FIVE NEW GENERA OF CONODONTS FROM THE CARNIAN-NORIAN BOUNDARY BEDS OF BLACK BEAR RIDGE, NORTHEAST BRITISH COLUMBIA, CANADA

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Abstract—A high-level taxonomic revision of conodonts from the Carnian-Norian boundary (CNB) interval in the Western Canada Sedimentary Basin is provided as a prelude to a monographic report. Five new genera - Acuminatella, Kraussodontus, Parapetella, Primatella, and Quadralella - are introduced, four of which are represented by newly described type species: Acuminatella acuminata, Kraussodontus peteri, Parapetella prominens, and Quadralella lobata. In addition, Acuminatella angusta, Carnepigondolella eozae, C. medioconstricta, Primatella asymmetrica, and P. conservativa are newly described. Amended diagnoses are provided for the genera Carnepigondolella, Epigondolella, Metapolygnathus, and Paragondolella. Based on both new and established species, and many others as yet undescribed, the CNB interval spanning the Welleri (part), Macrolobatus and Kerri ammonoid zones is informally divided into eight conodont zones and subzones, plus a further three intervals that can be potentially delineated near the top of these zones. The main zones are the Lower, Middle, and Upper samueli subzones, n. sp. Q Zone, “Lower primitia Zone,” parvus Zone, “Upper primitia Zone,” and quadrata Zone.

INTRODUCTION
The Upper Triassic Pardonet Formation in northeast British Columbia contains an unrivaled fauna of ammonoids (Tozer, 1994), bivalves (McRoberts, 2011), and conodonts (Orchard, 1983, 1991b, 2007b, c). At Black Bear Ridge on Williston Lake (Fig. 1), the upper Ludington Formation and overlying lower Pardonet Formation preserve a remarkable record of upper Carnian conodonts (Fig. 2) that complement the complete Norian record preserved in the Pardonet Formation (Orchard et al., 2000). At this locality in particular, the Carnian-Norian boundary interval is well displayed and has been intensively studied (Orchard, 2007c, Zonneveld et al., 2010, Williford et al., 2007). The present author is currently preparing a monograph on the prolific, diverse, and continuous conodont succession across this boundary. This provides a substantially new taxonomy, many new taxa, and a much refined biozonation for the interval. The present paper presents the high level taxonomic reevaluation of the conodont fauna whereby five new genera are introduced and four others (Carnepigondolella, Epigondolella, Metapolygnathus, and Paragondolella) are re-described (see Figs. 3 and 4). Two other extant pectiniform genera (Norigondolella, Misikella) are omitted from this report.

Upper Triassic conodont taxonomy has been in a state of flux since Hayashi (1968) first described a fauna that he erroneously regarded as Permain in age: later, it was recognized that the fauna was of mixed Triassic age. The work provided the genus Metapolygnathus and several key species that have, in the absence of clear definition, been variously interpreted in the decades since. Similar confusion plagued the type species of Epigondolella, E. abeptis (Huckriede), which led to many dissimilar ornate forms being assigned to that species. Some of these Carnian forms were later included in a new genus, Carnepigondolella (Kozur, 2003), which has also been variously interpreted since. Other taxa described by Mosher (1968, 1970, 1973) also proved unstable: e.g., E. primitia has been subjected to considerable revision, and his genus Paragondolella, introduced for the Middle Triassic P. excelsa, has continued to be used indiscriminately for many Carnian species. This work aims to stabilize the taxonomy by re-defining generic characteristics with particular emphasis on the differing morphologies of the anterior platform margins in the P elements, which I regard as a particularly diagnostic feature, as it is in many Paleozoic platform elements.

CONODONT BIOSTRATIGRAPHY
The conodont biostratigraphy of the Black Bear Ridge section facilitates subdivision of the interval into eight faunal intervals (Fig. 2), a mixture of range and assemblage zones. Previously, these zones were given several informal names and this is continued in the present paper pending formal definition utilizing both known and many as yet undescribed taxa (M.J. Orchard, unpubl. 2013). From the base of the section, these intervals are the Carnepigondolella samueli Zone, now divided into three subzones on the basis of the successive appearance of C. eozae sp. nov., C. zoae Orchard, and C. medioconstricta sp. nov.; these define Lower and Middle subzones (formerly combined as Fauna 1 of Orchard, 2010), and an Upper Subzone (formerly subdivided as Faunas 5 and 6 of Orchard, 2010) contains many new taxa, including the name bearer, plus P. mersinsensis, P. orchiardi, and Acuminatella angustus sp. nov.; some additional new species, including A. acuminata sp. nov. and Parapetella prominens sp. nov. appear in its topmost part (= Fauna 6). The “Lower primitia Zone” also contains uppermost Carnian Macrolobatus Zone ammonoids. The parvus Zone (= M. echinatus Zone of Orchard, 2007c, and Fauna 7 of Orchard, 2010) marks the appearance of many diminutive platform elements, including the name bearer, and the disappearance of many taxa including the new genera Quadralella and Kraussodontus that dominate Carnian collections. By the end of this relatively narrow zone, a major faunal turnover had occurred (Orchard 2007c, fig. 5) and in the “Upper primitia Zone” (= primitias Zone of Orchard 2007c, and Fauna 8 of Orchard, 2010) ornate Primatella species dominate in association with common but sporadic Norigondolella, fewer Acuminatella, and rare Parapetella. Note that the “Lower” and “Upper primitia” zones (which will be renamed in the monograph) do not correspond to the zones of that name identified by Orchard (1983, 1991b), which were differentiated on the first appearance of Norigondolella and were regarded as approximations of upper Carnian and lower Norian strata. However, Norigondolella is now known to be facies dependant and is known also from Carnian levels too, albeit rarely. The top of the lower Black Bear lower section has a succession of ammonoid beds that correspond to the lower Norian Kerri and Dawsoni ammonoid zones (Tozer, 1994), and a rapid turnover from Primatella faunas to those with Epigondolella quadrata (Fauna 9 of Orchard, 2010) and affiliated forms within the uppermost Kerri Zone. A few rare species appear just before this turnover, which marks the disappearance of other conodont genera.
**SYSTEMATIC PALEONTOLOGY**

**Order:** Ozarkodinida Dzik 1976  
**Superfamily:** Gondolelloidea (Lindstrom 1970)  
**Family:** Gondolellidae Lindstrom 1970  
**Genus:** Acuminatella gen nov.

**Derivation of name:** acuminatus/a (Latin), pointed, describing the posterior morphology of the platform P₁ elements.

**Type species:** Acuminatella acuminata sp. nov.

**Diagnosis:** The P₁ elements of this genus are typically arched with a posteriorly downturned and reduced platform and a prominent carina that extends to a pointed posterior termination. Anterior platform margins are weakly to strongly ornate, and the posterior margins are inornate. The lower surface characteristically has a pit located in a sub-medial position and a keel that extends to its posterior.

**Description:** The posterior platform is gradually tapered or narrows abruptly at a medial constriction posterior of the anterior nodes. In tapered forms, the posterior platform margins in upper view may be straight, plano-convex, biconvex, or slightly sinuous. When the platform narrowing is abrupt, the posterior platform margins may be very narrow to vestigial and its margins straight, curved, or sinuous. In all cases, the anterior platform margins are raised and each bears 1-6 variably developed, rounded nodes (in older species) to sharp denticles (in younger species). Both the denticles and the platform margins are covered by compact microreticulae. The free blade is about one-third element length, highest near the anterior end and forming a low convex crest as it descends onto the platform as a row of fairly discrete nodes, the largest of which often occur to the posterior. The carina extends to, or nearly to the posterior platform tip. The entire unit is posteriorly downarched. A pit is located slightly to the anterior or posterior of platform midlength, often beneath the constriction if present, and varies in position relative to the keel: it may be subterminal in small specimens, but it is generally anteriorly displaced within a terminally pointed keel.

**Comparisons:** Acuminatella species differ from most contemporaneous taxa in their reduced posterior platform and strongly developed posterior carina. Some early growth stages of Primatella species (e.g., P. conservativa) may have reduced posterior platforms but they broaden with growth, have a less developed carina with more discrete nodes, and often a wide posterior platform brim. Similarly, small specimens of some Quadraellula species have reduced posterior platforms but they also broaden with growth, have a carina that stops in front of a blunt posterior termination, and less developed anterior nodes. Pointed species of Parapetella have anterior parapets rather than nodes. The middle Norian Orchardella has high and sharp anterior denticles and less compact platform microreticulation.

**Remarks:** Elements combined here display variation in both platform shape and anterior node formation but they all have the distinctive narrow posterior and ornate anterior. As in Carnepigondolella and Primatella, there appears to be an evolutionary trend of increased differentiation of the anterior platform nodes in the P₁ elements of Acuminatella.

Kozur (2003) introduced Orchardella for four middle-late Norian species formerly referred to Epigondolella that he regarded as North American endemics (Moix et al., 2007, p. 294); he selected Epigondolella multidentata Mosher, a middle Norian species, as the type species. A fifth species of late Carnian-early Norian age, originally included within the "Epigondolella primitia population" by Orchard (1983, Fig. 2), was regarded by Kozur (2003, p. 70) as the forerunner of the middle Norian species but was questionably referred to Orchardella because of the stratigraphic gap between the species. I separate these early forms here as Acuminatella.

**Composition:** Thirteen new species are assigned to this new genus, two of them with question; most of these will be described in the monograph. Acuminatella is believed to have developed from Quadraellula through increased ornamentation of the anterior platform margins and increased lengthening and attenuation of the posterior platform.

**Age:** The first, questionable representatives appear within the
FIGURE 2. The stratigraphic section (after Zonneveld et al., 2010) in the lower part of the Black Bear Ridge section showing sedimentary units and facies associations described by Zonneveld, bed/sample numbers, the range of conodont genera, and on the right the conodont zonal intervals. The solid horizontal lines are the zonal boundaries; the dashed horizontal lines demarcate further potential subdivisions. The preferred option for the Carnian-Norian boundary is shown by the heavy line at the base of the parvus Zone.
upper range of *Carnepigondolella samueli* and the first true species appear soon after species of that genus disappear. Different species are recognized in the latest Carnian and earliest Norian, and all disappear immediately prior to the appearance of *Epigondolella quadrata*.

**Acuminatella acuminata** sp. nov.

*Fig. 4.16-4.18*

1983 *Epigondolella primitia* population – Orchard, fig. 2H, M, N.

**Derivation of name:** As for genus.

**Holotype:** GSC 132613, Figure 4.16-4.18.

**Type stratum:** Bed 17b (GSC cur. C-307807), within the Pardonet Formation.

**Age:** Uppermost “Lower *primitia* Zone,” uppermost Carnian.

**Diagnosis:** A species of *Acuminatella* in which the relatively long and narrow platform of the P element tapers progressively from near its anterior end to the posterior tip except for an indentation that may occur posterior to the lateral denticles on one or both margins, particularly in early growth stages. The posterior platform may be somewhat sinuous with one margin more convex in outline. Each anterior lateral platform bears 2-3, rarely up to 5, well developed, discrete, sometimes laterally elongate, and relatively sharp denticles; the denticles may become apically rounded in larger specimens. The posterior carina is composed of 2-5 separated to partly fused and prominent nodes that generally reach the posterior end of the element or terminate just in front. The pit is subcentral in position, commonly lying beneath the anterior half of the platform, and in all cases is anteriorly shifted within the keel.

**Comparisons:** The P elements of this species are distinguished by their relative length, the strong denticles of the anterior lateral platform margins, the evenly tapered rather than strongly constricted posterior platform, and the more anterior position of the pit. The smaller *A. angusta* differs in having an abruptly narrower posterior platform and high carina

**Stratigraphic range:** Uppermost “Lower *primitia* Zone,” uppermost Carnian through top “Upper *primitia* Zone,” lower Norian.

**Acuminatella angusta** sp. nov.

*Fig. 4.22-4.24*

1983 *Epigondolella primitia* population – Orchard, fig. 2O (only).

2007 *Metapolygnathus* n. sp. I. – Orchard (c), pl 2, figs. 1-3, 13-15

**Derivation of name:** *angusta* (Latin), narrow, describing the posterior morphology of the platform P elements.

**Holotype:** GSC 131166, Figure 4.22-4.24

**Type stratum:** Bed 15 (GSC cur. C-305879), within the Pardonet Formation.

**Age:** “Lower *primitia* Zone,” uppermost Carnian.

**Diagnosis:** A species of *Acuminatella* in which the P elements are narrow and elongate with a straight axis and a denticate platform mainly developed in the middle one-third of the element where there are 2-4 nodes on each lateral margin that are discrete, round, moderately high, and apically pointed. The anterior one-third consists of a free blade, and the posterior one-third is a process bearing a very narrow platform or lateral flanges. The carina posterior of the indistinct cusp extends to, or nearly to the posterior end of the element and is composed of 4-6 partly to strongly fused and high nodes.

**Comparisons:** In contrast with the present species, some similar early growth stages of *Primatella* species have a relatively shorter posterior platform that broadens with growth, and a posterior carina that is generally neither as high nor as well developed. See also *A. acuminata*.

**Remarks:** Elements of this species vary in the relative length of the posterior carina. Some, like the holotype, have 4(5) posterior carinal denticles, whereas others have a remarkably long and narrow posterior process with 6(7) denticles.

**Stratigraphic range:** “Lower *primitia* Zone,” uppermost Carnian through *parvus* Zone, lower Norian.
Stratigraphic range: My concept of this genus restricts typical species to the upper Carnian samueli Zone (Fig. 2) stratigraphically below the range of ornate Primatella and well below that of Epigondolella sensu stricto. The holotypes of both Carnepigondolella zoae and C. samueli come from Haida Gwaii where they were bracketed between ammonoids of the upper Welleri Subzone and the Macrolobatus Zone (Orchard 1991a, fig. 5; 1991b, p. 318, 319). The oldest species at Black Bear Ridge, C. samueli, is present already near the base of the Ludington Formation section and ranges up through the basal Pardonet Formation. A zone named after this interval can be subdivided into subzones by reference to the successive occurrences of C. eozae, C. zoae, and C. medioconstricta (formerly assigned to the C. n. sp. N and "pseudoechinatus" zones by Orchard, 2007c).

Carnepigondolella eozae sp. nov.

Fig. 3.1-3.3

Derivation of name: Referring to its apparently ancestral relationship to C. zoae.

Holotype: GSC 132598, Figure 3.1-3.3.

Type stratum: Bed C (GSC cur. C-426539), within the Ludington Formation.

Age: Lower samueli Subzone, upper Carnian.

Diagnosis: The P1 element of this Carnepigondolella species has well defined marginal platform nodes that are well rounded in both upper and lateral views, and which are more developed in the anterior half of the elongate platform and become less differentiated towards the posterior. A constriction occurs in the posterior 1/5 of the platform. The free blade is about one-third of the total element length, forms a convex crest, and passes into a low carina that extends to the center of the posterior constricted part; the cusp is indistinct. The pit lies at the posterior end of both the keel and the downturned platform.

Comparisons: The platform nodes of the new species are identical to those of C. zoae, but the latter has a less elongate platform, a platform constriction in a medial position, and an anteriorly shifted pit that lies slightly posterior of platform midlength. The posterior position of the constriction is unlike any other species of the genus.

Remarks: The platform ornament is identical to that of C. zoae, which could have arisen through anterior shifting of both the platform constriction and the pit in C. eozae.

Stratigraphic range: Carnepigondolella medioconstricta sp. nov.

Fig. 3.10-3.12

Derivation of name: Referring to the characteristic constriction in the middle of the platform of the P1 element.

Holotype: Figure 3.10-3.12

Type stratum: Bed 2 (GSC cur. C-305866), within the Pardonet Formation.

Age: Upper samueli Subzone, upper Carnian.

Diagnosis: P1 elements of have a relatively elongate, somewhat curved platform with a marked medial constriction, particularly in smaller growth stages, and a laterally expanded posterior platform, particularly on the inner side. The anterior platform bears generally 2-4 discrete and sharp nodes on each lateral margin, whereas the other asymmetrical, triangular to semicircular posterior platform is smooth or has weakly developed marginal nodes. The free blade is long, equal to one-half the element length in small specimens and a little shorter in larger specimens. One or two carinal nodes occur on the posterior platform, anterior of a wide platform brim. The cusp is inconspicuous above a pit that underlies the center of the platform; the posterior keel may be bifurcated.

Comparisons: The present species resembles Primatella orchardi but the latter is often larger, has more robust anterior platform nodes, a relatively shorter blade, more discrete carinal nodes, and lacks incipient nodes on the posterior margins.

Stratigraphic range: Only certainly known within Upper samueli Subzone.

Epigondolella Mosher 1968

Type species: Polygnathus abneptis Huckriede 1958.

Description: The P1 platform elements have high and sharp anterior platform denticles that may almost double the height of the platform; when viewed in profile, the denticles are commonly between about 35% and 45% of the total depth of the element measured from a lateral denticle tip to the basal keel margin. The platform basal margin is often straight or posteriorly stepped-up. Platform microreticulation is less compact and more subdued than in older genera and it does not extend onto the platform denticles (Orchard 1983, fig. 9). The posterior platform may be smooth or have weak to strong marginal platform nodes. The free blade is about one-third total element length and descends onto the platform as a carina that terminates in a central node, or continues onto the posterior platform as one or two additional nodes. The pit is subcentral and lies anteriorly within a keel that is often posteriorly bifurcate, particularly in large specimens.

Comparisons: Primatella P1 elements have lower, often blunter anterior denticles, a basal platform profile that is invariably downturned posteriorly, and a denser microreticulation that covers both the platform and anterior nodes (Orchard 1983, figs. 3A, B, F, E). Apically pointed anterior denticles of P1 elements of Carnepigondolella are typically more numerous and much smaller. The pit in both Primatella and Carnepigondolella often lies more to the posterior than in Epigondolella, although this is not the case in all species. In addition, a bifid keel is not unique to Epigondolella (contra Mazza et al., 2010, 2012a).

Remarks: All the ornate platform taxa of the upper Carnian and Norian were formerly referred to Epigondolella, particularly to the type species E. abneptis. Orchard (1991a, b) recognized this was inappropriate and established new Carnian species that he assigned to Metapolynathus. Some of these were later assigned to a new genus, Carnepigondolella (Kozur, 2003), although “Epigondolella” primitia remained assigned to Metapolynathus. Prior to the present work, there was disagreement about the generic identity of several species. Kozur (2003) described an older species, “Epigondolella” orchardi (Fig. 4.4-4.6), which he regarded as transitional between Carnepigondolella pseudodiebeli and Epigondolella quadrata (Fig. 4.25-4.27). Mazza et al. (2010, 2012a, b) agreed with this lineage but assigned orchardi to Carnepigondolella, and established an additional transitional species, Epigondolella miettoi, between orchardi and quadrata. In this work I restrict the use of both Carnepigondolella and Epigondolella and assign all the latest Carnian and earliest Norian taxa to Primatella gen. nov.

Composition: Six species of Epigondolella are recognized in the faunas that appear at or near the base of the quadrata Zone. All of these were formerly combined as the E. quadrata population (Orchard, 1983), but in addition to two morphotypes of the name-giver, I now recognize E. miettoi, E. aff. uniformis, E. viatovi, and two un-named taxa. Older species assigned to Epigondolella by authors are now referred to Primatella, which is regarded as the forebear.

Stratigraphic range: The oldest representatives of Epigondolella recognized in this work were formerly combined in the E. quadrata population (Orchard, 1983), which is well established as no older than the late Kerri Zone of the lower Norian in several localities in British Columbia (Orchard, 1983, 1991b). Epigondolella is the dominant genus in most collections that span the remainder of the lower Norian and, depending on one’s interpretation, into the younger Norian.

Kraussodontus gen. nov.

Derivation of name: Named for Peter Krauss, long-serving conodont preparator at GSC Vancouver.

Type species: Species Kraussodontus petersi sp. nov.

Diagnosis: The P1 platform elements are characterized by straight to curved, elongated or abbreviated ovoid platforms with largely...
subparallel lateral margins of generally uniform height, and a relatively rounded posterior margin of varying width. In some taxa, there is a medial to posterior platform narrowing on one or both sides; the posterior margin may be narrow and tapered, or broader and truncated but it is never broader than the anterior platform. The anterior margins are inornate to weakly ornate. Relative blade-platform length and pit position varies.

**Description:** P, platform elements are commonly elongate with a length to breadth ratio of about 3:1, but in some species this is reduced to 2:1. Long axes are usually straight or slightly curved, but a few are strongly curved so, in upper view, although the lateral margins are generally subparallel, the overall platform shape may be concavo-convex, plano-convex, or biconvex; in a few species a minor narrowing may occur on one or both sides in a medial or posterior position. The posterior platform varies in breadth but is always narrower than, or equal to, that of the anterior platform. The posterior outlines are essentially rounded but the posterior margin may be bulbous, tapered, or linguiform. In lateral view, the platform margins are quite variable but significant parapets do not occur: the profile commonly maintains a uniform height or gradually rises towards the anterior where it may either drop precipitously or decline in a gradual slope. A few nodes may occur at the anterior platform margin but they are rarely well formed.

Free blades are commonly one-third element length but the oldest representative has no free blade, whereas platform reduction in some species leads to a relatively long free blade equal to about one-half element length. The blade upper profile commonly forms a low convex crest but may be of uniform height. The carina is equally variable consisting of as few as three and as many as nine generally low nodes that may be of uniform size throughout or larger at the posterior end where a cusp may be distinguishable, or where several partly fused nodes may be higher than those to the anterior; the cusp is often indistinct.

The pit is posterior with respect to both the platform and keel in most older species, and migrates to a more submedial position in some younger representatives, in which a posterior keel occurs.

**Comparisons:** Species of *Kraussodontus* are most similar to *Quadralella* but they lack the typical quadratoform outlines, the commonly expanded or reduced posterior platforms, strong lateral constrictions, and the often ornate anterior margins. The rounded posterior platforms also contrast with those of *Metapolygnathus* species, which have a more anteriorly located pit than most species of the present genus. Species of *Parapetella* are distinguished by their strongly differentiated anterior margins.

**Composition:** Fourteen species or variants are differentiated in this new genus, only one of which resembles a named species, *K. reversus* (Mosher). All taxa will be described in the monograph.

**Stratigraphic range:** Elongate platforms of *Kraussodontus* first appear low in the *samueli* Zone of the upper Carnian Ludington Formation at Black Bear Ridge and range into the parvus Zone, in the basal part of the Norian as recognized herein. It is not known when the genus originated, but it is regarded as an offshoot of *Quadralella*.

**Quadralella lobata** gen. et sp. nov. 32-34

**Kraussodontus peteri** sp. nov. 20-22

**Derivation of name:** As for genus.

**Holotype:** GSC 132602, Figure 3.22-3.24.

**Type stratum:** Bed 3 (GSC cur. C-305867), within the Pardonet Formation.

**Age:** The interval informally named the n. sp. Q Zone, upper Carnian.

**Diagnosis:** A species of *Kraussodontus* in which the P element has an oval platform of variable length with sub-parallel to biconvex margins that taper to a narrow rounded posterior outline. Platform margins are upturned and in profile are slightly raised to the anterior where subdued nodes may occur. The blade is typically short (one-fourth total length), but appears longer in younger representatives that have a shorter platform. The carina terminates in a conspicuous cusp that lies well in front of the posterior margin and is surrounded by a broad brim. The pit lies near the posterior end of the keel.

**Remarks:** The stratigraphically oldest representative and holotype has a long platform and a relatively short blade, whereas younger specimens have shorter platforms and anteriorly shifted pits.

**Metapolygnathus Hayashi 1968**

1968 *Metapolygnathus* gen. nov. – Hayashi, p. 72.


**Type species:** *Metapolygnathus communisti* Hayashi 1968.

**Description:** The P, platform elements of this genus are subrectangular in outline, and have neither anterior parapets nor strong nodes; low nodes may be present at the geniculation point on one or both sides. The free blade is between one-fourth and one-half element length and extends onto the platform as a row of nodes of variable size and spacing; the cusp may be terminal or be followed by additional, sometimes bigger nodes. The carina terminates in front of the posterior platform and is separated from it by a brim of variable width. Compact microreticulae cover the platform margins. The pit is medial to anterior in position, and the keel extends far to its posterior where its termination is squared-off or bifurcated.

**Comparisons:** These elements differ from those of *Primatella* and *Quadralella* in lacking significant anterior marginal nodes, common platform constrictions, and/or posterior pits; from *Parapetella* in lacking strong anterior parapets; and from those of *Kraussodontus* in lacking rounded posterior outlines and/or posterior pits. Some stratigraphically young species of all these genera have anteriorly located pits, which is no longer regarded as a defining feature unique to *Metapolygnathus*. The older genus *Paragondolella* has P elements with a flat platform without geniculation points, a conspicuously high blade carina, a posteriorly located pit, and a different multielement apparatus (Orchard, 2005).

**Remarks:** Prior to the present revision, the author (e.g., Orchard, 1991a, b) referred all late Carnian and basal Norian platform elements with quadratoform outlines, geniculation points, and a free blade to *Metapolygnathus*, regardless of the pit position. This partly arose from the fact that an anterior pit and posterior prolongation of the keel, essential features of the genus, were observed in several different lineages in which anterior migration of the pit occurred through time. Grouping all taxa with such a lower surface morphology in *Metapolygnathus* is not
supported. Similarly, assigning other taxa to Paragondolella, as has been common practice, is equally inappropriate because the latter genus is based on Middle Triassic P. excelsa which has both a conspicuously high carina and particular multi-element attributes (Orchard, 2005). This work addresses this problem by narrowing the scope of both Metapolygnathus and Paragondolella and introducing several new genera.

Composition: At least six variants of Metapolygnathus ex gr. communissi (e.g., Fig. 3.31-3.33) are recognized at Black Bear Ridge, but none of them are common and they are identified as different morphotypes. The oldest representative appears about half way along the exposed Ludington Formation and is distinguished from otherwise similar and contemporaneous Quadraellela species by its mediital pit. Younger Metapolygnathus species have slightly elevated anterior platform margins and an increasingly anteriorly shifted pit. Metapolygnathus parvus (Fig. 3.34-3.36) differs from M. ex gr. communissi in its reduced platform, longer free blade, and anterior pit; an intermediate form will be described in the monograph.

Stratigraphic range: Metapolygnathus ex gr. communissi ranges from within the samuelii Zone through the “Upper primitia Zone” up to within a few meters of the basal quadra Zone. M. parvus is characteristic of basal Norian strata at Black Bear Ridge.

Paragondolella Mosher 1968

2005 Paragondolella Mosher – Orchard, p. 94-5, text-fig. 20.

Remarks: Mosher (1968) emphasized the high-crested blade-carina that characterized all growth stages of this genus as typified by its Middle Triassic type species P. excelsa. The relatively flat, oval platform is a distinctive feature of this taxon that is not exhibited by Carnian taxa. Furthermore, Orchard (2005) demonstrated that the multielement apparatus of typical Paragondolella differed from that of Neogondolella and its derivatives in the Carnian. Many species of Carnian age have been referred to Paragondolella by authors (e.g., Mazza et al., 2012a), whereas Orchard (1991b, 2007a) preferred to combine them with other Late Triassic species referred to Metapolygnathus. In this work, I introduce new genera to accommodate these taxa for which both Paragondolella and Metapolygnathus (q.v.) are now judged to be inappropriate.

Parapetella gen. nov.

Derivation of name: Referring to the formation of an elevated wall-like feature or parapet on the antero-lateral margins of the P1 platform elements.

Type species: Parapetella prominens sp. nov.

Diagnosis: The P1 platform elements have raised anterior platform margins that are increasingly differentiated into distinctive parapets that may be round-topped or angular in profile with an anterior edge that descends to meet the blade gradually or abruptly.

Description: The P1 elements include broad to narrow and long to short posteriorly downturned platforms with upper view outlines of considerable variety: they may be subrectangular, oval, pointed, linguiform, medially constricted, posteriorly attenuated or expanded, or strongly reduced. In all cases, the anterior platform margins are clearly higher (when viewed laterally) than the posterior parts and increasingly differentiated so as to produce high parapets or “buttons” that are round-topped or angular in profile; the anterior edge of the platform descends to meet the blade gradually or abruptly. Platform nodes occur rarely although the parapets may be weakly denticulate. Compact microreticulae cover both the platform and parapets. Free blades are one-third to two-thirds total unit length, depending on the extent of platform reduction. The carinal nodes may terminate in front of a wide brim, or continue close to the posterior end of the platform with a narrow brim: it may end in either a conspicuous cusp or two or more fused nodes. A pit is posterior in early forms, medial in later forms, and anterior in the youngest forms, with concomitant development of a posterior keel that may have a quadrate, pointed, or bifurcated termination, reflecting the platform shape.

Comparisons: Many species of Parapetella have a comparable platform outline to those of Primatella, but in all cases can be distinguished from them by having a parapet rather than strong anterior nodes or denticles. The less ornate or inornate genera Kraussodontus, Metapolygnathus, and Quadraellela may sometimes have raised anterior margins, but they lack well-differentiated parapets.

Remarks: The function of the anterior parapet in this genus is clearly comparable to that of the denticles in Primatella and Epigondolella and the genera evidently developed similar or even identical platform shapes to accompany those key features.

Composition: About 27, mostly new taxa are assigned to this genus and will be described in the monograph. They are regarded as having developed from inornate Quadraellela species that developed increasingly elevated anterior platform margins. Some species are characterized by a medial constriction, others by posterior attenuation, and both show anterior platform reduction through time (as in contemporaneous Metapolygnathus).

Stratigraphic range: The first appearance of Parapetella at Black Bear Ridge is just above the disappearance of Carneigondolella and is concurrent with the appearance of typical Acuminatella species. This corresponds to the base of the upper Carnian n. sp. Q Zone and the genus ranges upward to immediately beneath the lower Norian quadra Zone. Some constituent species were formerly assigned to “Metapolygnathus” n. sp. K, “M.” n. sp. P, “M.” n. sp. Q, “M.” n. sp. Y, and, in part, “M.” echinus (Orchard, 2007c; Zonneveld et al., 2010). There is some evidence that the genus appears earlier in Haida Gwaii (Carter and Orchard, this volume).

Parapetella prominens sp. nov.

Fig. 3.25-3.27

Derivation of name: prominens (Latin), projecting, referring to the distinctive upstanding parapet on each anterior platform margin.

Holotype: GSC 132604, Figure 3.25-3.27

Type stratum: Bed 18e (GSC cur. C-307184), within the Pardonet Formation.

Age: parvus Zone, basal Norian.

Diagnosis: The P1 elements of this species have a platform that is about twice as long as broad, and a free blade that is between one-third and one-half of the total element length. The long axes of the elements are straight to incurved and the posterior platform outlines vary from rect-angular to round to tapered and inturned. All specimens have high anterior parapets that double the height of the platform and are clearly differentiated from the relatively flat posterior platforms. In profile the parapets have a rounded to subtriangular outline. The carina is composed of 4-6 nodes that are commonly highest at the posterior end where they may be partly fused; platform brims are of variable width, and may include an accessory denticile. The pit underlies the center of the platform and has a posterior keel that reflects the platform shape.

Comparisons: The prominent parapet is a unique feature that separates this species from others of similar outline. There are several other new, as yet undescribed species of this genus that differ in platform shape, parapet differentiation, and pit position.


Primatella gen nov.

Derivation of name: Derived from the trivial name of the type species.

Type species: Epigondolella primitita Mosher, 1970.

Diagnosis: Anteriorly ornamented, downarched P1 platform elements of variable outline with generally inornate posterior and moderately high, apically blunt to sharp anterior marginal denticles that are commonly equal to between 20% and 40% of the total depth of the element measured from the denticle tip to the basal keel margin. Dense microreticulation covers both the platform and rounded nodes.
rinal usually terminates in front of the posterior margin and a platform brim is generally developed. Pit position is variable but commonly medial or posterior, and only rarely anterior.

**Description:** The P₁ platform elements are generally long with a length: breadth ratio ranging from 3:1 to 1.5:1. In some species, the elements are rectangular in outline, but others show a distinct medial constriction, particularly in early growth stages. The posterior margin, although often straight, may be obliquely truncated, rounded, or posterior-laterally expanded. In lateral view, *Primatella* species are arched with the posterior platform downturned; the anterior platform and blade also have a downward projecting lower surface.

The platform is often divided into two subequal parts, which is particularly evident in those elements with a constriction. The anterior part bears 2-6, commonly three moderately sized marginal nodes or denticles on each margin, although the two margins may be unequally developed. These denticles are usually well differentiated and have either sharp apices or may be round-topped, particularly in stratigraphically older species and in large specimens of descendant species. The posterior platform is generally unornamented but exceptionally may bear scalloped or incipiently nodose margins. Compact microreticulae cover the platform margins and nodes.

The free blade is approximately one-third total unit length with closely spaced, partly fused denticles forming an arcuate upper profile with maximum height at its midlength or, more commonly, near its anterior end. The denticles descend onto the platform and continue as often small nodes that increase in size to the posterior. The carina, consisting of 1-4 nodes, is variable to the posterior of the ornament anterior platform and forms the basis for further speciation: 2-3 variably separated nodes that extend close to the posterior platform margin, or stop far anterior of it with a distinct posterior platform brim. In many specimens the posteriormost carinal node is the largest, although it is not necessarily the cusp. In some younger species, the terminal carinal node lies close to the center of the platform.

The pit varies in position from the posterior of midlength and subterminal within the keel in early forms, to subcentral and anteriorly shifted within the keel in more advanced forms; in general, the pit lies beneath the platform constriction in those elements in which it is developed. Exceptionally, the pit is anterior of the platform center.

**Comparisons:** The ornate character of *Primatella* elements distinguishes them from the inornate or weakly ornate representatives of *Quadralella*, *Kraassodontus*, *Metapolygnathus*, and *Parapetella*. The P₁ elements of *Acuminatella* differ in being narrower, having smaller and more numerous platform nodes, and typically in their long and high carina that extends to the pointed posterior platform margin. *Epigondolella* has larger, consistently sharper anterior denticles, a lower lateral profile that is “stepped up” posteriorly rather than downturned, a consistently medial pit, and less compact microreticulation on the platform. *Carnepigondolella* species have smaller rounded nodes or sharp denticles at their less steep anterior platform margins, and commonly also on the posterior platform.

**Remarks:** Initial study of the Pardonet Formation conodonts throughout Williston Lake led to the characterization of an “*Epigondolella primitia*” population by Orchard (1983, fig. 2). This composite fauna included diverse morphotypes that commonly co-occur in the abundant faunas of the latest Carnian and earliest Norian age in that area. Initially, Kozur (1989, p. 402, 403) regarded “*Epigondolella primitia*” as an example of *E. abeptis* (Huckriede), but re-illustration of the holotype by Orchard (1991b) showed it had a more anteriorly located pit, less developed anterior denticles, a distinctive platform microreticulation, and a differing lower surface profile. The anterior location of the pit in particular led Orchard (1991b) to refer the species to *Metapolygnathus* because such a feature is characteristic of the type species of that genus, *M. communis* Hayashi.

Amongst the “*Epigondolella primitia*” population” of Orchard (1983), several independent species have subsequently been differentiated.

Kozur (2003) introduced “*Epigondolella orchardi*” for medially constricted P₁ elements with the terminal node of the carina in a central position and a more posteriorly situated pit, and “*Metapolygnathus mersinensis*” was introduced by Kozur and Moix (in Moix et al., 2007) on the basis of its shorter platform and differing carina. I further separate elongated elements with widely separated posterior carinal nodes and those having differing platform shapes. The stratigraphically oldest species have a more posteriorly located pit and round-topped and/or less differentiated nodes rather than sharp anterior denticles. *Primatella primitia* sensu stricto is now restricted to forms with three closely spaced posterior carinal nodes. All these species are united in having well developed anterior platform nodes or denticles, and strong microreticulation over both platform and nodes. However, they correspond neither to *Metapolygnathus* nor *Epigondolella* in key respects, so I establish this new genus, *Primatella*.

*Primatella* with relatively long platforms and posterior pits first appear concurrently with the last *Carnepigondolella* characterized, in contrast, by short, abbreviated platforms and medial pits. Although both genera are ornate, the latter is not regarded as ancestral to *Primatella*, which is regarded as having developed from *Quadralella* through increasing differentiation of relatively large anterior nodes compared with those found in typical *Carnepigondolella*.

**Composition:** At least 21 species or subspecies of *Primatella*, and several additional questionable taxa, are differentiated at Black Bear Ridge. Those that have previously been described (under various genera) are *P. primitia* (Fig. 4.13-4.15), *P. orchardi* (Fig. 4.4.4-6), *P. mersinensis* (Fig. 4.7.4-9), and *P. pseudoechinatus* (Fig. 4.10-4.12). Other taxa are described in the monograph. These fall into several subgroups characterized by differing platform shapes: namely both long and short rectangular platforms, medially constricted, ovoid, and asymmetrical outlines. Additional taxa questionably included in *Primatella* have less differentiated anterior denticles than is typical and are regarded as transitional from weakly ornate species of *Quadralella*.

**Stratigraphic Range:** The first *Primatella* species, characterized by less discrete anterior nodes, appear in the “n. sp. Q” Zone and are confined to the Carnian. Typical and better known species appear at the base of the “*Lower primitia*” Zone and all range into, and some to the top of, the “*Upper primitia*” Zone. They are less common in the former interval, but overwhelmingly dominant in the latter. Three undescribed species appear in the Norian.

**Primatella primitia** (Mosher, 1970)

*Fig. 4.13-4.15*

1970 *Epigondolella primitia* n. sp. – Mosher, p. 740-41, Pl. 110, figs. 8, 11, 12 (only).

1973 *Epigondolella primitia* Mosher – Mosher, p. 161, Pl. 18, figs. 1, 2, 11 (only).


**Description:** The P₁ element of this species is relatively long, with 2-5 anterior denticles on each margin, a medial constriction more evident in earlier growth stages, an unornamented rectangular posterior platform, and carinal nodes that extend onto the posterior platform. Three closely spaced carinal nodes lie posterior of a gap that separates them from the cusp; a tiny fourth accessory node may occur to the posterior. A broad platform brim generally separates the posterior carina from the platform margin. The posterior platform tends to widen with growth and in later growth stages; the constriction present earlier is commonly “overgrown” so as to produce elements of uniform breadth. The pit generally occupies a position beneath the platform midlength or a little to the anterior in mature specimens, and is anteriorly shifted within the keel, which may have a straight, oblique, or bifid termination.

**Comparisons:** *Primatella conservativa* differs from *P. primitia* in having two separated carinal nodes on the posterior platform. *Primatella*
**Remarks:** The holotype has two unique attributes not present in three other specimens illustrated by Mosher (1970): a pit that is located slightly to the anterior of the platform midlength compared with the more common medial position, and a posterior carina composed of three closely spaced nodes plus a small posteriormost accessory node. The presence of the latter is a variable feature seen only in some of the larger specimens of this species, so emphasis is placed here on the occurrence of the three adjacent nodes.

**Stratigraphic range:** Mosher (1970) illustrated specimens from both the early Norian Kerri Zone of Brown Hill, and the late Carnian Macrolobatus Zone of Pardonet Hill, but the holotype, and only typical specimen, came from Subzone II of the Kerri Zone. At Black Bear Ridge, the species occurs sporadically throughout the late Carnian “Lower primitia” Zone and the lower Norian parvus and “Upper primitia” zones.

**Primatella asymmetrica sp. nov.**

**Derivation of name:** Referring to the asymmetrical platform outline.

**Holotype:** GSC 132616, Figure 4.19-4.21.

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**Primatella mersinensis** has a relatively shorter rectangular platform.

Type stratum: Bed 18h (GSC cur. C-307817), from within the Pardonet Formation.

Age: parvus Zone, basal Norian.

Diagnosis: The distinctive P1 element of this species has an expanded, strongly convex outer platform margin that meets the straight inner platform margin at one postero-lateral corner; this imparts an asymmetric lobate posterior outline. Rarely, the posterior margin is crenulated but otherwise it is unornamented. The anterior platform margins bear 3-5 discrete sharp denticles or, in larger specimens, round-topped discrete nodes on each margin. The blade is about one-third element length and continues as a carina composed of 4-5 discrete nodes that either terminate well in front of the posterior margin and a broad platform brim, or as an additional isolated posterior node in front of a narrow brim. The pit is subcentral and lies within an arcuate keel that extends posteriorly far beyond it.

Comparisons: The lobate posterior outline and lack of a posterior carina distinguishes this species from others assigned to Primatella. Some elements referred to A. acuminata have slightly asymmetric but much narrower posterior platforms and a carina that continues to the posterior tip.

Stratigraphic range: This species appears near the base of the parvus Zone and appears to be one of the few Primatella species that is largely, or exclusively, Norian in age. It extends to high in the “Upper primitia Zone.”

Primatella conservativa sp. nov.

Fig. 4.1-4.3

1970 Epigondolella primitia n. sp. – Mosher, p. 740-41, Pl. 110, figs. 10, 13, 16, 17 (only).
1973 Epigondolella primitia Mosher – Mosher, p. 161, Pl. 18, figs. 7, 8, 9, 10 (only).
1983 Epigondolella primitia Mosher – Orchard, p. 178-9, Fig. 15A-C.
2012 Metapolygnathus cf. primitius – Mazza et al. (a), p. 117-8, Pl. 8, fig. 12.

Derivation of name: conservativa (Latin), referring to the relatively common and conservative morphology of the posterior carina in this member of the primitia group.

Holotype: GSC 132608, Figure 4.1-4.3.

Type stratum: Bed 21d (GSC cur. C-307827), within the Pardonet Formation.

Age: parvus Zone, basal Norian.

Diagnosis: An elongate Primatella with a posterior carina composed of two well separated carinal nodes, the posterior of which lies well in front of the posterior end of the platform, with the consequent development of a broad platform brim.

Comparisons: This species is closely allied to P. primitia (q.v.).

Remarks: Mazza (2012a) included similar forms in Metapolygnathus cf. primitius, which he noted was very common in Pizzo Mondello, in contrast to Primatella primitia sensu stricto, which was abundant in, and confined to North America. In fact, the latter taxon, in the restricted scope described by Kozur and Moix (in Moix et al., 2007), is uncommon in the Canadian sections. P. conservativa, which was included in the species primitia by Mosher (1970, 1973), is the more common species at Black Bear Ridge. Lateral elongation of the anterior nodes or denticles is seen in some specimens of each species, and both species also have a distinct platform brim posterior of the carina.

Stratigraphic range: At Black Bear Ridge, the species is the first of the “typical” Primatella species to appear near the base of the upper Carnian “Lower primitia Zone,” and it ranges through the lower Norian “Upper primitia Zone.” The two specimens illustrated by Mosher (1970) and included here came from matrix of the Carnian Macrolobatus Zone of Pardonet Hill (GSC cur. 64628), whereas those illustrated by Orchard (1983) come from the Norian Kerri Zone. Similarly, Mazza et al. (2012a) recorded their Metapolygnathus cf. primitius specimens from both the uppermost Tuvalian and lower Lacistian.

Quadralella gen. nov.

Derivation of name: Refers to the often rectangular or quadrate outline of the P1 platform elements in many species.

Type species: Quadralella lobata sp. nov.

Diagnosis: P1 platform elements are generally elongate, posteriorly downturned, with a straight to curved longitudinal axis. Many species have straight, subparallel lateral margins, but others have a distinct posterior to medial platform constriction, or the platform expands in width progressively or abruptly to the posterior. A few have asymmetric outlines. The anterior platform margins, which may be higher than the posterior, commonly bear poorly differentiated nodes. The blade is commonly between one-third to one-half total element length, and the carinal nodes are variable, ending in a large terminal node with a wide posterior brim, or extending close to the posterior platform margin. The pit varies in position from posterior to subcentral within the keel, in the latter case with a posterior prolongation of the keel.

Description: The P1 platform elements are generally elongate with a straight to curved longitudinal axis and a length: breadth ratio ranging from 3:1 to less commonly 1.5:1. In many cases, the elements are subrectangular in outline and have a squared-off posterior margin, but some are subtriangular with postero-lateral expansion. Some smaller species exhibit a distinct posterior to medial constriction. Rarely the elements are curved or have a posterior linguiform process. In lateral view, species are arched with the posterior platform downturned; the anterior platform and blade also have a downward projecting lower surface.

In stratigraphically older species, the lateral profile of the platform remains at a constant height but, particularly in some elements with a platform constriction, the platform margins anterior of the constriction are raised. The elements commonly have several subdued or incipient nodes on the anterior platform margins, but these are generally not well developed, and often the margins appear inornate. When present, the nodes may occur on the down sloped anterior margins and/or the anterior lateral margins. Compact microreticulae cover the platform margins and nodes.

The high-standing blade is commonly between one-quarter to one-half total element length but a free portion is often absent due to the development of anteriorly tapered platform flanges (anterior trough margins), particularly in stratigraphically older species. The blade bears closely spaced, partly fused denticles forming a straight to weakly convex upper profile. The denticles descend onto the platform and continue as a row of discrete nodes that become larger towards the posterior. In many species the posteriormost carinal node is the largest although it is not necessarily the cusp. Commonly, the terminal carinal node/ cusp lies well in front of the posterior platform margin and there is a wide posterior brim. Some species have 2-3 variably separated, sometimes partly fused, carinal nodes that extend beyond an indistinct cusp and terminate close to the posterior platform margin. Secondary carinal nodes may be developed in postero-laterally expanded elements.

The pit varies in position from posterior and subterminal within the groove keel in early forms, to subcentral and anteriorly shifted within the keel in younger forms; in general, the pit lies beneath the platform constriction in those elements in which it is developed. The keel expands progressively to a variable distance posterior of the pit where it is either truncated or bifurcated.

Comparisons: Some Metapolygnathus species appear similar to Quadralella but, whereas the latter has a pit in the posterior half of the platform, the former characteristically has a pit that is central or anterior in position. Furthermore, Metapolygnathus species are commonly inornate or have only a single anterior node in contrast to the ornate anterior platform of some Quadralella species in which the pit is shifted towards the centre. Parapetella species are also commonly inornate with anteriorly shifted pits but they differ most clearly in their well differentiated
anterior buttress or parapet development. Species of Quadralella and Primatella may have similar platform outlines but the latter have clearly differentiated anterior platform nodes or denticles that are often apically pointed. Carnepigondolella species are generally smaller and have flatter platforms and more ornate margins. Some Acuminatella species have similar anterior nodes but are characterized by a more developed posterior carina and a strongly reduced tapered platform.

**Remarks:** The new genus is introduced to accommodate taxa that were previously referred to Metapolygnathus by the present author, and often to Paragondolella by others. Some have been also referred previously to Carnepigondolella. Phylectic trends include a shortening of the platform and concomitant lengthening of the free blade, anterior platform margins that become progressively higher and more ornate, and an anteriorly migrating pit.

**Composition:** Quadralella includes many of the Carnian species previously referred to Metapolygnathus or Paragondolella, neither of which is regarded as appropriate (see above). About 23 taxa are differentiated from Black Bear Ridge, of which *Q. angulata* (Mazza, Cau and Rigo), *Q. carpathica* (Mock), *Q. praecommunisti* (Mazza, Rigo and Nicora) (Fig. 3.28-3.30), and *Q. tuvalica* (Mazza and Rigo) (Fig. 3.19-3.21) are known elsewhere. It is probable that several other known taxa are also best referred to this new genus, including *Q. polygnathiformis* (Budurov and Stefanov) and *Q. nodosus* (Hayashi). Other new species will be described in the monograph.

**Stratigraphic range:** Quadralella is present in the stratigraphically lowest *samueli* Zone at Black Bear Ridge and is thought to have a long history earlier in the Carnian where it provides the root stock for most if not all the other genera described here. About 12 taxa extend into the basal Norian *parvus* Zone, but all disappear thereafter (Orchard, 2007c, fig. 5).

*Quadralella lobata* sp. nov.

**Composition:** *Quadralella* includes many of the Carnian species previously referred to *Metapolygnathus* or *Paragondolella*, neither of which is regarded as appropriate (see above). About 23 taxa are differentiated from Black Bear Ridge, of which *Q. angulata* (Mazza, Cau and Rigo), *Q. carpathica* (Mock), *Q. praecommunisti* (Mazza, Rigo and Nicora) (Fig. 3.28-3.30), and *Q. tuvalica* (Mazza and Rigo) (Fig. 3.19-3.21) are known elsewhere. It is probable that several other known taxa are also best referred to this new genus, including *Q. polygnathiformis* (Budurov and Stefanov) and *Q. nodosus* (Hayashi). Other new species will be described in the monograph.

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*Quadralella lobata* sp. nov.

**Derivation of name:** lobat (new Latin), lobed, as produced by the posterior platform constriction.

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