Research Article

THE CARNIAN-NORIAN BOUNDARY GSSP CANDIDATE AT BLACK BEAR RIDGE, BRITISH COLUMBIA, CANADA: UPDATE, CORRELATION, AND CONODONT TAXONOMY

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Abstract – Re-assessment of conodonts from the Carnian-Norian boundary (CNB) at Black Bear Ridge (BBR), British Columbia and Pizzo Mondello (PM), Sicily improves correlation. Fossil endemism is less of a problem than are differing taxonomic approaches. Re-evaluation of literature suggests that most platform genera differentiated at BBR can also be recognized at PM. These are *Carnepigondolella, Ancyrogondolella, ?Kraussodontus, Metapolygnathus, Norigondolella, Parapetella, Primatella*, and *Quadralella*. Only *Acuminatella* at BBR is endemic, whereas use of *Hayashiella* and *Paragondolella* at PM is discounted. Hence, faunal turnovers PM-T1 and PM-T3 are not strongly endemic. Standardization of the conodont nomenclature facilitates improves correlation of the two GSSP candidates: top *Carnepigondolella samueli* Zone at BBR is equivalent to a position within the "*Epigondolella*" vialovi Zone at PM; the *Primatella primitia* Zone can be recognized in both sections; correlation of the *Metapolygnathus parvus* Subzone is strengthened by 14 new conodont identifications at PM, including relatives of the *Pr. gulloae* Zone index; the lower Norian succession of *Ancyrogondolella quadrata* succeeded by *An. triangularis*, well-known in western Canada, appears corrupted at PM.

The FAD of *Metapolygnathus parvus* alpha morphotype can be correlated between sections, as can the simultaneous demise of typical Carnian taxa. At BBR, the concurrent appearance of diminutive conodont species corresponds to geochemical excursions implying anoxia and a temperature maximum during the *Me. parvus* Subzone. Within 1 m above this datum, the FAD of other fossil proxies occur, including an array of conodonts, the bivalve *Halobia austriaca*, and the ammonoid *Pterosirenites* sp.. The *Me. parvus* Subzone corresponds to the uppermost part of the traditional Carnian ammonoid zone of *Klamathites macrolobatus*.

INTRODUCTION

This paper provides a summary of the conodont biostratigraphy and other salient features of the Carnian-Norian boundary (CNB) succession at Black Bear Ridge (BBR), British Columbia, Canada, a candidate for the Global Stratotype Section and Point (GSSP) for the stage boundary (Orchard, 2007b, c). It also presents a further rationale for the BBR conodont taxonomy presented earlier (Orchard, 2013, 2014) and, through that filter, re-assesses the conodont succession described from Pizzo Mondello (PM), Sicily, Italy (Mazza et al., 2011, 2012a, b, 2018; Mazza & Martinez-Perez, 2015; Rigo et al., 2018): similarities between the two successions are greater than previously recognized, but significant anomalies remain. Alternative horizons for CNB definition are considered.

A thorough description of the conodonts and their succession across the CNB at BBR was provided by Orchard (2014) following the earlier introduction of new genera (Orchard, 2013). The conodonts and ammonoids from the entire BBR succession on Williston Lake identify strata ranging from within the upper Carnian up to the Hettangian of the Lower Jurassic (Orchard et al., 2001a, b). The studied CNB interval represents the lowest ~90 m of the succession, starting within the upper Carnian Ludington Formation and extending into the Pardonet

Published online: Septermber 13, 2019

Orchard, M.J. 2019. The Carnian-Norian GSSP candidate at Black Bear Ridge, British Columbia, Canada: update, correlation and conodont taxonomy. *Albertiana*, vol. 45, 50–68.

Formation as high as the base of the lower Norian *Malayites dawsoni* (ammonoid) Zone.

The succession of Ludington and Pardonet formations formed under low energy conditions in a deep water, lower slope - basin paleoenvironment, as a distal ramp facies at the passive western margin of Pangaea (Zonneveld et al., 2010; Onoue et al., 2016). A rich pelagic fauna occurs in the Pardonet Formation and ammonoids occurring at multiple levels show that the studied section includes both the upper Carnian Klamathites macrolobatus Zone and the succeeding lower Norian Stikinoceras kerri Zone (see Tozer, 1994; McRoberts & Krystyn, 2011; Balini et al., 2012). Conodont faunas occur throughout the section, and are often abundant in the Pardonet Formation (Orchard, 2014, fig. 5). Pelagic bivalves are common and have been described by McRoberts (2011). Some ichthyoliths (Johns et al., 1997; Johns, in Orchard et al., 2001a, b) and brachiopods (Sandy, in Orchard et al., 2001a, b) have been described, as have several ichthyosaurians from nearby localities (Gowan 1995, 1996). Geochemical analyses across the boundary interval have been undertaken for $\delta^{13}C_{org}$ (Williford, 2007); for ${}^{87}Sr/{}^{86}Sr$, $\delta^{13}C_{carb}$, $\delta^{18}O_{carb}$, and the redox sensitive elements (V, Ni, and Cr) (Onoue et al., 2016); and for $\delta^{18}O_{PO4}$ in conodont apatite (Sun et al., 2019; in press). Magnetostratigraphic sampling failed to reveal a primary signal (Muttoni et al., 2001).

CONODONT DIVERSITY AND ENDEMISM

Different taxonomic approaches have been taken by conodont researchers in the Upper Triassic (Orchard, 2014; Mazza et al., 2012b, 2018). This has resulted in different morphological scope for several genera, variable diagnoses of species, and a resulting nomenclature that makes comparison of the primary candidate successions at Black Bear Ridge (BBR) and Pizzo Mondello (PM) in Sicily more challenging. Mazza et al. (2018, p. 82-3) noted that correlations between the two were problematic, citing differing paleolatitudes and paleoecologically induced endemism. The extent of this provincialism is examined here and found to be less than was previously thought.

Conodonts from all CNB successions are generally dominated by gondola-shaped platform elements of variable shape and oral ornament. These features have been weighted differently by authors. The taxonomy of the less common scaphate elements (Sweet, 1988), of *Neocavitella* and *Misikella*, and the coniform *Zieglericonus* is more straightforward, but these genera are rare or absent at BBR.

The generic classification of platform conodonts from BBR (Orchard, 1991a, 2013, 2014) focuses primarily on the configuration of anterior platform margins (see taxonomy). There is an increase in the amplitude of anterior platform nodes and denticles displayed by platform elements through the Upper Triassic. Platform shape, posterior ornament, relative blade-carina length, and pit position differentiate species within genera, with several of them showing similar evolutionary trends that involve concurrent platform reduction, blade lengthening, and anterior pit migration. Within the study interval, diminutive platform species evolve iteratively, near the top of the *C. samueli* Zone and particularly around the base of the *Me. parvus* Subzone within the *Pr. primitia* Zone.

In addition to eight platform genera described from the CNB interval at BBR (see below), about 150 lesser taxonomic entities (species, subspecies, morphotypes) have been differentiated (Orchard, 2014). This diversity underpins the precise placement of significant faunal horizons expressed as three zones and nine subzones, one of which (the Me. parvus Subzone) is further divided into three intervals (Orchard, 2104, figs. 3-6; Figure 1). At PM, about 45 conodont taxa representing 6 platform genera are described by Mazza et al. (2012, amended Rigo et al., 2018, Mazza et al., 2018) from the same CNB interval; they are: Carnepigondolella, Epigondolella, Hayashiella, Metapolygnathus, Norigondolella, and Paragondolella. For reasons described below, and based on published illustrations, these are re-interpreted as species of the genera Carnepigondolella, Ancyrogondolella, ?Kraussodontus, Metapolygnathus, Norigondolella, Parapetella, Primatella, and Quadralella. These are most of the genera described from BBR, although the numbers of species/ morphotypes differentiated are far fewer at PM. Only the platform genus Acuminatella appears to be totally absent at PM and can reasonably be regarded as a North American endemic.

The comparatively high numbers of taxa differentiated at BBR compared with PM arises from contrasting taxonomic approaches, summarized as 'splitting' and 'lumping'. The former is adopted at BBR (Orchard, 2014) where a typological approach promulgates a richness of taxa that enables stratigraphic and geographic ranges of distinct morphospecies to be discovered, and a potential increase in points of correlation. This is particularly important because many species have previously been broadly interpreted by authors, as is evident in the PM literature. Standardization of the taxonomies used at BBR and PM is the key to optimize correlation of the two CNB successions.

KEY CONODONT DATUMS AT BBR & CORRELATION WITH PM

Significant stratigraphic horizons established at BBR are shown as zones and subzones in Figure 1, which also shows conodont abundance through the entire section and the ranges of genera. Figure 2 shows ranges of both conodonts and macrofossils across the narrower CNB interval. Lower and upper boundary boundaries for the Pr. primitia Zone mark significant faunal turnovers, with the disappearance and appearance of genera, each preceded by accelerated evolution and peak abundances (Orchard, 2014, fig. 5). Species of Carnepigondolella are also relatively small at the top of the C. samueli Zone (C. spenceri Subzone), prior to their extinction. A third turnover showing similar attributes occurs within the Pr. primitia Zone, where the Me. parvus Subzone shows a major reduction in typical Carnian taxa and element diminution in several lineages. The top of the Me. parvus Subzone is marked by the virtual disappearance of all Carnian platform genera other than Primatella and Acuminatella, which are later joined by common Norigondolella. Other than these three turnover events, boundaries between subzones of the C. samueli and succeeding Pr. primitia zones are defined by an



Figure 1 – Conodont zonation, conodont yield, and stratigraphic ranges of genera across the Carnian-Norian boundary interval at Black Bear Ridge. Columnar section on left adapted from Zonneveld et al. (2010), to which the reader is referred for a discussion of the sedimentary units on the left (modified from Orchard, 2014, fig. 5).



Figure 2 – The CNB boundary interval at Black Bear Ridge showing (from left) sample numbers, macrofossil (bivalve, ammonoid) occurrences (gray dots) and ranges, conodont subzones, and key conodont occurrences (black dots) and ranges for the ~5 m interval; clear dots mean uncertain occurrence. Conodont genera abbreviations are *Ac.= Acuminatella*, *K.= Kraussodontus*, *Me.= Metapolygnathus*, *Pa.= Parapetella*, *Pr.= Primatella*; *Q. = Quadralella*. (Modified from Orchard, 2014, fig. 28).

evolutionary succession of species (Orchard, 2014, figures 7-25).

At PM, three conodont faunal turnovers - termed T1, T2 and T3 – were identified by Mazza et al. (2010) and slightly revised by Rigo et al. (2018, fig. 6.4), who also introduced new Tethyan conodont zones. In terms of the latter, turnover T1 corresponds to the base of the "*Epigondolella*" vialovi Interval Zone at PM, and T2 and T3 correspond respectively to the base and top of their *Me. parvus* Zone (see also Mazza et al., 2018, fig. 5). This correlation differs from that proposed by Orchard (2014, fig. 5), who was misguided by the differing scope of genera and their apparent ranges in the two sections. The equivalence of BBR and PM zonation are considered here in the light of taxonomic revisions discussed in detail below.

The *Carnepigondolella* clade and the range of *"Epigondolella"*

Carnepigondolella is the common ornate platform conodont that occurs globally in the upper Carnian. In North America, its

range is thought to lie largely or wholly within the *Tropites welleri* ammonoid Zone, although no direct association of the conodont and ammonoid zone is currently known. The genus disappears by end of the *C. samueli* Zone at BBR, which is believed to correspond to the beginning of the final ammonoid zone of the Carnian, the *K. macrolobatus* Zone. No such correlation has been suggested at PM, where the scope of *Carnepigondolella* has been very different. However, Mazza et al. (2018, p. 87-8, fig. 2; not correct in fig. 5) concluded that turnover T1 at PM corresponds to the top *C. samueli* Zone at BBR because of the disappearance of *Carnepigondolella* at that level has parallels with the reduction in *Carnepigondolella* at PM.

There are two problems with this correlation. First, at PM, *Carnepigondolella* species typical of the *C. samueli* Zone range upward into the "*E.*" *vialovi* Zone alongside "*Epigondolella*" species, which progressively replace the former genus according to Mazza et al. (2018). This correlation fails to take into account that the "*Epigondolella*" species like those identified by Mazza

et al. (2012a; Rigo et al., 2018) in the "*E.*" vialovi Zone are included in *Carnepigondolella* by Orchard (2014). The *C. spenceri* Subzone at the top of the *C. samueli* Zone at BBR is marked by a rapid succession of *Carnepigondolella* species showing reduced platforms, lengthening blades, and anterior migration of the pit (Orchard, 2014, fig. 17, 18). The anterior denticles of these species are comparable to other *Carnepigondolella* species and they are viewed as advanced representatives of that genus rather than a separate genus, and certainly not *Epigondolella* sensu stricto, a genus that occurs first in middle Norian strata (Orchard, 2018).

The same evolutionary trends are common to both BBR and PM. They are manifest in the successive appearance of the alpha and beta morphotypes of *Carnepigondolella pseudodiebeli* sensu Orchard (2014) at BBR, and in the appearance of *C. spenceri* and allied forms. Morphotypes of *C. pseudodiebeli* at BBR are comparable at PM to *C. pseudodiebeli* and "*Epigondolella*" vialovi sensu Mazza & Martínez-Pérez (2015, pl. 2), and *C. spenceri* is

comparable with "*Epigondolella*" *heinzi* (Rigo et al., 2018, p. 206). Hence, the upper part of the *C. samueli* Zone at BBR is equivalent to some part of the "*E.*" *vialovi* Zone, and its top is best drawn within the latter zone (Figure 3).

A second anomaly of the earlier proposed correlation of base "E." vialovi Zone with top C. samueli Zone concerns the range of other genera. Many Quadralella species (called Hayashiella and Paragondolella by Mazza et al., 2018) disappear at that level at PM, whereas Q. angulata, Q. carpathica, Q. oertlii, and Q. tuvalica, as well as others newly described, range well above the C. samueli Zone at BBR. The explanation for this difference may lie in the ecological competition, as invoked for these taxa by Mazza et al. (2009), although the competition is not evident at BBR. It is also notable that other species such as Q. kathleenae, Me. dylani and Me. praecommunisti (Quadralella sensu Orchard), as well as other species formerly included in the latter species (Parapetella clareae, ?Kraussodontus roberti) occur within the C. samueli Zone



Figure 3 – The Pizzo Mondello section, Sicily showing sample numbers (after Mazza et al., 2012b) and the Tethyan conodont zonation and faunal turnovers T1-T3 (after Rigo et al., 2018) on left; on the right, the conodont and ammonoid zonations at Black Bear Ridge, British Columbia with suggested equivalence, including correlation of top *C. samueli* Zone, and base and top of *Me. parvus* Subzone. Revised conodont occurrences at PM (dots) based on published illustrations (see taxonomy text for details). Abbreviations as in Fig. 2, plus *An. = Ancyrogondolella* and '*E* = '*Epigondolella*'. Thin vertical bars connect multiple new records; thick vertical bars are ranges of selected taxa at PM (from Rigo et al., 2018; Mazza at al., 2018); broken lines connect early records of *An. uniformis* and *An. triangularis* that appear out-of-place based on Canadian data.

equivalent at PM. None of these are known from BBR prior to the *Pr. primitia* Zone. On the contrary, the distribution of *Q. lobata* (see taxonomy) at PM correlates well with BBR occurrences, where it ranges midway through the *C. samueli* Zone.

Younger representatives assigned to *Carnepigondolella* at PM, i.e., *C. pseudoechinata* and *C.? gulloae*, are herein re-assigned to *Primatella*, so *Carnepigondolella* sensu Orchard (2014) does indeed disappear within the "*E.*" *vialovi* Zone. This reconciles the apparently different successions at BBR and PM and counters the suggestion (Mazza et al., 2018, p. 88) that the "proliferation of the endemic North American genera absent in the Tethys, allowed the epigondolellids to proliferate earlier in the Tethys." In fact, the same late stage *Carnepigondolella* evolutionary trends and appearance of "*Epigondolella*" occur in both regions.

The *Carnepigondolella* fauna is replaced at BBR by species of *Acuminatella*, *Primatella*, and *Parapetella*, none of which are explicitly recorded at PM. However, rather than being endemic, species of *Primatella* do occur in the younger parts of the "*E*." *vialovi* Zone, and sporadic examples of *Parapetella* occur (Fig. 3). A reinterpretation of illustrated specimens of long-ranging "*Epigondolella" vialovi* from PM identifies within it examples of upper Carnian *C. samueli*, CNB *Primatella* aff. *permica*, and lower Norian *Ancyrogondolella uniformis* (Mazza et al., 2010, 2012b) (see taxonomy). The holotype of *E. vialovi* actually resembles *An. uniformis*, and *An*. aff. *vialovi* has been interpreted as a lower Norian species by Orchard (2014).

In the higher part of the "E." vialovi Zone, several additional species assigned to *Epigondolella* are reported by Rigo et al. (2018), namely E. triangularis, E. uniformis, E. rigoi, and E. quadrata. These species were all established in the lower Norian and are now assigned to Ancyrogondolella (Orchard, 2018). Their presence in the upper Carnian and basal Norian is doubtful based on available illustrations, for example: E. quadrata from PM (Nicora et al., 2007; Balini et al., 2010) have either been previously reassigned to 'Epigondolella' miettoi (Balini et al., 2010), or are here re-assigned to Primatella species; Me. mersinensis from the upper Carnian (Mazza et al., 2012b) resembles Pr. subquadrata; E. rigoi from the upper Carnian (Nicora et al., 2007) resembles the ornate Pr. permica; E. rigoi from the Me. parvus Zone (Nicora et al., 2007; Mazza et al., 2010) is close to Pr. triangulare; and a Norian specimen of E. uniformis illustrated by Mazza et al. (2012b) resembles Pr. rhomboidale (see Fig. 3) None of these are to be confused with younger, lower Norian occurrences of Ancyrogondolella quadrata (Mazza et al., 2012b; Mazza & Martinez-Perez, 2015) and An. rigoi (Nicora et al., 2007; Mazza et al., 2010; Mazza et al., 2012b; Mazza & Martinez-Perez, 2015).

Concerning illustrated specimens of Ancyrogondolella triangularis and An. uniformis from PM, none of the alleged upper Carnian occurrences of those species have been illustrated. In North America, examples of these posteriorly ornate Ancyrogondolella species, often determined as An. ex gr. triangularis, typically occur in the younger lower Norian M. dawsoni and Juvavites magnus ammonoid zones and their appearance within the "C.?" gulloae Zone at PM (sample NA43, in Mazza & Martinez-Perez, 2015, pl. 5), equivalent to the Pr. asymmetrica - Norigondolella Subzone and prior to the An. quadrata Zone at BBR, is problematic: these records need verification.

In summary, the conodont successions at both BBR and PM are interpreted to consist of a diverse *Carnepigondolella* clade that disappears in the upper Carnian and is superseded by faunas that include *Metapolygnathus*, *Quadralella* and the first *Primatella*.

The Carnian-Norian boundary turnover

A second major conodont turnover at BBR involving the disappearance of several Carnian genera begins in the *Acuminatella acuminata – Parapetella prominens* Subzone of the *Pr. primitia* Zone (Fig. 2). This interval represents both a period of evolutionary innovation, and the initial die-off of long-ranging Carnian taxa, which reaches its peak midway through the overlying *Me. parvus* Subzone. At BBR, species with anteriorly shifted pits (*Metapolygnathus* sensu Mazza et al., 2018) are common at this level and therefore probably equate with the original faunal turnover T2 at PM (Mazza et al., 2010, p. 131), which is within the *Me. communisti* Zone of Rigo et al. (2018), where *Metapolygnathus* becomes dominant over "*Epigondolella*".

Faunal turnover PM-T2 has recently been updated to equate with sample NA35 and to approximate the base of the Metapolygnathus parvus Zone (Mazza et al., p. 83, tab.1; Rigo et al., 2018). That revision lowers the base of the Me. parvus Zone (=boundary interval of Mazza et al., 2012b, fig. 2) and reduces the Me. communisti Zone of Rigo et al. (2018) to a single sample (Mazza et al., 2018, tab.1, FNP117). Reassessment of published illustrations from both the Me. communisti and Me. parvus zones at PM confirms that, as at BBR, a mixture of Metapolygnathus, Parapetella, Primatella, and Quadralella species dominate the interval (Fig. 3). Besides Me. communisti, Me. dylani, and Me. parvus, these additional BBR species are recognized (see taxonomy for details): Pa. destinae (Mazza et al., 2012b), Pa. irwini (Mazza et al., 2012b); ?Pa. n. sp. D of Orchard, 2014 (Mazza et al., 2018); Pr. asymmetrica (Mazza & Martinez-Perez, 2015), Pr. bifida (Mazza et al., 2012b); and Pr. triangulare (Nicora et al., 2007; Mazza et al., 2010). The diminutive Pa. johnpauli, Pa. pumilio, and Pa. willifordi are also stated to occur at PM as "Tethyan morphotypes of the Me. communisti fauna" (Mazza et al., 2018), but none of these diminutive species have been illustrated, or their range documented. Quadralella multinodosus and similarly ornate ?Me. dylani also occur at PM but are not found at BBR (see taxonomy).

As recently discussed by Mazza et al. (2018), the FAD of *Metapolygnathus parvus*, which defines the base of the *Me. parvus* (Sub-)Zone, is a datum recognized at both BBR and PM. However, the concept of *Me. parvus* currently embraces several morphotypes (Orchard, 2014; Mazza et al., 2018) with variable platform shape and ornament. The subrectangular-oval alpha morphotype, close to the holotype of the species, appears to be the more stable concept and occurs in both sections. The elongate beta morphotype, which lacks strong nodes or denticles, was erroneously called *Me. echinatus* by Orchard (2007b), a determination that was followed by Mazza et al. (2012b, 2018) both for elements that lacked pronounced ornament (*=Me. parvus* beta morphotype of Orchard, 2014) and others that had a distinctive pair of anterior nodes or denticles, which were

assigned to *Pa. destinae* by Orchard (2014). Finally, the gamma morphotype of *Me. parvus* described by Orchard (2014) has a much longer posterior process than that illustrated by Mazza et al. (2018) and is not clearly the same taxon.

The successive first occurrences of the alpha, beta, and gamma morphotypes of *Metapolygnathus parvus* occur in that order at BBR. According to Mazza et al. (2018, fig. 4), a comparable succession of the BBR morphotypes occurs at PM, but the revisions above imply a somewhat different succession involving *Parapetella destinae* and *Me. parvus* new morphotype. Notably, *Pa. destinae* first appears in the *Ac. acuminata – Pa. prominens* Subzone at BBR, prior to the *Me. parvus* Subzone (Fig. 2; Orchard, 2014, fig. 28), so it is important to specify the scope of the chosen index species.

The substantial and rapid faunal turnover in the Canadian section begins below the base of the *Me. parvus* Subzone and continues through the entire span of the subzone, which is further subdivided into three divisions. The lowest 40 cm of the *Me. parvus* Subzone contains the FAD of *Me. parvus* and of five *Primatella* species, including *Pr. asymmetrica*; the next 40 cm of the *Me. parvus* Subzone contains the first appearance of several more diminutive *Parapetella* species. Most larger Carnian species other than *Acuminatella* and *Primatella* disappeared within this middle division of the *Me. parvus* Subzone is assigned to its upper division (~2+ m at BBR), which is characterized by a bloom of diminutive elements (Fig. 2; Orchard, 2014, Fig. 6). No such division or succession is currently identified at PM.

Norian stasis

At BBR, the top of the *Metapolygnathus parvus* Subzone is defined by the disappearance of the name-giver and its associated diminutive taxa (Fig. 2). Above the *Me. parvus* Zone, faunas are dominated by relatively stable populations of *Acuminatella* and *Primatella* +/- Norigondolella species. There are very few first occurrences about the top of the *Me. parvus* Zone through the remainder of the *Pr. primitia* Zone at BBR, the rare occurrence of *Acuminatella curvata* being an exception. Hence, recognition of the *Pr. asymmetrica* – Norigondolella Subzone of the *Pr. primitia* Zone is generally based on *Primatella* dominated faunas lacking *Me. parvus* Subzone indicators, or by the common association of *Norigondolella*.

The end of the extinction of typical Carnian taxa at BBR approximates PM-T3, which corresponds to the base of the *Carnepigondolella? gulloae* Zone of Rigo et al. (2018, fig. 2). The top of the range of *Me. parvus* at PM is above the base of the "*C.?*" *gulloae* Zone, so the upper boundary of the *Me. parvus* Subzone sensu Orchard (2014) correlates to that higher level (Fig. 3). Illustrated examples of the *Carnepigondolella? gulloae* from PM (Mazza et al., 2012b) are variable and show affinity with several species of *Primatella*, including *Pr. subquadrata*, *Pr. triangulare*, and *Pr. rotunda*. These similarities emphasize the re-assignment here of the PM index species to *Primatella*, and again suggests there was less endemism than previously assumed. Each of these similar *Primatella* species range through the boundary interval at BBR, which suggests that *Pr. gulloae* and its predecessors might

be located at BBR. However, the species lacks clear ancestry and is too poorly known to be a suitable index.

The "C.?" gulloae Zone post-T3 turnover at PM also corresponds to the occurrence of "abundant epigondolellids" (Mazza et al., 2018, p. 83), but in view of the previous observations these may be species of Primatella rather than 'Epigondolella' (=Ancyrogondolella). The presumably correlative Pr. asymmetrica - Norigondolella Subzone strata of the Pr. primitia Zone at BBR appears to have been a relatively stable time without notable evolutionary developments. Then, the wholesale replacement of Primatella by Ancyrogondolella occurred near the top of the S. kerri ammonoid Zone, which is at the base of the "type" An. quadrata Zone. Similar platform shapes occur in populations of both Primatella and early Ancyrogondolella but the anterior denticles of the latter are higher and sharper, which is also reflected in their differing platform microreticulation (Orchard, 1983, figs. 3, 9). This late S. kerri Zone event may correlate with the appearance of "advanced forms of E. quadrata" at PM (Mazza et al., 2012b, fig. 2). The earlier occurrence of An. ex gr. triangularis low in the PM succession (sample NA43) remains an anomaly because strongly sculptured posterior platforms like those illustrated from PM (see taxonomy) are only known to occur above the An. quadrata Zone in western Canada. Notable endemism in the Pr. primitia Zone and equivalent strata are shown by some Norigondolella species, with N. trinacriae occurring at PM, and N. norica at BBR.

CONODONT TAXONOMY & NOMENCLATURE

In this section, the conodont taxonomy developed in North America is explained and compared with that adopted at PM. Although there are faunal differences that can be attributed to endemism, there is far more commonality than hitherto documented.

Generic differentiation of the Upper Triassic platform conodonts is based primarily on the nature of the anterior platform margins (Figure 4; Orchard, 1991a, pl. 3). Ornament is absent or consists of rudimentary to poorly differentiated, low or incised nodes in Quadralella (Fig. 4 a-c), Kraussodontus, and Metapolygnathus; elevated anterior buttresses occur in Parapetella (Fig. 4 k, l); well differentiated nodes becoming relatively short and sharp denticles characterize Acuminatella and Carnepigondolella (Fig. 4 g-j); discrete and high, often apically rounded and microreticulated nodes occur in Primatella (Fig. 4 d-f); and very high and sharp denticles occur in Ancyrogondolella (Epigondolella sensu Orchard, 1991a, 2014; Fig. 4 m-o). Younger, largely middle to upper Norian Mockina, Orchardella, and Epigondolella (Fig. 4 p) also have very high and sharp denticles (see Orchard, 2018) that reach a peak development in Mockina englandi (Fig. 4 q).

Within each of the CNB genera, the pit migrates anteriorly through time producing a longer posterior keel. At PM, many species with medial to anteriorly shifted pits were combined as *Metapolygnathus* (Mazza et al., 2012b), which results in the combination of species of several BBR genera. The BBR taxonomy works well in formerly distant Panthalassan terranes



Figure 4 – Lateral profiles of some Upper Triassic genera: a-c, *Quadralella*; d-f, *Primatella*; g-l, *Carnepigondolella*; k-l, *Parapetella*; m-o, *Ancyrogondolella*; p, *Epigondolella*; q, *Mockina*. Specifically, a (flipped) = *Q. carpathica* (Mock), GSC 131354, sample C; b = *Q. carpathica* (Mock), GSC 131248, sample 0; c = *Q. tuvalica* (Mazza and Rigo), GSC 132604, sample 7; d (flipped) = *Pr. asymmetrica* Orchard, GSC 132947, sample PHE-24, Pardonet Hill east; e (flipped) = *Pr. stanleyi* Orchard, beta morphotype, GSC 132591, sample PHE-23, Pardonet Hill east; f = *Pr. vanlierae* Orchard, GSC 131340, sample PHE-23. Pardonet Hill east; g = *C. zoae* (Orchard), GSC 95203, Peril Formation, Huston Inlet, Haida Gwaii; h (flipped) = *C. anitae* Orchard, GSC 132681, sample 1a; i (flipped) = *C. samueli* (Orchard), GSC 132718, sample C; j (flipped) = *C. spenceri* Orchard, GSC 132714, sample 4; k = *Pa. beattyi* Orchard, GSC 132832, sample 5; l = *Pa. prominens*, GSC 132920, sample 18e; m (flipped) = *An.* aff. *vialovi* (Buryi), GSC 132741, sample 10/06; n = *An. quadrata* (Orchard), GSC 95265, sample PH-213b, Juvavites Cove; o = *An. equalis* (Orchard), GSC 95290, sample C-87005, Lewes River Group, Laberge. Samples are from the Pardonet Formation of Black Bear Ridge unless stated otherwise. Flipped images have been re-orientated 180° horizontally for uniform views.

such as Wrangellia (e.g., Orchard & Carter, 2013), and more southerly, low paleolatitude regions such as Nevada in the USA (Balini et al., 2014), where species of *Acuminatella*, *Parapetella*, *Primatella* and *Quadralella* are recorded. Further afield, this nomenclature has been adopted in Japan (Zhang et al., 2018; Yamashita et al., 2016, 2018), South China (Sun et al., 2016; Zhang et al., 2017, 2018; Jiang et al., 2019), and Turkey (Chen & Lukeneder, 2017). These examples suggest that the BBR taxonomic framework is widely, if not globally, applicable. The following review is arranged alphabetically.

Genus: Acuminatella Orchard, 2013

Type species: Acuminatella acuminata Orchard, 2013

Acuminatella species differ from most contemporaneous taxa in the strongly reduced and tapered posterior platform and well developed posterior carina. Species bear well differentiated anterior platform nodes or small, apically rounded denticles that become more pronounced through the BBR section, hence their use as subzonal indices (*Ac. sagittale, Ac. acuminata*) in the lower *Pr. primitia* Zone. The genus is allied with *Primatella* and, like that genus, appears near the base of the *Pr. primitia* Zone and extends through the entire zone, including the *Me. parvus* Zone extinctions.

Kozur (2003) introduced *Orchardella* for similar but more denticulate 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* as the type species. Kozur (2003) also suggested that CNB species was ancerstral to the younger species, but because there is no stratigraphic continuity between the two, the older homeomorph were referred to the new genus *Acuminatella* (Orchard, 2013). The genus has been described from Haida Gwaii (Carter & Orchard, 2013) and Nevada (Balini et al., 2014), but not outside North America.

Genus: Ancyrogondolella Budurov, 1972

Type species: Ancyrogondolella triangularis Budurov, 1972

This genus is now used for mostly lower Norian species that were previously assigned to *Epigondolella* by Orchard (1991b; 2014), plus others introduced in a recent revision (Orchard, 2018). The genus accommodates platform elements with high and sharp anterior denticles and a bifid basal keel, features of the first representatives in the '*E*.' *quadrata* fauna (Orchard, 2014, figs. 40, 41). A bifid keel may be developed in other broadplatform Late Triassic genera, but the anterior platform ornament is never as pronounced as in *Ancyrogondolella*. Sharp denticles in *Carnepigondolella* are shorter, while those of *Primatella* are typically high nodes or apically rounded denticles (Fig. 4). At PM, only the "advanced Epigondolellae species" identified by Mazza et al. (2012b) in the lower Norian are included in *Ancyrogondolella*.

Keel bifurcation generally arises during growth close to the subcentral pit, with the secondary keels being widely divergent in older representatives and much less so in the youngest species. *Ancyrogondolella* is believed to have evolved from *Primatella* in the early Norian, as documented in many Canadian sections where the former replaces the latter near the top of the *S. kerri* Zone (Orchard, 1991b, 2001a, b, 2014). Populations of *Ancyrogondolella* and *Primatella* have convergent platform shapes, but differing anterior ornamentation. *Ancyrogondolella* is regarded as ancestral to middle Norian *Epigondolella* sensu stricto, *Mockina*, and *Orchardella* (Orchard, 2018), all of which differ in their carina development and lack of a primary bifid keel.

Several species of *Ancyrogondolella* are common to BBR and PM, including Norian *An. quadrata, An. triangularis* sensu lato, and *An. uniformis*. Other species differentiated within the *An. quadrata* Zone at BBR (Orchard, 2014) have not been recorded at PM, while *An. rigoi* is not yet found at BBR. New species of *Ancyrogondolella* are anticipated in abundant undescribed faunas of *An.* ex gr. *triangularis* from the *M. dawsoni* and *J. magnus* ammonoid zones in B.C. The following revisions are proposed for illustrated PM material (sample numbers in bold):

- *An. rigoi* (= *E. rigoi* in Mazza et al., 2012b, pl. 6, figs. 1-7. NA59, NA61; Mazza & Martinez-Perez, 2015, pl. 4). NA68
- *An. quadrata* (= *E. quadrata* in Mazza et al., 2012b, pl. 5, figs. 2-10. NA60, NA58, NA56; Mazza & Martinez-Perez, 2015, pl. 3). NA56, NA60
- *An.* ex gr. *triangularis* (= *E. triangularis* in Nicora et al., 2007, pl. 4, fig. 10; =Mazza et al., 2010, pl. III, fig. 9). **NA68**
- An. ex gr. triangularis (= E. triangularis in Mazza & Martinez-Perez, 2015, pl. 5, figs. 1-12). NA43
- An. uniformis (= E. triangularis in Nicora et al., 2007, pl. 4, figs. 8, 9). NA43.
- An. uniformis (= E. vialovi in Mazza et al., 2012b, pl. 7.3). NA66
- An. uniformis (=E. uniformis in Mazza & Martinez-Perez, 2015, pl. 5, figs. 24, 25 only). NA43

Genus: Carnepigondolella Kozur, 2003

Type species: Metapolygnathus zoae Orchard, 1991a

This genus includes upper Carnian platform conodonts with characteristic short, sharp denticles on anterior platform margins, and sometimes on the posterior margins too. The type species, *C. zoae*, is atypical in having very well-defined, rounded nodes, but its ancestral relationship to the denticulate species is evident in *C. anitae*, in which both ornament styles are present as anterior denticles and posterior nodes. The origin of the genus lies in older strata than is preserved at BBR (*C. gibsoni* is already present near the base), and there may be more than one lineage represented (Orchard, 2014, figs. 17, 18).

At BBR, a succession of *Carnepigondolella* species ends with the *C. spenceri* Subzone of the *C. samueli* Zone, which is characterized by relatively small species with reduced platforms, long blades, and anteriorly shifted pits. The same evolutionary development occurs at PM within the "*E.*" *vialovi* Zone where Mazza et al. (2012b; Martinez Perez, 2016) have characterized these taxa as the beginning of the *Epigondolella* clade. Hence, as discussed above, realignment of the top *C. samueli* Zone at BBR with a position within the "*E.*" *vialovi* Zone at PM is suggested.

Several PM species that were formerly assigned to *Carnepigondolella* by Mazza et al (2012b) are here assigned to

Quadralella (e.g., *Q. carpathica, Q. tuvalica*) or *Primatella* (*Pr. pseudoechinata, Pr. gulloae*). The elements described as *C. orchardi* by Mazza et al. (2012b) are examples of the genus but not the species, which was interpreted as a *Primatella* species by Orchard (2014)(see below).

The succession of *Carnepigondolella* species in the Ludington and basal Pardonet formations at BBR (Orchard, 2014) includes several species identical or allied to those recognized at PM, some of which were assigned to *Epigondolella* (see above). Although informal morphotype designations have also been assigned to variants of *C. zoae*, *C. pseudodiebeli*, and *C. samueli*, all occurrences fall within the *C. samueli* Zone.

- *C. anitae* (= *C. zoae* B in Mazza et al., 2010, pl. I, fig. 8. **FNP53a**
- *C. anitae* (= *C. zoae* in Nicora et al., 2007, pl. 3, figs. 6a-c.). **PM19**
- *C.* ex gr. *milanae* (= *C. zoae* morphs in Mazza et al., 2012b, pl.4, figs. 1-3). **PM19**, **NA8**
- *C. pseudodiebeli* (= *Me. mersinensis* in Mazza et al., 2012b, pl. 4, fig. 10). **NA32**
- *C. pseudodiebeli* (= *C. orchardi* in Mazza, 2009, pl. I, fig. 11; 2012b, pl. 2, figs. 1, 2). **FNP53**, **FNP88a**
- C. samueli (= E. vialovi in Mazza et al., 2012b, pl. 7.2). FNP88a
- *C. miettoi* holotype (= *E. quadrata* in Nicora et al., 2007, pl. 3, fig. 8). **FNP88a**
- *C. miettoi* paratype (= *E. quadrata* in Balini et al., 2010, pl. 3, fig. 5). **FNP88a**
- *C.* ex gr. *spenceri* (= *E. heinzi* in Mazza, Cau & Rigo, 2012a, fig. 9. C-E). NA25, NA27
- C. spenceri (= C. pseudoechinata in Mazza et al., 2012, pl. 2, fig. 5). NA25

Genus: Epigondolella Mosher, 1968

Type species: Polygnathus abneptis Huckriede, 1958

As discussed previously by several authors (e.g., Kozur, 2003), the holotype of *Epigondolella abneptis* is of Middle Norian, Alaunian age and differs from similar lower Norian elements. Orchard (2018) has argued that *Epigondolella* is best used for middle Norian species that, in common with the holotype, are broad and lack both a primary bifid keel and a strong posterior carina. These attributes separate the genus from contemporary *Mockina* and *Orchardella*, and the lower Norian *Ancyrogondolella* (see above).

Species from the upper Carnian of PM were also assigned to *Epigondolella* by Mazza et al. (2012a, b; 2018) but, as discussed above, these were included in *Carnepigondolella* by Orchard (2014). These species are considered here as end-members of that clade, but if a separate genus was to be used, it should not be *Epigondolella* because neither that genus nor its lower Norian replacement, *Ancyrogondolella*, are directly related.

As discussed above, at least some records of *Epigondolella* from high Carnian and low Norian strata at PM can be reassigned to *Primatella* (q.v.; Fig. 3). These specimens provided Mazza et al. (2012b) the basis for proposing continuity between *Carnepigondolella* and *Epigondolella*, which is disputed here. Rather, Orchard (2014) proposed a lineage from *Quadralella* to *Primatella* to *Ancyrogondolella* (formerly *Epigondolella*).

Genus: Kraussodontus Orchard, 2013

Type species: Kraussodontus peteri Orchard, 2013

Platform elements of this genus are characterized by largely subparallel lateral margins of generally uniform height, and a relatively rounded posterior margin that is never broader than the anterior platform. The anterior margins are smooth to weakly ornate. Both relative blade length and pit position varies. Species of *Kraussodontus* are most similar to some *Quadralella* but differ in their rounded, unexpanded posterior platforms.

Kraussodontus has not been widely differentiated in the past, but has now been recognized in the late Carnian of Okinawajima, Japan (Yamashita et al., 2016), and from the Taurus Mts., Turkey (Chen & Lukeneder, 2017). Some elements similar to *K. roberti* were included in *Metapolygnathus praecommunisti* by Mazza et al. (2011, fig. 3, D).

Genus: Metapolygnathus Hayashi, 1968

Type species: Metapolygnathus communisti Hayashi, 1968

The taxonomic scope of *Metapolygnathus* has changed in recent decades. Orchard (1991a, b) assigned almost all platform conodonts of Carnian age to the genus, although he recognised revision was necessary. Many of these species were later assigned to the new genus *Carnepigondolella*, or to those introduced more recently by Orchard (2013). A more restricted scope for *Metapolygnathus* limits it to the late Carnian clade around the type species, *Metapolygnathus communisti*, and its cohorts with mostly inornate platforms and an anteriorly shifted pit (Orchard, 2014). The origins of *Me. dylani* and *Me. parvus* lie in the diverse but uncommon older elements identified as morphotypes of *Me.* ex gr. *communisti* by Orchard (2014, see front-piece), and not within the more ornate *Quadralella praecommunisti*.

Noyan & Kozur (2007, p. 176) included four species in *Metapolygnathus: Me. communisti* with two subspecies (*Me. c. communisti* and *Me. c. parvus* – now elevated to species), *Me. linguiformis, Me. angustus*, and *Me. multinodosus*. The last of these was exceptional in bearing common anterior nodes. Later Mazza et al. (2012b, p. 112) restricted the genus to include only elements with an ".. absence of ornamentation or, at most, the presence of tiny nodes at geniculation points", a diagnosis followed by Orchard (2014). However, more recently Mazza & Martinez-Perez (2015, pl. 6) have divided the *Me. communisti* group into three morphotypes: A bears 1-2 anterior nodes; B corresponds to *Me. multinodosus*, and C has no nodes. At BBR, morphotypes A and B are included in *Me.* ex gr. *communisti* by Orchard (2014), whereas morphotype C, or *Quadralella multinodosus*, does not occur.

Other species previously assigned to *Metapolygnathus* that bear larger, more developed anterior nodes, i.e. *Me. mersinensis* and *Me. primitia*, are now referred to *Primatella* (see below). This includes *Me. mazzai*, the growth series of which (Mazza & Martínez-Pérez, 2015) includes *Pr. asymmetrica*. Notably, these authors also illustrated growth series of *Me. communisti* morphotypes that included elements close to *Pr. asymmetrica* (as morphotype B) and of *Parapetella irwini* (as morphotype C). This diversity appears to be a consequence of a focus on the anteriorly shifted pits of these elements, a feature that is seen also in species of *Parapetella*, *Primatella*, and *Quadralella*.

Metapolygnathus communisti is rare at BBR, where Orchard (2014, fig. 46) differentiated five uncommon morphotypes of Me. ex gr. communisti, all of which either lack anterior nodes or have one or two poorly developed; they differ from one another in their anterior profile and platform outline. Morphotypes 1-4 appear well below the CNB at BBR, before the common occurrence of the Quadralella praecommunisti. The inclusion of Morphotypes 1-4 into Me. praecommunisti by Mazza et al. (2018) broadens the scope of that species even more than its already substantial variability (Mazza et al., 2011), and obscures a more complex phylogeny. Two lineages may be represented - one with ornate Quadralella species (including Q. praecommunisti, Q. multinodosus), and a second with inornate Metapolygnathus species - both showing anterior pit migration, and ultimately reduction of the platform. The types of Me. dylani from BBR are mostly inornate like those of Me. ex gr. communisti, whereas most of those illustrated from PM are ornate. The final expression in these two lineages may be the diminutive and smooth Me. parvus, and some diminutive and noded specimens called Me. echinatus by Mazza et al. (2018, pl. 5).

Regarding Metapolygnathus parvus, Orchard (2014) differentiated three morphotypes (alpha, beta, and gamma) at BBR, each showing progressive reduction of the already small platform, ending in the platform-less gamma morphotype. As discussed above, the alpha morphotype corresponds broadly to the holotype of Me. parvus, but the beta and gamma morphotype of Mazza et al. (2018) differ. The beta morphotype of Orchard (2014) does not correspond to Gladigondolella echinata Hayashi, whose short platform has a distinctive anterior node on each margin. The identification of Me. echinatus in Orchard (2007c, pl. 2, figs 10-12, 22-24) was incorrect because those specimens, which were subsequently re-assigned to the Me. parvus beta morphotype (Orchard, 2014), are smooth or have only a few low nodes. Rather, strongly noded specimens like those referred to Me. echinatus by Mazza et al. (2018) are examples of Parapetella destinae, and one is closer to Pa. n. sp. D of Orchard, 2014 (Mazza et al., 2018).

Regarding the holotype of *Gondolella echinata*, the age of which is uncertain, Carter & Orchard (2013, p. 72, fig. 3. 10-12) discussed and illustrated a specimen from the top of the *C. samueli* Zone in Haida Gwaii that strongly resembles the holotype: they assigned it to *Carnepigondolella* and regarded it an end-member of that clade. Therefore, use of the specific name *echinatus* for *Me. parvus* Subzone CNB indices is discouraged.

Genus: Paragondolella Mosher, 1968

Type species: Paragondolella excelsa Mosher, 1968

Mazza et al. (2009) emphasized the lower side morphology as diagnostic for this genus, namely a posteriorly situated pit and no bifurcation of the keel, as well as a lack of any platform nodes on the upper surface. Also regarded as important features of the type species, *P. excelsa*, are the high anterior carina, and the absence of anterior geniculation points. The latter distinguishes it from all *Quadralella* species. Typical Ladinian *Paragondolella* species often have a broad, relatively flat platform, above which the carina is conspicuous in lateral view. Although platform ornament is generally absent, some species, e.g., P. *inclinata*, occasionally exhibit some weak anterior nodes (e.g., Orchard, 2007a, fig. 3. 1-3). Furthermore, according to Orchard (2005), the genus has a distinctive multielement apparatus.

Paragondolella certainly ranges into the lower Carnian, but probably no higher. Most of the species assigned to the genus by Mazza et al. (2009) should be assigned to *Quadralella*. This includes elements from PM assigned to *P. praelindae* that, unlike the holotype, display a geniculation point and free blade. These PM elements (Mazza et al., 2012b; Rigo et al., 2018) are probable examples of *Q. lobata*, characteristic of the *C. samueli* Zone at BBR.

Genus: Parapetella Orchard, 2013.

Type species: Parapetella prominens Orchard, 2013.

The genus *Parapetella* was introduced for conodont elements from BBR with mostly smooth anterior margins that become increasingly elevated into prominent buttresses. This genus has an uncertain origin but appears widespread in the upper Carnian (e.g., Carter & Orchard, 2013; Orchard, 2014), and apparently occurs in the lower Carnian of South China (Jiang, 2016). In common with several contemporaneous genera, species exhibit anterior pit migration and progressive diminution in the *Me. parvus* Subzone.

Parapetella was not explicitly differentiated at PM (Rigo et al., 2018; Mazza et al., 2018) although, as discussed above, *Pa. destinae* is one species that does occur there (identified as *Metapolygnathus echinatus*). Mazza et al. (2018, p. 88) also stated that *Parapetella pumilio*, *Pa. irwini*, *Pa. johnpauli*, and *Pa. willifordi* occurred at PM as "Tethyan morphotypes of the *Me. communisti* fauna", although only *Pa. irwini* was illustrated (i.e. Mazza et al., 2012b, see list below). Similarly, Mazza et al. (2018) synonymized *Metapolygnathus* n. sp. Y of Orchard, 2007c, as one of many morphotypes combined in an equally broad *Metapolygnathus praecommunisti*; they did not figure a specimen of the species, which was subsequently described by Orchard (2014) as *Parapetella broatchi*. Hence, up to eight species of *Parapetella* differentiated at BBR may also occur at PM:

- *Pa. broatchi* (= *Me.* n. sp. Y Orchard, 2007c = in synonymy with *Me. praecommunisti* in Mazza et al., 2018, p. 90.
- *Pa. clareae* (= *Me. praecommunisti* in Mazza et al., 2011, pl. 2E only). NA18
- *Pa. destinae* (= *Me. echinatus* in Mazza et al., 2012b, pl. 8, figs. 7, 8; =Mazza et al., 2010, pl. II, fig. 12; =Mazza et al., 2018, fig. 5.4 only). **NA39**
- *Pa. irwini* (= *Me. communisti* in Mazza et al., 2012b, pl. 8, fig. 6 only). NA37
- Pa. aff. irwini (= Me. communisti morphotype C, in Mazza & Martinez-Perez, 2015, pl. 6, fig. 25). NA36–NA39
- Pa. johnpauli, Pa. willifordi, Pa. pumilio (= recorded but not figured as "Tethyan morphotypes of the Me. communisti

fauna" in Mazza et al., 2018, p. 88).

?Pa. n. sp. D of Orchard, 2014 (=Me. echinatus in Mazza et al., 2018, fig. 5.2). PM27

Genus: Primatella Orchard, 2013

Type species: Epigondolella primitia Mosher, 1970

Primatella is characterized by larger and higher nodes or denticles than those of *Carnepigondolella*, and much more differentiated than those of *Quadralella*; those of *Ancyrogondolella* are much higher and sharper than in *Primatella* (Fig. 4). The genus appears rarely at the end of the *C. samueli* Zone at BBR and thereafter becomes more common until it dominates the lower Norian fauna above the *Me. parvus* Subzone in BBR. *Primatella* bridges the gap between the disappearance of *Carnepigondolella* (top *C. samueli* Zone) and the appearance of the *Ancyrogondolella* late in the *S. kerri* ammonoid Zone. *Primatella* is regarded as the precursor to *Ancyrogondolella*, but not as a derivative of *Carnepigondolella* but rather evolving from ornate *Quadralella* species (Orchard, 2014, figs. 20, 23). *Pr. primitia* itself is rather rare but it is retained as the zonal name-giver for sake of consistency.

Several ornate species previously assigned to Metapolygnathus - namely Epigondolella primitia, Me. mersinensis, and Me. mazzai - are assigned to Primatella. Also, a variety of elements from PM assigned to Carnepigondolella and Epigondolella are regarded as examples of Primatella. As discussed by Orchard (2014, p. 97), the holotype of Me. mazzai (in Mazza et al., 2012b) from PM (chosen by Karádi et al., 2013) appears to be fall within the range of Me. mersinensis. Those elements included in Me. mersinensis and illustrated by Mazza et al. (2012b) are regarded as a variety of Primatella and Quadralella species (see synonymy in Orchard, 2014, p. 94), including *Pr.* aff. *asymmetrica* and *Pr. subquadrata*. The Me. mazzai growth series of elements illustrated by Mazza & Martínez-Pérez (2015, pl. 7, fig. 15) also includes Pr. asymmetrica, whereas those illustrated by Karádi et al. (2013) have much larger anterior denticles than in Primatella and are regarded as closer to Ancyrogondolella quadrata.

In addition to the *Primatella* species discussed above, two other species have been misinterpreted at PM but are clearly useful for trans-Panthalassan correlation, namely *P. bifida* and *Pr. triangulare*. Orchard (2014, p. 89-90) included *Metapolygnathus linguiformis* sensu Mazza et al. (2012b) in synonymy with *P. bifida* but he did not regard the holotype of *Me. linguiformis* as conspecific as claimed by Mazza et al. (2018, p. 88). In contrast to *P. bifida* (and *Me. linguiformis* sensu Mazza et al.), Hayashi's species differs in having no anterior nodes, as previously discussed by Noyan & Kozur (2007, p. 172).

A second example concerns *Ancyrogondolella rigoi*. Mazza et al. (2018, p. 88) synonymized *Primatella triangulare* with *Epigondolella rigoi* but, as described by Orchard (2014, p. 105), *Pr. triangulare* differs in its posterior platform, lower anterior denticles, longer carina, and less pronounced keel bifurcation. Younger specimens of typical *An. rigoi*, which Noyan & Kozur (2007) regarded as diagnostic of a zone occurring above that of *An. quadrata*, are well illustrated by Mazza et al. (2012b). The long range attributed to *An. rigoi* by Rigo et al. (2018) apparently

combines both that species and Pr. triangulare.

Other species assigned to *Primatella* at BBR include *Epigondolella orchardi*, and *E. pseudoechinata*, both of which have been included in *Carnepigondolella* at PM (Rigo et al., 2018). The type species of *E. orchardi* is from the lower Norian *E. orchardi* – *N. navicula* Zone of Slovakia (Kozur, 2003), the same age as attributed to *Primatella orchardi* at BBR. Specimens of *C. orchardi* illustrated by Mazza (2009, 2012b) are older and close to *C. pseudodiebeli* beta morphotype at BBR, whereas those illustrated by Nicora et al. (2007) and Balini et al. (2010) are probably true *Pr. orchardi*. As interpreted by Orchard (2014), *Pr.* ex gr. *pseudoechinata* embraces broad variation, but the only example of "Carnepigondolella" pseudoechinata illustrated from PM (Mazza et al., 2012b) is re-interpreted here as *C. spenceri* (see above).

The youngest species assigned by Mazza et al. (2018) with question to *Carnepigondolella*, *C.? gulloae*, is also interpreted here as a *Primatella* species with affinity with, and a possible origin in, *Pr. rotunda*. The appearance of the species at PM is sudden and without clear ancestry, so its FAD (T3 of Rigo et al., 2018) lacks context.

- *Pr.* aff. *asymmetrica* (= *Me. communisti* morphotype B in Mazza & Martínez-Pérez, 2015, pl. 6, fig. 15). NA36–NA39
- *Pr. asymmetrica* (= *Me. mazzai* in Mazza & Martinez-Perez, 2015, pl. 7, fig.15 only). FNP117
- *Pr. bifida* (= *Me. linguiformis* in Mazza et al., 2012b, pl. 8, fig. 11; = Balini et al., 2010, pl. 4, fig. 1). **NA39**
- *Pr. mersinensis* (= *Me. communisti* B in Mazza et al., 2010, pl. III, fig. 4). **NA46**
- *Pr. orchardi* (= *C. orchardi* in Nicora et al. 2007, pl. 3, fig. 11). NA33
- *Pr. orchardi* (= *C. orchardi* in Balini et al., 2010, pl. 3, fig. 30. NA53
- *Pr.* aff. *permica* (= *E. rigoi* in Nicora et al., 2007, pl. 3, fig. 12). NA33
- *Pr*. aff. *permica* (= *E. vialovi* in Mazza et al., 2010, pl. II, fig. 4). **NA29**
- *Pr. rhomboidale* (= *E. uniformis* in Mazza et al., 2012b, pl. 7, fig. 1). NA46.
- *Pr.* ex gr. *rotunda* (= *C.*? *gulloae* in Mazza et al., 2012b, pl. 1, figs. 4, 6-9). **FNP134**, **PM30a**
- *Pr. subquadrata* (= *Me. mersinensis* in Mazza et al., 2012b, pl. 4, fig. 7, 9). NA30, NA34
- *Pr. subquadrata–Pr. permica* (=*E. quadrata* in Nicora et al., 2007, pl. 3, fig. 9. NA30; in Mazza et al., 2010, pl. II, fig. 3). FNP112
- *Pr. triangulare* (= *E. rigoi* in Nicora et al., 2007, pl. 4, fig. 6 = Mazza et al., 2010, pl. II, fig. 5). **NA28**
- Pr. aff. triangulare (= C.? gulloae in Mazza et al., 2012b, pl. 1, fig. 5 only). FNP134

Genus: Quadralella Orchard, 2013

Type species: Quadralella lobata Orchard, 2013

The oldest upper Carnian species at BBR are assigned to *Quadralella*, a genus introduced by Orchard (2013) with a type species, *Q. lobata*. The genus is characterized by anterior

geniculation points and anterior ornament that varies from absent to low, weakly differentiated, and irregular nodes. In lateral view, these nodes are often defined by incisions into the anterior platform margins whereby the nodes do not rise above the posterior platform margins as they do in *Primatella* (Fig. 4). *Paragondolella* lacks geniculation points, and both *Carnepigondolella* and *Ancyrogondolella* have more organized and sharper anterior denticulation.

Although focussed on upper Carnian taxa, Orchard (2013, p. 456) thought it probable that older taxa should be referred to Quadralella, including Gondolella polygnathiformis and Metapolygnathus nodosus. This comment seems to have been overlooked by Kiliç et al. (2015), who subsequently introduced a new genus, Hayashiella, with the unfortunate choice of Me. nodosus as the type species. The holotype of that species is of uncertain age and unknown morphological range because it originated in a poorly preserved and stratigraphically mixed fauna extracted from chert in Japan (Hayashi, 1968). In fact, the holotype of Me. nodosus has been favourably compared to 'Epigondolella' carnica (see discussion in Noyan and Kozur, 2007, p. 173), which was chosen as the type species of a second new genus Mazzaella Kiliç et al. Notwithstanding those uncertainties, the scope of Hayashiella Kiliç et al. is embraced by Quadralella. Besides, the name Hayashiella is preoccupied for a beetle (Vives & Ohbayashi, 2001). Hence, Hayashiella is both a junior synonym and a junior homonym.

Mazza et al. (2018) have recently argued for the suppression of *Quadralella* because the lower Carnian *Metapolygnathus lobatus* was erroneously mislabelled "*Quadralella lobatus*" (sic) in a review paper on Middle to Upper Triassic conodonts (Chen at al., 2015, fig. 4). This apparent homonymy arose due to an uncritical re-assignment of all lower Carnian species formerly referred to *Metapolygnathus* by Orchard (2007a) to *Quadralella* subsequent to the former genus being more narrowly defined in the upper Carnian (Orchard, 2014). The lower Carnian *Me. lobatus* is not a *Quadralella* but an example of *Paragondolella*, probably derived from *P. inclinata. Quadralella lobata* Orchard, 2013 remains the type species of the genus *Quadralella*.

The species *Quadralella praecommunisti*, which first appears in the *Ac. angusta – Me. dylani* Subzone of the *Pr. primitia* Zone at BBR, is regarded as an advanced *Quadralella* with a forward shifted pit, and not a precursor to the inornate *Metapolygnathus communisti*. Elements of the latter group, which are rare at BBR, occur much earlier at BBR and are thought to be unrelated to *Q. praecommunisti*, which is common in the latest Carnian there. At PM, *Q. praecommunisti* appears earlier but is much broader in scope (Mazza et al., 2011), including some elements similar to *Parapetella* and *Kraussodontus*. There appears to be no examples at BBR of more advanced species with a more anteriorly shifted pit, as in *Q. multinodosus*, or with reduced platforms, as in some ornate elements referred to *Me. dylani* by Mazza et al. (2018).

More ornate species of *Quadralella*, such as *Q. kathleenae* and *Q. willistonensis*, may also occur at PM although it is difficult to evaluate isolated specimens. They too occur in the *C. samueli* Zone, earlier than at BBR. The two species mentioned above are characterized by posterior pits, unlike the similar *Q. praecommunisti* and *Q. mcrobertsi*, which are also noded species but with more medial pits (see below). The following species assigned to *Quadralella* explicitly occur at both BBR and PM (from Mazza et al., 2012b; Rigo et al., 2018, with their former generic assignment):

- Q. angulata (previously Carnepigondolella)
- Q. carpathica (previously Carnepigondolella, then Hayashiella)
- Q. noah (previously Paragondolella)
- Q. oertlii (previously Paragondolella)
- Q. praecommunisti (previously Metapolygnathus)
- Q. tuvalica (previously Carnepigondolella, then Hayashiella)

Additional species of *Quadralella* interpreted from the literature may include:

- ?Q. kathleenae (= C. pseudodiebeli Morphotype A in Mazza et al., 2012b, pl. 2, fig. 8). FNP53a
- *Q. lobata* (= *P. praelindae* in Mazza et al., 2012b, pl. 7, fig. 13; Rigo et al., 2018, fig. 6.6d). **NA4a**
- *Q. lobata* (= *P. noah* in Mazza & Martinez-Perez, 2015, pl. 1, figs.1-5 only). **NA2**, **PM3a**
- Q. praecommunisti (= Me. praecommunisti in Mazza et al., 2011, fig. 2C, fig. 3C, F, G, H).
- ?Q. willistonensis (= Me. mersinensis in Mazza et al., 2012b, pl. 4, figs., 5, 8). FNP53, NA22

PLACEMENT OF THE CARNIAN-NORIAN BOUNDARY

Event horizons recognized at BBR and suggested primary options for definition of the CNB cluster around the range of *Metapolygnathus parvus*: the base (T2 at PM), top (-T3 at PM), or a datum within *Me. parvus* Subzone. The earlier end-*Carnepigondolella* event (top *C. samueli* Zone) is also a primary biostratigraphic marker but it clearly lies within the upper Carnian even though the position of PM-T1 is disputed.

The highest suggested position for the CNB is at the base of the Carnepigondolella? gulloae Zone at PM, or the top of the Me. parvus Subzone at BBR, which are close but not coincident. The event is marked at BBR by the disappearance of all the diminutive conodont species that dominate the upper division of the Me. parvus Subzone. This might be viewed as a natural Norian base after disappearance of Carnian stocks, but the datum does not clearly correspond to the appearance of any common conodont taxon. At PM, the first appearance datum (FAD) of Primatella gulloae is suggested to be an approximation of this level, although Metapolygnathus parvus ranges higher there (Fig. 3). However, as discussed above, Pr. gulloae is regarded as a member of the Pr. rotunda group, which appears at BBR below the Me. parvus Subzone and may contain a precursor for Pr. gulloae. At the moment, in the absence of a known ancestry, the choice of *Pr*. gulloae as a CNB index is problematic.

In support of defining the CNB at the top of the *Me. parvus* Subzone is the totality of ammonoid data from British Columbia. Ammonoid fauna of the traditionally latest Carnian *Klamathites macrolobatus* Zone (see Tozer, 1994) is known from many western Canadian localities and many of them have also yielded conodonts. Figure 5 shows the subzonal assignment

conodont zones/ subzones		Locality	Curation number	macrofauna ammonoids/ bivalves
Ancyrogondolella quadrata Zone		Black Bear R.		
	(<i>Pr.</i> sp. nov. A - <i>Pa</i> . sp. nov. G)	Black Bear R.	V-002455	Subzone 2 o Stikinoceras
<i>Primatella primitia</i> Zone	<i>Pr. asymmetrica -</i> Norigondolella sp.			Zone
	(Pr. curvata - Pr. bifida - Pr. rotunda)	Black Bear R. Huxley Island	C-307862 C-157123	Guembelites subzone 1 Styrites dawsoni, Gonionotites sp., Thisbites sp. Halobia austriaca
	upper Me. parvus middle lower	Huxley Island	C-157119	Anatropites sp., Tropceltites pacificus, Thisbites huxleyi, Tropithisbites denticostatus, ?H. austriaca
		Pardonet Hill	O-064628	Anatropites cascadensis, Thisbites selwyini, Goniotites nobilis, Griesbachites auctoris
	Ac. acuminata - Pa. prominens	Pardonet Hill	O-064616	Anatropites pardoneti, Thisbites selwyni
	/	Mt. McLearn (Black Bear R.)	O-068202	Anatropites maclearni, A. sulphurensis, Goniotites avarus, G. nobilis, Hadrothisbites taylori
	Ac. angusta - Me. dylani	Mt. Laurier	O-094738	Anatropites cupressus, A. maclearni, A. silberlingi, A. ausoniformis, Goniotites avarus
		Kunghit Island	C-157382	Tropithisbites densicostatus, Margarijuvavites carlottensis
	Ac. sagittale - Pa. beattyi	Black Bear R. Black Bear R.	C-201931 C-201930	Anatropites sp. Thisbites sp.
Carnepigondolella samueli Zone				Welleri Zone?

Figure 5 – Composition of *Klamathites macrolobatus* Zone ammonoid faunas (partly after Tozer, 1994), accompanying halobiids, and their assignment to conodont subzones of the *Pr. primitia* Zone. The oldest collections are in section at Black Bear Ridge, two are archive from Pardonet Hill (see Orchard, 2014, fig. 30), two are archive from elsewhere in northeastern B.C. (Mount Laurier, Mount McLearn), and three are from Kunghit and Huxley islands, Haida Gwaii (Wrangell Terrane). These collectively demonstrate that the stratigraphic scope of the *K. macrolobatus* Zone embraces the *Pr. primitia* Zone up to and including the *Me. parvus* Subzone at Black Bear Ridge, including the ~5 m CNB interval that lacks ammonoid zonal indices. The occurrences of the lower and upper *S. kerri* Zone indices (vertical bars) at BBR are also shown. (Modified from Orchard, 2014, fig. 31).

of nine conodont collections, which are from a variety of *K. macrolobatus Zone* faunas and localities, most of them characterized by the diagnostic ammonoid *Anatropites*. At BBR it has been demonstrated that this ammonoid zone corresponds to the *Acuminatella sagittale - Parapetella beattyi* and *Ac. angusta - Metapolygnathus dylani* subzones of the lower *Pr. primitia* Zone, while other localities support that calibration and extend it upward through the *Me. parvus* Subzone and just beyond. A single *K. macrolobatus* Zone collection (lacking *Anatropites*) from Huxley Island, Haida Gwaii contains only *Primatella* conodonts and is regarded as younger than the *Me. parvus* Subzone. Both this latter collection and a second from nearby on Huxley Island may also contain *Halobia austriaca*, which is consistent with the FAD of that species in the *Me. parvus* Subzone of BBR.

Hence, it appears that the totality of the *Me. parvus* Subzone, as well as the entire lower *Pr. primitia* Zone, is embraced by the traditionally uppermost Carnian *K. macrolobatus* Zone. This also conforms to the lowest occurrence of the lower Norian *S. kerri* Zone species *Guembelites clavatus* immediately above

the *Me. parvus* Subzone at BBR, low in the *Pr. asymmetrica -Norigondolella* sp. Subzone. A consequence of a position at the base of the *Me. parvus* Zone for the CNB places the upper part of the "Carnian" *K. macrolobatus* ammonoid Zone in the Norian.

The choice of the base *Me. parvus* Subzone/ Zone as the definitive CNB datum, as advocated by Mazza et al. (2018), has many advantages in spite of the realignment of the ammonoid zones. These are summarized in Figure 6. As has been noted previously, the major faunal turnover occurs around the *Me. parvus* Subzone where most long-ranging Carnian genera and numerous species disappear over several metres of strata. Prior to this, there is a rise in the abundance of small conodont elements, the forebears of which are known in the preceding beds (Orchard, 2014, figs. 13, 15, 16), and then they too disappear (Fig. 6, A). Two genera, *Acuminatella* and *Primatella*, continue on and in higher strata are joined by *Norigondolella*. This turnover is complete by the end of the *Me. parvus* Subzone, whereas its lower division is marked by most of the extinctions and by first appearances of key macrofaunal elements, including *Halobia*

austriaca and *Pterosirenites* (Fig. 2); these latter taxa have been regarded as Norian indicators.

Geochemical data from BBR point to underlying causes for the biological events. Williford et al. (2007; Fig. 6, B) identified a small but significant negative excursion of the carbon isotope of total organic carbon with a minimum precisely between the lower and middle divisions of the *Me. parvus* Subzone. This suggests the presence of low oxygen conditions that were conducive to efficient burial of organic matter (Williford et al., 2007). Later, Onoue et al. (2015) presented further geochemical data that they interpreted as recording a period of deep-water anoxic deposition (indicated by the V/(V + Ni) and V/Cr indices), and reflecting a transition from dysoxic conditions in the *Ac. acuminata–Pa. prominens* Subzone to anoxic conditions in the *Me. parvus* Subzone; $\delta^{13}C_{carb}$ values increased through these zones and then decreased in the *Pr. asymmetrica–Norigondolella* sp. Subzone (Fig. 6, C). Onoue et al. (2015) linked the conodont faunal turnover event with a widespread oceanic anoxic event, but noted $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ and $\delta^{13}\mathrm{C}_{_{\mathrm{carb}}}$ isotopic data largely exclude the possibility that the event was triggered by dissociation of methane hydrates and degassing related to large-scale volcanic activity.

Very recent work has looked at the oxygen isotopes preserved in conodont apatite (Sun et al., 2019; in press; Fig. 6, D). These indicate temperature increase of several degrees into the *Me. parvus* Subzone followed by lower temperatures in the *Pr. asymmetrica* – *Norigondolella* Subzone. Sun et al. (2019) also determined that *Quadralella* and *Norigondolella* were cooler/ deeper water genera. The first of these conodonts disappears as both deep water anoxia and elevated temperatures are indicated, whereas *Norigondolella* appears and becomes common during the cooling trend in the earliest Norian. All these events provide boundary proxies for definition of the CNB. The FAD of



Figure 6 – Conodont fauna and zonation through a 5 m boundary interval in the Pardonet Formation between the highest *K. macrolobatus* (*Anatropites*) Zone and lowest *S. kerri* (*Guembelites*) Zone ammonoid indicators. A. Shows replacement of typical Carnian conodonts (pale gray bars) by *Primatella* and *Acuminatella* (medium gray bars) with an intervening bloom of diminutive derivatives (black bars) during the *Me. parvus* Subzone (after Orchard, 2014, fig. 6). B. Peak negative organic carbon isotope excursion at the lower-middle division boundary of the *Me. parvus* Subzone (after Williford et al., 2007). C. Isotope geochemistry showing excursions at the base and top of the *Me. parvus* Subzone (after Oncue et al., 2016). D. Paleotemperatures derived from conodont apatite $\delta^{18}O_{PO4}$ showing an increase in temperature in the *Me. parvus* Subzone and subsequent drop. Data are calibrated to NBS 120c with an analytical uncertainty of ±0.14 ‰ (1 σ). Genus-specific depth corrections are applied; circle, hexagon and square stand for data measured on *Quadralella*, *Primatella* and *Carnepigondolella*, respectively (after Sun et al., 2019; in press).

Metapolygnathus parvus alpha morphotype at the base of the *Me. parvus* Subzone/ Zone may serve that purpose. However, the scope of this index fossil and its ancestry need to be well defined. Notably, *Primatella asymmetrica* and *Pr. rhomboidale* also appear at the base of the *Me. parvus* Zone at BBR and are known to occur at PM. Similarly, the FAD of *Parapetella johnpauli* and *Pa. willifordi* mark the base of the middle division of the *Me. parvus* Subzone at BBR, and these too are noted to occur at PM. None of these species have been well documented at PM so their full utility remains unknown.

SUMMARY

The conodont taxonomy about the Carnian-Norian boundary (CNB) interval at the GSSP candidate at Black Bear Ridge (BBR), British Columbia is reviewed and compared with that used at Pizzo Mondello (PM), Sicily. Correlation of these sections has been impeded to some extent by fossil endemism but it is concluded that differing taxonomic approaches have obscured similarities. Both the North American (BBR) and Tethyan (PM) conodont successions contain species of the platform genera Carnepigondolella, Ancyrogondolella, ?Kraussodontus, Metapolygnathus, Norigondolella, Parapetella, Primatella, and Quadralella; only Acuminatella and some non-platform genera appear to be endemic, although there may be endemic species. Further nomenclatural and taxonomic revisions revise the use of several generic names at PM: Quadralella is valid and a senior synonym of Hayashiella; Paragondolella is an inappropriate name for upper Carnian species; "Epigondolella" species at PM are revised as Carnepigondolella in the upper Carnian, as Primatella around the CNB, and as Ancyrogondolella in the lower Norian. The evolutionary trend of anterior pit migration is recognized in all 6 genera that exist in the lower part of the Pr. primitia Zone at BBR (Orchard, 2014) so the practise of combining in a single genus all specimens with an anterior pit (as in *Metapolygnathus*) obscures relationships.

These revisions suggest that faunal turnover intervals at PM-T1 and -T3 were not endemic events (Mazza et al., 2018, pp. 83, 88, 90) but can be recognized at BBR by reference to evolutionary events in, respectively, *Carnepigondolella* and *Primatella*. At PM, these are cast as, respectively, a transition from *Carnepigondolella* to *Epigondolella* (T1), and as a sudden appearance of *C*.? *gulloae* (T3). At BBR, the transitional species near the top of the *C*. *samueli* Zone are all included in *Carnepigondolella*, whereas the *C*.? *gulloae* fauna is allied to, and is now assigned to, the *Primatella* fauna that dominates above the *Me. parvus* Subzone.

Hence, it is concluded that: the top of the *C. samueli* Zone at BBR is equivalent to a position within the "*E*." vialovi Zone at PM; the overlying zone containing *Primatella* species crosses the CNB in both sections, including *Pr. asymmetrica*, *Pr. bifida*, *Pr.* aff. permica, ?*Pr. rhomboidale*, *Pr. subquadrata*, and *Pr. triangulare*; correlation of the *Me. parvus* Subzone within the *Pr. primitia* Zone is strengthened by these and other revised conodont occurrences, including *Parapetella destinae*, *Pa. johnpauli*, *Pa. willifordi*, *Pa. pumilio*, and *Pa. irwini*; and the well-known lower Norian succession of *Ancyrogondolella quadrata* followed

by *An. triangularis* in western Canada appears corrupted at PM (sample NA43).

As previously concluded, the *Me. parvus* Sub-/ Zone can be correlated between both sections based on the FAD of the nominal conodont (PM-T2) as well as the demise of many typical Carnian taxa, and is a suitable datum for definition of the CNB. However, the morphological scope of the index species and its morphotypes needs agreement, as does its evolutionary cline. Orchard (2014, front piece) illustrated the progression from *Metapolygnathus* ex gr. *communisti* to *Me. dylani* to *Me. parvus*, but these did not include ornate elements like those shown by Mazza et al. (2018), for which reason *Quadralella praecommunisti* and *Q. multinodosus* are excluded from that genus.

It is demonstrated that, based on both BBR and other British Columbian locations from where diagnostic ammonoid faunas are known in association with conodonts, a CNB defined at the base of the *Me. parvus* Subzone has the effect of placing the upper part of the traditional Carnian *K. macrolobatus* ammonoid Zone in the Norian. On the plus side, additional fossil (e.g., *Halobia austriaca*, *Pterosirenites* sp.) and geochemical proxies coincide with the *Me. parvus* Subzone.

At BBR, the highly resolved taxonomy provides numerous morphospecies as guide fossils. It also provides documentation of a progressive diminution of surviving clades around the CNB, particularly in *Metapolygnathus* and *Parapetella*. These observations have not been explicitly recorded at PM where the *Me. parvus* Zone (~12 m thick) is undifferentiated, although the presence of diminutive taxa is indicated. This biological event appears related to geochemical observations at BBR that imply paleoecological stress in terms of both anoxia and temperature. Considering generic preferences, the disappearance of *Quadralella* and the later appearance of common *Norigondolella* may reflect the direct impact of these changes.

ACKNOWLEDGEMENTS

I thank Martyn Golding, Leo Krystyn, Chris McRoberts for their reviewer comments. In so much as this work draws on data reported in a previous publication (Orchard, 2014), I acknowledge the support of the Geological Survey of Canada and the collaboration of those cited in that work.

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