterior platform shape.

Element 10: sample KL2-15, Klaskino Inlet. Displays the variation of a slowly tapering anterior platform.

a younger species, *M. n. sp. C* Orchard (2006) wherein one side of the anterior platform margin is elevated above the other anterior platform margin when viewed in profile. This element is not assigned to *M. n. sp. C* due to its longer free blade and stronger anterior nodes as compared to *M. n. sp. C*.

3) Carina and Cusp: Most specimens of the population have a line of three to five carinal nodes and a terminal cusp at the posterior end of the element. The carina consist of distinct, individual nodes that run from the blade to the posterior of the platform. The arrangement of carina and cusp can differ from the holotype by having an extra node posterior of the cusp. Element numbers 6 (Figure 3.14) and 7 (Figure 3.13) both display this extra node, which is smaller than the terminal cusp. The extra node on these specimens of *M. carpathicus* is much larger in relation to that seen in the *M. polygnathiformis* s.l. population.

Another variation that is present in the *M. carpathicus* population, but is not common, is the presence of a carinal node of equal size to the cusp immediately anterior of the cusp. This node, as illustrated by element number 4 (Figure 3.14), is equal in size to the cusp, but by comparison it is not as pronounced as the same variation in the *M. polygnathiformis* s.l. population.

The length of the fused carina that form the blade is another feature that varies from the holotype morphology. In the majority of observed *M. carpathicus* specimens, the fused denticles of the blade become distinct nodes where the platform begins to taper anteriorly. In conodont element numbers 5 and 8 (Figure 3.14) the fused denticles continue further down the platform in the posterior direction.

4) Presence of Anterior Nodes: The specimens of the *M. carpathicus* population have nodes on the anterior portion of the platform margin. These nodes can be strongly developed or quite

weak where only a hint of a node is visible. Element numbers 3 (Figure 3.11) and 2 (Figure 3.14) are good examples of well developed anterior nodes. These nodes are easily visible on the upper and profile views but only occupy the anterior third of the platform margin. Weak anterior nodes are shown by element numbers 3 (Figure 3.14) and 2 (Figure 3.13). These weakly developed nodes are rarely visible in profile and there is only a hint of nodes in the upper view. Like the well developed nodes, the weak nodes only occupy the anterior third of the platform margin.

5) Basal Pit and Keel: As in *M. polygnathiformis* s.l., the width of the keel varies from specimen to specimen. The keel width to the width of the element platform has a ratio of approximately 1:5 at its narrowest and 2:5 at its broadest. Element number 7 (Figure 3.14) shows a fairly narrow keel width, while element number 2 (Figure 3.14) shows a rather broad keel.

The keel commonly forms a rounded, semi-circular ridge around the basal pit. This semi-circular shape tends to be more common in juvenile specimens, whereas adult specimens most commonly have a more quadrate, sub-round ridge around the basal pit.

The posterior end of the keel which wraps around the basal pit can take a variety of shapes. Generally, the shape of the basal keel reflects the shape of the platform. A triangular posterior keel is observed in element numbers 2 through 4 (Figure 3.11) where the sides of the keel are extended outwards in the direction of the edges of the platform margin. This triangular shaped posterior keel is also seen in element number 2 (Figure 3.14), although in this element the keel is asymmetrically developed.

The last variation on the keel that is observed in the *M. carpathicus* population is the presence of a branched keel. Element number 7 (Figure 3.14) appears to have a keel which is forming two buds on the right and left posterior edges that could become the branches. Element

7 (Figure 3.12) is more developed and the buds on the edges of the keel are defined and branch-like. The most defined branched keel is observed in element number 5 (Figure 3.14). The branches are much longer and stretch closer to the posterior edge of the platform than any other element in the *M. carpathicus* population.

Similar to the *M. polygnathiformis* s.l. population, the *M. carpathicus* population shows variation in the position of the basal pit. In the most common specimens, the pit is located approximately 50 microns or less from the posterior edge of the keel. Elements 5 and 7 (Figure 3.13) are good examples of the most common position of the basal pit. Element numbers 2 (Figure 3.14), and 2 and 7 (Figure 3.12) are good examples of the specimens which exhibit the “*communisti* trend” where the basal pit is located more than 50 microns from the posterior edge of the keel. This phenomenon is not a common occurrence but neither is it rare.

Metapolygnathus carpathicus morphotype “A”

(Figure 3.12, elements 1, 2; Figure 3.13, elements 1, 2, 3, 4)

Material: 4 complete specimens and 2 incomplete specimens contributed to this description.

Description: *Metapolygnathus carpathicus* morphotype with a varying number of small nodes situated mostly on the anterior platform margin. The free blade is relatively short when compared to the length of the platform and comprises only one-third or less of the total length of the element. The posterior end of the platform is sub-round and all specimens demonstrate the “*communisti* trend” with regard to the location of the basal pit.

Discussion: This morphotype is placed in the *M. carpathicus* species group because of anterior platform nodes and the uniform level of the platform margin profile in side view. The “*communisti* trend” distinguishes this morphotype from morphotype “B.” It is differentiated from morphotype “C” by its sub-round posterior platform end.

Occurrence and Age: Found from KL-2-15, 2-17, 2-18, and 2-20 in the Quatsino limestone. Late Carnian, lower to middle *nodosus* zone (Welleri Zone 1 and possibly Welleri Zone 2).

Metapolygnathus carpathicus morphotype "B"

(Figure 3.12, elements 4, 5, 6; Figure 3.13, elements 5, 6, 7, 8, 9)

Material: 7 complete specimens and 8 incomplete specimens contributed to this description.

Description: *Metapolygnathus carpathicus* morphotype with similar characteristics to *M. polygnathiformis* s.l. morphotype "A." Juvenile specimens have a posterior constriction, while adult specimens have a sub-round to triangular posterior margin. *Metapolygnathus carpathicus* morphotype "B" has a rounded posterior cusp and small anterior nodes on the platform margin.

Discussion: This morphotype is distinguished from *M. carpathicus* morphotype "A" by its posteriorly positioned basal pit, which is common to the more primitive metapolygnathids.

Morphotype "C" is differentiated from "B" by its highly rounded posterior end. This morphotype is comparable to *M. polygnathiformis* s.l. morphotype "A," but it is differentiated by the presence of small, moderately developed nodes on the anterior margin of the platform.

Occurrence and Age: Found from KL-2-9, 2-11, 2-12, 2-15, 2-17 – 2-22, 2-25 – 2-27, with a questionable occurrence at 2-26, in the Quatsino limestone. Late Carnian, lower to middle *nodosus* zone (Welleri Zone 1 and possibly Welleri Zone 2).

Metapolygnathus carpathicus morphotype "C"

(Figure 3.12, element 7; Figure 3.14, elements 4, 9)

Material: 4 incomplete specimens were contributed to this description.

Description: *Metapolygnathus carpathicus* morphotype with a highly rounded posterior end of the platform. The strength of the anterior platform nodes varies from being weakly to strongly exhibited. This morphotype also displays the "*communisti* trend."

Discussion: This morphotype varies from the others by having a highly rounded posterior platform end. It is differentiated from morphotype "B" by displaying the "*communisti* trend."

Occurrence and Age: Found in the QCI at Houston Point and Houston Inlet South and at Klaskino Inlet, KL2-14 and KL2-15. Late Carnian, lower *nodosus* zone (Welleri Zone 1).

3.3.4 *Metapolygnathus nodosus* Population

Metapolygnathus nodosus (Hayashi, 1968)

1968a *Gladigondolella abneptis nodosa* n. subsp. – HAYASHI (a,b), p. 69, Pl. 2, figs. 9a-c.

1991a *Metapolygnathus nodosus* (HAYASHI) – ORCHARD, p. 176, Pl. 2, figs. 8-13; Pl. 3, fig. A.

Diagnosis of *Metapolygnathus nodosus*

The holotype of *Metapolygnathus nodosus* was described from a collection from Japan (Hayashi, 1968a). *Metapolygnathus nodosus* is a metapolygnathid with a quadrate to triangular platform, free blade about one-half the length of the platform, and anterior nodes on the platform margin which are conspicuous in both upper and lateral views. This species also shows a bi-leveled platform margin when viewed in profile.

Description of *Metapolygnathus nodosus* holotype morphology

The holotype of *Metapolygnathus nodosus* (Hayashi, 1968a) has a squat, triangular shape and a small free blade and is characterized by a bi-leveled platform margin. The term “bi-leveled” refers to the platform margin being relatively more elevated in the anterior region of the platform than it is at the posterior end of the element in profile view.

Metapolygnathus nodosus has a row of five carinal nodes on the central platform which run posteriorly from the free blade to a single terminal cusp and are sub-equal in size. The cusp

of the holotype is not larger than any of the carinal nodes. The holotype of *M. nodosus* appears to have four to five anterior nodes which are visible in profile.

The keel is similar to the other specimens of *Metapolygnathus*. It runs from the tip of the blade posterior to the basal pit and mirrors the platform morphology with a squat shape. The keel on the illustration of the holotype specimen is difficult to see, but it appears that the ratio of the width of the keel to the width of the element is approximately 1:2.

Comparison of *Metapolygnathus nodosus* to Other Species

Metapolygnathus nodosus is distinct from *M. polygnathiformis* s.l. in its bi-leveled platform margin with anterior nodes present. While the holotype of *M. nodosus* does not have a very long free blade, the specimens in the collections from British Columbia do have a longer free blade. This longer free blade of the British Columbia specimens further separates *M. nodosus* from *M. polygnathiformis* s.l.. The species which is most comparable to *M. nodosus* in this study is *M. carpathicus*. Because *M. nodosus* evolved from *M. carpathicus*, there are often intermediate forms which are difficult to classify. Typically, *M. nodosus* is distinguished from *M. carpathicus* by its bi-leveled platform, anterior nodes which cover up to one-half of the platform margin, and its much longer free blade.

Variation in the *Metapolygnathus nodosus* Population

1) Platform Shape: In the specimens studied from the Queen Charlotte Islands, *M. nodosus* most commonly has a more elongate, quadrate shaped platform than the holotype with a sub-rounded posterior end. Examples of *M. nodosus* from Klaskino Inlet tend to be smaller than those found in the Queen Charlotte Islands and northeastern British Columbia and, therefore, are interpreted to be mostly juvenile elements.

At Klaskino Inlet, the platform shape tends to be more irregular and rounded than the typical quadrate shape of specimens found elsewhere, as illustrated by element numbers 1-4 (Figure 3.15). The free blade is often not preserved, which greatly hinders the understanding of many of the Klaskino Inlet elements.

In element numbers 3 (Figure 3.16) and 6 (Figure 3.17) the width of the platform is almost constant along its length producing a quadrate shape. A triangular variation on the quadrate shape is seen in element numbers 2 and 5 (Figure 3.16). The posterior end of these elements is still quadrate but the overall shape of the platform is triangular. The free blade is preserved well enough on element number 2 (Figure 3.16) to illustrate the relative length of the free blade to the platform. In typical *M. nodosus* elements, the length of the free blade is approximately one-half of the total length of the element. A highly rounded posterior end of the platform is another variation that is seen in element number 4 (Figure 3.16) of the *M. nodosus* population. Element numbers 1 (Figure 3.15) and 7 (Figure 3.16) illustrate the posterior constriction of the platform which is common of juvenile elements of *M. nodosus*.

2) Lateral Profile of the Platform Margin: The major variations in platform margin shape of the *M. nodosus* population occur on the anterior margin. Element numbers 2, 3 (Figure 3.16) and 8 (Figure 3.17) for example, all have an anterior margin that steeply slopes creating a distinct shoulder and often a long free blade. In contrast, element numbers 5, 6 (Figure 3.16), and 5 (Figure 3.17) all have slowly tapering anterior margins, which manifests as a gentle curve towards the free blade. The characteristic bi-leveled margin of *M. nodosus* is best illustrated by element number 3 (Figure 3.16). An extreme example of this quality is observed in element number 4 (Figure 3.16).

Figure 3.15 Growth Series of *Metapolygnathus nodosus*

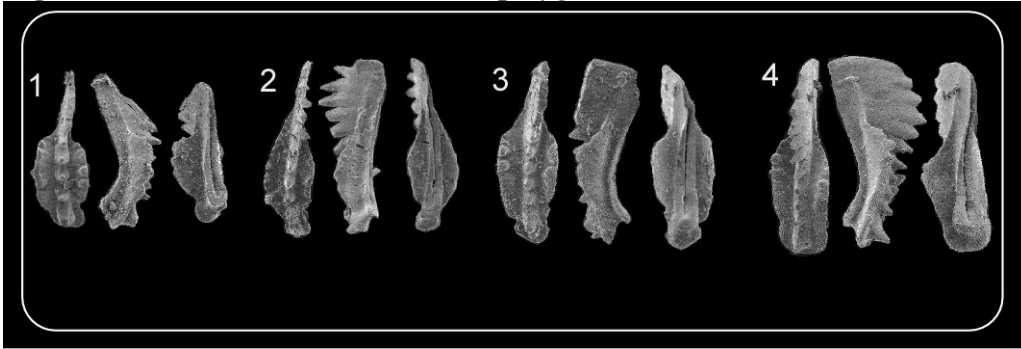


Figure 3.15: There are no specimens that closely resemble the holotype, so only the growth series commonly found from Klaskino Inlet is presented. All elements are shown in an upper, side, and lower view at 50x magnification.

Element 1: sample KL2-17.

Element 2: sample KL2-23.

Element 3: sample KL2-23.

Element 4: sample KL2-17.

Figure 3.16 Population of *Metapolygnathus nodosus*

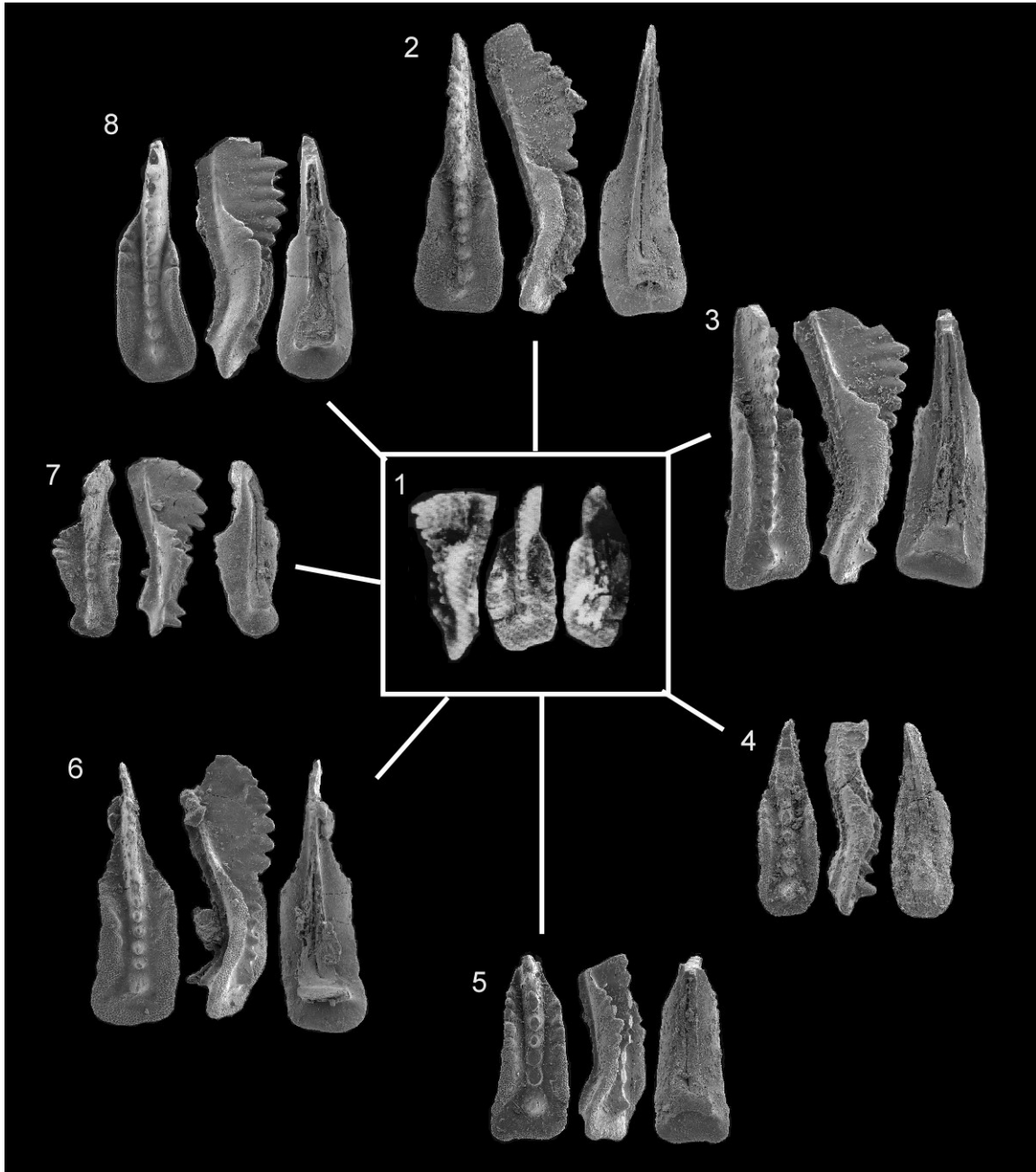


Figure 3.16: Illustrates the various morphologies present within the species population of *Metapolygnathus nodosus*. There are no specimens that closely resemble the holotype, so the holotype of *M. nodosus* is shown in the central box. All elements are shown in three views: upper, side, and lower. All images are 50x magnification.

Element 1: Metapolygnathus nodosus holotype (Hayashi, 1968a), p. 69, Pl. 2, figs 9a-c, Adoyama Formation, Japan.

Element 2: sample HP-8, Queen Charlotte Islands (QCI). Displays the variations of a triangular platform shape, a steeply sloped anterior shoulder, and the presence of an extra carinal node posterior to the cusp which is smaller than the cusp.

Element 3: sample HP-8, QCI. Illustrates the variations of a quadrate platform shape, and a branched keel.

Element 4: sample KL2-19, Klaskino Inlet. Displays the variation of a rounded posterior platform.

Element 5: sample HP-8, QCI. Displays the variation of strong anterior nodes on the platform margin.

Element 6: sample BI-4D, QCI. Illustrates the variations of weak anterior nodes on the platform margin, and a tapering anterior shoulder.

Element 7: sample KL2-18, Klaskino Inlet. Displays the variation of the presence of an extra carinal node posterior to the cusp which is equal in size to the cusp.

Element 8: sample SP-7, QCI. Illustrates a weakly bi-leveled platform and a posterior keel with potential buds forming.

Figure 3.17 *Metapolygnathus*, *Carniepigondolella*, and *Ichthyolith* Illustrations

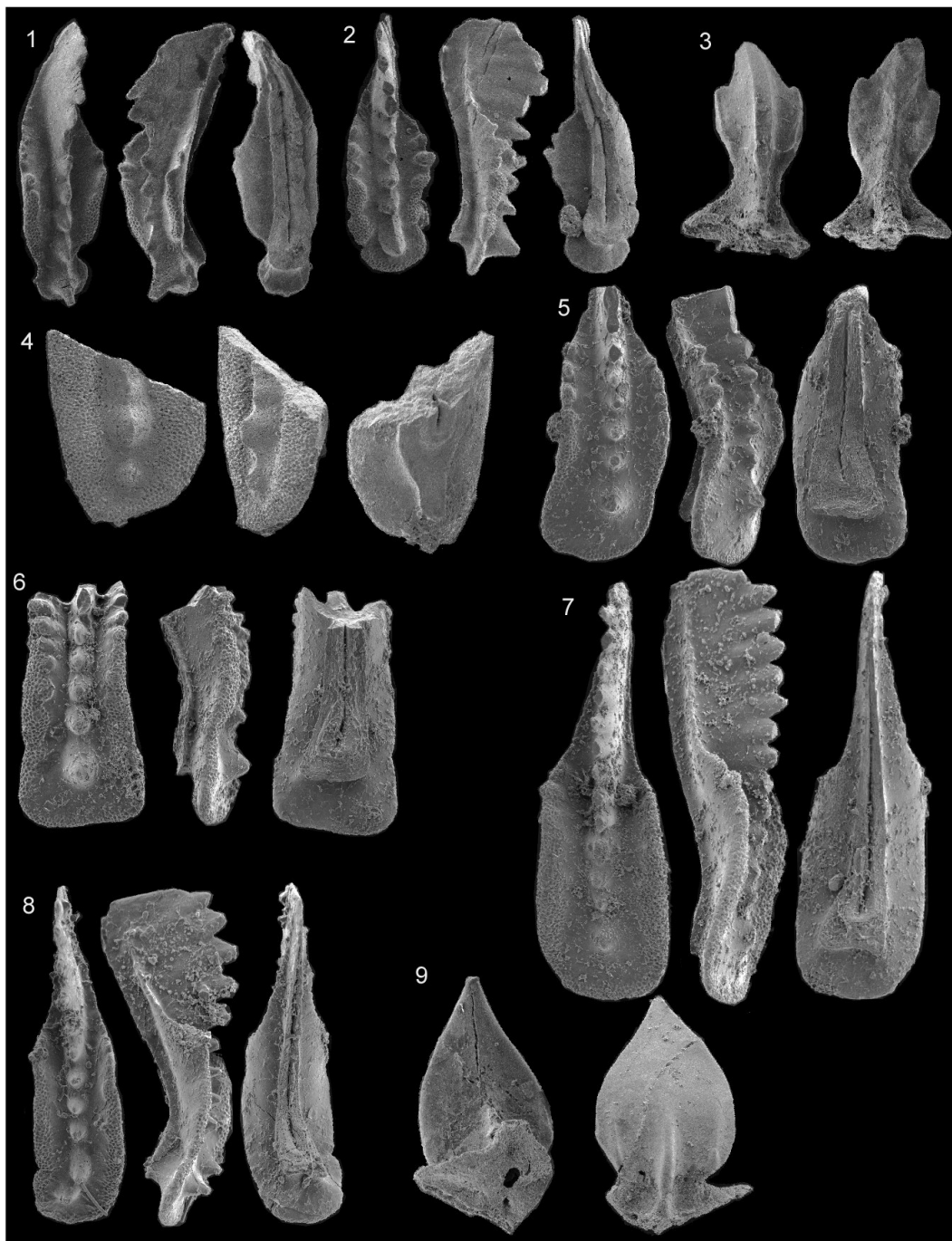


Figure 3.17: Illustrations of *Metapolygnathus nodosus*, *Metapolygnathus* aff. *M. communisti*, *Carniepigondolella zoeae*, and various ichthyoliths. Conodont elements are presented in upper, side, and lower views when possible. Ichthyoliths are presented in upper and lower views only. All images are at 95x magnification.

Element 1 – Carniepigondolella aff. *C. zoeae* (Orchard). This specimen has bulbous nodes like *C. zoeae*, but the tapering anterior platform and posterior constriction more resemble *M. lindae*. This specimen varies from *M. nodosus* due to its short free blade and lack of a bi-leveled platform margin. This specimen is assigned to *C. aff. C. zoeae* due to its bulbous nodes and appearance as an intermediate form between *M. lindae* and *C. zoeae*. Sample KL2-20, Klaskino Inlet.

Element 2 – Carniepigondolella aff. *C. zoeae* (Orchard). Sample KL2-20, Klaskino Inlet.

Specimen 3 – Gracilisuggestus triapices ? Johns, *et al.*. Sample KL2-21, Klaskino Inlet.

Element 4 – Metapolygnathus aff. *M. communisti* Hayashi. Due to the fact that this specimen is incomplete, this assignment to *M. aff. M. communisti* was made based on the anteriorly shifted pit and branched keel. Sample KL2-14, Klaskino Inlet.

Element 5 – Metapolygnathus nodosus morphotype B (Hayashi). Sample SHU-3, Queen Charlotte Islands (QCI).

Element 6 – Metapolygnathus nodosus morphotype B (Hayashi). Sample HP-8, QCI.

Element 7 – Metapolygnathus nodosus (Hayashi). Sample HP-8, QCI.

Element 8 – Metapolygnathus nodosus morphotype A (Hayashi). Sample KT-A19, QCI.

Specimen 9 – Labrilancea glabrisubcuspis ? Johns, *et al.*. Sample KL2-21, Klaskino Inlet.

3) Carina and Cusp: The *M. nodosus* population has variations on the carinal nodes and cusp similar to those variations seen in the other conodont populations discussed; however, fewer specimens of *M. nodosus* exhibit these variations. The most common variation observed in this population is the addition of an extra carinal node posterior of the terminal cusp, as in element numbers 2 (Figure 3.16) and 8 (Figure 3.17). Element number 7 (Figure 3.16) has an equal sized node just anterior to the cusp, thus illustrating another variation. Two specimens of *M. nodosus* from the Queen Charlotte Islands, which are not illustrated, have fused carinal nodes on the platform instead of the more common discrete nodes. In juvenile specimens (e.g., element number 4 [Figure 3.15]) the cusp tends to be more pointed and tooth-like than adult specimens (e.g., element number 3 [Figure 3.16]) where the cusp is slightly more rounded.

4) Presence of Anterior Nodes: This species has a varying degree of anterior node development along its platform margin. Commonly this species has four nodes on the anterior margin but, some specimens have one to two anterior nodes (e.g. element 7 [Figure 3.17]), and others have five nodes along up to half of the anterior platform (e.g. element number 7 [Figure 3.16]). When the nodes are present and have good relief, they can be seen along the platform margin in side view. The nodes appear to give the platform margin a serrated edge, as is illustrated in element numbers 5 and 7 (Figure 3.16). When the nodes are not as well developed, the platform margin appears bumpy in profile, as in element number 6 (Figure 3.16).

5) Basal Pit and Keel: In juvenile specimens the posterior keel most often curves around the basal pit in a semi-circle, which is illustrated in element numbers 1 through 3 (Figure 3.15). In adult specimens, the keel is often a more quadrate, sub-round shape as it wraps around the basal pit. This shape is illustrated in element numbers 6 (Figure 3.16) and 5 (Figure 3.17). The variation of the branching keel is seen again in this species, with element numbers 5, 3, 2 (Figure

3.16), and 7 (Figure 3.17) all illustrating the beginning of the formation of a branching keel. The ratio of the width of the keel to the width of the element ranges from 1:3 to 1:2.

There does appear to be a certain degree of the "*communisti* trend" observed in this population. Elements 2 and 3 (Figure 3.16) are good examples of the basal pit at a distance of more than 50 microns from the posterior keel. Elements 4 and 7 (Figure 3.16) are specimens that do not display the "*communisti* trend." Unlike the *M. polygnathiformis* s.l. and *M. carpathicus* populations, in this collection of *M. nodosus* the smaller adults do not show the "*communisti* trend" as frequently as the larger adults do. In the other species populations both small and larger adults showed the trend.

Metapolygnathus nodosus morphotype A

(Figure 3.17, element 8; Figure 3.18, elements 5, 6, 7, 8, 10)

Material: 7 complete specimens and 2 incomplete specimens contributed to this description.

Description: *Metapolygnathus nodosus* morphotype that is primarily distinguished by not displaying the "*communisti* trend." Platform shape varies from being irregular (Figure 3.18, element 8) to regular and straight (Figure 3.18, element 10). This morphotype appears to be lacking larger platform elements, as all the examples of the morphotype in this collection are juveniles or small sized adults.

Discussion: The presence of nodes that do not continue all the way to the posterior end and that make the platform margin irregular makes *M. nodosus* an appropriate assignment for these specimens. The platform margin also exhibits a bi-leveled quality, characteristic of *M. nodosus*. This morphotype is differentiated from morphotype "B" in that it does not display the "*communisti* trend."

Figure 3.18 *Metapolygnathus* Species Illustrations

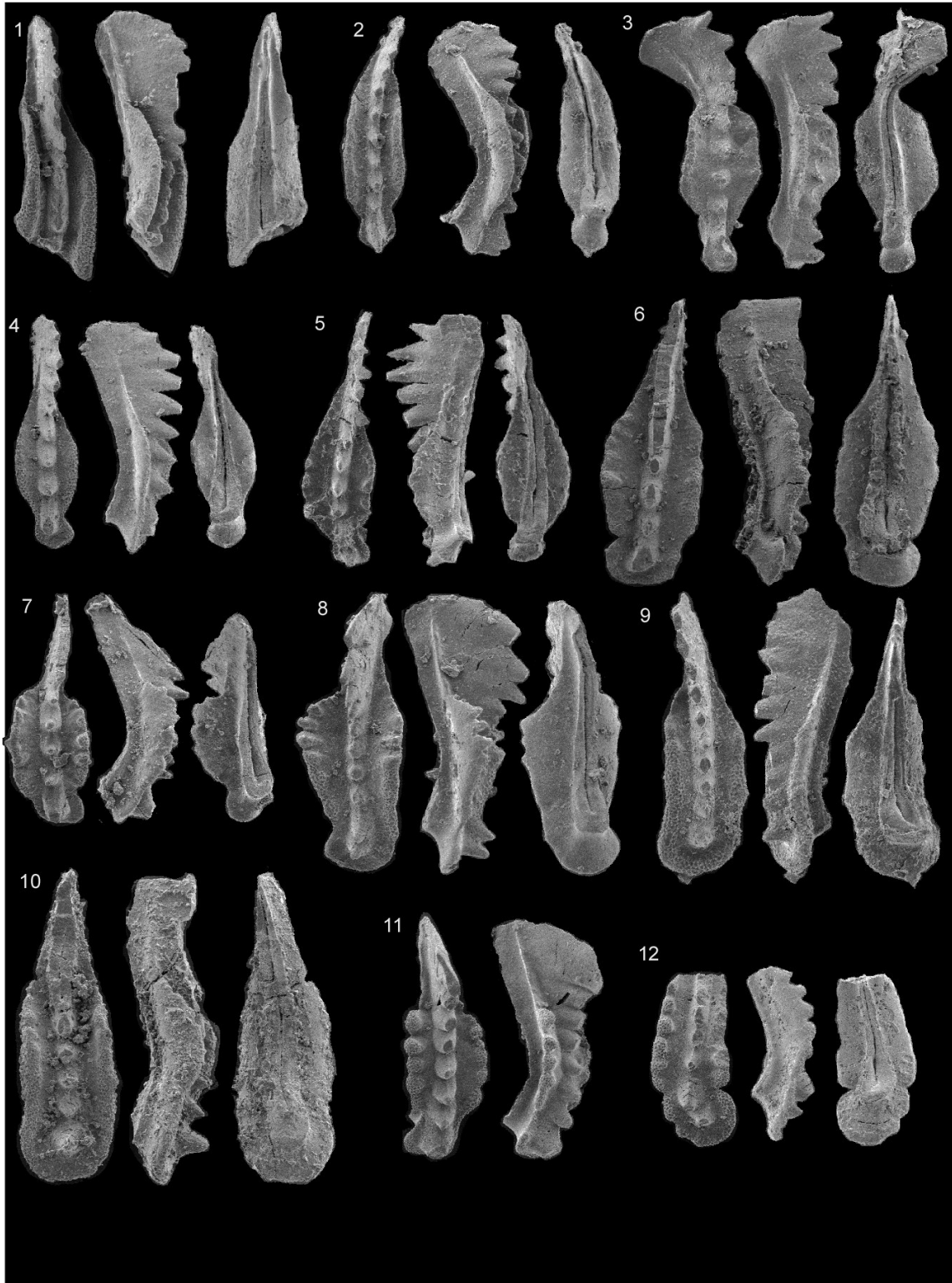


Figure 3.18: Illustrations of *Metapolygnathus lindae*, *M. nodosus*, *M. aff. M. nodosus*, *Carniepigondolella* ex. gr. *C. zoeae*, and *Carniepigondolella* aff. *C. zoeae*. All elements are presented in an upper, side, and lower view when possible. All elements are at 95x magnification.

Element 1: Metapolygnathus lindae Orchard. This specimen is missing the posterior end of the platform, so it is impossible to know if the specimen has the posterior constriction characteristic of *M. lindae*. It is assigned to *M. lindae* due to the narrow and slowly tapering anterior platform. Sample KL2-14, Klaskino Inlet.

Element 2: Metapolygnathus lindae Orchard. Sample KL2-15, Klaskino Inlet.

Element 3: Metapolygnathus lindae Orchard. Note distorted blade. Sample KL2-15, Klaskino Inlet.

Element 4: Metapolygnathus lindae Orchard. Sample KL2-17, Klaskino Inlet.

Element 5: Metapolygnathus nodosus (Hayashi). Sample KL2-23, Klaskino Inlet.

Element 6: Metapolygnathus nodosus (Hayashi). Sample KL2-18, Klaskino Inlet.

Element 7: Metapolygnathus nodosus (Hayashi). Sample KL2-17, Klaskino Inlet.

Element 8: Metapolygnathus nodosus (Hayashi). Assigned to *M. nodosus* due to its well defined nodes and slight bi-leveled margin, although the free blade is slightly short for a specimen of *M. nodosus*. Sample KL2-18, Klaskino Inlet.

Element 9: Metapolygnathus aff. M. nodosus (Hayashi). Assigned to *M. aff. M. nodosus* due to its long free blade and slight bi-leveled margin. Very weak anterior nodes differentiate this specimen from *M. nodosus*. Sample KL2-27, Klaskino Inlet.

Element 10: Metapolygnathus nodosus (Hayashi). This specimen displays a strongly bi-leveled margin, characteristic of *M. nodosus*, as well as weak anterior nodes. Sample KL2-19, Klaskino Inlet.

Element 11: Carniepigondolella ex gr. *C. zoeae* (Orchard). Sample KL2-20, Klaskino Inlet.

Element 12: Carniepigondolella aff. *C. zoeae* (Orchard). Sample KL2-18, Klaskino Inlet.

Occurrence and Age: Found from KL-2-17 – 2-19, 2-23 in the Quatsino limestone; and Kunghit Island - west, QCI. Late Carnian, lower to middle *nodosus* zone (Welleri Zone1, and possibly Welleri Zone 2).

Metapolygnathus nodosus morphotype "B"

(Figure 3.17, elements 5, 6, 8; Figure 3.16, elements 2, 3, 5, 6)

Material: 3 complete specimens and 4 incomplete specimens contributed to this description.

Description: *Metapolygnathus nodosus* morphotype which exhibits the presence of strong to weak anterior nodes and a distinctive bi-level platform margin. These characteristics provide the basis for assigning these specimens to the *M. nodosus* population. The free blade is often a length of one-half the total length of the platform. Platform shape can vary from quadrate to sub-round. These specimens are grouped together because they all display the "*communisti* trend."

Discussion: This morphotype is distinguished from morphotype "A" by exhibiting the "*communisti* trend." Morphotype "B" is differentiated from a similar species *M. carpathicus* by its bi-leveled margin profile and often its longer free blade.

Occurrence and Age: Found at Houston Point, Burnaby Island, Houston Inlet South, QCI. Late Carnian.

Metapolygnathus aff. *M. nodosus* (Hayashi, 1968a)

(Figure 3.18, element 9)

Material: 1 incomplete specimen has contributed to this description.

Description: *Metapolygnathus* with a rounded posterior end. The platform margin is not smooth in regards to both the margin's curvature and slightly nodose nature. Nodes occur on the anterior platform margin and weaker nodes, like slight swellings, occur in a more central position on the

platform margin. The free blade appears to be nearly one-half the total length of the platform with at least 6 denticles. Basal keel and pit are well developed in a loop shape and are in a posterior position on the platform.

Discussion: This species appears to be an intermediate between *Metapolygnathus carpathicus* and *M. nodosus*. The length of the free blade as well as the weakly bi-leveled posterior margin makes this species comparable to *M. nodosus* and is the reason the specimen is assigned here to *M. aff. M. nodosus*. The strength and position of the nodes on the platform margin draws comparison to *M. carpathicus*. Overall, this specimen is more similar to *M. nodosus* than *M. carpathicus*.

Occurrence and Age: Found only in KL-2-27 from the Quatsino limestone. Late Carnian, middle nodosus zone (Welleri Zone 1 or possibly Welleri Zone 2).

3.3.5 Systematic Descriptions of Less Common Species

Metapolygnathus aff. *M. communisti* Hayashi

1968a *Metapolygnathus communisti* gen. et sp. nov. – HAYASHI (a,b), p. 72, Pl. 3, fig. 11a-c.

(Figure 3.17, element 4)

Material: 1 incomplete specimen contributed to this description.

Description: *Metapolygnathus* with rounded posterior end. The basal pit exhibits the “*communisti* trend.” This is the only conodont specimen recovered to have a posteriorly elongated and pointed basal keel.

Discussion: This specimen is assigned to *M. aff. M. communisti* because of the relatively anterior position of the basal pit relative to the end of the keel. There is uncertainty as to where the basal pit is in relation to the anterior tip of the element because the blade is missing. This element differs from the holotype of *M. communisti* by having a more rounded posterior end and a pit that is not as far to the anterior. Both the illustrated specimen and the holotype exhibit keels

that have digitate extensions; however, the holotype has a branched keel with two digitate extensions and the illustrated specimen has one single extension.

Occurrence and Age: Found only at KL-2-14 from the Quatsino limestone. Late Carnian, lower *nodosus* zone (Welleri Zone 1).

Metapolygnathus lindae Orchard, 1991c

1991a *Metapolygnathus* n. sp. E – ORCHARD, p. 176, Pl. 1, figs. 1-6.

1991c *Metapolygnathus lindae* – ORCHARD, p. 316, Pl. 1, figs. 1-3.

(Figure 3.18, elements 1, 2, 3, 4)

Material: 4 complete specimens and 3 incomplete specimens contributed to this description.

Description: The holotype of *M. lindae* is elongate with an anteriorly tapering platform and no anterior platform margin nodes. The anterior tapering of the platform usually ends just short of the anterior end of the blade. There is a posterior constriction which remains present into adulthood that is characteristic of the species. The blade consists of 6 denticles which develop into discrete carinal nodes on the posterior platform. The cusp is slightly larger than the preceding carina, and opposite the cusp is posterior basal pit with a looped basal keel. Element 4 (Figure 3.18) of the Klaskino material is the most similar to the holotype.

Discussion: These specimens are assigned to *M. lindae* based on the elongate and anteriorly tapering platform in the upper view, and the posterior constriction observed in many of the specimens. These specimens differ from juvenile specimens of *M. polygnathiformis* s.l. with a posterior constriction in that specimens of *M. lindae* have a more narrow and elongate platform. They are different from the holotype because elements 3 and 4 (Figure 3.18) have a platform that does not taper all the way to the anterior tip of the blade. Compared to the holotype, these specimens also tend to have a wider platform.

Occurrence and Age: Found from KL-2-9, 2-14, 2-15, 2-17, and 2-18 in the Quatsino limestone.

Late Carnian, lower to middle *nodosus* zone (Welleri Zone 1).

Genus *Carniepigondolella* Kozur, 2003

Carniepigondolella ex gr. *C. zoeae* (Orchard 1991c)

(Figure 3.18, element 11)

1991a *Metapolygnathus* n. sp. *F* – ORCHARD, p. 176, Pl. 1, figs. 7-11; Pl. 3, fig. B.

1991c *Metapolygnathus zoeae* – ORCHARD, p. 319, Pl. 1, figs. 7-9.

Material: 1 complete specimen and 1 incomplete specimen contributed to this description.

Description: *Carniepigondolella* with very well developed, sometimes bulbous nodes that run along the entire margin of the platform. These marginal nodes are visible in profile view and cause an irregular marginal outline. Three of four specimens have a small posterior constriction and a large posterior cusp. The pits in these specimens are posterior in position, unlike the more medial pit position of the holotype.

Discussion: *Carniepigondolella* ex gr. *C. zoeae* closely resembles *M. nodosus*, as both have well developed nodes that line the platform margin and similar irregular margins in profile due to these nodes; however, *C. ex gr. C. zoeae* differs from *M. nodosus* in having more developed nodes that often run along the entire platform. The nodes on *C. ex gr. C. zoeae* also tend to be more bulbous-looking than in *M. nodosus*.

Occurrence and Age: Found in KL-2-20, and 2-25 in the Quatsino limestone. Late Carnian, middle *nodosus* zone (Welleri Zone 1 and possibly Welleri Zone 2).

Carniepigondolella aff. *C. zoeae* (Orchard, 1991c)

(Figure 3.17, elements 1, 2; Figure 3.18, element 12)

Material: 2 complete specimens and 1 incomplete specimen have contributed to this description.

Description: An elongate *Carniepigondolella* whose platform slowly tapers anteriorly, stopping just short of the anterior tip of the blade. Nodes are present along the anterior margins of the platform, but vary in intensity from weak to moderately strong. In profile, the nodes often produce spiky protrusions. The free blade is somewhat deformed in one specimen (element 1 [Figure 3.17]) but appears to be just under one-half the total length of the platform. The basal pit is in a posterior position on the platform. Both specimens illustrate a posterior constriction, although one specimen (element 1 [Figure 3.17]) has a more pronounced constriction than the other (Element 2 [Figure 3.17]).

Discussion: This species of *Carniepigondolella* shares characteristics of *C. zoeae*, *Metapolygnathus lindae* and *C. samueli* (Orchard, 1991c). Both *M. lindae* and *C. samueli* have elongate platforms that taper towards the blade. Like *C. samueli*, *C. aff. C. zoeae* has distinct, separated nodes along the platform margin. These specimens may be a transitional form between *C. zoeae* and *C. samueli*, however, they are assigned here to *C. aff. C. zoeae* because of the weaker strength and more rounded appearance of the marginal nodes than is observed in *C. samueli*. These specimens differ from *M. nodosus* by having more bulbous nodes, and no bi-leveled platform margin.

Occurrence and Age: Found at locality KL2-18 and KL2-20 from the Quatsino limestone. Late Carnian, middle *nodosus* zone (Welleri Zone 1 or possibly Welleri Zone 2).

3.4 Conclusions

There is considerable intraspecific variation within elements presently grouped as *Metapolygnathus polygnathiformis*, *M. carpathicus*, and *M. nodosus*. These variations are

observed in the characteristics of platform shape, lateral profile of the platform margin, carinal nodes and cusp, anterior nodes, and the basal pit and keel.

At present, *Metapolygnathus polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* are differentiated primarily on the basis of platform margin shape, the presence of anterior nodes, and to a lesser extent the character of the free or fixed blade.

These three species form an evolutionary lineage and show morphological change through time. It is apparent that some of the species population variations are shared between the species discussed herein. A summary of the variations present in the three species is detailed in Table 3.1. All species populations share the variations of extra carinal nodes, closely spaced carinal nodes, and fused nodes. They also have in common the variations of quadrate, rounded, and triangular platform shapes, and steeply sloped or tapering anterior margins, as well as the "*communisti* trend." Given that all three species share the "*communisti* trend," I think that they are related to *M. communisti*.

Metapolygnathus polygnathiformis and *M. carpathicus* share the most variations in common including the downturned anterior platform margin, and the inturning of the posterior platform. *Metapolygnathus carpathicus* also shows similarities in variations with *M. nodosus* including the branching keel and several platform shapes.

Species of *Metapolygnathus* described here are justifiably included within this genus. *Metapolygnathus polygnathiformis*, *M. carpathicus*, *M. nodosus*, and *M. lindae* all exhibit the characteristics of the genus: micro-reticulation on the upper platform, a longer than wide platform, and a basal keel with a loop-like structure. Despite the common variability between the three species populations, I do not think it is advisable at present to include these variations in the genus description for *Metapolygnathus*. Only three species of *Metapolygnathus* have been looked at in depth in this study and it is not known if the other species of *Metapolygnathus* share these variations or not. Secondly, the variations are not always present in the specimens

collected so they would not be appropriate additions to a genus definition. These variations would, however, be appropriate for inclusion into a species level description. Conodont workers should be aware of these variations to reduce species confusion in *Metapolygnathus*.

Based on this study, the criteria used to distinguish the species of *Metapolygnathus* appear to be sound. All the elements described here show the basic characteristics of their species, but they also show other variations in morphology. These variations should be included with the species descriptions but should not be weighed more heavily than the characteristics currently used for species definition.

The *Metapolygnathus* species described in this chapter are often misunderstood and placed in other genera. In this chapter I have described the conodonts found at Klaskino Inlet as well as at the Queen Charlotte Islands and northeastern British Columbia in order to establish a clearer understanding of the morphotypes of *Metapolygnathus*. Although no new biostratigraphic information is immediately clear from this thesis, the enhanced definition of three key species of *Metapolygnathus* will hopefully aid future Upper Carnian biostratigraphic works.

Table 3.1 Variations Present in *Metapolygnathus* Species Populations

	<i>M. polygnathiformis</i> s.l.	<i>M. carpathicus</i>	<i>M. nodosus</i>
Characteristics			
Platform			
quadrate platform	x	x	x
triangular platform	x	x	x
elongate platform	x		
rounded platform	x	x	x
marked inturning of posterior platform	x	x	
Profile			
steeply sloping anterior shoulder	x	x	x
tapering anterior towards blade	x	x	x
asymmetrical anterior shoulder		x	
bi-leveled platform profile			x
Carina/Cusp			
widely spaced carinal nodes	x		
closely spaced carinal nodes	x	x	x
fused carinal nodes	x	x	x
extra node posterior to cusp, equal in size to cusp	x	x	x
extra node posterior to cusp, smaller than cusp	x	x	x
Anterior Nodes			
absent	x		
present but weak strength, visible in upper view		x	x
present and strong, visible in upper view		x	x
present but weak strength, visible in profile view			x
present and strong, visible in profile view		x	x
Pit/Keel			
wide width keel	x	x	x
narrow width keel	x	x	x
quadrate keel	x		
triangular keel		x	
branched keel		x	x
" <i>communisiti</i> trend" present	x	x	x

Table 3.1: Displays the presence of the variations discussed in the text for the *Metapolygnathus polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* populations. An "x" indicates the presence of a characteristic.

Chapter 4: Paleobiogeography

4.1 Purpose

Paleobiogeography, given suitable faunal distribution, can help constrain the paleolatitude and hemispheric position of a terrane relative to the continent. Whereas paleomagnetic data have provided the prime constraint upon the paleolatitudinal positions of terranes relative to the craton in the geologic past, the technique cannot determine if a terrane was located in the northern or southern hemisphere due to potential terrane rotation and the symmetrical nature of Earth's magnetic field. This ambiguity makes paleobiogeography an important tool for understanding past tectonic movement because endemism and diversity correlate with latitude, and southern and northern faunas are usually distinct from each other and from the tropical faunas of the lower latitudes.

The position of the allochthonous terranes which make up western North America, including Wrangellia, is still a matter for debate. In addition to paleobiogeography, paleomagnetic techniques have been used on several Mesozoic rock formations making up Wrangellia (Yole and Irving, 1980; Ward *et al.*, 1997) to try and ascertain the terrane's past movements. Yole and Irving (1980) interpret Wrangellia's position during the Late Carnian to be at 18 degrees South latitude based on their paleomagnetic data from the Karmutsen Formation (Figure 4.1). However Trop *et al.* (2002) reasoned that the terrane was more likely at a northern latitude of around 12 degrees based on their sedimentologic and geochronologic data.

Smith (2006) uses the paleobiogeographic patterns of ammonoids and bivalves from the Early Jurassic to show the increasing linkage of the allochthonous terranes Quesnellia, Stikinia, and Wrangellia to the North American craton over time. This increased similarity is also complemented by a decreased similarity to ammonoids and bivalves on the South American craton. Smith (2006) places Wrangellia at a paleolatitude of around 30 degrees North in the Early Jurassic and demonstrates the ability of paleobiogeography to constrain the hemispheric

Figure 4.1 Hypothesized Locations of Wrangellia in the Late Triassic

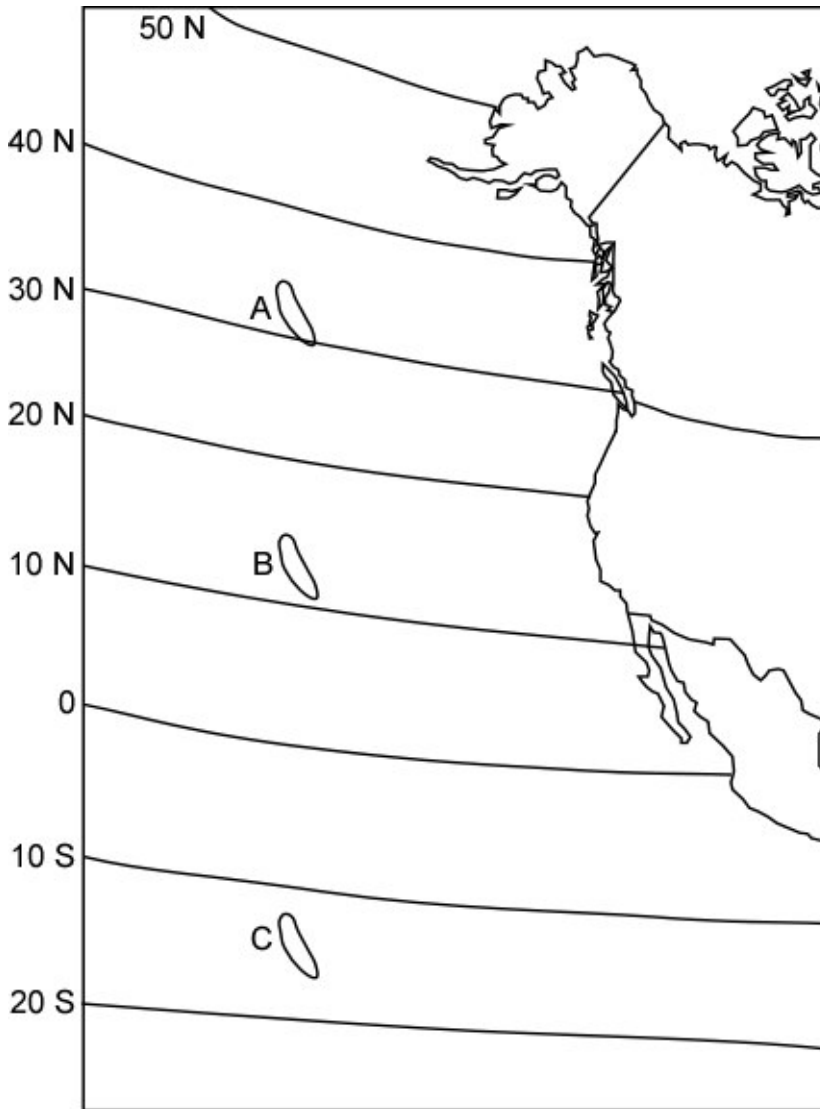


Figure 4.1: Various possible positions for Wrangellia in the Late Triassic in relation to the modern day craton. Paleolatitude lines in relation to the craton are based on paleomagnetic data from Yole and Irving (1980). Locations of Wrangellia are approximate. No longitudinal scale is intended. Wrangellia is not to scale.

A) Based on the ammonoid similarities presented in this thesis, Wrangellia shows the greatest similarity with the middle paleolatitude of the craton. As this is not an officially proposed location for Wrangellia, it is provided for reference only.

B) Position of Wrangellia as reported by Trop *et al.* (2002). Wrangellia is at around 12°N paleolatitude based on sedimentologic and geochronologic data.

C) Position of Wrangellia as reported by Yole and Irving (1980). Wrangellia is at 18°S paleolatitude based on paleomagnetic data from the Karmutsen Formation.

position of allochthonous terranes in the geologic past (Figure 4.2).

After several paleomagnetic and paleobiogeographic studies on the Cretaceous rocks of Wrangellia, there is still much debate regarding its location. The so-called "Baja BC" hypothesis estimates that the terrane was at a paleolatitude of around 25 degrees North, around the modern day Baja Peninsula in the Cretaceous (Figure 4.3). Many workers refute this hypothesis on the basis of conflicting paleomagnetic and paleontological data, stating instead that this terrane was more likely at a paleolatitude of 40 or 53 degrees North in the Late Cretaceous (Kodama and Ward, 2001; Stamatakis *et al.*, 2001). Regardless of the path Wrangellia took while migrating towards the craton, it is likely that Wrangellia was docked to North America by the Late Cretaceous (Trop and Ridgway, 2007).

With the Late Triassic position of Wrangellia still in question, the purpose of this chapter is to use paleobiogeographic methods with Upper Carnian ammonoids to help elucidate the location of the terrane relative to North America during the Late Carnian. A comparison of ammonoid faunal similarity between Wrangellia and the southern hemisphere is not possible for the Late Carnian because there are no known Upper Carnian rocks on the South American craton; therefore it is only possible to compare the similarity measurements of the various latitudes (high, mid, and low) within the northern hemisphere.

While I cannot compare Wrangellian fauna to the southern hemisphere, I can compare the fauna to the western Pacific. The Upper Carnian rocks in the western Pacific are not all cratonic, but I can compare them to Wrangellia to make a general conclusion as to the paleolongitude of the terrane. As with the north and south similarity measurements, similarities to east or west directions can also be ascertained using paleobiogeographic methods given suitable faunal distribution.

Figure 4.2 Hypothesized Location of Wrangellia in the Early Jurassic

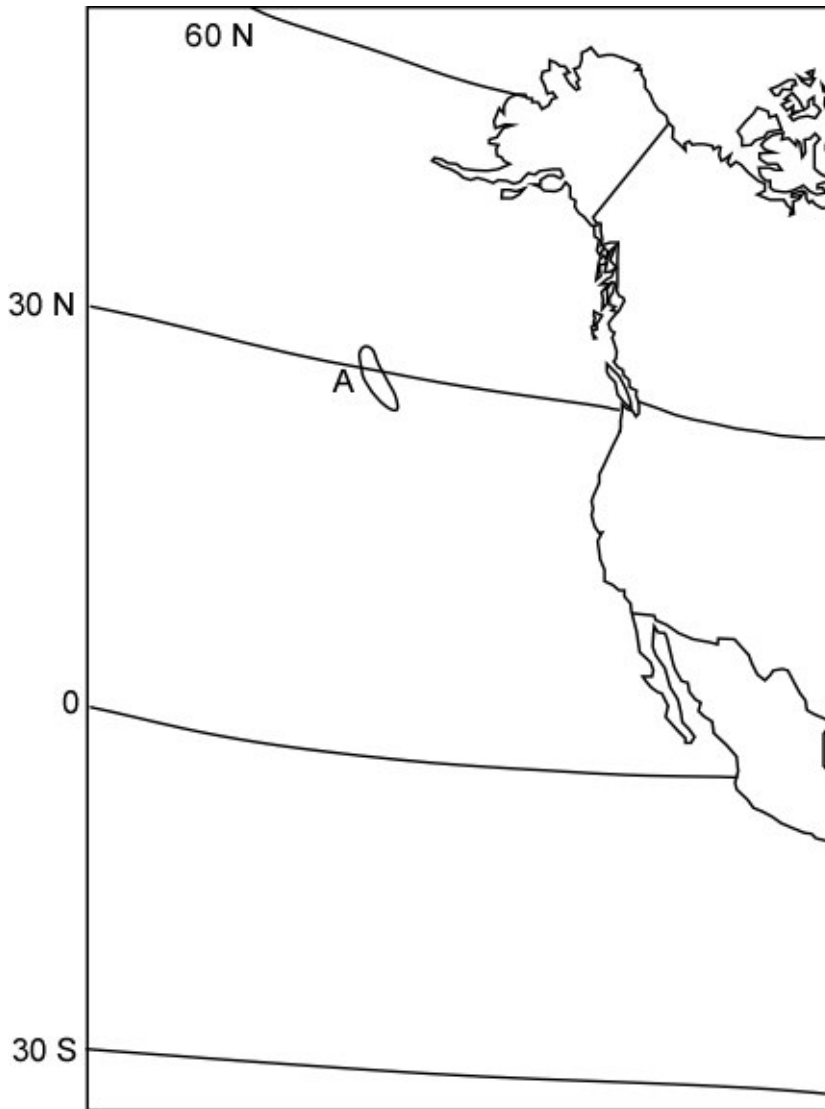


Figure 4.2: A possible location for Wrangellia in the Early Jurassic in relation to the modern day craton. Paleolatitude lines in relation to the craton are based on information provided in Smith (2006). Location of Wrangellia is approximate. No longitudinal scale is intended. Wrangellia is not to scale.

A) Position of Wrangellia as reported by Smith (2006). Wrangellia is located at approximately 30°N paleolatitude during the Hettangian based on ammonoid and bivalve paleobiogeographic patterns.

Figure 4.3 Hypothesized Locations of Wrangellia in the Late Cretaceous

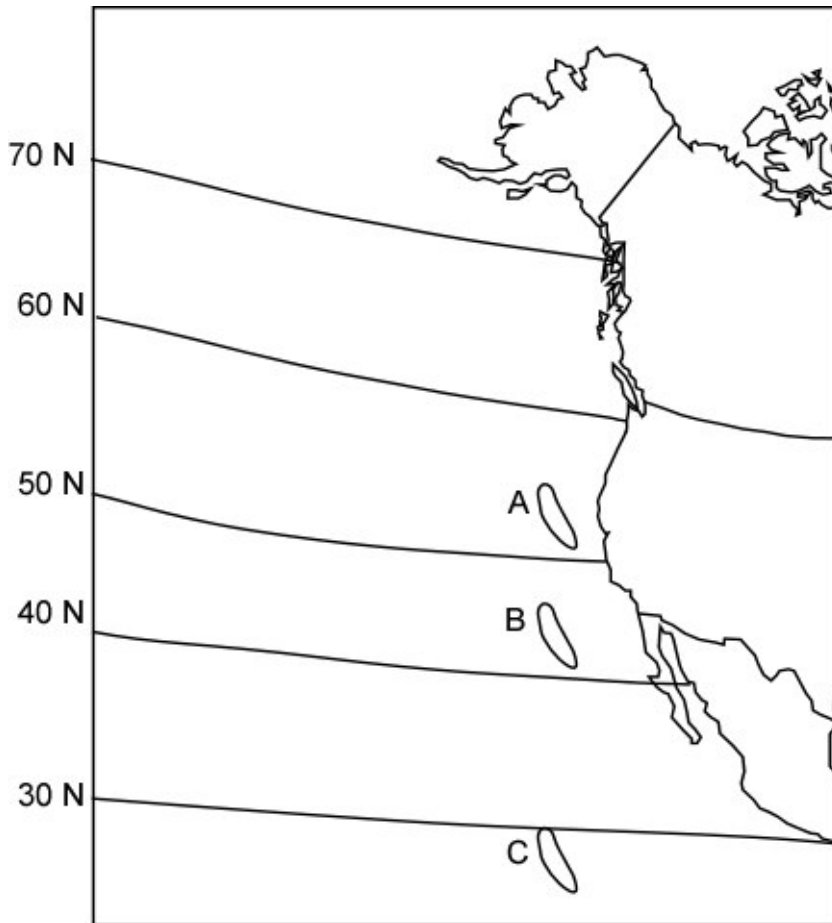


Figure 4.3: Potential locations of Wrangellia in the Late Cretaceous in relation to the modern day craton. Paleolatitude lines in relation to the craton are based on Ward *et al.* (1997). Locations of Wrangellia are approximate. No longitudinal scale is intended. Wrangellia is not to scale.

- A) Position of Wrangellia as reported by Stamatakis *et al.* (2001). Wrangellia is at a paleolatitude of around 53°N based on paleomagnetic results from the MacColl Ridge Formation.
- B) Position of Wrangellia as reported by Kodama and Ward (2001). "Baja BC" which includes Wrangellia is reported as being at a paleolatitude of no further south than 40°N.
- C) Position of Wrangellia in the traditional "Baja BC" hypothesis (e.g., Ward *et al.*, 1997).

4.2 Methods

After establishing the existence of low, middle, and high paleolatitude faunas for the Dilleri, Welleri, and Macrolobatus zones of North America (Figure 4.4), I collected presence-absence data for ammonoids from published literature. Jakobs (1992) noted that collecting ammonoid data on generic occurrences was the best taxonomic level to use in paleobiogeographic studies. The use of species data can be problematic due its subjective nature. Many authors have conflicting ideas about the appropriate definition of fossil species. This is the “lumping and splitting” conflict; some authors prefer to lump many varying morphologies into one species, while others split these morphologies into several unique species. Lumping and splitting affects the number of occurrences in paleobiogeographic studies, making studies comparing species somewhat dubious. This problem of taxonomic agreement is less evident in the generic and familial ranks, but generic data allows for a more precise comparison than familial data. Species and familial data were also collected, however, and analyzed for comparison with the generic data.

I also collected data on ammonoid occurrences from Japan, northeastern Russia, and Primorye so as to compare the similarity of the western circum-Pacific and Wrangellia to that of North America (Figure 4.5). It should be noted that both Primorye and Japan were terranes in the Late Triassic. These data were included in order to see how close Wrangellia may have been to the terranes that comprised Japan and Primorye. The similarities to the western and eastern Pacific could help determine a relative paleolongitude for Wrangellia.

Data were collected from many sources, which are listed in the appendix. Generic occurrences noted as questionable by the reporting author were not used in this study to avoid bias in the data. Similarly, taxa reported as “sp.,” “cf.,” or “aff.” were not included in the species analysis.

Figure 4.4 Upper Carnian Ammonoid Localities from North America

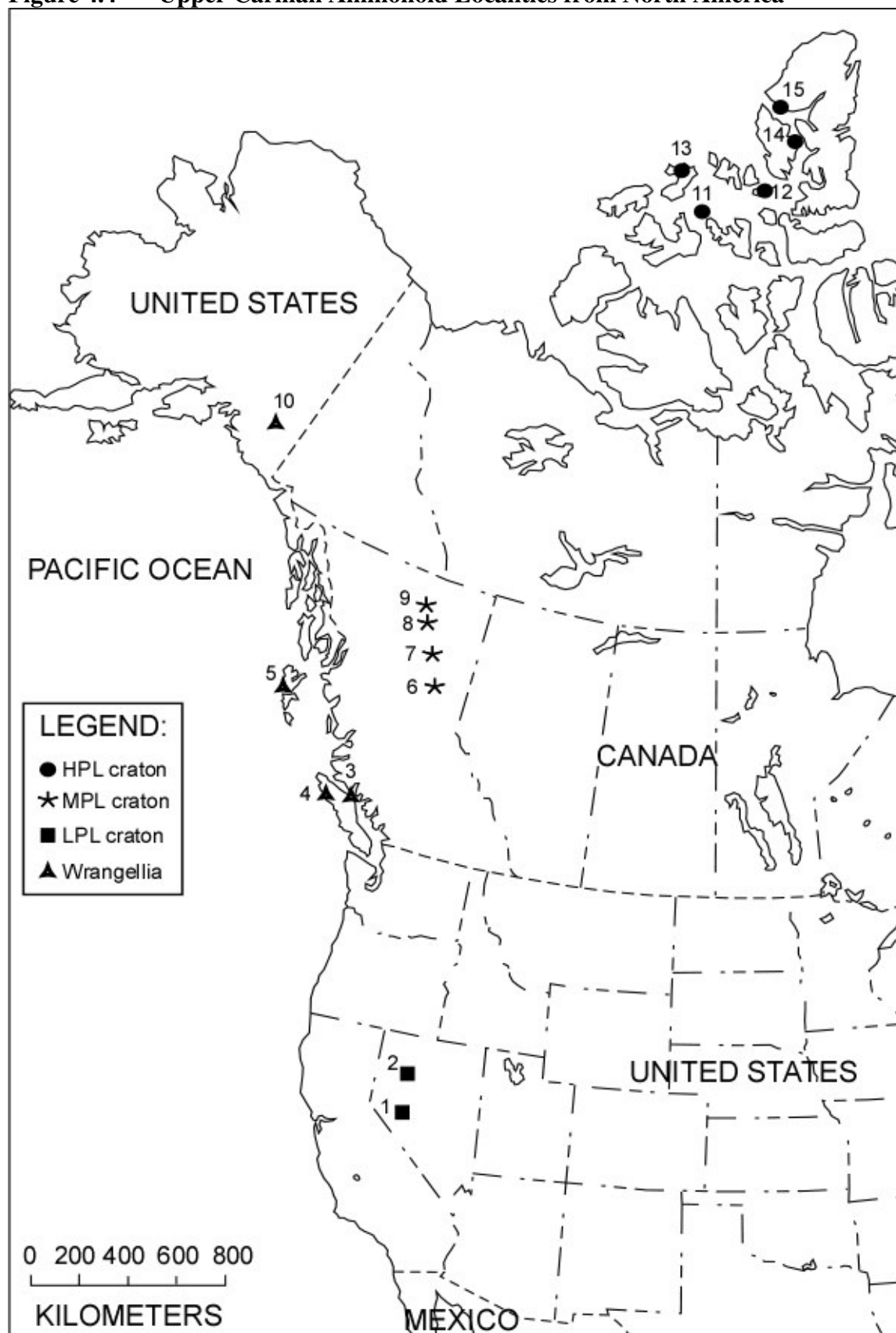


Figure 4.4: Localities from which ammonoid data was gathered for North America. (Modified from Nichols and Silberling, 1979). Square icons represent low paleolatitude cratonic localities; star icons represent mid paleolatitude cratonic localities; circle icons represent high paleolatitude cratonic localities; triangle icons represent localities on Wrangellia.

- 1, Shoshone Mountains, Union District, Nevada (Luning Formation), low paleolatitude.
- 2, Humboldt Range, Nevada (Cane Spring Formation), low paleolatitude.
- 3, Vancouver Island, British Columbia, including Quadra Island (GSC loc. 22691, 22692 Open Bay Formation); and Iron River (“Interlava Sediments” of Givens and Susuki, 1964), Wrangellia.
- 4, Northwestern Vancouver Island, British Columbia, including Ououkinsh Inlet (GSC loc. 23147, 23939, 23161, 23066 Quatsino Formation); Klaskino Inlet (GSC loc. 53340, 82936, 86293, 86284 Quatsino Formation and occurrences of Parson Bay Formation); Union Island (GSC loc. 24033 Karmutsen Formation); Hisnit Islands (GSC loc. 82852 Quatsino Formation or Karmutsen Group); Kyuquot Sound (GSC loc. 20236 Quatsino Formation); and Izard Point (GSC loc. 22270 Quatsino Formation), Wrangellia.
- 5, Queen Charlotte Islands, British Columbia, including Moresby Island (GSC loc. C-157006 Saddler Limestone); Kunghit Island (GSC loc. C-157373, C-157382 Peril Formation); Burnaby Island (GSC loc. C-157295 Peril Formation); and Huxley Island (GSC loc. C-157123, C-157119 Peril Formation), Wrangellia.
- 6, Northeastern British Columbia, Pardonet Hill (GSC loc. 9687, 9688, 64616, 64617, 64627, 64628 Pardonet Formation), mid paleolatitude.
- 7, Northeastern British Columbia, Mount Laurier (GSC loc. 94736, 94738, 56250, 51265 Ludington Formation), mid paleolatitude.
- 8, Northeastern British Columbia, Alaska Highway near mile post 428 (GSC loc. 42377, 42378, 42379, 42386, 42388, 42389 Pardonet Formation; 42306 Ludington or Pardonet Formation; 42384 Ludington Formation), mid paleolatitude.
- 9, Northeastern British Columbia, including Mount McLearn (GSC loc. 68208 Ludington Formation; 42320, 42321, 42322, 42398, 68179, 68179, 68360 Baldonnel Formation; 68202 Pardonet Formation); “Grey Beds;” and Mount Prudence (GSC loc. 68221 Pardonet Formation), mid paleolatitude.
- 10, Southern Wrangell Mountains, Alaska (Chitistone Limestone), Wrangellia.
- 11, Queen Elizabeth Islands, Nunavut, Cameron Island (GSC loc. 25868, 35611 Schei Point Formation), high paleolatitude.
- 12, Queen Elizabeth Islands, Nunavut, Cornwall Island (GSC loc. 30369 Schei Point Formation), high paleolatitude.
- 13, Queen Elizabeth Islands, Northwest Territories, Borden Island (GSC loc. 37216, 37218 Schei Point Formation), high paleolatitude.
- 14, Queen Elizabeth Islands, Nunavut, Axel Heiberg Island (GSC loc. 26167, 28429, 28435, 28454, 89714, 89716 Blaa Mountain Formation), high paleolatitude.
- 15, Queen Elizabeth Islands, Nunavut, Ellesmere Island (GSC loc. 28428, 55479 Blaa Mountain Formation), high paleolatitude.

Figure 4.5 Upper Carnian Ammonoid Localities of the Western Pacific

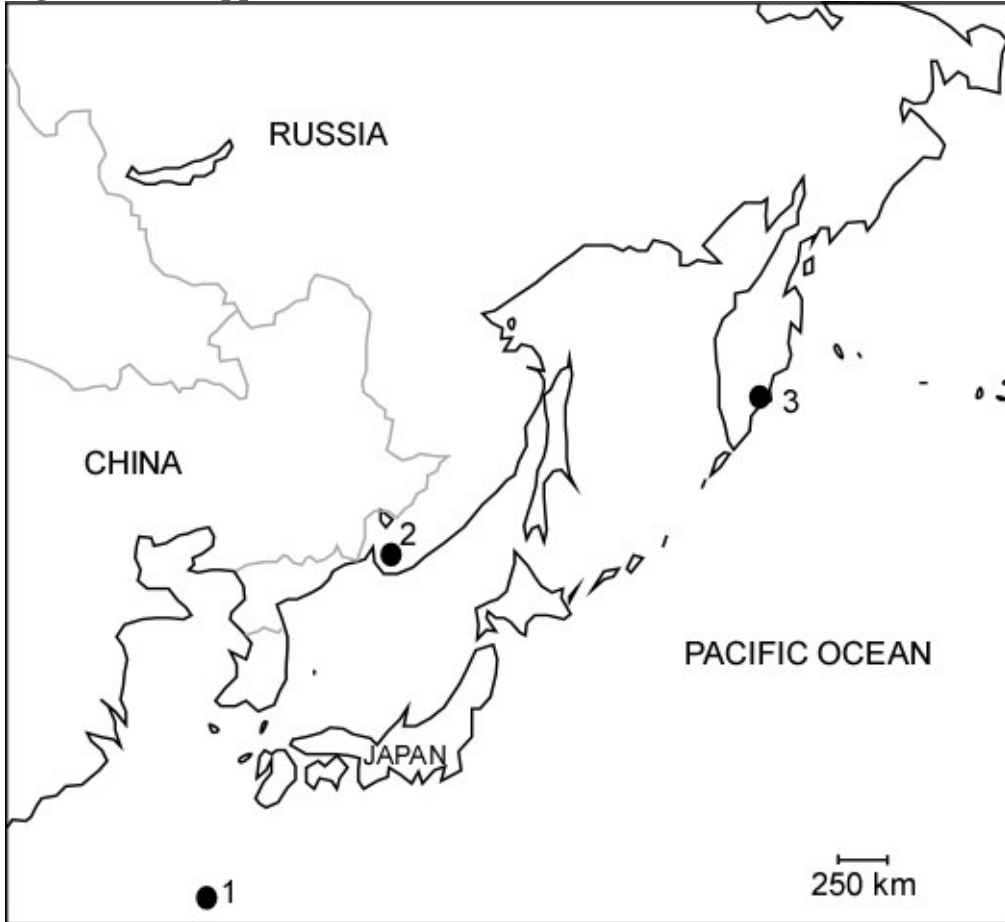


Figure 4.5: Localities of Upper Carnian ammonoids from the Western circum-Pacific.

1, Okinawa-Jima, Japan. Nakijin Formation.

2, Primorye, Russia. Kievka River.

3, Northeastern Russia. This is an approximate placement, as exact locality information was unavailable.

The presence-absence data was first compared using the Dice similarity coefficient. This coefficient is particularly useful when data sets are small (Jakobs, 1992; Maples and Archer, 1988), as it records the least amount of bias. The Dice coefficient is calculated using the following equation,

$$2A \div (2A + B + C)$$

where A is the number of taxa in common between two localities, B is the number of taxa present in locality 1, and C is the number of taxa present in locality 2. The data was also compared by a simple percent similarity measure. This measure is calculated using the following equation,

$$\text{percent similarity} = (A \div D) \times 100$$

where A is the number of taxa in common between two localities, and D is the total number of taxa present at both localities.

4.3 Results and Discussion

Ammonoids are not generally considered to be an ideal fossil group to use for paleobiogeographic studies. As with recent nautiloid shells, ammonoid shells had the potential to float after the organism's death and drift around the ocean. This tendency towards post-mortem drift would mean that many ammonoids did not live in the region in which the fossils are later found; therefore, this could be a potential source of error in paleobiogeographic studies using ammonoids. However, Neumayer (1883) recognized endemic Boreal and Tethyan ammonoids in Europe which confirms that some ammonoid genera were not subject to post-mortem drift. Also, a recent study by Wani *et al.* (2005) has called into question the degree to which ammonoid shells floated after death. They make a comparison between the ratio of the body chamber volume to the phragmocone volume of extinct ammonoids to that of the modern

Nautilus pompilius. It is their opinion that this ratio is important in determining whether a *N. pompilius* shell, and by extrapolation an ammonoid shell, will sink or float. Their conclusion was that shells with a diameter of 200 mm or less should sink relatively close to where the animal died, but that larger shells did have the potential for post-mortem drift. If this is the case, then the relatively small ammonoids of the Triassic may indeed be reliable paleobiogeographic fossils.

Another factor which can determine if an ammonoid family is a good paleobiogeographic indicator is whether it was cosmopolitan or endemic. Specific ammonoids have been found to show endemism and diversity patterns that correlate with paleolatitude during the Early Jurassic (Smith, 2006) which allows them to be very useful in determining the location of the various terranes that make up western Canada. Certain families of ammonoid appear to have the cosmopolitan or endemic distinction in the Late Triassic as well.

During the Late Triassic, ammonoid faunas from the western Cordillera are unique enough from the eastern Cordillera and the arctic that they could be considered a separate zoogeographic province (Tozer, 1970). My data support Page's (1996) conclusion that the East Pacific Province, which includes British Columbia and the western United States, during the Late Carnian was primarily made up of the ammonoid superfamilies Tropitaceae and Trachycerataceae. Many of the East Pacific ammonoid genera are also found in the Tethyan Subrealm, but some are endemic to the East Pacific Province (Page, 1996). Based on my data of global ammonoid occurrences, it appears that there are six genera of ammonoid that are endemic to the East Pacific Province in the Late Carnian: *Spirogmoceras*, *Trachystenoceras*, *Pleurotropites*, *Sympolycyclus*, *Klamathites*, *Margarijuvavites*, and *Hadrothisbites*. Of these six genera, four of them are found in the Upper Carnian rocks of Wrangellia possibly indicating that Wrangellia was in the east Pacific during the Late Carnian.

In a paleomagnetism study conducted on the Karmutsen Formation on Vancouver Island, Yole and Irving (1980) concluded that Wrangellia was at a latitude of 18 degrees North or South of the paleoequator during the Late Triassic. Based on their data, they favored the interpretation of 18 degrees South latitude. Because there is no published occurrence of Upper Carnian cratonic rocks on South America, there is no way to directly verify their interpretation using paleobiogeography. While it seems plausible that my low similarity results for North America could support Wrangellia not being in the Northern hemisphere during the Late Carnian, I do not think that this is the case. Using the 30 degrees North latitude of Zonneveld *et al.* (2007) for the middle paleolatitude of North America, Wrangellia would be 48 degrees away from the mid-latitude craton if it were at a latitude of 18 degrees South. I think that the Dice coefficient and percent similarity measurements for the middle paleolatitude would be much lower than they are if this were the correct interpretation of Wrangellia's location.

In total, 46 ammonoid genera were recognized from the Upper Carnian Dilleri, Welleri, and Macrolobatus zones on Wrangellia and the North American craton (Table 4.1). Only 17 genera were recognized from the Upper Carnian of the Western Pacific (Table 4.2). The results of this paleobiogeography study are inconclusive. Percent similarity measurements show that the ammonoid fauna on Wrangellia has the greatest similarity with the middle latitude of the craton, but with a value of 33.3%, the similarity is not striking (Figure 4.6). Low paleolatitude has the next highest percent similarity with Wrangellia at 13.3%, and the high paleolatitude is unsurprisingly low at 2.9% similarity (Table 4.3). The Dice coefficient measurements show a similar trend. The middle latitude fauna on the craton has a coefficient of 0.33 when compared to Wrangellia. The low latitude fauna comes next with a 0.19 coefficient, and the high latitude fauna has a 0.05 coefficient (Table 4.3). These similarity measurements are low in the case of the low to middle latitudes and dissimilar in the case of the high latitude data.

Table 4.1 Ammonoid Presence-Absence Data for Wrangellia and North America

Family	Genus	Species	Locality	Wrangellia	LPL Craton	MPL Craton	HPL Craton	Used in Species Analysis
Trachyceratidae	<i>Spirogmoceras</i>	<i>shastense</i>		X	X	X		X
		sp.		X				
	<i>Trachystenoceras</i>	aff. <i>T. gabbi</i>				X		
	<i>Trachysagenites</i>	<i>herbichi</i>		X				X
		sp.		X				
	<i>Hisnitites</i>	<i>janmulleri</i>		X				X
	<i>Sirenites</i>	<i>senticosus</i>					X	X
		sp. gr. <i>S. betulinus</i>					X	
		<i>yakutensis</i>					X	X
	<i>Arctosirenites</i>	<i>columbianus</i>				X		X
		<i>canadensis</i>					X	X
		<i>southeri</i>					X	X
	<i>Yakutosirenites</i>	<i>pentastichus</i>					X	X
	<i>Arctoarpadites</i>	<i>costatus</i>					X	X
Sandlingitidae	<i>Traskites</i>	<i>Pamphagosirenites</i>						X
		<i>pamphagus</i>		X				X
		<i>pacificus</i>		X				X
		sp.		X		X		
		cf. <i>T. careyi</i>		X				
Tropitidae	<i>Sandlingites</i>	cf. <i>T. compressus</i>		X				
		cf. <i>T. rugosus</i>		X				
	<i>Paratropites</i>	<i>oribasus</i>		X				X
		<i>sellai</i>		X		X		X
	<i>Discotropites</i>	cf. <i>P. sulcatus</i>		X	X			
		sp.		X				
		<i>arcticus</i>					X	X
		<i>teres</i>				X		X
		<i>sandlingensis</i>				X		X
		cf. <i>D. sandlingensis</i>		X				
		<i>smithi</i>		X		X		X
		cf. <i>D. lineatus</i>		X				
		cf. <i>D. mojsvarensis</i>		X				
		<i>theron</i>				X		X
	<i>Tropites</i>	<i>dilleri</i>		X		X		X
		sp.		X				
		cf. <i>T. welleri</i>		X				
		<i>keliformis</i>		X				X
		<i>izardi</i>		X				X
	<i>Pleurotropites</i>	<i>latiumbilicatus</i>			X			X
		<i>subquadratus</i>			X			X
		<i>crassicostratus</i>			X			X
		<i>nodosus</i>			X			X
		<i>nevadanus</i>			X			X
	<i>Gymnotropites</i>	<i>gracillis</i>		X		X		X
		<i>gabbi</i>		X		X		X
		sp.		X				
	<i>Indonesites</i>	<i>americanus</i>		X				X
		cf. <i>G. californicus</i>		X				
	<i>Margaritropites</i>	<i>sphaericus</i>		X				X
	<i>Jovites</i>	<i>johnsoni</i>				X		X
		<i>bosnensis</i>				X		X
	<i>Homerites</i>	<i>borealis</i>					X	X
		<i>semiglobosus</i>		X				X

Table 4.1 continued

Family	Genus	Species	Locality	Wrangellia	LPL Craton	MPL Craton	HPL Craton	Used in Species Analysis
Tropitidae	<i>Homerocheras</i>	<i>grandis</i>				X		X
	<i>Hoplotropites</i>	<i>mari</i>				X		X
		<i>auctus</i>				X		X
		<i>circumspinitus</i>		X				X
	<i>Arctotropites</i>	<i>richardsi</i>					X	X
	<i>Anatropites</i>	<i>silberlingi</i>				X		X
		<i>cupressus</i>				X		X
		<i>cascadensis</i>				X		X
		<i>ausoniformis</i>				X		X
		<i>maclearni</i>				X		X
		<i>sulfurensis</i>				X		X
		<i>pardoneti</i>				X		X
		sp.		X				
	<i>Eusculites</i>	<i>krystyni</i>				X		X
Thisbitidae	<i>Thisbites</i>	sp.				X		
		<i>selwyni</i>				X		X
		<i>huxleyi</i>		X				X
	<i>Hadrothisbites</i>	<i>taylori</i>				X		X
Juvavitidae	<i>Tropithisbites</i>	<i>densicostatus</i>		X				X
	<i>Bacchites</i>	<i>hyatti</i>		X		X		X
		cf. <i>B. bacchus</i>		X				
	<i>Projuvavites</i>	<i>brockensis</i>				X		X
		<i>strongi</i>		X		X		X
	<i>Goniojuvavites</i>	<i>kellyi</i>				X		X
	<i>Juvavites</i>	cf. <i>J. elegans</i>						
		sp.			X			
		<i>inflatus</i>			X			
	<i>Gonionitites</i>	<i>avarus</i>				X		X
Clionitidae		<i>nobilis</i>				X		X
	<i>Margarijuvavites</i>	<i>carlottensis</i>		X		X		X
	<i>Griesbachites</i>	<i>auctoris</i>				X		X
	<i>Leconteiceras</i>	<i>californicum</i>		X				X
		sp.		X				
	<i>Sympolycyclus</i>	<i>gunningi</i>		X				X
		<i>kellyi</i>				X		X
	<i>Choristoceratidae</i>	<i>Hannaoceras</i>		X				
	<i>Arcestidae</i>	<i>Arcestes</i>		X	X			
	<i>Klamathitidae</i>	<i>Klamathites</i>				X		
Badioditidae		<i>schucherti</i>			X			X
		<i>macrolobatus</i>			X			X
Cycloceltitidae	<i>Orthoceltites</i>	<i>belcheri</i>					X	X
Tropiticeltitidae	<i>Neotenoceras</i>	<i>simplex</i>		X				X
	<i>Styrites</i>	<i>dawsoni</i>		X				X
	<i>Tropiceltites</i>	<i>pacificus</i>		X				X
	<i>Tardeceras</i>	<i>parvum</i>		X				

Table 4.1: Presence-Absence data of Upper Carnian ammonoids from the North American craton and Wrangellia is presented. The species used for similarity measurements are indicated by the X's in the "Used in Species Analysis" column.

Table 4.2 Ammonoid Presence-Absence Data for Wrangellia and the Western Pacific

Family	Genus	Location				
			Wrangellia	NE Russia	Japan	Primorye
Arcestidae	<i>Arcestes</i>		X		X	X
	<i>Proarcestes</i>			X	X	X
	<i>Stenarcestes</i>				X	X
Choristoceratidae	<i>Hannaoceras</i>		X		X	X
Clionitidae	<i>Leconteiceras</i>		X			
	<i>Sympolycyclus</i>		X			
Cycloceltidae	<i>Neotenoceras</i>		X			
Discophyllitidae	<i>Discophyllites</i>			X		X
Juvavitidae	<i>Bacchites</i>		X			
	<i>Juvavites</i>				X	X
	<i>Projuvavites</i>		X			
	<i>Margarijuvavites</i>		X			
Sandlingitidae	<i>Traskites</i>		X			
	<i>Sandlingites</i>		X			
Thisbitidae	<i>Thisbites</i>		X		X	X
	<i>Tropithisbites</i>		X			
Trachyceratidae	<i>Spirogmoceras</i>		X			
	<i>Trachysagenites</i>		X			
	<i>Hisnites</i>		X			
	<i>Sirenites</i>			X		X
	<i>Pamphagosirenites</i>		X			
	<i>Neosirenites</i>			X		X
	<i>Striatiosirenites</i>			X		X
	<i>Neoprotrachyceras</i>					X
Tropiceltites	<i>Tardeceras</i>		X			
	<i>Styrites</i>		X			
	<i>Tropiceltites</i>		X			
	<i>Arietoceltites</i>				X	X
Tropitidae	<i>Amioceltites</i>				X	X
	<i>Paratropites</i>		X			
	<i>Discotropites</i>		X	X		X
	<i>Tropites</i>		X	X		X
	<i>Pleurotropites</i>		X			
	<i>Gymnotropites</i>		X			
	<i>Indonesites</i>		X			
	<i>Jovites</i>				X	X
	<i>Homerites</i>		X			
	<i>Hoplotropites</i>		X	X		X
	<i>Anatropites</i>		X			

Table 4.2: Presence-absence data of ammonoids for Wrangellia and localities of the western Pacific are presented.

Figure 4.6 Percent Similarity Measurements and Amount of Diversity of Various Localities with Wrangellia

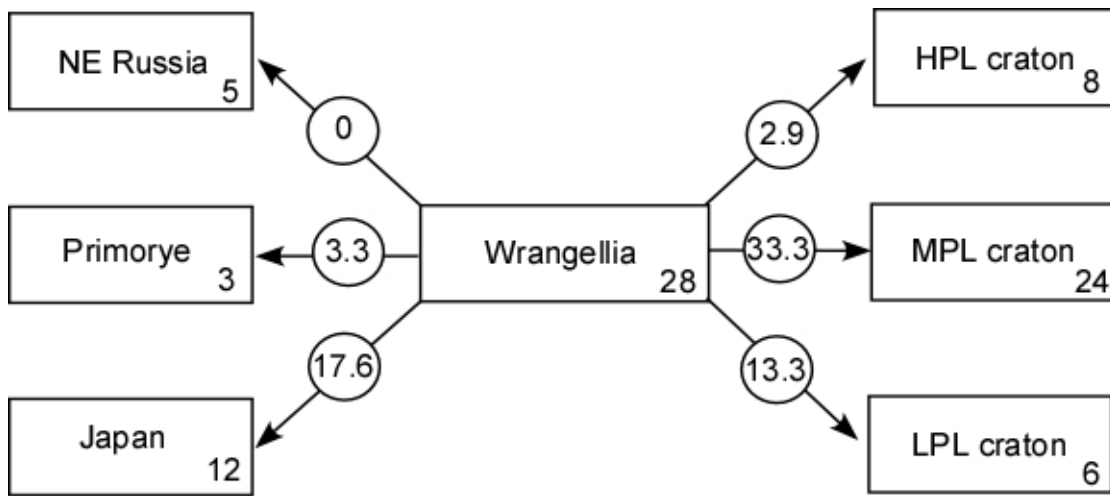


Figure 4.6: Numbers in circles illustrate the percent similarity measurements for ammonoid genera of the various localities mentioned in the text as compared to Wrangellia. Diversity is reported as number of ammonoid genera at the locality and is shown as a number in the lower right corner of each locality's box. No reference to paleolatitude is intended by the order of the western Pacific localities.

Table 4.3 Dice Coefficients and Percent Similarity Measurements for North America

Families	Wrangellia	LPL	MPL	HPL
A	n/a	4	6	2
B	n/a	5	7	3
C	10	n/a	n/a	n/a
D	n/a	11	11	11
Dice Coefficient	n/a	0.34	0.41	0.24
Percent Similarity	n/a	36.4	54.5	18.2
Genera				
A	n/a	4	13	1
B	n/a	6	24	8
C	28	n/a	n/a	n/a
D	n/a	30	39	35
Dice Coefficient	n/a	0.19	0.33	0.05
Percent Similarity	n/a	13.3	33.3	2.9
Species				
A	n/a	1	9	0
B	n/a	9	34	10
C	28	n/a	n/a	n/a
D	n/a	36	52	39
Dice Coefficient	n/a	0.05	0.225	0
Percent Similarity	n/a	2.77	17.3	0

Table 4.3: Dice coefficients and percent similarity measurements of ammonoids from North America and Wrangellia using family, genera, and species data. A: number of taxa common to the cratonic locality and Wrangellia; B: number of taxa present at the cratonic locality; C: number of taxa present on Wrangellia; D: number of taxa present at either locality.

Despite the fact that the Late Triassic spans nearly 35 million years of the approximately 50 million years in the Triassic Period, comparatively little Upper Triassic rock is actually preserved in the craton's low paleolatitude region. There are only a few Upper Carnian localities that are on the North American craton: these are the Cane Spring Formation in the Star Peak Group of the Humboldt Range and the Luning Formation in the Shoshone Mountains, both of which are in Nevada. These formations were deposited on allochthonous terranes that had accreted to the craton by Early to Middle Triassic time (Speed, 1979). Unfortunately, ammonoids collected from these sites are abundant but not particularly diverse (Silberling and Wallace, 1969; Silberling, 1959). This fact may explain why the low latitude similarity measurements with *Wrangellia* are so low.

It is possible that there truly is little similarity between *Wrangellia* and the craton. Perhaps *Wrangellia* was too far away from North America during the Late Carnian to share more similar ammonoid faunas. I find this conclusion unsatisfactory because approximately 5 million years after the Late Carnian in the Lower Norian rocks of *Wrangellia* other fossils such as corals occur. These corals indicate an affinity with low latitude cratonic faunas (Tozer, 1982). Species of the bivalve *Monotis* have also been used to indicate a low latitude affinity for the Pacific margin of Cordilleran North America in Middle to Upper Norian rocks (Silberling, 1985). It seems unlikely that *Wrangellia* would have been so far removed from the craton during the Late Carnian when there is similarity with the low latitude just 5 million years later in the Early Norian.

Fossil corals are often used in paleogeography to indicate deposition in low latitudes. Interestingly, Zonneveld *et al.* (2007) have located the oldest scleractinian coral from the North American craton, *Retiophyllia*, at Pardonet Hill in the Peace River area of northeastern British Columbia from the Carnian Baldonnel Formation. This region of British Columbia is a cratonic reference of the middle latitude for the Upper Triassic. Because this area is thought to be at a

paleolatitude of 30 degrees north (Zonneveld *et al.*, 2007), there may not be enough differentiation between the Upper Carnian middle and low latitude references to allow paleobiogeographic discrimination between the two.

Ammonoid faunal data were also collected from the western Pacific areas of Japan, northeastern Russia, and Primorye (Figure 4.5). This data set is unfortunately sparse due to several factors, mainly the lack of definition of Late Triassic time in some publications. Many publications list a particular ammonoid as being generically Carnian or Upper Triassic. Without the assignment to at least the Late Carnian, I wasn't able to include that particular data in my study. As with the North American data, preservation was also a problem with the ammonoids from Japan. Ishibashi (1970) noted that there is a lack of preserved Upper Triassic marine sediments in Japan. This results in there only being a small number of ammonoids preserved in Japan's Upper Carnian rocks.

Wrangellia shows the greatest similarity coefficient with Japan out of all the other western Pacific localities studied, but this similarity is still low (Table 4.4). The Dice similarity coefficient at the generic level between Wrangellia and Japan is 0.23. The similarity coefficient for Japan is slightly higher than that for the North American low paleolatitude, perhaps indicating that Wrangellia's paleolatitude was more similar to Japan's in the Late Carnian. Primorye has a coefficient of 0.06, and northeastern Russia has a coefficient of 0.00 when compared to Wrangellia. Both seem to indicate a dissimilarity with Wrangellia.

In order to determine if the eastern or western side of the Pacific margin shows the greatest similarity to Wrangellia, I combined the data for North America as one data set and the data from the western Pacific as a second data set. The comparison of genera in the western Pacific did not change very much from that of Japan, the largest data source. The Dice coefficient of similarity for the western Pacific is 0.21 with Wrangellia. The Dice coefficient for the combined North American data is 0.325. Even though neither coefficient indicates a strong

Table 4.4 Dice Coefficients and Percent Similarity Measurements for Western Pacific Localities

Families	Wrangellia	NE Russia	Japan	Primorye
A	n/a	2	6	3
B	n/a	3	6	3
C	10	n/a	n/a	n/a
D	n/a	11	10	10
Dice Coefficient	n/a	0.24	0.431	0.32
Percent Similarity	n/a	18.2	60	30
Genera				
A	n/a	0	6	1
B	n/a	5	12	3
C	28	n/a	n/a	n/a
D	n/a	32	34	30
Dice Coefficient	n/a	0	0.23	0.06
Percent Similarity	n/a	0	17.6	3.3

Table 4.4: Dice coefficients and percent similarity measurements of ammonoids from western Pacific localities and Wrangellia using family and genera data. A: number of taxa common to the Pacific locality and Wrangellia; B: number of taxa present at the Pacific locality; C: number of taxa present on Wrangellia; D: number of taxa present at either locality.

relationship with the terrane, Wrangellia was most likely closer to North America than the western Pacific, and therefore in the eastern Pacific during the Late Carnian.

4.4 Conclusions

In this study, I cannot conclude with certainty the position of Wrangellia during the Late Carnian. This is because similarity measurements between Wrangellia and the North American craton and the western Pacific are low. Despite the low similarities in the data, I can make some generalized conclusions.

Wrangellia certainly has a dissimilar ammonoid fauna when compared to the North American high paleolatitude and northeastern Russia. The greatest similarity is shown between Wrangellia and the mid paleolatitude. This fact leads me to infer that during the Late Carnian Wrangellia was most likely in the eastern Pacific and closer to the mid paleolatitude of North America than the other localities.

There are a few genera that appear to be endemic to North America based on my compilation of ammonoid occurrences. Some of these endemic genera also occur on Wrangellia, strengthening the connection of this terrane to the eastern Pacific.

Chapter 5: Conclusions

This thesis addresses two questions: Can we improve the Triassic biochronology through a better understanding of the Late Carnian conodont genera *Metapolygnathus* and *Carniepigondolella*; and where was *Wrangellia* during the Late Carnian?

The conodont genus *Metapolygnathus*, in particular, is valuable in refining the Late Triassic biochronology. Unfortunately, this genus is poorly understood which hinders its usefulness. This thesis provides a detailed description of the Late Carnian representatives of the genus found at Klaskino Inlet, British Columbia. I think these descriptions enhance the understanding of the variations within these species, which will lead to them being more useful in the pursuit of an integrated conodont and ammonoid Triassic biochronology. The conclusions reached about the conodont genus *Metapolygnathus* are as follows:

- 1) *Metapolygnathus polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* are differentiated primarily on the characteristics of nodosity and platform shape, specifically the slope of the platform margin. To a lesser extent, free blade length is also a consideration in identifying the species.
- 2) There is morphological variability within the discussed species of *Metapolygnathus*. This variability is not grounds for splitting the species as the characteristics the species are based on are sound.
- 3) Certain morphological variations are shared between some of the described species. Extra carinal nodes, closely spaced carinal nodes and fused nodes are variations shared between all the species populations discussed. Also shared are the variations of quadrate, triangular, and

rounded posterior platform shapes, steeply and gently sloping anterior margins, and the “*communisti* trend.” *Metapolygnathus polygnathiformis* s.l. and *M. carpathicus* share a downturned anterior platform margin, and a postero-lateral extension of the element platform. *Metapolygnathus carpathicus* and *M. nodosus* share the branching keel variation and the presence of anterior platform nodes which vary in strength.

4) The presence of the “*communisti* trend” in *M. polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* indicates that these species are related to the younger *M. communisti*.

5) There are no indications that the morphological variants of *M. polygnathiformis* s.l., *M. carpathicus*, and *M. nodosus* found at Klaskino Inlet currently provide any new stratigraphic zones, but the enhanced understanding of the genus will allow for more detailed biochronology in the future.

The uncertainty of the location of Wrangellia during the Late Carnian is a different matter than conodont morphology, and as such it requires a different approach. Using paleobiogeographic methods and records of ammonoid occurrences, I reached the following conclusions:

1) The data set of Late Carnian ammonoid genera is small. This means that significance levels of generic similarity are difficult to assess.

2) Ammonoid occurrence data for the Late Carnian age show low similarity measurements between Wrangellia and all paleolatitudes of the North American craton. Because no paleolatitudes on the craton show a high degree of similarity with Wrangellia, only inferences

can be made as to the location of Wrangellia in the Late Carnian. The similarity of the Wrangellian ammonoid fauna is the greatest with that of the mid-paleolatitude fauna. Therefore, I infer that Wrangellia was most likely of similar latitude to the mid-paleolatitude of the North American craton in the Late Carnian.

3) The ammonoid fauna of Wrangellia was more like the fauna of North America than the fauna of the western Pacific. I infer that Wrangellia was closer to North America than to the western Pacific in the Late Carnian.

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Appendix References Used to Compile Ammonoid Occurrences

References Consulted	Age	Relative Location
Armstrong, MacKevett, and Silberling, 1969	Late Carnian	Wrangellia
Carlisle and Susuki, 1965	D	Wrangellia
Carlisle and Susuki, 1974	W	Wrangellia
Ishibashi, 1970	D, W, M	Japan
Krystyn, 1982	D, W	Nepal
Mojsisovics, 1873, 1893, 1902	D, W	Austria
Silberling, 1959	W	LPL North American Craton
Silberling and Wallace, 1969	D	LPL North American Craton
Silberling and Tozer, 1968	D, W, M	Wrangellia and North American Craton
Smith, 1927	D, W	California
Tozer, 1961	W	HPL
Tozer, 1965	D	Wrangellia
Tozer, 1967	D, W, M	Wrangellia and North American Craton
Tozer, 1970	D, W, M	HPL and MPL North American Craton
Tozer, 1994	D, W, M	Wrangellia and North American Craton
Tozer and Thorsteinsson, 1964	W	HPL North American Craton
Zacharov, 1997	D, W, M	NE Russia and Primorye

Additional References	Age	Relative Location
Givens and Susuki, 1964	D	Wrangellia
Jeletzky, 1954	D	Wrangellia
Jeletzky, 1976	D	Wrangellia
Muller, 1969	D	Wrangellia
Surdam <i>et al.</i> , 1964	D	Wrangellia

Appendix 4.1: Ammonoid occurrences referred to in the text were collected from the “References Consulted” list. The “Additional References” list is often where an ammonoid occurrence was first reported, but these works were not directly consulted in this study. “D” is Dilleri Zone, “W” is Welleri Zone, and “M” is Macrolobatus Zone.