



## OPEN ACCESS

## EDITED BY

Yanlong Chen,  
Northwest University, China

## REVIEWED BY

Guichun Wu,  
Chinese Academy of Geological Sciences  
(CAGS), China  
Dmitry Ruban,  
Southern Federal University, Russia  
Weiping Zeng,  
Huanggang Normal University, China

## \*CORRESPONDENCE

Michael J. Orchard,  
✉ mike.orchard@nrca-nrcan.gc.ca

RECEIVED 10 May 2023

ACCEPTED 01 August 2023

PUBLISHED 24 August 2023

## CITATION

Orchard MJ (2023), The utility of the  
Upper Triassic conodont *Primatella* in  
Tethyan-Panthalassan correlation  
around the Carnian-Norian boundary.  
*Front. Earth Sci.* 11:1220590.  
doi: 10.3389/feart.2023.1220590

## COPYRIGHT

© 2023 Orchard. This is an open-access  
article distributed under the terms of the  
[Creative Commons Attribution License  
\(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or  
reproduction in other forums is  
permitted, provided the original author(s)  
and the copyright owner(s) are credited  
and that the original publication in this  
journal is cited, in accordance with  
accepted academic practice. No use,  
distribution or reproduction is permitted  
which does not comply with these terms.

# The utility of the Upper Triassic conodont *Primatella* in Tethyan-Panthalassan correlation around the Carnian-Norian boundary

Michael J. Orchard\*

Geological Survey of Canada, Vancouver, BC, Canada

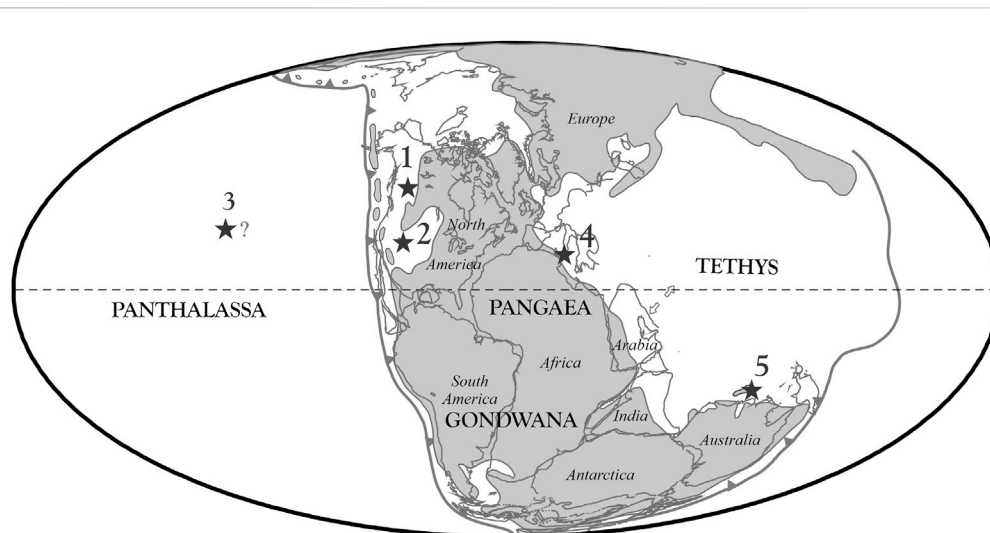
The Upper Triassic conodont genus *Primatella* is important for recognizing the Carnian-Norian stage boundary in Panthalassan and Tethyan domains. Originally based on Canadian material from Black Bear Ridge in the Western Canada Sedimentary Basin, two key species are highlighted, and their occurrence is documented in the allochthonous Wrangellia and Alexander terranes in the North American Cordillera; in the Great Basin in Nevada, western United States; at Pizzo Mondello, Sicily, in western Tethys; and in Timor-Leste on the southeastern margin of the Meso-Tethys Ocean (northeastern Gondwana). The correlation potential of *Primatella* species is compromised by a differing nomenclature employed in Tethyan regions of Europe where *Primatella* species have been assigned to other genera, namely, *Ancyrogondolella* (formerly *Epigondolella*), *Carnepigondolella*, and *Metapolygnathus*. This has obscured phyletic relationships and impacted the stratigraphic utility of two demonstrably cosmopolitan species, *P. asymmetrica* and *P. bifida*. These species are shown to occur widely in a variety of paleoenvironments and have a restricted stratigraphic range around the CNB for which they can be adopted as useful indices.

## KEYWORDS

Upper Triassic, conodont, *Primatella*, taxonomy, paleogeography

## 1 Introduction

Conodonts have proven to be a pre-eminent stratigraphic tool for dating and correlating Paleozoic and Triassic strata. As index fossils, they are invaluable in the recognition of events and for the definition of stratigraphic boundaries. In the Triassic, they define the base of the period as well as play an important role in at least supporting its constituent stage boundaries. Recent deliberations of the Carnian-Norian boundary (CNB) have been no exception and conodonts featured prominently in studies of the two candidate sections for the Global Stratigraphic Section and Point (GSSP) at Pizzo Mondello, Sicily (Mazza et al., 2012), and Black Bear Ridge, British Columbia (Orchard, 2014). Although both sections contain the distinctive *Metapolygnathus parvus* faunal interval that in North America corresponds to the latest Carnian *Macrolobatus ammonoid* zone, the associated conodont taxa, including those that characterize the basal Norian stage immediately above, are controversial.



**FIGURE 1**

Simplified paleogeographic world map for the Triassic showing the locations of the cited areas: 1. Black Bear Ridge, northeast B.C.; 2. Berlin, western Nevada; 3. Sadler Point, Haida Gwaii—Kuiu Island, Alaska; 4. Pizzo Mondello, Sicily; 5. Timor-Leste [Based on [Scotese \(1998\)](#)]. Note that the northern Tethys margin differs in the updated reconstruction of [Kocsis and Scotese \(2021\)](#), but this does not impact the location of the studied sections.

Recent reclassification of Upper Triassic conodonts based on rich faunas from Black Bear Ridge ([Orchard, 2013; Orchard, 2014](#)) included the separation of a new genus, *Primatella*, that spans the CNB interval. This genus largely ranges within and helps define the *primitia* Zone sensu Orchard ([Orchard, 1983; Orchard, 1991a](#)), which was internally subdivided by [Orchard \(2014\)](#). The now agreed definition of the CNB is at the appearance of the bivalve *Halobia austriaca* ([Hounslow et al., 2021](#)), which corresponds broadly to the base of the *P. asymmetrica*-*Norigondolella* Subzone at Black Bear Ridge, and of the “*Carnepigondolella*” *gulloae* Zone in Pizzo Modello. The latter has been interpreted as a probable *Primatella* species by [Orchard \(2019\)](#).

Although *P. primitia* sensu stricto is uncommon and to date only known from Canada, the zonal name is retained for the sake of stability. The volume of the genus, which was originally assigned to a single species of *Epigondolella*, includes many similar species that have been assigned to a variety of other genera in Europe ([Orchard, 2019](#)), including the older *Carnepigondolella* (e.g., *C. orchardi* in [Balini et al., 2010](#), pl. 3, fig. 30), the younger *Ancyrogondolella* (e.g., *E. = A. rigoi* in [Mazza et al., 2010](#), pl. II, fig. 5 = *Primatella triangulare*), and the partly contemporaneous *Metapolygnathus* (e.g., *Me. mersinensis* in [Mazza et al., 2012](#), pl. 4, fig. 7, 9). This paper reasserts the value of *Primatella* as a distinct genus for both intercontinental correlation and the recognition of the CNB by documenting the global distribution of two representative species established in Canada and now recognized in the United States, Europe, and Southeast Asia.

In this study, North American occurrences of *Primatella asymmetrica* and *P. bifida* are documented from northeastern British Columbia (B.C.), their type area; from Haida Gwaii, B.C. and Keku Islands, southeast Alaska, representative of, respectively, the allochthonous Wrangel and Alexander terranes that occupied an unknown but probably more southerly paleolatitude in the Late Triassic Panthalassan Ocean; and from lower latitude Nevada in the Great Basin of western United States. These successions are from

various parts of Panthalassa, whereas records from the GSSP at Pizzo Mondello in Sicily are from western Tethys, and new collections from Timor-Leste come from the southeastern margin of Tethys, which was rifting from the northern edge of Gondwana in the Late Triassic ([Metcalf, 2021](#)) ([Figure 1](#)). The two distinctive species are the focus of the present study, particularly as they occur widely but have not been consistently identified. Other *Primatella* species are thought to be equally widespread, and the genus is clearly a valuable indicator of the CNB.

## 2 Materials and methods

### 2.1 The locations

This report arises from the investigation over several decades of numerous Upper Triassic conodont collections from several areas of western North America, where studies have recently focused on defining a GSSP for the CNB. In particular, the Black Bear Ridge (BBR) candidate and nearby sites were sampled in considerable detail, with closely spaced bulk limestone samples subjected to standard processing procedures ([Jeppsson et al., 1999](#)). Numerous rich faunas were recovered, providing an outstanding conodont record through the boundary interval. This resulted in a substantially revised taxonomy for the interval ([Orchard, 2013; Orchard, 2014](#)) that has had some, but not universal, uptake. The taxonomy was successfully applied in both Haida Gwaii in the Wrangel terrane ([Carter and Orchard, 2013](#)) and in Nevada ([Balini et al., 2015](#)). Together, the conodont collections from these Panthalassan locations, which incidentally represent the sites from which much of the North American Carnian and Norian ammonoid zonation was developed ([Silberling, 1959; Tozer, 1994](#)), demonstrate the broad applicability of the BBR classification.

Further afield, conodont research at Pizzo Mondello (PM) in Sicily, Italy (Mazza et al., 2012), pre-dated the taxonomic revisions of Orchard (2014) but later descriptions of conodont faunas from the Tethys Realm (e.g., Rigo et al., 2018) have employed a nomenclature that has generally remained unchanged. Nevertheless, published illustrations from Europe enabled a preliminary revision of PM conodonts by Orchard (2019), who recognized several species of *Primatella* among those illustrated by Nicora et al. (2007), Balini et al. (2010), Mazza et al. (2010, 2012), and Mazza and Martínez-Pérez (2015) as species of *Carnepigondolella*, *Epigondolella*, and *Metapolygnathus*.

Far from both regions, in the southeastern Tethys on the margins of Gondwanaland, extensive investigations in Timor-Leste (McCartain, 2014; Haig et al., 2021) included the processing of numerous small conodont samples. The recovered collections have been studied by the present author, who has identified many species of *Primatella*, including examples of the two focus species.

## 2.2 The conodonts

*Primatella* accommodates a comparatively ornate clade that arose from *Quadralella* concurrent with the disappearance of *Carnepigondolella* in the late Carnian (Tuvalian) (Orchard, 2013). The youngest species of the latter genus (Orchard, 2014, figs. 17, 18) have been regarded by Mazza et al. (2012) as the earliest representatives of *Epigondolella* (now called *Ancyrogondolella*). However, in western Canada, a succession of *Primatella* species follows the disappearance of *Carnepigondolella*, which shows progressive diminution in size prior to its demise at the end of the *samuelyi* Zone (Orchard, 2014, figs. 17, 18). This trend is repeated later in the *parvus* Zone, which also contains diminutive taxa with reduced platforms. *Epigondolella* sensu stricto is now recognized as a middle Norian (Alaunian) genus, and similar lower Norian (Lacian) species have been reassigned to *Ancyrogondolella* (Orchard, 2018). The first representatives of the latter genus appear near the end of the Lower Norian Kerri ammonoid Zone in North America (Orchard, 1991a). In the author's view, the most distinctly ornate taxa of the latest Tuvalian and early Lacian are probably species of *Primatella* (e.g., see Orchard, 2019).

*Primatella asymmetrica* and *P. bifida* are typical representatives of the genus in that they bear well-differentiated anterior nodes that rise above the platform margin as high apically blunt nodes compared with the low broadly rounded or incised nodes of some *Quadralella* species, and the high and sharply terminated denticles of *Ancyrogondolella* species (Orchard, 2019; fig. 4). Apart from the anterior ornament, the diagnostic morphology of *P. asymmetrica* is the asymmetric posterior platform with a strongly convex outer margin and inturred posterior. *P. bifida* has a bifurcated keel and an indented posterior margin. The supporting taxonomy is provided below.

## 3 Results

### 3.1 Northeast British Columbia

Both *Primatella asymmetrica* and *P. bifida* were first described from the CNB candidate section at BBR in northeastern B.C., located in the Peace River valley where the North American Norian

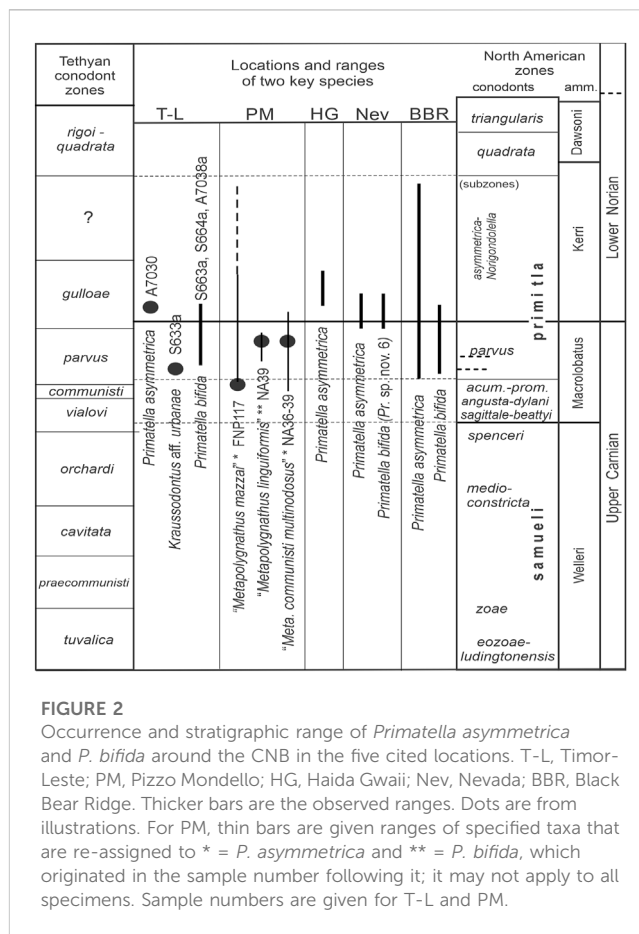


FIGURE 2

Occurrence and stratigraphic range of *Primatella asymmetrica* and *P. bifida* around the CNB in the five cited locations. T-L, Timor-Leste; PM, Pizzo Mondello; HG, Haida Gwaii; Nev, Nevada; BBR, Black Bear Ridge. Thicker bars are the observed ranges. Dots are from illustrations. For PM, thin bars are given ranges of specified taxa that are re-assigned to \* = *P. asymmetrica* and \*\* = *P. bifida*, which originated in the sample number following it; it may not apply to all specimens. Sample numbers are given for T-L and PM.

zonation of ammonoids (Tozer, 1967; 1994) and conodonts (Orchard, 1983; Orchard, 1991a) was developed in the Pardonet Formation. This formation is primarily composed of gray carbonaceous limestone, calcareous and silty dolostone and shale indicative of deposition in an offshore deep marine setting on the northwestern margin of the Pangea supercontinent (Zonneveld et al., 2010).

At BBR and nearby localities, *Primatella asymmetrica* and *P. bifida* appear in upper Tuvalian strata near the base of the *parvus* Subzone and disappear in the lowest zone of the Norian, which is in the North American ammonoid Zone of *Stikinoceras kerri* and within the *asymmetrica-Norigondolella* conodont Subzone (Orchard, 2014). The nominal species of this conodont subzone ranges throughout the interval, whereas *P. bifida* disappears low in the subzone, a little above the CNB (Figure 2). Conodont associates of these *Primatella* species in the Pardonet Formation include diverse *Primatella* species as well as *Acuminatella* spp. and, in the Norian, common *Norigondolella*. In the Tuvalian part of their range, they are accompanied by *Kraussodontus*, *Metapolygnathus*, *Parapetella*, and *Quadralella* species, most of which disappear by the CNB.

### 3.2 Nevada

Upper Triassic conodonts from the Berlin-Ichthyosaur State Park in the Shoshone Mountains of central Nevada were recovered

from samples collected during a restudy of the CNB in the Luning Formation (Balini et al., 2015). This site is important for both its articulated vertebrate remains and as the type section for the latest Carnian *Klamathites macrolobatus* ammonoid Zone (Silberling, 1959). The Triassic succession lies within the Berlin Allochthon of the Paradise terrane, a lithotectonic assemblage linked with several others thought to have originally lain along the same continental margin but possibly separated by major structural dislocations (Stewart et al., 1997).

Carbonate strata of the Upper Triassic Luning Formation are considered to have been deposited in both shallow-water and relatively deep-water marine environments. In West Union Canyon, the calcareous shale member is dominated by marls with rare intercalations of thin bedded limestones that carry ammonoids of both the Carnian *Macrolobatus* and Norian *Kerri* zones. Conodont faunas include *Primatella bifida*, provisionally identified earlier as *P. sp. nov. 6*, and *P. asymmetrica*, both of which are common in the Brick Pile and North sections (Balini et al., 2015, figs. 5, 6). These species were mostly recovered from strata recognized as lower Norian, based on their ammonoids, or from underlying undated strata.

In total, the Nevadan conodont fauna is dominated by *Primatella* species as is commonly the case in the *asymmetrica-Norigondolella* Subzone of the *primitia* Zone in Canada; however, *Norigondolella* is absent, presumably reflecting some ecological barrier. Other associates are the same as in Canada, including *Acuminatella*. As discussed by Balini et al. (2015), the lowest collections at the Brick Pile section may date from the uppermost Carnian, whereas those from some 50 m higher and above, are typical of the Norian part of the *primitia* Zone.

Overlying the Luning Formation, the Gabbs Formation includes Rhaetian strata bearing *Misikella posthernsteini* and *Zieglericonus rhaeticus* (Orchard et al., 2007a), taxa that are unknown in northeast B.C. but are common in the Eurasian Tethyan successions and in allochthonous terranes in North America, including Wrangellia (Orchard, 1991b), Cache Creek (Golding et al., 2016), and Baja California (Orchard et al., 2007b). This suggests a more southerly paleolatitude for the Canadian terranes, although their longitude is uncertain. Despite differing Rhaetian provinciality, *Primatella* is common in all these areas around the CNB.

### 3.3 Haida Gwaii—Keku Islands

The North American Cordillera is composed of many allochthonous tectonostratigraphic terranes, of which Wrangellia and the Alexander terranes are the largest. The former includes both Vancouver Island and Haida Gwaii, whereas the Alexander terrane is well displayed in the Keku Islands area of southeast Alaska. The Alexander terrane is characterized by a long Paleozoic history culminating in amalgamation with Wrangellia as a composite terrane (Beranek et al., 2014), which later accreted to the western margin of the Intermontane terranes by the Middle Jurassic but was exotic with respect to the Laurentian margin during the Late Triassic. At that time, the Alaskan portion of Wrangellia in the Wrangell Mountains was estimated to lie at approximately 12°N (Trop et al., 2002). All these regions include Upper Triassic

conodont-bearing successions in which *Primatella* is a common component.

The Upper Triassic conodont succession in Haida Gwaii was first summarized by Orchard (1991b) and later by Carter and Orchard (2013), who focussed on integrating the conodont and radiolarian successions around the CNB. These faunas occur in the Peril Formation, which mainly consists of thinly bedded siliceous dark gray to black limestone (Desrochers and Orchard, 1991) that accumulated on an intraoceanic carbonate platform built on a remnant volcanic arc. The Peril Formation carries a wholly pelagic fauna that implies deposition in deep water under low oxygen conditions. At Sadler Point in northwest Graham Island, *Primatella asymmetrica* occurs in association with radiolarian Assemblage 5 (Carter and Orchard, 2013), which is assigned to the “Upper *primitia* Zone”, or in current terminology the *asymmetrica-Norigondolella* Subzone of the *primitia* Zone. In common with BBR, associated species around the CNB in Haida Gwaii include additional *Primatella* species plus *Acuminatella*, *Kraussodontus*, *Metapolygnathus*, *Norigondolella*, *Parapetella*, and *Quadralella* species. As noted about Nevada, younger Rhaetian strata in Haida Gwaii include ‘Tethyan’ species, in this case, *Misikella posthernsteini* and *Oncodella paucidentata*.

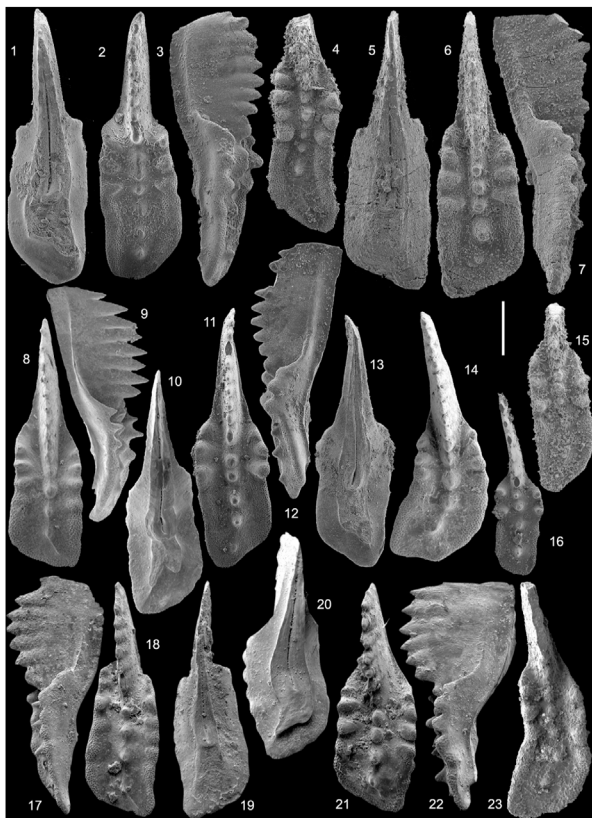
Upper Triassic strata in the Keku Islands in southeast Alaska are assigned to the Hyd Group (Muffler, 1967; Katvala and Stanley, 2008). In that area, CNB *Primatella* occurs in the Cornwallis Limestone on Kuiu Island (Katvala and Stanley, 2008), an often oolitic fossiliferous limestone formed in a shallow-marine environment receiving clastic sediment input from terrestrial erosion. This is a very different sedimentary environment from that of the Peril Formation on Haida Gwaii, yet *Primatella* species dominate some collections and include *P. bifida* (see Supporting Taxonomy).

### 3.4 Pizzo Mondello

The Pizzo Mondello (PM) section in the Sicani Mountains of western Sicily, Italy, is the newly agreed locality for the CNB GSSP. It exposes the Scillato Formation, a Carnian-Rhaetian pelagic-hemipelagic succession of cherty limestones that accumulated in the western Tethyan realm (Balini et al., 2010). There, conodont zones recognized around the CNB are based on a variety of taxa (Nicora et al., 2007; Mazza et al., 2012; Rigo et al., 2018) and include *Neocavitella cavitata*, *Norigondolella trinacriae*, and *Zieglericonus sp.*, which are unknown from contemporaneous strata in North America. Despite this provinciality, many conodont taxa are common to both regions, although neither *Quadralella* nor *Primatella* have featured in the PM literature. Orchard (2019) recognized both genera among species identified by authors as *Carnepigondolella*, *Epigondolella*, *Metapolygnathus*, and *Paragondolella*.

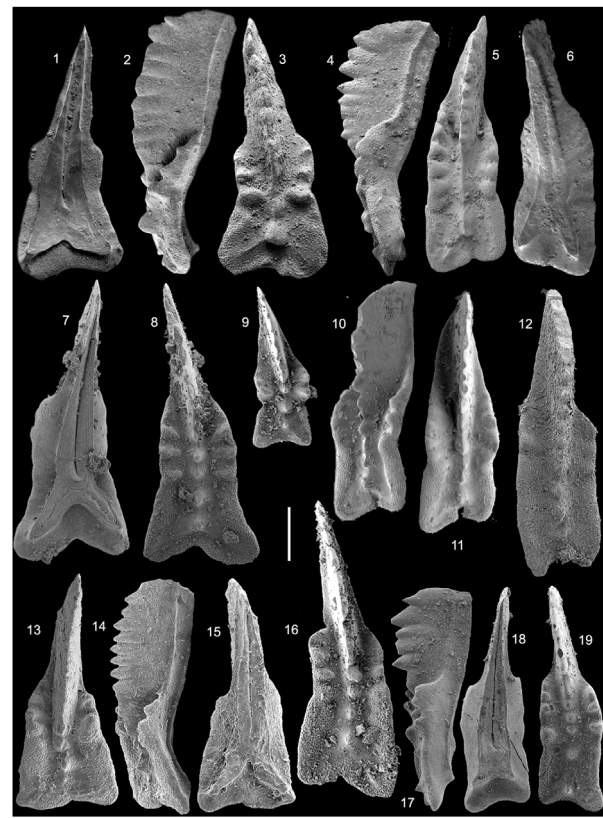
For example, an element of *Primatella asymmetrica* was regarded as a growth stage (GS5) of *Metapolygnathus mazzaei* by Mazza and Martínez-Pérez (2015). It came from a sample from the *comunisti* Zone immediately beneath the *parvus* Zone occurrence of a similar element included in *M. comunisti* by those authors. These align with the Tuvalian appearance of *P. asymmetrica* at BBR.





**FIGURE 3**

1-22. *Primatella asymmetrica* Orchard, 2013. 1-3. GSC 136630 from sample 90SP-U11 (GSC cur. no. C-176937), Peril Formation, Sadler Point, Haida Gwaii; 4. NMMNH P-67736 from sample from sample BIS36, Brick Pile section, Union Canyon, Nevada; 5-7. NMMNH P-67735 from sample BIS4, Luning Formation at Berlin-Ichthyosaur State Park, central Nevada; 8-10. Micro-Unimi no. 2007 from sample FNP117, Scillato Formation, Pizzo Mondello, Sicily; 11-13. GSC 132616 from sample 18 h, Pardonet Formation, Black Bear Ridge, NE B.C.; 14. Micro-Unimi no. 2006 from sample NA36-NA39, Scillato Formation, Pizzo Mondello, Sicily; 15. NMMNH P-67736 from sample BIS34, Luning Formation, Berlin-Ichthyosaur State Park, central Nevada; 16. GSC 132944 from sample 21h, Pardonet Formation, Black Bear Ridge, NE B.C.; 17-19. Element T507 from sample 7030b, Aitutu Formation, Timor-Leste; 20-22. Element T505 from sample 7030b, Aitutu Formation, Timor-Leste. 23. *Kraussodontus* aff. *urbanae* Orchard. T190 from sample S633a, Aitutu Formation, Timor-Leste. Scale bar = 200  $\mu$ m.



**FIGURE 4**

1-19. *Primatella bifida* Orchard, 2014. 1-3. Element T498 from sample A7038a, Aitutu Formation, Timor-Leste; 4-6. Element T209 from sample S664a, Aitutu Formation, Timor-Leste; 7, 8. GSC 132955 from sample 21g, Pardonet Formation, Black Bear Ridge, NE B.C.; 9. GSC 132951 from sample 23, Pardonet Formation, Black Bear Ridge, NE B.C.; 10, 11. Element T205 from sample S663a, Aitutu Formation, Timor-Leste; 12. NMMNH P-67724 from sample BIS45, Luning Formation, Berlin-Ichthyosaur State Park, central Nevada; 13-15. Sample NA39, Scillato Formation, Pizzo Mondello, Sicily; 16. GSC 132954 from sample 23, Pardonet Formation, Black Bear Ridge, NE B.C.; 17-19. GSC 132956 from sample 07-22, Pardonet Formation, Black Bear Ridge, NE B.C. Scale bar = 200  $\mu$ m.

The occurrence of *Primatella bifida* at PM has been discussed by Orchard (2014, 2019). An element identified as *Metapolygnathus linguiformis* by Balini et al. (2010) and Mazza et al. (2012) clearly has anterior nodes unlike the holotype of that species from Japan (Hayashi, 1968). On that basis, two species can be distinguished (see Supporting Taxonomy). As at BBR, this specimen of *P. bifida* from PM occurs in the *parvus* Zone.

### 3.5 Timor-Leste

Recent work in Timor-Leste has involved a wide-ranging study of Triassic strata (McCartain, 2014; Haig et al., 2021) that accumulated in marine basins along northeastern Gondwana on

the southeastern margin of the Meso-Tethys Ocean. Upper Triassic strata include the Aitutu Formation (Audley-Charles, 1968), which includes a range of different lithological and facies associations, such as dark gray bioturbated mud-wackestone, interbedded siliciclastic mudstone beds, grainstone, and conglomerates.

Strata of the Aitutu Formation have yielded diverse CNB faunas, including most of the taxa known from the other locations described above, namely, species of *Kraussodontus*, *Metapolygnathus*, *Norigondolella*, *Primatella*, and *Quadralella*. Included among these are *Primatella asymmetrica* and *P. bifida*, which mostly occur in *Primatella*-dominated faunas that are interpreted, in the absence of typical Tuvalian taxa, to date from the lower Lacin (see Supporting Taxonomy). Both species occur in eastern Timor, while two additional faunas with *P. bifida* have been recovered from the central part of the country, where a nearby locality has yielded the slightly older but similar *Kraussodontus* aff. *urbanae*.

Unlike North American faunas, *Acuminatella* and *Parapetella* have not been found in Timor-Leste, but the presence of both *Neocavitella cavitata* and *Norigondolella trinacriae* in the CNB faunas mirror the Sicilian Tethyan record. Younger collections from the upper Norian and Rhaetian include Tethyan *Misikella* and *Bajadontus*, the latter being previously reported only from peri-Pacific allochthonous terranes in Mexico (Orchard et al., 2007b) and Japan (Zhang et al., 2017).

## 4 Conclusion

The conodont genus *Primatella* is a distinctive indicator for the Carnian-Norian boundary that bridges Tuvalian *Carnepigondolella* and Lacial *Ancyrogondolella*. Two representative species, *P. asymmetrica* and *P. bifida*, are shown to have a broad environmental tolerance in shallow and deep water and a cosmopolitan distribution that spans a range of North American (Pangean) paleolatitudes, distant locations in western and eastern Tethys, and in allochthonous Panthalassan terranes occupying an intermediate location.

In North America, the two species occur in the Pardonet Formation of northeastern British Columbia within the late Carnian (Tuvalian) *parvus* and succeed Norian (Lacial) *asymmetrica*-*Norigondolella* conodont subzones, which are equivalent to the upper *Macrolobatus* and *Kerri* ammonoid zones. The same age is given by collections in which these *Primatella* species occur in the Peril Formation of Haida Gwaii and the Cornwallis Limestone of Keku Islands, parts of the allochthonous Wrangell and Alexander terranes, and in the Luning Formation in the Great Basin of western Nevada. *Acuminatella* species also occur around the CNB in all these areas but not further afield, leading to the suggestion that the genus is an eastern Panthalassan endemic.

Some younger Tethyan conodont elements found in Haida Gwaii support a low paleolatitude (as is the case with younger Rhaetian strata in Nevada) and/or a more westerly longitude for Wrangellia. Typical Tethyan CNB successions in Sicily and Timor include some elements unknown in North America, but *Primatella* is an important element in all regions.

## 5 Supporting taxonomy

Taxonomic data for the genus and focus species, including their distribution is provided below. This is accompanied by photographic illustration (Figures 3, 4) from Orchard (2014) for BBR; Carter and Orchard (2013) for Haida Gwaii; Balini et al. (2015) for Nevada; and Mazza et al. (2012) and Mazza and Martínez-Pérez (2015) for PM. Illustrations from Timor-Leste are original unpublished images provided by E. McCartain (The University of Western Australia).

### 5.1 Genus: *Primatella* Orchard, 2013

2013 *Primatella* gen. nov.—Orchard, p. 452-3.

2014 *Primatella* Orchard—Orchard, p. 87-8.

*Type species: Epigondolella primitia* Mosher, 1970, p. 740-41, pl. 110, figs. 8, 11, 12 (type number GSC 25051). From GSC curation number O-64654, *asymmetrica*-*Norigondolella* Subzone (Kerri Zone) of the Pardonet Formation at Brown Hill, northeast B.C.

*Diagnosis-Description-Comparisons:* see Orchard, 2014.

*Remarks:* Early studies of the Pardonet Formation conodonts led to the characterization of an “*Epigondolella primitia* population” in the latest Carnian and earliest Norian (Orchard, 1983; fig. 2), a composite of diverse morphotypes that commonly co-occur during this interval. These are united by the nature of the anterior platform ornament that consists of moderately high and well-differentiated but blunted nodes covered in compact microreticulation (op. cit., fig. 3). Initially, Orchard (Orchard, 1991a; Orchard, 1991b) excluded these elements from younger more strongly ornate epigondolellids (*Ancyrogondolella*) and re-assigned the holotype to *Metapolygnathus* because its pit was anteriorly shifted like that of the type species of that genus, *M. communisti* Hayashi. However, further study showed that several Late Triassic clades show pit migration through time, so this feature alone is judged to be insufficient for genus definition. *Metapolygnathus* species, which are far more common in the Tethys Realm, are now distinguished by an anterior pit and a minimal or absent platform ornament.

Orchard (2013) reviewed the classification and differentiation of Upper Triassic genera and proposed that members of the “*Epigondolella primitia* population” be assigned to a new genus, *Primatella*. This genus is thought to have evolved from *Quadrалеlla* through the acquisition of a more differentiated anterior ornament of increasing amplitude (Orchard, 2014, fig. 23; 2019; fig. 4) concomitant with anterior pit migration. This trajectory later led to *Ancyrogondolella* in the late Kerri ammonoid Zone, represented by the “*Epigondolella abneptis* A” population (Orchard, 1983), in part later renamed *E. quadrata* (Orchard, 1991a) and now *A. quadrata* (Orchard, 2018). Compared with *Primatella*, the younger Lacial *Ancyrogondolella* has larger, more elevated, and sharper anterior denticles devoid of compact microreticulae (Orchard, 1983), whereas the older *Carnepigondolella* species generally have smaller more rounded nodes (as in *C. zoeae*), small sharp denticles (as in *C. samueli*), or both (as in *C. anitae*), developed on less steep anterior platform margins.

The recognition of “*Epigondolella quadrata* and other species of that genus (e.g., *E. heinzi* and *E. miettoi*) in the Tuvalian in Europe (Mazza et al., 2012; Rigo et al., 2018) is judged to be based on the last representatives of *Carnepigondolella* (e.g., *C. spenceri*; Orchard, 2014, figs. 17, 18) and the occurrence of unidentified *Primatella* species.

### 5.2 *Primatella asymmetrica* Orchard, 2013

Figure 3. 1-22.

aff. 2010 *Metapolygnathus mersinensis* Kozur and Moix—Balini et al., pl. 3, fig. 2a-c.

2013 *Primatella asymmetrica* sp. nov.—Orchard, p. 454-55, fig. 4, 19-21.

2013 *Primatella asymmetrica* Orchard—Carter and Orchard, fig. 7, 6-18.

2014 *Primatella asymmetrica* Orchard—Orchard, p. 88, fig. 61, 4–27.

2015 *Primatella asymmetrica* Orchard—Balini et al., fig. 11 k1–3, l1–3.

p2015 *Metapolygnathus communisti* Hayashi, Morphotype B—Mazza and Martínez-Pérez, pl. 6. 15.

p2015 *Metapolygnathus mazzai* Karádi, Kozur, and Görög—Mazza and Martínez-Pérez, . pl. 7. 15, 16.

**Holotype:** Orchard, 2013, p. 554–55, fig. 4 19–21 (type number GSC 132616). From bed 18h (=GSC cur. no. C-307817), middle *parvus* Subzone of the *primitia* Zone (=Macrolobatus Zone) of the Pardonet Formation at Black Bear Ridge, northeast B.C.

**Diagnosis-Comparisons:** see Orchard, 2014.

**Remarks:** *Primatella asymmetrica* is characterized by an asymmetric posterior platform that is expanded on its outer margin and incurved beyond that, often carrying a weak carina; the basal attachment reflects this asymmetry in the development of either a short secondary keel or lobe beneath the expansion. The pit lies at platform midlength. Mazza and Martínez-Pérez (2015) presented a growth series of *Metapolygnathus mazzai* from the *communisti* Zone of Pizzo Mondello (Figure 2). One specimen, characterized as GS5, corresponds to *Primatella asymmetrica*. Note that the holotype of *M. mazzai* (*M. cf. primitius* sensu Mazza et al., 2012, pl. 8, fig. 12) and additional elements assigned to that species from the Csovár borehole, Hungary (Karádi et al., 2013), do differ.

Another element illustrated from PM as a growth stage of *M. communisti* Morphotype B may belong here, although its posterior platform is shorter and more strongly curved than in typical *P. asymmetrica* (but see Orchard, 2014, fig 61. 19–21) The element figured as *M. mersinensis* by Balini et al. (2010), which pre-dates the known range of the present species, has a similar platform asymmetry but the anterior nodes are smaller and not as well differentiated.

In one sample from Timor-Leste, an element similar to *Kraussodontus urbanae* (Figure 3. 23) co-occurs with *Primatella* species. This element is uniformly narrow and more elongate than *P. asymmetrica* and has less differentiated anterior nodes, but it does have a slightly expanded outer posterior platform margin, unlike *K. urbanae* sensu stricto. The latter species is common in the *angustadyani* through the lower subdivision of the *parvus* subzones of the *primitia* Zone at BBR, a range that overlaps with the appearance of *P. asymmetrica*. The specimen is included here as a further example of similarities between the Canadian and Timor faunas.

**Stratigraphic occurrence:** At its type locality at Black Bear Ridge, *Primatella asymmetrica* occurs in at least twelve collections from the base of the Tuvalian *parvus* Subzone through the lower part of the Lacia *asymmetrica-Norigondolella* Subzone of the *primitia* Zone (Orchard, 2014, tables 7, 8). The inferred range of occurrences in Haida Gwaii and Nevada are consistent with this, as shown in Figure 2. In Nevada, *P. asymmetrica* occurs in seven collections, mostly from the Brick Pile section (Balini et al., 2015). At Pizzo Mondello, a slightly older occurrence of the species is confirmed in the *communisti* Zone but younger records of ‘*Metapolygnathus*’ *mazzai* in the Norian are of undetermined identity. The specimen of *Metapolygnathus communisti* questionably included here came from the *parvus* Zone at PM. In eastern Timor-Leste, sample A7030 (latitude  $-8.796^{\circ}$ ; longitude  $126.6026^{\circ}$ ) contains several additional *Primatella* species but no

typical Carnian taxa, so is judged to be Lacia in age. The slightly older Timor collection (sample S633a) with *K. aff. urbanae* occurs in the central part of the country ( $-8.8945^{\circ}$ ;  $125.5515^{\circ}$ ).

### 5.3 *Primatella bifida* Orchard, 2014

Figure 4. 1–19.

p2008 *Metapolygnathus primitius* (Mosher, 1970). Katvala and Stanley, fig 40. 14 (only).

2012 *Metapolygnathus linguiformis* Hayashi—Mazza et al., p. 114, 116, pl. 8, fig 11.

2014 *Primatella bifida* sp. nov. —Orchard, p. 89–90a, fig 62. 1–15.

2015 *Primatella* sp. nov. 6—Balini et al., fig. 10 j1.

**Holotype:** Orchard, 2014, p. 89–90, fig 62. 13–15 (type number GSC 132956). From bed 07–22 (=GSC cur. no. C-307831), *asymmetrica-Norigondolella* Subzone of the *primitia* Zone (=Kerri Zone) of the Pardonet Formation at Black Bear Ridge, northeast B.C.

**Diagnosis-Comparisons:** See Orchard, 2014.

**Remarks:** *Primatella bifida* is characterized by a bifid variably expanded posterior platform margin and distinct well-differentiated anterior platform nodes. The basal pit lies beneath the center of the platform, posterior to which the basal scar divides and extends close to each posterolateral corner. Illustrated specimens show variation in posterior platform expansion, anterior node formation, and keel bifurcation.

The holotype of *Metapolygnathus linguiformis* Hayashi, 1968, despite being damaged, clearly lacks well-differentiated anterior marginal nodes, unlike the specimen illustrated by Mazza et al. (2012). Hayashi (1968) made no mention of ornament in *M. linguiformis*, and that species appears to lie closer to two others in which ornament is minimal: “*Neogondolella*” *bisecta* Igo, 1989, from a mixed fauna in the Mino Terrane in central Japan, and “*Metapolygnathus*” *slovenicus* Ramovs, 1994, from northwest Slovenia. The few illustrations of these taxa show incipient nodes or marginal undulation like many species of *Quadralella*. These two species may be synonyms, and both may be assignable to *M. linguiformis*, but all are excluded from *P. bifida*. The character of nodose ornament, or its absence, is the basis for distinguishing many Triassic conodonts and is regarded as sufficient for separating *P. bifida* from *M. linguiformis*.

**Stratigraphic occurrence:** At the type locality at Black Bear Ridge, *Primatella bifida* is common in the Tuvalian *parvus* Subzone through the lower part of the Lacia *asymmetrica-Norigondolella* sp. Subzone of the *primitia* Zone. Mazza et al. (2012) recorded their element of *M. linguiformis* from “lower Lacia” strata. The identity of unillustrated specimens is unknown, although, like *P. bifida*, these elements all occur in the “boundary interval” (op. cit., Figure 2). In West Union Canyon, Nevada *P. bifida* (provisionally identified as *P. sp. nov.* 6) occurs in six collections from the Brick Pile and North sections (Balini et al., 2015, figs. 5, 6), all of them within strata recognized as early Norian based on ammonoids, or from stratigraphically older but undated strata above Carnian beds. In the Keku Islands, southeast Alaska, the single specimen figured by Katvala and Stanley (2008) came from the Cornwallis Limestone, sample CPE-F2 at their locality #70 ( $56^{\circ}56.099'$ ,  $134^{\circ}14.534'$ ) on the northeasternmost shore of Cornwallis Peninsula on Kuiu Island: there, it also occurs with other *Primatella* species and is



regarded as Lacián. In Timor-Leste, three occurrences of *P. bifida* are recorded from the Aitutu Formation: sample S663a (−8.8663°; 125.6355°) from the center of the country appears Tuvalian as it also contains *Quadralella*, and nearby sample S664a (−8.8658°, 125.6353°) is probably Lacián as it contains only *Primatella* species, as does a third sample A7038a (−8.6344, 126.8395) from eastern Timor-Leste.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

## Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

## Acknowledgments

Thanks to Eujay McCartney (The University of Western Australia), whose wide-ranging study of the Triassic in Timor-Leste included the recovery, documentation, and photography of diverse conodont faunas that were shared for this study and

## References

- Audley-Charles, M. G. (1968). *The Geology of Portuguese Timor*. London, England: Memoir of the Geological Society of London.
- Balini, M., Bertinelli, A., Di Stefano, P., Guaiumi, C., Levera, M., Mazza, M., et al. (2010). The late Carnian-Rhaetian succession at Pizzo Mondello (Sicani Mountains). *Albertiana* 39, 36–61.
- Balini, M., Jenks, J. F., Martin, R., McRoberts, C. A., Orchard, M. J., and Silberling, N. J. (2015). The Carnian/Norian boundary succession at Berlin-Ichthyosaur State Park (Upper Triassic, central Nevada, USA). *Paläontologische Z.* 89, 399–433. doi:10.1007/s12542-014-0244-2
- Carter, E. S., and Orchard, M. J. (2013). “Intercalibration of conodont and radiolarian faunas from the Carnian-Norian boundary interval in Haida Gwaii, British Columbia, Canada,” in *The Triassic System*. Editors L. H. Tanner, J. A. Spielman, and S. G. Lucas (Albuquerque, NM, United States: New Mexico Museum of Natural History and Science Bulletin) 64, 139.
- Desrochers, A., and Orchard, M. J. (1991). “The Kunga Group (Late Triassic - Early Jurassic), Queen Charlotte Islands, British Columbia: stratigraphic revisions and carbonate sedimentology,” in *Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia*. Editor G. W. Woodsworth (Ottawa, Ontario: Geological Survey of Canada), 163–172.
- Golding, M. L., Orchard, M. J., and Zagorevski, A. (2016). Microfossils from the Cache Creek complex in northern British Columbia and southern Yukon. *Geol. Surv. Can. Open File* 8033, 25. doi:10.4095/298696
- Haig, D. W., Rigaud, S., McCartney, E., Martini, R., Barros, I. S., Brisbout, L., et al. (2021). Upper Triassic carbonate platform facies, Timor-Leste: foraminiferal indices and regional tectonostratigraphic association. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 570, 110362. doi:10.1016/j.palaeo.2021.110362
- Hayashi, S. (1968). The Permian conodonts in chert of the Adoyama Formation, Ashio Mountains, central Japan. *J. Earth Sci. Jpn.* 22 (2), 63–77.
- Hounslow, M. W., Bachmann, G. H., Balini, M., Benton, M. J., Carter, E. S., Konstantinov, A. G., et al. (2021). The case for the global stratotype section and Point (GSSP) for the base of the Norian stage. *Albertiana* 46, 25–57.
- Igo, H. (1989). Mixed conodont elements from Hachiman town, Mino terrane, Central Japan. *Trans. Proc. Paleontol. Soc. Jpn. New Ser.* No. 156, 270–285.
- Jepsson, L., Anehus, R., and Fredholm, D. (1999). The optimal acetate buffered acetic acid technique for extracting phosphatic fossils: acetic acid technique for extracting phosphatic fossils. *J. Paleontology* 73, 964–972. doi:10.1017/s0022336000040798
- Karádi, V., Kozur, H. W., and Görög, A. (2013). “Stratigraphically important Lower Norian conodonts from the Csövar borehole (CSV-1), Hungary - comparison with the conodont succession of the Norian GSSP candidate Pizzo Mondello (Sicily, Italy),” in *The Triassic System*. Editors L. H. Tanner, J. A. Spielman, and S. G. Lucas (Albuquerque, NM, United States: New Mexico Museum of Natural History and Science Bulletin).
- Katvala, E. C., and Stanley, G. D., Jr. (2008). “Conodont biostratigraphy and facies correlations in a Late Triassic island arc, Keku strait, southeast Alaska,” in *The terrane puzzle: New perspectives on paleontology and stratigraphy from the North American Cordillera*. Editors R. B. Blodgett and G. D. Stanley Jr (Boulder, Colorado, USA: Geological Society of America Special Paper).
- Kocsis, A. T., and Scotese, C. R. (2021). Mapping paleocoastlines and continental flooding during the Phanerozoic. *Earth Sci. Rev.* 213, 103463. doi:10.1016/j.earscirev.2020.103463
- Mazza, M., Furin, S., Spötl, C., and Rigo, M. (2010). Generic turnovers of Carnian/Norian conodonts: climatic control of competition? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 290, 120–137. doi:10.1016/j.palaeo.2009.07.006
- Mazza, M., and Martínez-Pérez, C. (2015). Unravelling conodont (Conodont) ontogenetic processes in the Late Triassic through growth series reconstructions and X-ray microtomography. *Boll. della Soc. Paleontol. Ital.* 54 (3), 161–186. doi:10.4435/BSP1.2015.10
- Mazza, M., Rigo, M., and Gullo, M. (2012). Taxonomy and stratigraphic record of the Upper Triassic conodonts of the Pizzo Mondello section (western Sicily, Italy), GSSP candidate for the base of the Norian. *Riv. Ital. Paleontol. Stratigr.* 118 (1), 85–130.
- McCartain, E. (2014). *Stratigraphic studies on Timor-Leste, School of Earth Sciences*. Perth, Australia: The University of Western Australia, 505.
- Metcalfe, I. (2021). Multiple Tethyan ocean basins and orogenic belts in Asia. *Gondwana Res.* 100, 87–130. doi:10.1016/j.gr.2021.01.012
- Mosher, L. C. (1970). New conodont species as Triassic guide fossils. *J. Paleontology* 44 (4), 737–742.
- Muffer, L. J. P. (1967). *Stratigraphy of the Keku islets and neighboring parts of Kuiu and Kupreanof Islands southeastern Alaska*. Denver, CO, USA: U.S. Geological Survey Bulletin.
- Nicora, A., Balini, M., Bellanca, A., Bertinelli, A., Bowring, S. A., Di Stefano, P., et al. (2007). The Carnian/Norian boundary interval at Pizzo Mondello (Sicani Mountains),

are the subject of a future paper in preparation. This compilation represents a legacy contribution to *Triassic Time and trans-Panthalassan correlations*, the International Geological Correlation Program (IGCP) 467 (2003-08), and Geological Survey of Canada-funded programs to understand the evolution and assembly of the Canadian Cordillera. Viktor Karádi, Dmitry Ruban, Guichun Wu, Weiping Zeng, and one anonymous reviewer prompted improvement of this manuscript.

## Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.



- sically) and its bearing for the definition of the GSSP of the Norian stage. *Albertiana* 36, 102–129.
- Orchard, M. J. (1983). *Epigondolella* populations and their phylogeny and zonation in the Norian (Upper Triassic). *Fossils Strata* 15, 177–192.
- Orchard, M. J. (1991a). “Upper Triassic conodont biochronology and new index species from the Canadian Cordillera,” in *Ordovician to Triassic conodont paleontology of the Canadian Cordillera*. Editors M. J. Orchard and A. D. McCracken (Boulder, Colorado, USA: Geological Survey of Canada Bulletin).
- Orchard, M. J. (1991b). “Late Triassic conodont biochronology and biostratigraphy of the Kunga Group, Queen Charlotte Islands, British Columbia,” in *Evolution and hydrocarbon potential of the Queen Charlotte Basin, British Columbia*. Editor G. W. Woodsworth (Boulder, Colorado, USA: Geological Survey of Canada Paper).
- Orchard, M. J. (2013). “Five new genera of conodonts from the Carnian-Norian Boundary beds, northeast British Columbia, Canada,” in *The Triassic system*. Editors L. H. Tanner, J. A. Spielman, and S. G. Lucas (Albuquerque, NM, United States: New Mexico Museum of Natural History and Science).
- Orchard, M. J. (2014). *Conodonts from the Carnian-Norian boundary (Upper Triassic) of Black Bear Ridge, northeastern British Columbia, Canada*. Albuquerque, NM, United States: New Mexico Museum of Natural History and Science.
- Orchard, M. J. (2018). “The lower-middle Norian (Upper Triassic) boundary: new conodont taxa and a refined zonation,” in *Conodont studies dedicated to the careers and contributions of Anita Harris, Glenn Merrill, Carl Rexroad, Walter Sweet, and Bruce Wardlaw*. Editors D. Jeffrey Over and Charles M. Henderson (Bulletins of American Paleontology).
- Orchard, M. J. (2019). The Carnian-Norian boundary GSSP candidate at Black Bear Ridge, British Columbia, Canada: update, correlation, and conodont taxonomy. *Albertiana* 45, 50–68.
- Orchard, M. J., Carter, E. S., Lucas, S. G., and Taylor, D. G. (2007a). Rhaetian (Upper Triassic) conodonts and radiolarians from New York Canyon, Nevada, USA. *Albertiana* 35, 59–65.
- Orchard, M. J., Whalen, P. A., Carter, E. S., and Taylor, H. (2007b). Latest Triassic conodonts from radiolarian-bearing successions in Baja California sur. *N. M. Mus. Nat. Hist. Sci. Bull.* 41, 355–365.
- Ramovš, A. (1994). Conodonten aus den obersten Amphiclinen-Schichten und die Karn/Nor-Grenze im voralpinen Raum der Julischen Alpen. *Cl. 4, Hist. Nat.* 35 (5), 101–109.
- Rigo, M., Mazza, M., Karádi, V., and Nicora, A. (2018). “New Upper Triassic conodont biozonation of the Tethyan Realm,” in *The Late Triassic world*. Editor L. Tanner (Berlin, Germany: Springer).
- Scotese, C. R. (1998). Paleogeographic map archive. PALEOMAP project. Dept. Of Geology, University of Texas. <http://www.scotese.com>.
- Silberling, N. J. (1959). *Pre-Tertiary stratigraphy and Upper Triassic paleontology of the Union District, Shoshone Mountains, Nevada*. Denver, CO, USA: U. S. Geological Survey Professional Paper.
- Stewart, J. H., Silberling, N. J., and Harwood, D. S. (1997). *Triassic and Jurassic stratigraphy and paleogeography of west-central Nevada and eastern California, with a correlation diagram of Triassic and Jurassic rocks*. Denver, CO, USA: U.S. Geological Survey Open-File Report.
- Tozer, E. T. (1967). A standard for Triassic time. *Geol. Surv. Can. Bull.* 156, 103.
- Tozer, E. T. (1994). Canadian Triassic ammonoid faunas. *Geol. Surv. Can. Bull.* 467, 663.
- Trop, J. M., Ridgway, K. D., Manuszak, J. D., and Layer, P. (2002). Mesozoic sedimentary-basin development on the allochthonous Wrangellia composite terrane, Wrangell Mountains basin, Alaska: A long-term record of terrane migration and arc construction. *GSA Bull.* 114 (6), 693–717. doi:10.1130/0016-7606(2002)114<0693:msbdot>2.0.co;2
- Zhang, L., Orchard, M. J., Algeo, T. J., Chen, Z-Q., Lyu, Z., Zhao, L., et al. (2017). An intercalibrated Triassic conodont succession and carbonate carbon isotope profile, Kamura, Japan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 519, 65–83. doi:10.1016/j.palaeo.2017.09.001
- Zonneveld, J-P., Beatty, T. W., Williford, K. H., Orchard, M. J., and McRoberts, C. A. (2010). Stratigraphy and sedimentology of the lower Black Bear Ridge section, British Columbia: candidate for the base-Norian GSSP. *Stratigraphy* 7, 61–82.