

Newly discovered Early to Middle Triassic Conodont faunas in the Shiquanhe area, western Lhasa Block, Xizang (Tibet) and their biostratigraphic and palaeobiogeographic implications

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ABSTRACT

Conodonts have taken on a significant role in elucidating the sedimentary setting as well as geological history of the Lhasa Block (LSB) of Xizang (Tibet). Conodont biostratigraphic research indicates that the LSB was in carbonate platform setting rather than an emergent land mass during Triassic. Lower Triassic sedimentary successions of the LSB are classified as limestone-dominated and dolomite-dominated types. A relatively complete Early to Late Triassic conodont succession has been established for the limestone-dominated sections. In contrast, only a rough Early Triassic *Hadrodontina-Pachycladina* fauna has been described from dolomite-dominated sections. Our investigations of the dolomite-dominated type succession of the Shiquanhe area of the western LSB document for the first time three Early Triassic and two Middle Triassic conodont faunas. They are, in ascending order, the Late Griesbachian to Early Smithian *Hadrodontina* (revised from previously described *Hadrodontina-Pachycladina*) fauna, the Smithian *Pachycladina shiquanica* n. sp. fauna, the Spathian *Triassospathodus homeri-Triassospathodus triangularis* Assemblage Zone, the Early Ladinian *Neogondolella transita*-*Neogondolella excelsa*-*Neogondolella cornuta* fauna, and the Late Ladinian *Budurovignathus* cf. *diebeli*-*Pseudofurnishius murcianus* fauna. The recovered Early to Middle Triassic conodont faunas permit more robust redefinition of the dolomite-dominated Triassic strata. Correlations of the conodont succession of the Shiquanhe area with those in other areas confirm that elloniids-bearing conodont successions existed preferentially along dolomite-dominated strata of low paleo-latitude. They also confirm that the Shiquanhe area had a closer relationship with Europe than with the western USA in palaeobiogeographic distribution in yielding the Lower Triassic species *Pachycladina* fauna and Ladinian species *Neogondolella excelsa* and a more diverse *Budurovignathus* species. Moreover, well-preserved platform-like elements of a newly described species *Pachycladina shiquanica* n. sp. provide clarification of the true P₁ and P₂ elements of the *Pachycladina* apparatus.

1. Introduction

The Lhasa Block (LSB) was a relatively stable tectonic unit of the Qinghai-Xizang Plateau (QXP). It is separated from the Himalaya Block (HB) by the Indus-Yarlungzangbo Suture Zone (IYSZ) to the south and from the South Qiangtang Block (SQB) by the Bangongco-Nujiang Suture Zone (BNSZ) to the north (Fig. 1A).

The LSB during Late Permian to Late Triassic time has been considered by many to have been an old land setting because of the lack of marine Triassic deposits (BGMRX, 1993; Zhao et al., 2001; Pan et al., 2004). However, advances in conodont biostratigraphy in recent years

have revealed the presence of Triassic marine deposits across nearly the entire central to western LSB (Fig. 1A), demonstrating that the region hosted a carbonate platform during Triassic time rather than emergent land (Ji et al., 2018; Wu et al., 2021a, 2024). Two distinct depositional successions have been identified: (1) a limestone-dominated succession, described from the Coqen and Wenbudangsang areas where a nearly complete Late Permian to Late Triassic conodont biostratigraphy has been established (Wu et al., 2007, 2014, 2024; Li et al., 2021, 2025); and (2) a more widely distributed but less biostratigraphically constrained dolomite-dominated succession (Zheng et al., 2007; Wu et al., 2017, 2018, 2021a, 2021b). Previous investigations of the latter have

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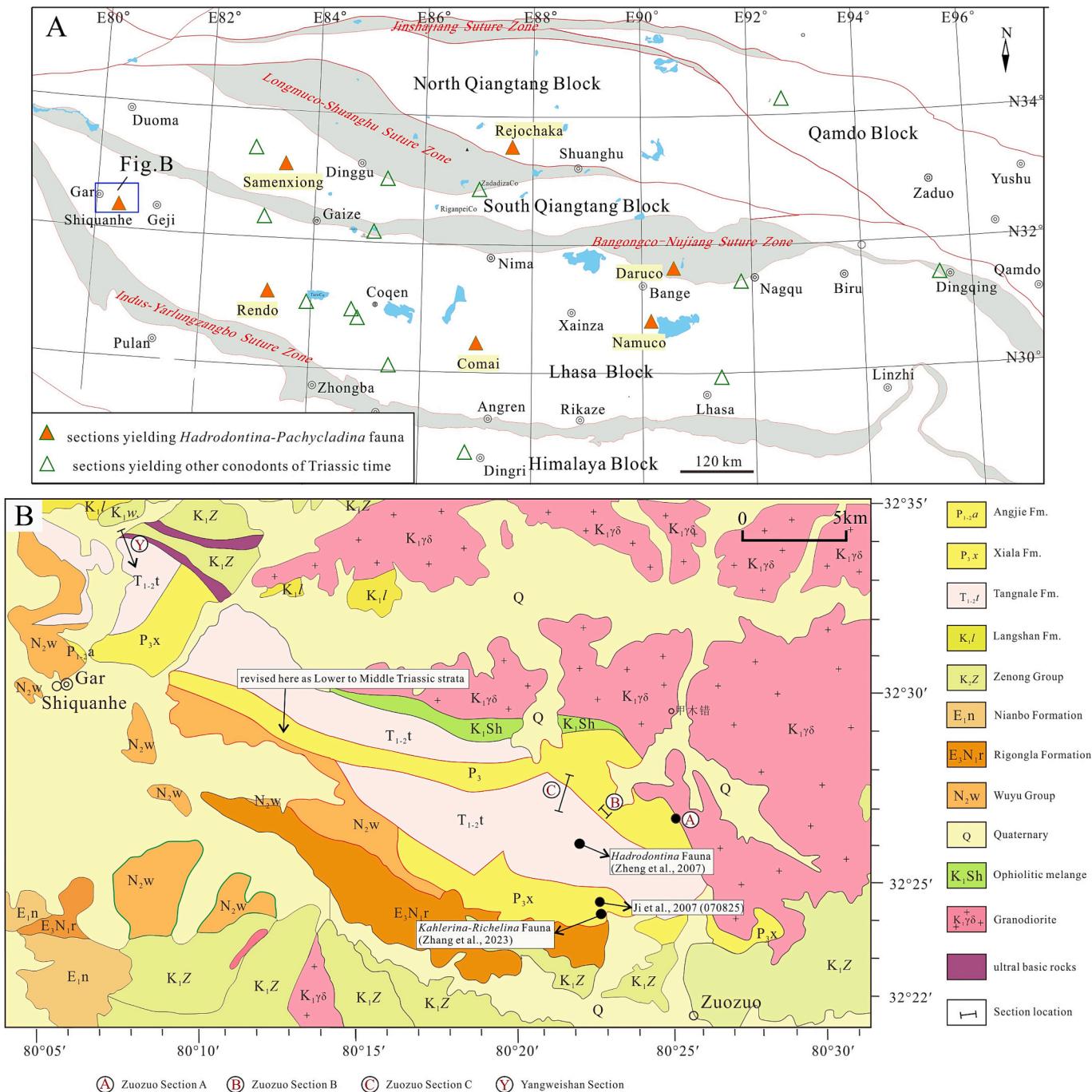


Fig. 1. A) Tectonic units of Xizang (Tibet) and location of the Shiquanhe area (the base is from Pan et al., 2004; B) Geological map of the study area (after Zheng et al., 2002).

recognized only a single, broadly defined Early Triassic *Hadrodontina-Pachycladina* Assemblage Zone (Zheng et al., 2007; Wu et al., 2017, 2018, 2021a, 2024). Middle to Upper Triassic deposits of the dolomite-dominated succession have yet to be confirmed by fossils or other age-indicative data. A more complete understanding of the sedimentary history requires detailed conodont biostratigraphic investigation of the upper part of the dolomite-dominated succession.

The dolomite-rich deposits have been documented from the Shiquanhe area, where they have been described as the Lower–Middle Triassic Tangnale Formation (Zheng et al., 2007). The inferred extension of this succession into the Middle Triassic is based solely on the occurrence of the *Hadrodontina-Pachycladina* fauna in the lower part of the ~3675 m-thick dolomite sequence (Zheng et al., 2007). However, the

presence of Middle Triassic strata remains unresolved due to the absence of definitive fossil evidence. Moreover, the Middle Permian Xiala Formation, previously considered to overly the Tangnale Formation in fault contact, lacks neither fossil nor geochronological data to support this age designation (Zheng et al., 2007). Our study aims to (1) provide new constraints on the age and stratigraphic relationships of the upper Tangnale Formation and overlying strata and (2) re-define the biostratigraphy of the dolomite-dominated Triassic succession of Shiquanhe area of the western LSB.

2. Geological setting

The study area is dominated by exposures of Cretaceous

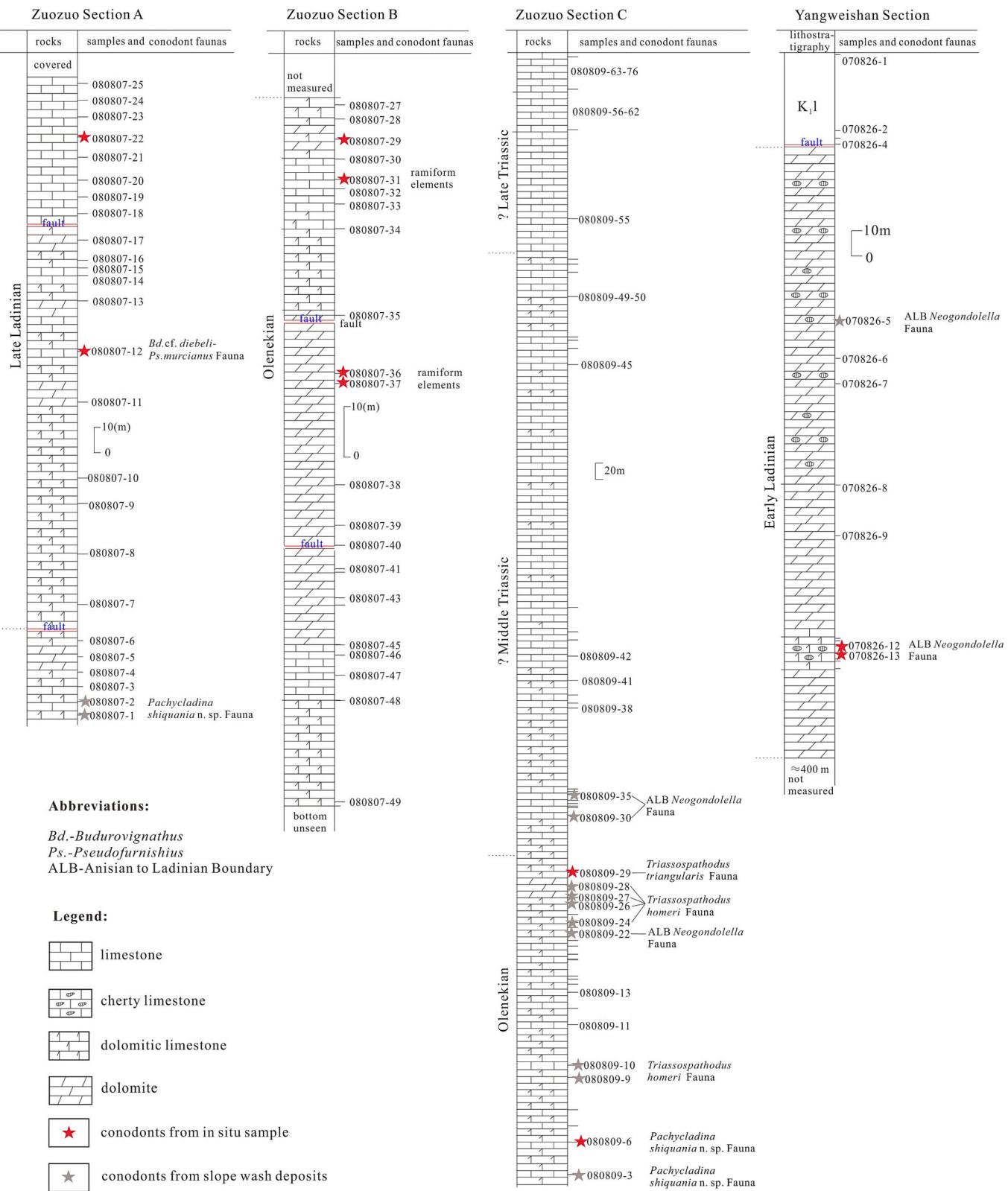


Fig. 2. Lithologic logs of the four measured sections illustrating conodont sample locations and principle conodont faunas.

granodiorites. Identified sedimentary strata include the Lower to Middle Permian Angie Formation (P_{1-2a}), Upper Permian Xiala Formation (P_{3x}), Lower to Middle Triassic Tangnale Formation (T_{1-2f}), Lower Cretaceous Zenong Group (K_1Z) and Langshan Formation (K_1l), and Cenozoic sediments (Xu et al., 2010). Among these units, the Xiala and

Tangnale formations are the most extensively distributed (Fig. 1B).

The Permian Xiala Formation, well-studied in the Zuozuo area, consists of thick-bedded limestone containing abundant chert nodules and bands, and hosts the Upper Permian Wuchiapingian fusuline *Kahlerina-Reichelina* Fauna (Zhang et al., 2023) and Upper Permian

sections	Samples		conodont types and numbers						
	in situ	slope wash	neospaphodid (P ₁)	neogondolellid (P ₁)	ellisoniid (P ₁ +P ₂)	Budurovignathus(P ₁)	Pseudofurnishius(P ₁)	Nicoraella (P ₁)	Ramiform
A	080807-22								1
	080807-12					1	1		1
	080807-2								7
	080807-1				2+2				70
B	080807-29								1
	080807-31								70
	080807-36								140
	080807-37								90
Zuozuo	080809-36								1
	080809-35			2					5
	080809-32								1
	080809-31			1					1
	080809-30								1
	080809-29		9						400
	080809-28		25						340
	080809-27		12						300
	080809-26		11						260
	080809-24		9						210
C	080809-22		8				1	3	
	080809-20							1	
	080809-14							3	
	080809-10		10						450
	080809-9		12						190
	080809-6								20
	080809-3			1(P ₁)					5
	070826-5			28					60
	070826-6			2					
	070826-7			5					3
Yangweishan	070826-11			11					
	070826-12			9					8
	070826-13			29			1	4	
	070826-14			1					1
	070826-15								2
	070826-16			4					4

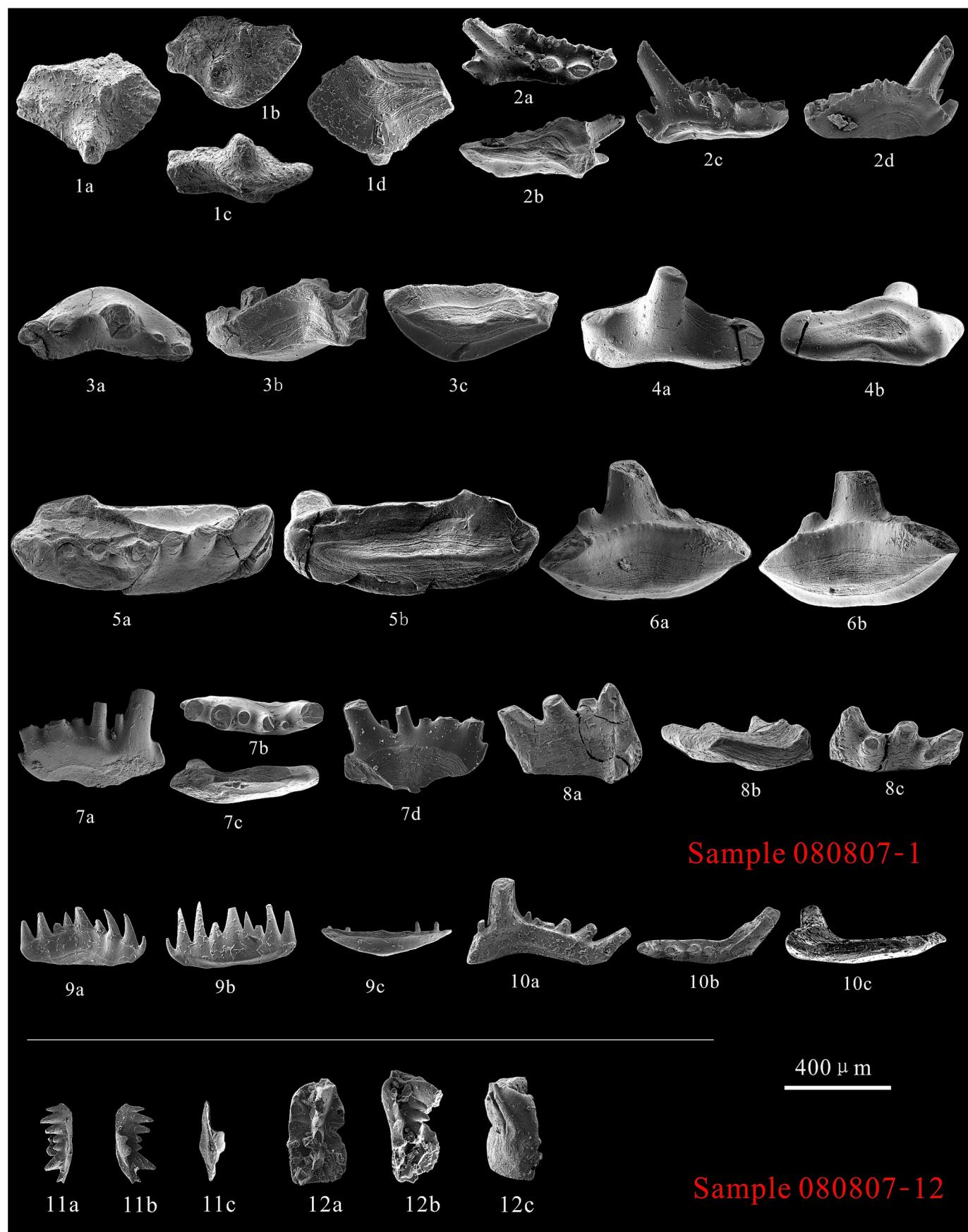
Fig. 3. Conodont occurrence, types and quantities of the studied sections.

Changhsingian to Lower Triassic conodont species (*Clarkina changxinensis*, *Neospaphodus* sp., *Gladigondrella* sp.) (Ji et al., 2007) (Fig. 1B). The overlying dolomite-dominated Tangnale Formation has been described as a Lower to Middle Triassic unit following the discovery of the Lower Triassic *Hadrodontina-Pachycladina* fauna in its lower part (Zheng et al., 2007). However, no age-diagnostic fossils or chronostratigraphic markers have been confirmed in the upper Tangnale Formation nor the immediately overlying Xiala Formation. Furthermore, extensive faulting and limited exposure have complicated stratigraphic characterization and regional correlation. Similar uncertainties persist in the Yangweishan area, where the presence of deposits of the Lower to Middle Triassic Tangnale Formation has not been confirmed by fossil evidence. The present study focuses on the upper Tangnale Formation and overlying strata (previously assigned to the Xiala Formation) in three Zuozuo sections (A, B, and C), as well as the Tangnale Formation in the Yangweishan area (Fig. 1B).

3. Methods

We measured and sampled three sections (A, B, C) in the Zuozuo area and one section in the Yangweishan area (Fig. 1B; Fig. 2). Each conodont sample weighs ~2.5 kg on average. The surveyed sections are not especially well exposed. In areas where rock exposure is poor, samples were collected from slope wash deposits along traverses that spanned the interval of interest. Although the original stratigraphic positions of these samples remain uncertain, recovered conodonts are useful to constraining age ranges when integrated with in situ data.

We adopted acid dissolution methods for conodont sample analysis as per the following procedures: rock samples were dissolved in 10 % buffered acetic acid that was changed every 7 to 10 days; residues were sieved into two size classes (N2 mm, N200 µm); the dried residues were picked under a binocular stereomicroscope and recovered fossils were stored in microcells. Scanning electron microscopic (SEM) images were



(caption on next page)

Plate 1. Early to Middle Triassic conodonts of the Zuozuo Section A.

Sample numbers are marked directly on the plate. Different samples are separated from each other by a white line.

- 1–2, *Pachycladina shiquanica* n. sp. 1, P₁; 2, P₂;
- 3–4, *Pachycladina* sp., S elemens;
- 5, *Pachycladina* sp. (?P₁);
- 6, *Pachycladina shiquanica* n. sp. (S₀);
- 7–10, *Ellisonia* sp.;
- 11, *Pseudofurnishius murcianus* (P₁), juvenile specimen;
- 12, *Budurovignathus* cf. *diebeli* (P₁).

collected at 10 keV on gold-coated samples. All fossils are housed at the Key Laboratory of Stratigraphy and Palaeontology, Institute of Geology, Chinese Academy of Geological Sciences.

4. Results

Age-diagnostic conodonts have been collected from the four measured sections. Their productivity and abundance in each section are shown in Fig. 3.

Zuozuo Section A extends from 32°26'51.4" N, 80°25'13.4" E, 4741 m H, and ends where strata are in contact with Cretaceous magmatic rocks. Section A is dominated by grey to blackish dolomite intercalated with dolomitic limestone that has previously been assigned to the Xiala Formation (Zheng et al., 2007) (Fig. 1B). We collected 19 conodont samples (numbers 080807–7 to 080807–25) from this section. Most of the samples were recovered in situ. We also recovered 6 samples (numbers 080807–1 to 080807–6) from underlying slope wash deposits comprised largely of dark grey dolomite. Early Triassic conodont specimens assigned to *Pachycladina* and *Ellisonia* are found from samples 080807–1 and 080807–2, and rare specimens of *Budurovignathus* and *Pseudofurnishius* are described from Sample 080807–12 (Plate 1).

Zuozuo Section B extends from 32°26'50.3" N, 80°23'05.3" E, 4948 m H to 32°27'01.7" N, 80°22'47.6" E, 5045 ± 2 m H. Strata of this section have been assigned to the Permian Xiala Formation (Fig. 1B) and are dominated by interlayered dark-grey dolomite and limestone. We collected 23 samples from this section (numbers 080807–27 to 080807–49). Three in situ samples provided relatively abundant ramiform conodont elements. The generally limited use of these elements in biostratigraphic correlation has been attributed to their equivocal morphological evolution compared that of P elements. However, the recovery of similar ramiform elements from rocks of the neighboring Zuozuo Section C, where associated P₁ elements have also been identified, increase the utility of the ramiform faunas for biostratigraphic correlation of the Zuozuo Section B.

Zuozuo Section C starts from the 32°26'57.4" N, 80°21'26.2" E, 5005 ± 3 m H, and ends at 32°27'51.7" N, 80°21'49.1" E, 4872 m H. This section is thicker than the other two, comprising the upper part of the Tangnale Formation and an interval of the overlying Xiala Formation though the contact of these units remains unclear (Fig. 2). We collected 71 conodont samples (numbers 080809–6 to 080809–76) from Section C. Eleven samples recovered from the lower part of the section yielded abundant conodonts (Plate 2, Plate 3). Samples 080809–3 and 080809–6 are dominated by species of *Pachycladina*. Samples 080809–22 and 080809–35 have yielded neogondolellid elements, including *Neogondolella excelsa*, a juvenile specimen of *Neogondolella constricta* group, *Neogondolella cornuta*, and *Neogondolella transita*. *Nicarella* sp. has also been documented from sample 080809–22. The remaining seven samples (080809–9, 080809–10, 080809–24, 080809–26 to 080809–29) are dominated by species of *Novispathodus* and *Triassospathodus*.

Yangweishan Section. This section starts at the location 32°34'8.64" N, 80°07'24" E, 4648 ± 7 m H (Figs. 1B and 2). Strata of this Yangweishan Section were originally correlated with the Lower to Middle Tangnale Formation though fossil evidence is lacking. The section is comprised of grey-black dolomite and cherty nodules. We collected 13 conodont samples from this section. Recovered conodonts from seven

samples (070826–5, 070826–6, 070826–7, 070826–11, 070826–12, 070826–13, 070826–16) include neogondolellid elements (Plate 4). The recognized species include *Neogondolella excelsa*, *Neogondolella constricta*, *Neogondolella cornuta* group, *Neogondolella transita*, and *Neogondolella aldae*.

5. Newly identified Early to Middle Triassic conodont faunas

Two Early Triassic and two Middle Triassic conodont faunas are for the first time identified from the Shiqianhe area. The faunas include, in ascending order, the *Pachycladina shiquanica* n. sp. fauna, the *Triassospathodus homeri-Triassospathodus triangularis* Assemblage Zone, the *Neogondolella transita-Neogondolella excelsa-Neogondolella cornuta* fauna, and the *Budurovignathus* cf. *diebeli-Pseudofurnishius murcianus* fauna.

1) *Pachycladina shiquanica* n. sp. fauna.

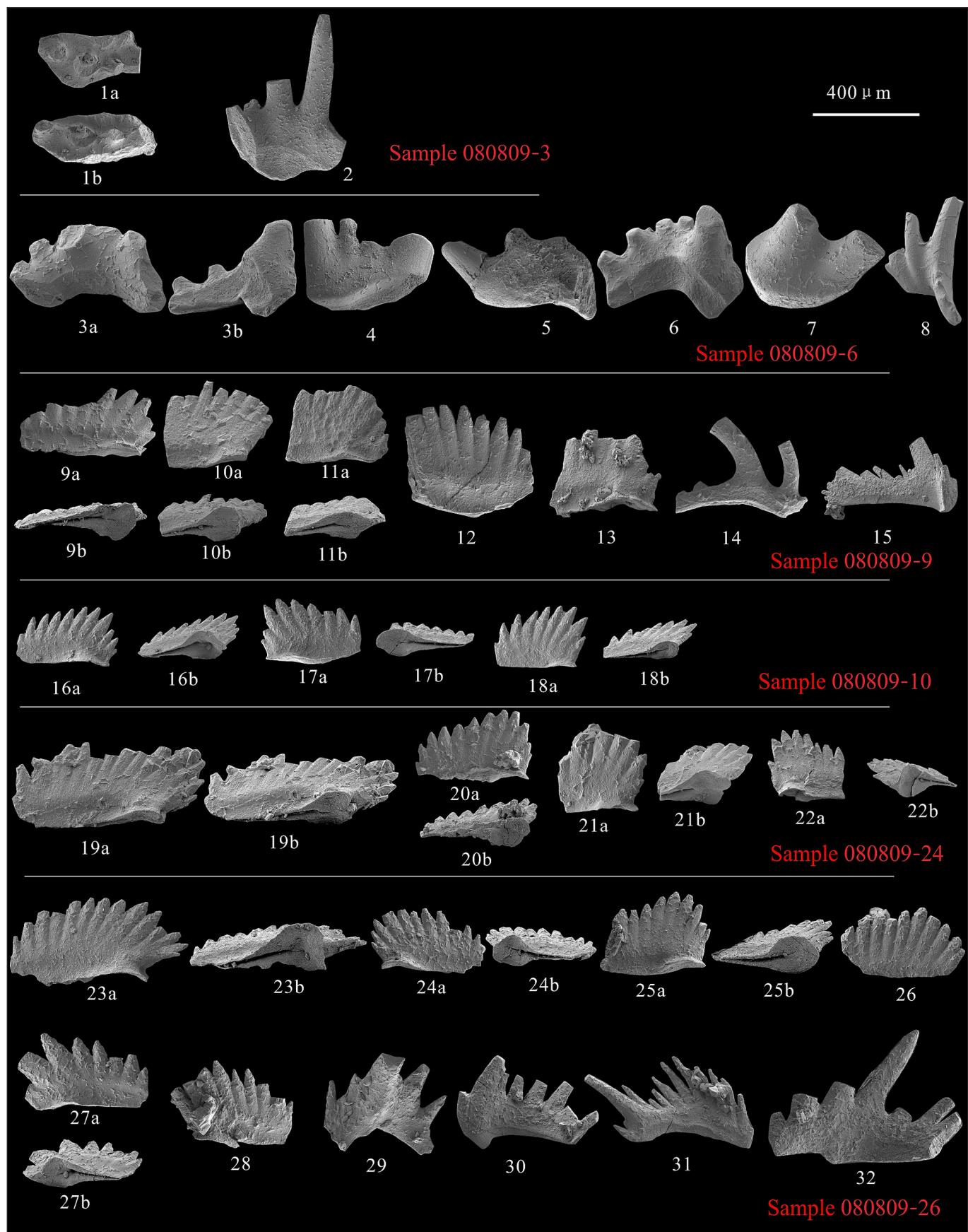
This fauna is identified in four samples: two from the Zuozuo Section A (080807–1, 080807–2) and two from the Zuozuo Section C (080809–3, 080809–6). Conodonts are abundant in sample 080807–2 but rare in the other samples. The assemblage is characterized by Early Triassic elloniid specimens characterized by robust denticles and denticle bars. Recognized species include *Ellisonia* sp., *Pachycladina shiquanica* n. sp., and *Pachycladina* sp. Among them, *Pachycladina shiquanica* n. sp. is the most prevalent.

Pachycladina is well-known for its sturdy morphology that has generally been interpreted as an adaptation to high-energy and shallow water depositional environments (Staesche, 1964; Orchard, 2007). Its predilection for low paleo-latitude regions enhances their utility in paleobiogeographic reconstructions (Wu et al., 2021a). Morphologically and ecologically similar genera include *Hadrodontina* and *Parachirognathus*. Their evolutionary relationship remains unknown though the established *Hadrodontina-Pachycladina-Parachirognathus* succession of the middle Werfen Formation of the Southern Alps of Northern Italy (Staesche, 1964; Perri and Andraghetti, 1987; Perri, 1991) and Slovenia (Kolar-Jurkovšek and Jurkovšek, 2019) suggests that *Hadrodontina* appeared in the Dienerian, followed by *Pachycladina* in the Early Smithian, with *Parachirognathus* representing the youngest occurrence of this morphological group in the Late Smithian (Staesche, 1964; Perri and Andraghetti, 1987; Perri, 1991; Orchard, 2007; Posenato, 2008).

The *Pachycladina shiquanica* fauna described herein occurs in the upper Tangnale Formation, stratigraphically above the "*Hadrodontina-Pachycladina*" fauna reported by Zheng et al. (2007) from the lower Tangnale Formation and below the Spathian *Triassospathodus homeri-Triassospathodus triangularis* Assemblage Zone (see below). Notably, we reassigned "*Pachycladina*" specimens described by Zheng et al. (2007) to *Hadrodontina* based on their distinct basal cavity and furrow morphology (for detailed generic differentiation, see Wu et al., 2025). This conodont succession, from the *Hadrodontina* fauna through the *Pachycladina shiquanica* fauna to the *Triassospathodus triangularis-Triassospathodus homeri* Assemblage Zone, correlates well with that documented from Southern Alps of Italy (Perri, 1991) and Slovenia (Chen et al., 2016a; Kolar-Jurkovšek and Jurkovšek, 2019), confirming the Smithian age of the present *Pachycladina shiquanica* fauna.

2) *Triassospathodus homeri*-*Triassospathodus triangularis* Assemblage Zone.

This fauna has been recovered from in situ sample 080809–29 and slope wash samples 080809–9, 080809–10, 080809–24, 080829–26,



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Plate 2. Early Triassic conodonts of the Zuozuo Section C.

Sample numbers are marked directly in the plate. Different samples are separated from each other by a white line.

- 1, *Pachycladina shiquania* n. sp. (P₂);
- 2–8, ramiform elements of *Pachycladina* sp.;
- 9, *Triassospathodus homeri* (P₁);
- 10, *Triassospathodus* cf. *symmetricus* (P₁);
- 11, 13, *Triassospathodus* cf. *homeri* (P₁);
- 12, *Novispathodus* sp. (P₁);
- 14–15, ramiform elements;
- 16–18, *Triassospathodus homeri* (P₁);
- 19–20, *Triassospathodus homeri* (P₁);
- 21–22, *Novispathodus* cf. *waageni* (P₁);
- 23, *Triassospathodus sosioensis* (P₁);
- 24–25, *Triassospathodus homeri* (P₁);
- 26, 28, *Novispathodus* sp. (P₁);
- 27, *Neospathodus tulongensis* (P₁);
- 29–32, ramiform elements.

080809–27, 080809–28, and 080809–29. All of these samples have yielded similar segminate elements of Olenekian time, indicating that the slope wash samples have experienced minimal transport from their in situ stratigraphic level. *Triassospathodus homeri* and *Triassospathodus triangularis* dominate this fauna. Other species of this fauna include *Novispathodus* cf. *pingdingshanensis*, *Triassospathodus sosioensis*, *Triassospathodus* cf. *symmetricus*, and *Neospathodus tulongensis*, all of which are typical Spathian species.

Triassospathodus homeri and *TTriassospathodus triangularis* have been widely recognized as index species for the Spathian stage (Sweet, 1970; Kozur, 2003; Wu et al., 2007, 2021b; Yan et al., 2013; Chen et al., 2015, 2023; Sun et al., 2021; Kolar-Jurkovsek et al., 2023). Both species possess diagnostic P₁ elements with distinct morphological characteristics. Specifically, *Triassospathodus homeri* P₁ elements are relatively elongate, characterized by a short posterior process that deflects laterally to varying degrees, and a basal cavity that tapers posteriorly beneath the posterior process. *Triassospathodus triangularis* P₁ elements are comparatively shorter and feature a posteriorly expanded, triangular-shaped basal cavity and a distinctive folded basal cup near the posterior portion (Orchard, 1995).

3) *Neogondolella transita*-*Neogondolella excelsa*-*Neogondolella cornuta* fauna.

This fauna has been recovered from both the Zuozuo C (samples 080809–22 and 080809–35) and the Yangweishan (samples 070826–5, 070826–12, 070826–13) sections. They are most abundant in strata of the Yangweishan Section though they display low diversity in both sections. *Neogondolella transita*, *Neogondolella excelsa*, and *Neogondolella cornuta* are recognized in both sections. Associated species documented in the Zuozuo Section C include a junior element of *Neogondolella constricta* group, *Nicarella* sp., and rare ramiform elements. Associated other species documented from the Yangweishan Section include *Neogondolella constricta* and *Neogondolella aldae*.

Neogondolella cornuta and *Neogondolella constricta* are dominant species in strata of the Anisian - Ladinian boundary (ALB) interval of both Europe (Kozur, 1990; Kovács, 1994; Karádi et al., 2022) and North America (Orchard and Golding, 2024). *Neogondolella transita* is identified from Lower Ladinian strata of Europe (Kozur, 1990; Kovács, 1994; Vörös et al., 1996; Karádi et al., 2022). A morphologically similar species is also found from North America though it referred to as *Neogondolella excentrica sigmoidalis* (Orchard and Golding, 2024). *Neogondolella excelsa* has occurrence mainly on Lower Ladinian deposits of Tethys area (Wang and Wang, 1976; Durkoop et al., 1986; Chen et al., 2016a, 2016b; Karádi et al., 2022). Thus, the present described ALB interval *Neogondolella* fauna is suggested to be of Early Ladinian age.

4) *Budurovignathus* cf. *diebeli*-*Pseudofurnishius murcianus* fauna.

This fauna has been identified in Sample 080807–12 of the Zuozuo Section A. Only one broken adult specimen and one juvenile specimen are recognized, which are assigned respectively as *Budurovignathus* cf.

diebeli and *Pseudofurnishius murcianus*. Both are characterized by a forward shifted basal cavity with a posteriorly extended keel and obvious platform margin denticulation that are consistent with the definition of *Budurovignathus* (=*Sephardiella*) (Plasencia et al., 2007; Ishida and Hirsch, 2011; Chen et al., 2016b).

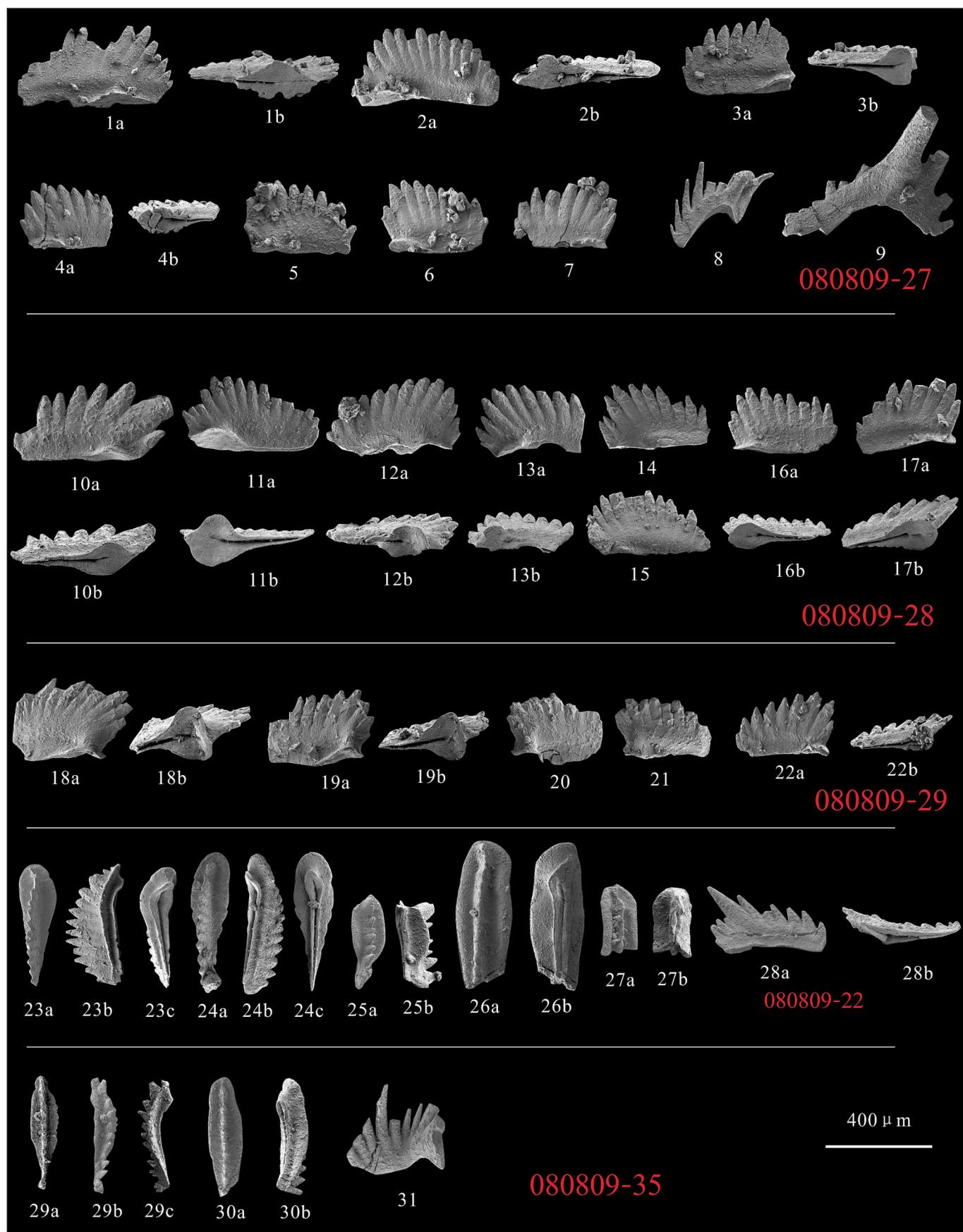
The specimen assigned to *Budurovignathus* cf. *diebeli* exhibits a broad platform with a nearly square posterior termination. The carina deflects toward one posterior-lateral corner, mirroring the curvature of the posteriorly elongated basal keel. The anterior platform tapers sharply to a free blade, much of which is broken. These features, including the broad platform morphology, abrupt anterior narrowing, and posteriorly extended curved keel, closely align with those of *Budurovignathus diebeli*. However, the incomplete preservation of the free blade necessitates a provisional designation of this specimen as a comparative form of *Budurovignathus diebeli*.

The specimen assigned to *Pseudofurnishius murcianus* is a juvenile one, but it is fully intact and displays an exceptionally narrow platform at its midpoint with two marginal denticles on one lateral edge and only a faint ridge on the opposite side, consistent with the definition of *Pseudofurnishius huddlei* (Plasencia et al., 2007; Kolar-Jurkovsek et al., 2023).

Budurovignathus diebeli and *Pseudofurnishius murcianus* range from late Longobardian (Late Ladinian) to early Julian (Early Carnian) (Chen et al., 2016b; Plasencia et al., 2007; Rigo et al., 2018; Kolar-Jurkovsek and Jurkovsek, 2019). When accompanied by typical Early Carnian species such as *Paragondolella polygnathiformis*, it is definitely of Early Julian time (Jiang et al., 2018). The present fauna do not include elements of *Paragondolella polygnathiformis*, so it is tentatively assigned to be of Late Ladinian age.

6. Conodont correlations and their palaeobiogeographic implications

The Shiquanhe conodont succession reveals a much more complete ellisoniids dominated Lower Triassic zonation. It is comprised of *Hadrodontina* fauna, *Pachycladina* fauna, and *Triassospathodus* fauna in an ascending order. It is noteworthy the “*Hadrodontina*” fauna of the present study is revised from the “*Hadrodontina-Pachycladina*” described by Zheng et al. (2007) as the illustrated specimens of *Pachycladina* are actually *Hadrodontina* as noted earlier. The Shiquanhe succession also consists of two Middle Triassic faunas, the Early Ladinian *Neogondolella* fauna and the Late Ladinian *Budurovignathus*-*Pseudofurnishius* fauna (Fig. 4). Correlation of the Lower to Middle Triassic conodont succession of the Shiquanhe area with succession of Coqen area, Himalaya, Europe, and western USA, further confirm that the ellisoniids- characterized conodont succession is preferentially distributed along low paleo-latitude areas, illustrating a strong palaeobiogeographic character (Fig. 4).



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Plate 3. Early to Middle Triassic conodonts of the Zuozuo Section C.

Sample numbers are marked directly in the plate. Different samples are separated from each other by a white line.

- 1–2, *Triassospathodus homeri* (P₁);
- 3, *Novispathodus* sp. (P₁);
- 4–7, 17, 21–22, *Novispathodus cf. pingdingshanensis* (P₁);
- 8–9, ramiform elements;
- 10, *Neospathodus tulongensis* (P₁);
- 11–16, *Triassospathodus homeri* (P₁);
- 18–20, *Triassospathodus triangularis* (P₁);
- 23–24, *Neogondolella excelsa* (P₁);
- 25, *Neogondolella aff. Excelsa* (P₁);
- 26–27, *Ng. excentrica transita* (P₁);
- 28, *Nicoraella* sp. (P₁);
- 29, a juvenile specimen (P₁) of *Neogondolella constricta* group;
- 30, *Neogondolella cornuta* (P₁);
- 31, ramiform element.



1) Correlation with the Coqen area.

The Lower Triassic conodont succession of the Coqen area is dominated by gondolellid and neospathodid species. It can be correlated with the Shiquanhe succession by sharing common Spathian *Triassospathodus* fauna.

The ALB interval *Neogondolella* fauna of the Shiquanhe succession has not been described from the Coqen area, where only rare juvenile specimens of the *Neogondolella constricta* group have been identified. Both successions host Late Ladinian species of *Budurovignathus* though *Pseudofurnishius* species has not been described from Coqen. It is noteworthy that *Budurovignathus mungoensis* has been documented from both the Coqen (Ji et al., 2006, 2018; Li et al., 2025) and Angren (Li et al., 2020) areas of the LSB though it has been wrongly assigned as the Late Triassic epigondolellid species (Ji et al., 2006, 2018; Li et al., 2020).

2) Correlation with South China.

The Lower Triassic conodont succession comprised of hindeodid, gondolellid, and neospathodid species has been well established in South China areas, including in Anhui (Zhao et al., 2007), Hubei (Zhao et al., 2013), and Guizhou (Yan et al., 2013; Chen et al., 2015; Lehrmann et al., 2015; Leu et al., 2022; Chen et al., 2023). Lower Triassic ellisoniid specimens have also been collected from the dolomite-dominated deposits of Sichuan of South China, but no such complete succession as that of the Shiquanhe area has been recovered to present (Wang and Cao, 1981; Wang and Dai, 1981; Tian et al., 1983; Zhao et al., 2024).

Much of the Middle Triassic conodont succession of South China has been recovered from Guizhou, where conodont zones except for ALB interval *Neogondolella* faunas have been confirmed (Wang et al., 2005; Wu et al., 2008; Sun et al., 2014; Qin et al., 2021, 2023; Orchard and Golding, 2024). The Ladinian conodont succession, including *Budurovignathus truempi*, *Budurovignathus hungarica*, and *Budurovignathus mungoensis* in an ascending order, has also been identified from Guizhou (Wang et al., 2005; Qin et al., 2023). It is noteworthy that *Budurovignathus diebeli*, proposed as the final stage of the *Budurovignathus* lineage (Plasencia et al., 2007), has not been described from South China (Tong et al., 2019; Qin et al., 2023).

3) Correlation with Himalaya.

The Lower Triassic conodont succession of Himalaya is known to be comprised of hindeodid, gondolellid, and neospathodid species. The biostratigraphy is well known in the Kashmir region of India (Sweet et al., 1971; Lyu et al., 2021), the Spiti region of India (Krystyn et al., 2004; Sun et al., 2021), and the Tulong Section of Southern Xizang (Wang and Wang, 1976; Tian, 1982; Chen et al., 2022; Bai et al., 2025). Among them, the Lower Triassic conodont succession of Kashmir has been accepted as international standard zonation (Sweet et al., 1971).

The Middle Triassic Ladinian conodont succession of Himalaya is poorly defined primarily due to stratigraphic condensation (Krystyn et al., 2004; Sun et al., 2021). Nevertheless, the Ladinian species *Neogondolella excelsa* has been confirmed in the Tulong Section of Southern Xizang (Tian, 1982). Moreover, *Budurovignathus mungoensis* has been

recognized in the Tulong Section where associated species include *Paragondolella foliata inclinata* and *Paragondolella foliata foliata* (Xia and Zhang, 2005).

4) Correlation with Europe.

The Lower Triassic conodont succession of Europe is characterized by the presence of ellisoniid faunas. This occurrence is especially well known from the southern Alps and Slovenia areas, where *Hadrodontina* fauna appears earlier than *Pachycladina* fauna though both are demonstrated to overly the Griesbachian hindeodid zones and are overlain by the Spathian neospathodid zone (Staesche, 1964; Perri and Andraghetti, 1987; Perri, 1991; Posenato, 2008; Kolar-Jurkovšek and Jurkovšek, 2019).

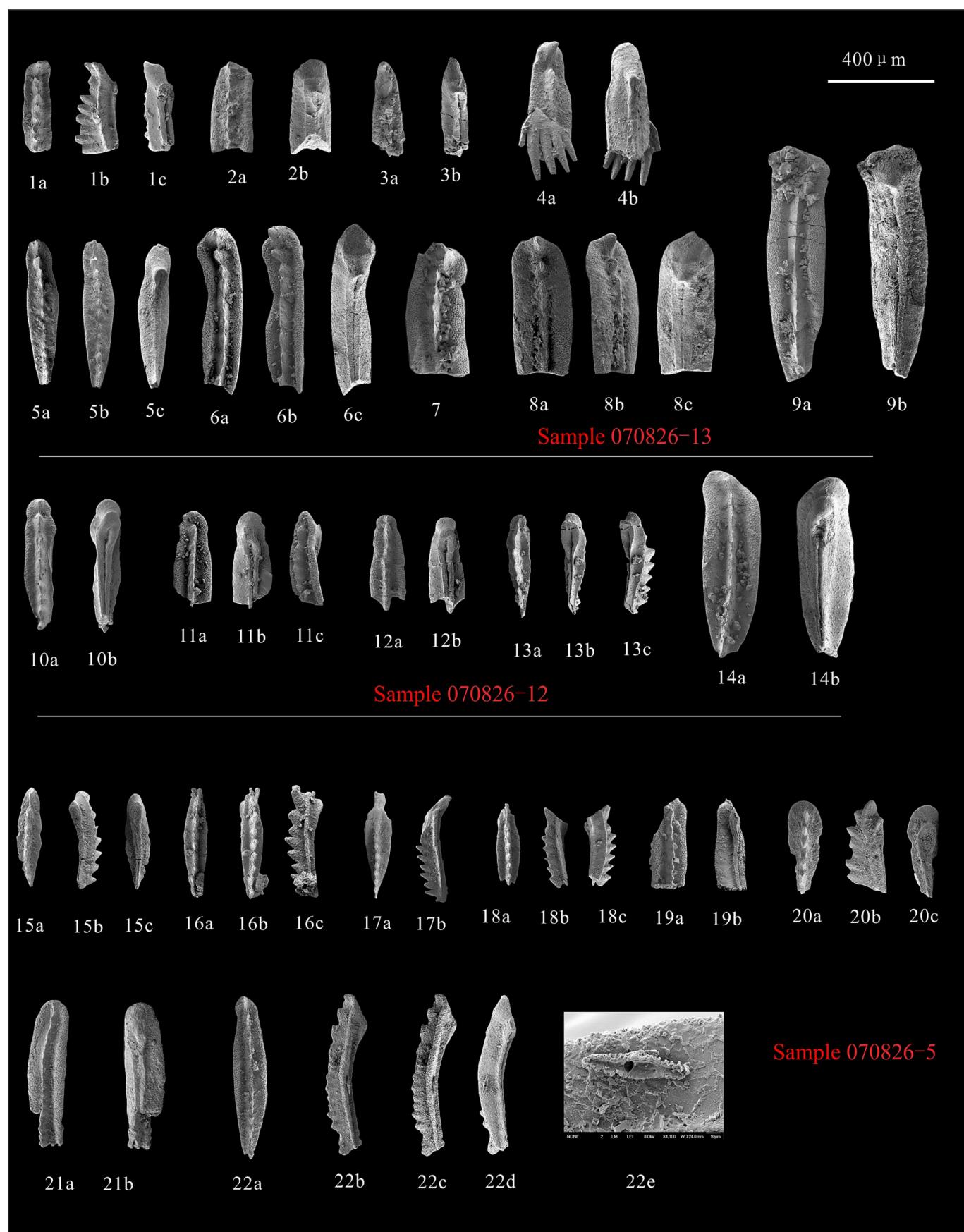
Middle Triassic conodont succession of Europe is not especially well defined despite the presence of the Global Boundary Stratotype Section and Point (GSSP) for the base and top of the Ladinian Stage in this part of the world (Broglio Loriga et al., 1999; Brack et al., 2005; Ogg et al., 2020). Conodont zones are primarily assembled from different areas. For example, the ALB interval conodont succession is best observed in Bulgaria (Budurov and Stefanov, 1972) and the Balaton Highlands, Hungary (Kovács, 1994; Vörös et al., 1996) (Fig. 6). Kozur (1980, 1990) described the ALB succession as being comprised of the Illyrian (Late Anisian) *Neogondolella cornuta* and *Neogondolella postcornuta* zones and the early Fassanian (Early Ladinian) *Neogondolella transit-a-Neogondolella excelsa* fauna. Ladinian conodont faunas are present in Slovenia where they comprise the *Budurovignathus hungaricus* fauna and the *Budurovignathus mungoensis-Pseudofurnishius murcianus* fauna, in ascending order (Kolar-Jurkovšek and Jurkovšek, 2019).

The Europe conodont succession, which is similar to the Shiquanhe succession, comprises the Lower Triassic ellisoniid succession, the ALB interval *Neogondolella* fauna, and the Late Ladinian *Budurovignathus-Pseudofurnishius* fauna.

5) Correlation with USA.

The Lower Triassic conodont succession of Nevada and Utah, western USA, is characterized by the ellisoniid *Parachirognathus* and *Furnishius* overlain by the gondolellid *Scythogondolella* and neospathodid *Icriospathodus* species (Clark, 1959; Solien, 1979).

ALB interval conodonts are well known in the Fossil and Saurian hills of Nevada (Mosher and Clark, 1965; Bucher and Orchard, 1995; Orchard and Golding, 2024). The ALB conodont succession there includes the Upper Anisian *Neogondolella constricta* Zone and the Lower Ladinian *Neogondolella mombergensis* Zone (Sweet et al., 1971; Nicora and Kovács, 1984). Orchard and Golding (2024), however, modified the ALB conodont succession there to be made up of the Upper Anisian *Neogondolella constricta* and *Neogondolella cornuta* faunas, and the Lower Ladinian *Neogondolella posterolonga* fauna. They further noted that the associated species *Neogondolella excentrica sigmoidalis* of the *Neogondolella posterolonga* fauna is morphologically similar to *Neogondolella transit-a* of Europe (Orchard and Golding, 2024). *Budurovignathus mungoensis* has been described from the Ladinian-Carnian boundary interval at South



(caption on next page)

Plate 4. Middle Triassic conodonts of the Yangweishan Section.

Sample numbers are marked directly in the plate. Different samples are separated from each other by a white line.

1–7, 9, *Neogondolella cornuta* (P₁) group. The upper side of 4 is attached by a specimen temporarily assigned to *Nicoraella* sp. (P₁);

8, *Neogondolella constricta* (P₁).

10–13, juvenile specimens of *Neogondolella constricta* (P₁) group, with typical posterior platform constriction.

14, *Neogondolella transita* (P₁).

15–19, juvenile specimens of *Neogondolella constricta* (P₁) group, with typical posterior platform constriction.

20, *Neogondolella excelsa* (P₁) (Mosher, 1968), a juvenile specimen. The round posterior platform as well as the high carina denticles that increase anteriorly are both typical characters of this species, even in this juvenile specimen.

21, *Neogondolella cornuta* (P₁).

22, *Neogondolella aldae* (P₁). fig. 22d shows a weird structure in one lateral side of basal field; this part is magnified as seen in fig. 22e.

Canyon, western USA, though it is less common than in Europe (Orchard and Balini, 2007).

6) Palaeobiogeographic implications.

Correlation of the Lower to Middle Triassic conodont succession of the Shiquanhe area with that of other areas further confirms that the ellisoniids dominated conodont succession displays strong palaeobiogeographic implications. First, ellisoniid faunas recovered from the dolomite-dominated deposits appear to occur extensively along low latitude regions, including South China (Tian et al., 1983; Zhao et al., 2024), southern Qinling (Lai, 1992; Li et al., 2019, 2022), Yunnan (Dong and Wang, 2006), northern Xizang (Xia and Zhang, 2005; Zheng et al., 2007; Wu et al., 2017, 2018, 2019, 2021a, 2025), Jordan (Powell et al., 2019), Iran (Isaa et al., 2022), Europe (Staesche, 1964; Perri, 1991; Posenato, 2008; Chen et al., 2016a; Kolar-Jurkovšek and Jurkovšek, 2019), and the western USA (Solien, 1979). Second, the Shiquanhe conodont succession displays a more intimate relationship with European successions than with western USA biostratigraphy in yielding the Lower Triassic species *Pachycladina* fauna and Ladinian species *Neogondolella excelsa* and a more diverse *Budurovignathus* species.

7. Re-definition of the Triassic deposits of the Shiquanhe area

As noted earlier, the absence of fossils from the upper part of the Tangnale Formation as well as from its immediately overlying strata interpreted to be exposed as fault-bounded blocks, hinders recognition of Lower and Middle Triassic strata in the Shiquanhe area (Fig. 1B). However, we collected age-diagnostic conodonts from these deposits confirming that (1) the Middle Triassic deposits are indeed present in the Shiquanhe area, as demonstrated by the *Neogondolella cornuta*-*Neogondolella excelsa* fauna from the Yangweishan and Zuozuo C sections, and the Late Ladinian *Budurovignathus* cf. *diebeli*-*Pseudofurnishius murcianus* fauna recovered from Zuozuo Section A; (2) the originally described upper Tangnale Formation of the Zuozuo area does not extend into the Middle Triassic as demonstrated by the fossils of both the Zuozuo C and B sections; and (3) inferred strata of the Permian Xiala Formation overlying the Tangnale Formation are actually of Early to Middle Triassic age as demonstrated by conodonts recovered at sections A, B, and C of the Zuozuo area. Combining the lithostratigraphy of the studied succession with the newly recognized conodont faunas allows for re-definition of the Lower and Middle Triassic deposits of the Shiquanhe area, though the current sample resolution remains preliminary and warrants further investigation.

Lower Triassic deposits are present in the Zuozuo area, comprising the originally described Tangnale Formation and the lower part of the overlying unit (originally described as Xiala Formation) (Fig. 1B). The dolomite-dominated Tangnale Formation can be further separated into two members. The lower member is made up of grey-white coarse grained dolomite that yields the *Hadrodontina* fauna (revised herein from the originally described *Hadrodontina*-*Pachycladina* fauna by Zheng et al., 2007) and rare elements of *Neospathodus* sp. and *Gladigondolella* sp. (Ji et al., 2007). The upper member of the Tangnale Formation as well as the lower part of its overlying strata is comprised of dark grey fine-grained dolomite that yields *Pachycladina shiquania* n. sp. fauna and the *Triassospathodus triangularis*-*Triassospathodus homeri* fauna in an

ascending order. Defining the boundary of the two members requires further detailed investigation.

Middle Triassic deposits are distinctly darker in color than underlying Lower Triassic strata, exhibiting a grayish-black hue. They have been confirmed from the Yangweishan and Zuozuo A sections. Recognized Middle Triassic strata can be divided into two intervals: 1) Anisian-Ladinian boundary (ALB) strata described from the Yangweishan area are dolomited by dolomite interlayered with subordinate nodular chert and yield the *Neogondolella transita*-*Neogondolella excelsa*-*Neogondolella cornuta* fauna. It is noteworthy that a similar fauna has also been recognized in slope wash samples of the Zuozuo Section C suggesting that the ALB interval spread extensively in the Shiquanhe area. 2) Upper Ladinian strata described from the Zuozuo Section A, are comprised of dolomitic limestone that yields *Budurovignathus* cf. *diebeli*-*Pseudofurnishius murcianus* fauna.

It is noteworthy that dark, thin- to thick-layered limestone that may represent Upper Triassic deposits have been recognized at the top of Section C (Fig. 2). However, this interpretation remains tentative pending further fossil evidence. Future studies should prioritize higher-resolution sampling to refine these age constraints and clarify the disputed Upper Triassic interval.

8. Implications of P elements of *Pachycladina* apparatus

Confirmation of P₁ and P₂ elements of the *Pachycladina* apparatus is a long-standing taxonomic challenge of conodont studies (Staesche, 1964; Perri and Andraghetti, 1987; Orchard, 2007) mainly because specimens of this type are quite rare. In most cases, P elements are poorly preserved. Rare P elements have been described from Iran (Isaa et al., 2022) and Slovenia (Kolar-Jurkovšek and Jurkovšek, 2019) though they are usually broken.

Typical P elements have been recognized from the Rendo and Comai areas of the southern LSB (Wu et al., 2017, 2018, 2021a). Though no bed assemblage conodonts that would confirm their being P elements of *Pachycladina* have been observed, developed platforms associated with typical ramiform elements of this type make us believe that they are P elements. P₁ elements of *Pachycladina rendoensis* (Wu et al., 2021a) are characterized by broadly triangular platforms whereas P₂ elements display narrow and long platforms. The cusp of P₁ is present in one corner of the triangular platform whereas the cusp of P₂ is present in the posterior part with a short posterior dental carina comprising 1 or 2 denticles exists.

The P₁ and P₂ elements of *Pachycladina shiquania* n. sp. exhibit morphological similarities with those of *Pachycladina rendoensis*, but are readily distinguished by their diagnostic serrated platform margins (see taxonomic description below). This morphological continuity between species strongly supports the assignment of both P₁ and P₂ elements to the *Pachycladina* apparatus, as previously proposed for *Pachycladina rendoensis*.

9. Conclusions

- 1) Four newly described Early to Middle Triassic conodont faunas have been described from the Shiquanhe area, western LSB. They include,

Age/Stage/Substage		South China	Himalaya	Europe	USA	Coen	LSB Shiquanhe (this study)	
240	Ladinian	Longobardian	<i>Bd. mungoensis</i>	<i>Bd. mungoensis</i>	<i>Bd. mungoensis/ Pseudofurnishius murcianus</i>	<i>Paragondolella inclinata</i>	<i>Bd. mungoensis</i>	
	Fassanian		<i>Bd. hungaricus</i>		<i>Bd. hungaricus</i>		<i>Bd. cf. diebeli/ Pseudofurnishius murcianus</i>	
		Illyrian	<i>Bd. truempyi</i>		<i>Bd. truempyi</i>			
	Anisian	Pelsonian		<i>Ng. excelsa</i>	<i>Ng. transita</i> <i>Ng. excelsa</i>	<i>Ng. posterolonga</i>	<i>Ng. transita-</i> <i>Ng. excelsa-</i> <i>Ng. cornuta</i>	
		Bithynian	<i>Ng. bulgarica</i>		<i>Ng. postcornuta</i>	<i>Ng. cornuta</i>		
245	Aegean		<i>Ni. kockeli-</i> <i>Ni. germanica</i>		<i>Ng. cornuta</i>	<i>Ng. constricta</i>	<i>Ng. praezaboi</i>	
	Spathian		<i>Ch. timorensis</i>	<i>Ch. timorensis</i>	<i>Ch. timorensis</i>	<i>Ch. timorensis</i>		
	Olenekian		<i>Ns. anhuiensis</i>	<i>Tr. homeri</i>	<i>Tr. triangularis</i>	<i>Ng. jubata</i>	<i>Tr. homeri-</i> <i>Tr. triangularis</i>	
	Smithian		<i>Tr. homeri</i>	<i>Nv. abruptus</i>		<i>Ic. collinsoni</i>	<i>Tr. homeri-</i> <i>Tr. triangularis</i>	
	Dienerian		<i>Nv. pingd.</i>	<i>Nv. pingd.</i>				
250	Induan			<i>Scy. mosheri</i>		<i>Scy. milleri</i>		
	Griesbachian		<i>Nv. waageni</i>	<i>Nv. waageni</i>	<i>Pachycladina obliqua</i>	<i>Parachirognathus</i> <i>Furnishius</i>	<i>Nv. waageni</i>	
			<i>Ns. cristagalli</i>	<i>Ns. pakistanensis</i>	<i>H. anceps</i>	<i>Furnishius</i>	<i>Pachycladina</i> <i>serrata</i>	
			<i>Ns. dieneri</i>	<i>Ns. dieneri</i>	<i>H. aequabilis-</i> <i>Ns. dieneri</i>	<i>Eu. costatus</i>	<i>Hadrodontina</i>	
			<i>Nc. krystyni</i>	<i>Nc. krystyni</i>		<i>C. planata</i>		
			<i>Isarcicella</i>	<i>Isarcicella</i>	<i>I. isarcica</i>	<i>H. postparvus</i>	<i>Isarcicella</i>	
			<i>H. parvus</i>	<i>H. parvus</i>	<i>H. parvus</i>		<i>H. parvus</i>	

Fig. 4. Correlations of the Lower to Middle Triassic conodont succession of the Shiquanhe area with sections of other regions. Sources of regional conodont biostratigraphy: South China - Tong et al. (2019) and Qin et al. (2023); Himalaya - Lyu et al. (2021), Tian (1982), and Xia and Zhang (2005); Europe - Kozur (1990), Perri (1991), and Kolar-Jurkovšek and Jurkovšek (2019); USA - Solien (1979), Orchard and Balini (2007), and Orchard and Golding (2024).

Abbreviations: *Bu.*-*Budurovignathus*; *C.*-*Clarkina*; *Ch.*-*Chiosella*; *Eu.*-*Eurygnathus*; *H.*-*Hindeodus*; *I.*-*Isarcicella*; *Nc.*-*Neoclarkina*; *Ng.*-*Neogondolella*; *Ni.*-*Nicoraella*; *Ns.*-*Neospathodus*; *Nv.*-*Novispathodus*; *Scy.*-*Scythogondolella*; *Tr.*-*Triassospathodus*; *pingd.*-*pingdingshanensis*.

- in ascending order, the Smithian *Pachycladina shiquania* n. sp. fauna, the Spathian *Triassospathodus homeri-Triassospathodus triangularis* Assemblage Zone, the ALB *Neogondolella cornuta-Neogondolella excelsa* fauna, and the Late Ladinian *Budurovignathus* cf. *diebeli* fauna.
- 2) The originally described *Hadrodontina-Pachycladina* of the Shiquanhe area is revised as the *Hadrodontina* fauna of Late Griesbachian to Dienerian age.
 - 3) Correlations of Lower to Middle Triassic conodont succession of the Shiquanhe area with those in other areas confirm that ellisoniids-bearing conodont successions existed preferentially along dolomite-dominated strata of low paleo-latitude. They also confirm that the Shiquanhe area had a closer relationship with Europe than with the western USA in palaeobiogeographic distribution in yielding the Lower Triassic species *Pachycladina* fauna and Ladinian species *Neogondolella excelsa* and a more diverse *Budurovignathus* species.
 - 4) The newly described Early to Middle Triassic conodont succession compels us to re-define the originally described Lower and Middle Triassic Tangnale Formation as well as overlying strata in the Shiquanhe area.
 - 5) Well preserved platform-like elements of the *Pachycladina shiquania* n. sp. provide clues to the true P₁ and P₂ morphology of the *Pachycladina* apparatus. P₁ elements display a triangular platform with cusp located in a corner. P₂ elements are characterized by relatively narrow and straight platforms that contain large cusps standing near posterior parts of the unit.

10. Taxonomic note

Pachycladina shiquania nov. sp.

Etymology: Refers to the Shiquanhe (=Shiquan River) where the species is first found.

Holotype: Fig. 1 of Plate 1 is designated as the holotype of the P₁ element; Fig. 2 in Plate 1 is the holotype of the P₂ element.

Type locality: Zuozuo Section A, Shiquanhe area, Xizang.

Materials: 1 P₁ element; 3 P₂ elements; 2 S₀ elements.

Repository: Institute of Geology, Chinese Academy of Geological Sciences.

Diagnosis: The P₁ element displays a broad triangular platform with a prominent, erect node-like cusp located at one corner. A narrow posterior platform margin is behind the cusp. Despite partial breakage, two carinal denticle branches are discernible anterior to the cusp. Platform margins exhibit well-developed serrations.

The P₂ platform element exhibits a relatively narrow, elongated morphology compared to P₁ elements. The platform reaches its maximum width near the mid-posterior region, tapering progressively toward both anterior and posterior terminations. The prominent cusp is reclined and substantially larger/longer than adjacent denticles. The anterior carina comprises four discrete, reclined denticles, while one or two smaller inwardly-curved denticles occur posterior to the cusp. Distinct platform margin serrations are throughout their length. In basal view, a small pit occurs beneath the cusp, and a faint keel with well-developed growth lamellae extends along lower denticular surfaces.

Moreover, the assemblage contains symmetrical S₀ elements displaying symmetry-transition morphology along with asymmetrical S elements (S₁-S₄). All recovered elements exhibit variably developed platform margin serrations.

Remarks: The presence of platform margin serrations serves as a key diagnostic feature distinguishing these elements from other *Pachycladina* species that exhibit smooth platform margin.

Occurrence: Tangnale Formation, Shiquanhe area, western LSB of Xizang.

CRediT authorship contribution statement

Gui-chun Wu: Writing – original draft, Funding acquisition, Formal

analysis, Conceptualization. **Zhan-sheng Ji:** Investigation, Conceptualization. **Gary G. Lash:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

References

- Bai, R.Y., Dai, X., Chen, J., Li, M.T., Wang, F.Y., Tian, L., Chu, D.L., Song, H.Y., Song, H.J., 2025. Lower-Middle Triassic conodont biostratigraphy and evolution from South Tibet, China: Implications for global correlations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 675, 113055.
- BGMRX, 1993. Regional Geology of Xizang (Tibet) Autonomous Region. Bureau of Geology and Mineral Resources of Xizang Autonomous Region. Geological Publishing House, Beijing (in Chinese with English Abstract).
- Brack, P., Rieber, H., Nicora, A., Mundil, R., 2005. The Global boundary Stratotype Section and Point (GSSP) of the Ladinian Stage (Middle Triassic) at Bagolino (Southern Alps, Northern Italy) and its implications for the Triassic time scale. *Episodes* 28 (4), 233–244. <https://doi.org/10.18814/epiugs/2005/v28i4/001>.
- Broglio Loriga, C., Cirilli, S., De Zanche, V., di Bari, D., Gianolla, P., Laghi, G.R., et al., 1999. The Prati di Stuores/Stuores Wiesen section (Dolomites, Italy): a candidate Global Stratotype Section and Point for the base of the Carnian stage. *Riv. Ital. Paleontol. Stratigr.* 105, 37–78.
- Bucher, H., Orchard, M.J., 1995. Intercalibrated ammonoid and conodont succession, upper Anisian–lower Ladinian of Nevada. *Albertiana* 15, 66–71.
- Budurov, K., Stefanov, S., 1972. Plattform-Conodonten und ihre Zonen in der Mittleren Trias Bulgariens. *Mitt. Ges. Geol. Bergbaustud.* 21, 829–852.
- Chen, Y.L., Jiang, H.S., Lai, X.L., Yan, C.B., Richoz, S., Liu, X.D., Wang, L.N., 2015. Early Triassic conodonts of Jiarong, Nanpanjiang Basin, southern Guizhou Province, South China. *J. Asian Earth Sci.* 105, 104–121.
- Chen, Y.L., Kolar-Jurkovšek, T., Jurkovšek, B., Aljinović, D., Richoz, S., 2016a. Early Triassic conodonts and carbonate carbon isotope record of the Idrija–Žiri area, Slovenia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 444, 84–100.
- Chen, Y.L., Krystyn, L., Orchard, M.J., Lai, X.L., Richoz, S., 2016b. A review of the evolution, biostratigraphy, provincialism and diversity of Middle and early late Triassic conodonts. *Papers in Palaeontology* 2 Part 2, 235–263. <https://doi.org/10.1002/spp.2.1038>.
- Chen, A.F., Zhang, Y., Lyu, Z.Y., Wu, H.T., Zhang, K.X., 2022. A new study of OlenekianAnisian boundary conodont biostratigraphy of the Tulong section in Himalaya Terrane, southern Tibet. *Palaeoworld* 31, 428–442.
- Chen, A.F., Zhang, Y., Golding, M.L., Wu, H.T., Liu, J.Q., 2023. Upper Changhsingian to lower Anisian conodont biostratigraphy of the Datuguwan section, Nanpanjiang Basin, South China. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 616, 111470. <https://doi.org/10.1016/j.palaeo.2023.111470>.
- Clark, D.L., 1959. Conodonts from the Triassic of Nevada and Utah. *J. Paleontol.* 33, 305–312.
- Dong, Z.Z., Wang, W., 2006. The Cambrian-Triassic Conodont Faunas in Yunnan, China—Correlative Biostratigraphy and the Study of Palaeobiogeographic Province of Conodont. Yunnan Science and Technology Press, Kunming, pp. 1–347 (in Chinese).
- Durkoop, A., Richter, D.K., Stritzke, R., 1986. Facies, Age, and Correlation of Triassic Red Limestones (“Hallstatt Type”) from Epidavros, Ahlhami and Hydra (Greece). *Facies* 14, 105–150 (in German).
- Isaa, A., Ghaderi, A., Khanehabad, M., Kolar-Jurkovšek, T., 2022. Early Triassic conodonts of the Sorkh-Shale Formation in Rabat-Shor section (West of Tabas, East of Central Iran); investigation of their alteration index concerning the hydrocarbon production capacity. *Iranian. J. Pet. Geol.* 21, 33–53 (in Farsi with English abstract). [10.52547/ispg.39722.11.21.33](https://doi.org/10.52547/ispg.39722.11.21.33).
- Ishida, K., Hirsch, F., 2011. The Triassic conodonts of the NW Malayan Kodiang Limestone revisited: Taxonomy and paleogeographic significance. *Gondwana Res.* 19, 22–36. <https://doi.org/10.1016/j.gr.2010.05.008>.
- Ji, Z.S., Yao, J.X., Wu, G.C., Liu, G.Z., 2006. Discovery of late Triassic Norian *Epigondolella* in the Xiala Formation in the Dibu Co area, Coqen County, Tibet, China. *Geol. Bull. China* 25, 138–141 (in Chinese with English Abstract).

- Ji, Z.S., Yao, J.X., Wu, G.C., 2007. Discovery of Permian and Triassic conodonts in the Shiquanhe area, Ngari, western Tibet, China and their significances. *Geol. Bull. China* 26 (4), 383–397 (in Chinese with English Abstract).
- Ji, Z.S., Yao, J.X., et al., 2018. Land submerged to carbonate platform by conodonts: paleoenvironment reconstruction of the western Gangdese in Tibet during Triassic. *China Geology* 3, 450–452. <https://doi.org/10.31035/cg2018053>.
- Jiang, H.S., Chen, Y., Liu, F., 2018. Research prospects on marine Ladinian-Carnian boundary in Guizhou Province. *Earth Sci.* 43 (11), 3947–3954 (in Chinese with English Abstract). <https://doi.org/10.3799/dqkx.2018.144>.
- Karádi, V., Budai, T., Haas, J., Vörös, A., Piros, O., Dunkl, I., Tóth, E., 2022. Change from shallow to deep-water environment on an isolated carbonate platform in the Middle Triassic of the Transdanubian Range (Hungary). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 587, 110793.
- Kolar-Jurkovšek, T., Jurkovšek, B., 2019. Conodonts of Slovenia. Geological Survey of Slovenia, Ljubljana, p. 260.
- Kolar-Jurkovšek, Martínez-Pérez C., Hrvatović, H., Aljinović, D., Goričan, Š., Skopljak, F., Jurkovšek, B., 2023. *Pseudofurnishius* (Conodonta) from the Triassic Drenica section, Bosnia and Herzegovina. *Mar. Micropaleontol.* 183, 102271.
- Kovács, S., 1994. Conodonts of stratigraphical importance from the Anisian–Ladinian boundary interval of the Balaton Highland, Hungary. *Riv. Ital. Paleontol. Stratigr.* 99, 473–514.
- Kozur, H., 1980. Revision der Conodontenzonierung der Mittel- und Obertrias des Tethyan Faunenreichs: Geologisch-Paläontologisch Mitteilungen Innsbruck, 10, 79–172.
- Kozur, H., 1990. The taxonomy of the gondolellid conodonts in the Permian and Triassic. *Cour. Forschungsinst. Senck.* 117, 409–469.
- Kozur, H., 2003. Integrated ammonoid, conodont and radiolarian zonation of the Triassic and some remarks to stage/Substage subdivision and the numeric age of the Triassic stages. *Albertiana* 28, 57–74.
- Krystyn, L., Balini, M., Nicora, A., 2004. Lower and Middle Triassic Stage and Substage boundaries in Spiti. *Albertiana* 30 (Supplement), 39–52.
- Lai, X.L., 1992. Conodont. In: Yin, H.F., Yang, F.Q., Huang, Q.S., Yang, H.S., Lai, X.L. (Eds.), Triassic in Qinling and Adjacent Areas. China University of Geosciences Press, Wuhan, pp. 66–68 (in Chinese).
- Lehrmann, D.J., Stephinski, L., Altiner, D., Orchard, M.J., Montgomery, P., Enos, P., Ellwood, B.B., Bowring, S.A., Ramezani, J., Wang, H.M., Wei, J.Y., Yu, M.Y., Griffiths, J.D., Minzioni, M., Schaal, E.K., Li, X.W., Meyer, K.M., Payne, J.L., 2015. An integrated biostratigraphy (conodonts and foraminifers) and chronostratigraphy (paleomagnetic reversals, magnetic susceptibility, elemental chemistry, carbon isotopes and geochronology) for the Permian–Upper Triassic strata of Guandao section, Nanpanjiang Basin, South China. *J. Asian Earth Sci.* 108, 117–135.
- Leu, M., Bucher, H., Vennemann, T., Bagherpour, B., Ji, C., Brosse, M., Goudermand, N., 2022. A Unitary Association-based conodont biozonation of the Smithian–Spathian boundary (early Triassic) and associated biotic crisis from South China. *Swiss J. Palaeontol.* 141 (19), 18–61. <https://doi.org/10.1186/s13358-022-00259-x>.
- Li, H.X., Jiang, H.S., Chen, Y.L., Wignall, P.B., Wu, B.J., Zhang, Z.T., Zhang, M.H., Ouyang, Z.M., Lai, X.L., 2019. Smithian platform-bearing gondolellid conodonts from Yiwagou Section, northwestern China and implications for their geographic distribution in the early Triassic. *J. Paleontol.* 93, 496–511. <https://doi.org/10.1017/jpa.2018.93>.
- Li, J., Liu, H., Huang, J.Y., Gou, Z.B., An, X.Y., Zhang, S.Z., 2020. Discovery of Norian conodonts from Mujiuco Formation in Konglong Area of Ngamring County in Tibet and its geological significance (in Chinese). *Earth Sci.* 45, 2957–2963.
- Li, Y.X., Ji, Z.S., Wu, G.C., 2021. New progress on the early Triassic conodont biostratigraphy in the Coqen area, Lhasa Terrane. *Acta Micropaleontologica Sinica* 38, 334–351 (in Chinese with English Abstract).
- Li, H.X., Dong, H.X.S., Jiang, H.S., Wignall, P.B., Chen, Y.L., Zhang, M.H., Ouyang, Z.M., Wu, X.L., Wu, B.J., Zhang, Z.T., Lai, X.L., 2022. Integrated conodont biostratigraphy and $\delta^{13}\text{C}_{\text{carb}}$ records from end Permian to early Triassic at Yiwagou Section, Gansu Province, northwestern China and their implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 601, 111079.
- Li, Y.X., Ji, Z.S., Wu, G.C., Wignall, B.P., Chen, Y., Zhang, Z.T., Zhang, S.W., Lai, X.L., 2025. Early to late Triassic conodont biostratigraphy in the Lhasa Terrane, Palaeogeography, Palaeoclimatology, Palaeoecology 669, 112927. <https://doi.org/10.1016/j.palaeo.2025.112927>.
- Lyu, Z.Y., Orchard, M.J., Golding, M.L., Henderson, C.M., Chen, Z.Q., Zhang, L., Han, G., Wu, S.L., Huang, Y.G., Zhao, L.S., Bhat, G.M., Baud, A., 2021. Lower Triassic Conodont biostratigraphy of the Gurul Ravine section, Kashmir. *Glob. Planet. Change.* 207, 103671.
- Mosher, L.C., Clark, D.L., 1965. Middle Triassic conodonts from the Prida Formation of northwestern Nevada. *J. Paleontol.* 39, 551–565.
- Nicora, A., Kovács, S., 1984. Conodont fauna from the Rotelliforme, Meeki and Occidentalis zones (Middle Triassic) of Humboldt Range, Nevada, Western North America. *Riv. Ital. Paleontol. Stratigr.* 90, 135–164.
- Ogg, J., Chen, Z.Q., Orchard, M.J., Jiang, H.S., 2020. The Triassic Period. In: book: Geologic Time Scale 2020, pp. 903–953. <https://doi.org/10.1016/B978-0-12-824360-2.00025-5>.
- Orchard, M.J., 1995. Taxonomy and correlation of lower Triassic (Spathian) segminate conodonts from Oman and revision of some species of *Neopathodus*. *Journal of Paleontology* 60, 110–122.
- Orchard, M.J., 2007. Conodont diversity and evolution through the latest Permian and early Triassic upheavals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 93–117. <https://doi.org/10.1016/j.palaeo.2006.11.037>.
- Orchard, M.J., Balini, M., 2007. Conodonts from the Ladinian–Carnian boundary beds of South Canyon, New Pass Range, Nevada, USA. In Lucas and Spielmann (eds.): the Global Triassic. N. M. Mus. Nat. Hist. Sci. Bull. 41, 333–340.
- Orchard, M.J., Golding, M.L., 2024. The Neogondolella constricta (Mosher and Clark, 1965) group in the Middle Triassic of North America: speciation and distribution. *J. Paleontol.* 97 (6), 1161–1191.
- Pan, G.T., Ding, J., Wang, L.Q., 2004. Qinghai-Tibet Plateau and its adjacent areas explanation book of 1:1500000 Geological Map. Chengdu Cartographic Press, Chengdu 43–45 (in Chinese).
- Perri, M.C., 1991. Conodont biostratigraphy of the Werfen Formation (lower Triassic), Southern Alps, Italy. *Boll. Soc. Paleontol. Ital.* 30, 23–46.
- Perri, M.C., Andraghetti, M., 1987. Permian–Triassic boundary and early Triassic conodonts from the Southern Alps, Italy. *Riv. Ital. Paleontol. Stratigr.* 93, 291–328.
- Plasencia, P., Hirsch, F., Márquez-Alaña, A., 2007. Sephardiellinae, a new Middle Triassic conodont subfamily. *J. Iber. Geol.* 33 (2), 163–172.
- Posenato, R., 2008. Global correlations of mid early Triassic events: the Induan/Olenekian boundary in the Dolomites (Italy). *Earth Sci. Rev.* 91, 93–105. <https://doi.org/10.1016/j.earscirev.2008.09.001>.
- Powell, J.H., Nicora, A., Perri, M.C., Rettori, R., Posenato, R., Stephenson, M.H., Masri, A., Borlenghi, L.M., Gennari, V., 2019. Lower Triassic (Induan to Olenekian) conodonts, foraminifera and bivalves from the Al Mamalah area, Dead Sea, Jordan: constraints on the P-T boundary. *Riv. Ital. Paleontol. Stratigr.* 125, 147–181. <https://doi.org/10.13130/2039-4942/11270>.
- Qin, B.X., Golding, M.L., Jiang, H.S., Chen, Y., Zhang, M., Kang, L., Wang, D., Yuan, J., 2021. Middle Triassic (Anisian) conodont biostratigraphy at the Shaiwa Section, Guizhou, South China. *J. Earth Sci.* 32, 592–615.
- Qin, B.X., Jiang, H.S., Chen, Y., Wu, X.L., 2023. Restudy of conodont biostratigraphy across the Middle-late Triassic Boundary at the Guandao Section, Guizhou, South China. *J. Stratigr.* 47 (3), 306–323 (in Chinese with English Abstract).
- Rigo, M., Mazza, M., Karádi, V., Nicora, A., 2018. New Upper Triassic conodont biozonation of the Tethyan Realm. In: Tanner, L. (ed.) the late Triassic World. Springer, Cham. Top. Geobiol. 46, 189–235.
- Solien, M.A., 1979. Conodont biostratigraphy of the lower Triassic Thaynes Formation, Utah. *J. Paleontol.* 53 (2), 276–306, 3 plates.
- Staesche, U., 1964. Conodonten aus dem Skyth von Sudtirol. *Neues Jahrbuch für Geologie Und Paläontologie-Abhandlungen* 119, 247–306 (in German).
- Sun, Z.Y., Jiang, D.Y., Sun, Y.L., et al., 2014. Conodont Biostratigraphy of the Upper Member of the Guanling Formation in Yangjiao-Chupiwa Section, Guizhou Province, South China. *Acta Sci. Nat. Univ. Pekin.* 50 (2), 269–280 (in Chinese with English Abstract).
- Sun, Y.D., Richoz, S., Krystyn, L., Grasby, S.E., Chen, Y.L., Banerjee, D., Joachimsky, M.M., 2021. Integrated bio-chemostratigraphy of lower and Middle Triassic marine successions at Spiti in the Indian Himalaya: implications for the early Triassic nutrient crisis. *Glob. Planet. Chang.* 196, 103363. <https://doi.org/10.1016/j.gloplacha.2020.103363>.
- Sweet, W.C., 1970. Uppermost Permian and lower Triassic conodonts of the Salt Range and Trans-Indus Ranges, West Pakistan. University of Kansas, Department of Geology, Special Publications 4, 207–275.
- Sweet, W.C., Mosher, L.C., Clark, D.L., Collinson, J.W., Hasenmueller, W.A., 1971. Conodont biostratigraphy of the Triassic. In: Sweet, W.C., Bergstrom, S.M. (Eds.), Symposium on Conodont Biostratigraphy: Geological Society of America, Memoir, vol. 127, pp. 441–465.
- Tian, C.R., 1982. Triassic conodonts in the Tulong section from Nyalam County, Xizang (Tibet), China. In: Geological Collection of Tibetan Plateau, Series 7. Geological Publishing House, Beijing, pp. 153–165 (in Chinese with English abstract).
- Tian, C.R., Dai, J., Tian, S.G., 1983. Triassic conodonts. In: Chengdu Institute of Geology and Mineral Resources, Paleontological Atlas of Southwest China, Volume of Microfossils, Geol. Publ. House, Beijing, pp. 1–802 (in Chinese).
- Tong, J.N., Chu, D.L., Liang, L., et al., 2019. Triassic Integrative Stratigraphy and Timescale of China. *Sci. China Earth Sci.* 62 (1), 189–222. <https://doi.org/10.1007/s11430-018-9278-0>.
- Vörös, A., Szabó, I., Kovács, S., Dosztály, L., Budai, T., 1996. The Felsőörs section: a possible stratotype for the base of the Ladinian stage. *Albertiana* 17, 25–40.
- Wang, Z.H., Cao, Y.Y., 1981. Early Triassic conodonts from Lichuan, western Hubei. *Acta Palaeontol. Sin.* 20 (4), 363–375 (3 plates in Chinese with English Abstract).
- Wang, Z.H., Dai, J.Y., 1981. Triassic conodonts from the Jiangyou-Beichuan area, Sichuan Province. *Acta Palaeontol. Sin.* 20 (2), 138–150 (3 plates in Chinese with English Abstract).
- Wang, C.Y., Wang, Z.H., 1976. Triassic Conodonts in Himalaya Region. In: Scientific Investigation Report, Paleontology Part (2). Science Press, Beijing, pp. 387–424 (in Chinese).
- Wang, H.M., Wang, X.L., Li, R.X., Wei, J.Y., 2005. Triassic conodont succession and stage subdivision of the Guandao Section, Luodian, Guizhou. *Acta Palaeontol. Sin.* 44, 611–626 (in Chinese with English abstract).
- Wu, G.C., Yao, J.X., Ji, Z.S., 2007. Triassic conodont biostratigraphy in the Coqen area, western Gangdese, Tibet, China. *Geol. Bull. China* 26, 938–946 (in Chinese with English Abstract).
- Wu, G.C., Yao, J.X., Ji, Z.S., et al., 2008. Discovery of the Upper Qingyanian Conodonts in the Qingyan Cross-section of Guizhou and its significance. *Acta Geol. Sin.* 82 (2), 145–154 (in Chinese with English Abstract).
- Wu, G.C., Ji, Z.S., Trotter, J.A., Yao, J.X., Zhou, L.Q., 2014. Conodont biostratigraphy of a new Permo-Triassic boundary section at Wenbudangsang, North Tibet. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 411, 188–207. <https://doi.org/10.1016/j.palaeo.2014.06.016>.
- Wu, G.C., Ji, Z.S., et al., 2017. Age revision of the dolomite to the west of Namtso and the significance of the discovered oil immersed dolomite. *Acta Geol. Sin.* 91, 2867–2880 (in Chinese with English Abstract).

- Wu, G.C., Ji, Z.S., et al., 2018. The early Triassic conodonts in Rendo area of Zhongba County, Tibet, and paleogeographic pattern of the West Gangdise Block in early Triassic. *Acta Geosci. Sin.* 39, 409–418 (in Chinese with English Abstract).
- Wu, G.C., Ji, Z.S., Liao, W.H., Yao, J.X., 2019. New biostratigraphic evidence of late Permian to late Triassic deposits from Central Tibet and their paleogeographic implications. *Lithosphere* 11, 683–696, 10.1130/L1046.1.
- Wu, G.C., Ji, Z.S., Kolar-Jurkoviček, T., Yao, J.X., Lash, G.G., 2021a. Early Triassic Pachycladina fauna newly found in the southern Lhasa Terrane of Tibet and its palaeogeographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 562, 110030. <https://doi.org/10.1016/j.palaeo.2020.110030>.
- Wu, G.C., Ji, Z.S., Lash, G.G., Yao, J.X., Zhang, S.W., Li, Y.X., 2021b. Newly discovered Wuchiapingian to Olenekian conodonts from the Longgar area, southern Lhasa Terrane and their palaeobiogeographical implications. *Lethaia* 54, 723–735.
- Wu, G.C., Ji, Z.S., Lash, G.G., Zeng, Q.G., Yao, J.X., 2024. Triassic integrative stratigraphy, biotas, and paleogeographical evolution of the Qinghai-Tibetan Plateau and its surrounding areas. *Sci. China Earth Sci.* 67, 1152–1194. <https://doi.org/10.1007/s11430-023-1188-5>.
- Wu, G.C., Ji, Z.S., Li, H.Q., Lash, G.G., Zhang, S.W., Yao, J.X., 2025. New biostratigraphic data and U-Pb geochronology for the Middle Permian to Triassic succession of the South Qiangtang Block, Xizang. *J. Geol. Soc. Lond.* 182. <https://doi.org/10.1144/jgs2024-244>.
- Xia, F.S., Zhang, F., 2005. Conodonts. In: Jingeng, S. (Ed.), *Micropalaeontology of the Qiangtang Basin*. Science Press, Beijing, pp. 172–229 (in Chinese with English Abstract).
- Xu, R.K., Zheng, Y.Y., Ciqiong, 2010. Chinese Regional Geological Survey Report 1: 250000 Sinuowashan and Shiquanhe sheets). Geological Publishing House, Beijing [in Chinese].
- Yan, C.B., Wang, L.N., Jiang, H.S., Wignall, P.B., Sun, Y.D., Chen, Y.L., Lai, X.L., 2013. Uppermost Permian to lower Triassic conodonts at Biyang section, Guizhou Province, South China. *Palaios* 28, 509–522.
- Zhang, Y.C., Shen, S.Z., Xu, H.P., Qiao, F., Yuan, D.X., Ju, Q., 2023. Permian Strata and Faunas from the Lhasa Block. Science Press, Beijing (in Chinese), Tibet.
- Zhao, Z.Z., Li, Y.T., Ye, H.F., Zhang, Y.W., 2001. Stratigraphy of the Qinghai-Tibet Plateau (in Chinese with English Abstract). Science Press, Beijing, pp. 1–210.
- Zhao, L.S., Orchar, M.J., Tong, J.N., Sun, Z.M., Zuo, J.X., Zhang, S.X., Yun, A.L., 2007. Lower Triassic conodont sequence in Chaohu, Anhui Province, China and its global correlation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 252, 24–38.
- Zhao, L.S., Chen, Y.L., Chen, Z.Q., Cao, L., 2013. Uppermost Permian to lower Triassic conodont zonation from three Gorges Area, South China. *Palaios* 28, 523–540.
- Zhao, Y.L., Chen, Y.L., Wang, J.Q., Ma, X.Y., Xue, C.L., Topper, T.P., Zhang, Z.F., 2024. Early Triassic conodonts from the Liangshan area, Hanzhong, Shaanxi, South China. *J. Micropalaeontol.* 43, 423–439. <https://doi.org/10.5194/jm-43-423-2024>.
- Zheng, Y.Y., Xu, R.K., Wang, C.Y., Ma, G.T., Lai, X.L., Ye, D.J., Cao, L., Liang, J.W., 2007. Discovery of early Triassic conodonts in western Gangdise and the establishment of the Tangnale Formation. *Science in China Series D: Earth Science* 50, 1767–1772. <https://doi.org/10.1007/s11430-007-0099-4>.