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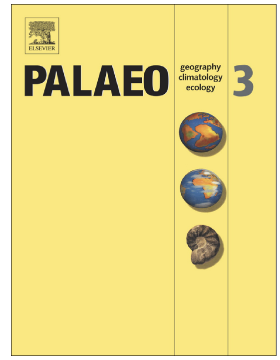

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Early Carnian conodont fauna at Yongyue, Zhenfeng area and its implication for Ladinian-Carnian subdivision in Guizhou, South China

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Abstract

The subdivision of Ladinian and Carnian strata in Guizhou, South China has been a matter of intense debate because of the paucity of age-diagnostic faunas. Here we have carried out a detailed conodont biostratigraphic investigation on the Yangliujing, Zhuganpo and Wayao formations in the Yongyue section of western Guizhou Province. Conodonts are only prolific in the Zhuganpo and Wayao formations. Three genera and twenty species are identified, including two new species *Quadralella wanlanensis* n. sp. and *Quadralella yongyueensis* n. sp. They represent a rather endemic fauna of latest Ladinian to early Carnian age. Four conodont zones are established. They are, in the ascending order, the *Paragondolella foliata, Quadralella polygnathiformis, Quadralella tadpole,* and *Quadralella* aff. *praelindae* zones.

Thus in the study area, the Zhuganpo Formation is generally of early Carnian (Julian 1) age whilst the Wayao Formation probably extends from the Julian 2 into the late Carnian (Tuvalian substage). The Ladinian–Carnian boundary (LCB) cannot be precisely defined due to the absence of the ammonoid *Daxatina Canadensis* and the paucity of conodonts. However, the LCB is unlikely lower than the Yangliujing–Zhuganpo formation contact. The Julian 1–Julian 2 (early Carnian) substages boundary is defined in the uppermost Zhuganpo Formation by the occurrence of basal Julian 2 ammonoid *Austrotrachyceras* ex gr. *A. austriacum* and is also evidenced by the disappearance of most short-range Julian 1 conodonts in the overlying Wayao Formation.

Key words: biostratigraphy; Middle Triassic; Late Triassic; Wayao Formation; Zhuganpo Formation

1. Introduction

Age assignments for many Middle and Late Triassic lithological units in Guizhou Province, South China are historically controversial and have been intensively debated for almost a century. As a classic location for Triassic studies, however, systematic investigations in this area started in the 1920s when Loh (1929) undertook a stratigraphic study. The carbonates in the southern suburbs of Guanling city, assigned to the Late Triassic, were of particular interest to Loh and named as the Falang Formation after a nearby village (Loh, 1929). The unit later proved to be widely distributed in the Middle to Upper Triassic of South China.

However, controversies concerning the age and subdivision of Falang Formation began during this earliest research. Hsu (1939) and Hsu and Chen (1944) suggested a Middle Triassic (Ladinian) age, based on the abundant occurrence of the bivalve *Halobia comatoides*. In the following 50 years, the age assignment of Hsu (1939) was used in later studies (Zhao et al., 1962; Yin, 1962; Wang et al., 1963; Chen et al., 1979) until the Bureau of Geology and Mineral Resources of Guizhou Province (1987) further subdivided the original Falang Formation into three separate units, in stratigraphically ascending order the Zhuganpo, Wayao and Laishike formations, and assigned a Carnian age to all three units. However, the evidence for the precise age of these units has been insubstantial. Yang et al. (1995; 2002) investigated strata in the Guanling and Zhenfeng areas of Guizhou and concluded, based on the "*Neogondolella" polygnathiformis–tadpole* conodont assemblage and the absence of the late Ladinian genus *Budurovignathus,* that the Zhuganpo Formation was most likely of Carnian rather than Ladinian age or partly Ladinian and partly Carnian age. Similarly, Sun et al. (2005) reported the first occurrence of "*Paragondolella" polygnathiformis* in the lower Zhuganpo Formation in the Guanling area and also assigned a Carnian age to most of the Formation. On the other hand, ammonoid biostratigraphy has provided contradictory age assignments. Enos et al. (2006) reported that the Zhuganpo Formation yielded a typical Ladinian ammoniod association, including age diagnostic *Anolcites* (=*Trachyceras*). Based on a large ammonoid collection, Zou et al. (2015) also suggested that most of the Zhuganpo Formation in the Xingyi area was of Ladinian age except for the upper part which was assigned to the Carnian.

Besides the possible diachronous nature of the Zhuganpo Formation and many other units in the region (e.g., Sun et al., 2016), the sedimentary hiatus caused by the regression in the Ladinian presents an additional complication. Yin (1982) first identified this sea-level lowstand and suggested that there was a widespread loss of Ladinian strata in most areas of South China, the Qaidam Basin of North China as well as in Central Asia due to subaerial erosion. The precise timing and amplitude of the Great Ladinian Regression (GLR, after Yin, 1982) remains unclear. However, paraconformities widely observed between the

Zhuganpo Formation and underlying Yangliujing Formation (e.g., Yang et al., 2002; Minzoni, 2007; Zeng et al., 2013; Minzoni et al., 2015) may be one of the manifestations of the GLR. Any attempts to resolve the biostratigraphic problems in this region must therefore be viewed in the context of the effect of this sea-level lowstand.

Robust biostratigraphy is essential to reconcile the discrepancies in age assignments of the Middle–Late Triassic strata of Guizhou. In the present study, a thorough investigation of conodont biostratigraphy has been carried out on a new section in the Zhenfeng area, southwestern Guizhou where a complete, early Carnian conodont assemblage has been recovered. We are able to show that, at least in the Zhenfeng area, the Zhuganpo Formation is mainly of early Carnian age. Part of the Ladinian succession is likely lost, probably due to sea level lowering and erosion at a level in the lower Zhuganpo Formation. The lower Wayao Formation, which overlays the Zhuganpo Formation, extends to the later Carnian (Julian 2 to possibly Tuvalian 1).

2. Geological Setting

During the Triassic, the South China plate was a large, isolated platform in eastern Tethys with extensive carbonate deposition (Yang et al., 1982; Yin et al., 2000). Guizhou was located in the southwest of the South China Plate and straddled the margin of the Yangtze Platform and adjacent Nanpanjiang Basin (Enos et al., 1998).

The Zhenfeng area of SW Guizhou is considered as a classic location for

Triassic studies, featuring diverse sedimentary facies, ease of access and excellent outcrop conditions (Yang et al., 1995; Enos et al., 1998; Li et al., 2003). The studied section at Yongyue (Wanlan town, Fig. 1) is located 8 km SW of Zhenfeng city and about 200 km SW of Guiyang (capital city of Guizhou). Triassic strata exposed at Yongyue are more expanded but generally similar to those reported from the Long Chang area (Sun et al., 2016) and are represented by the Yangliujing, Zhuganpo and Wayao formations (Fig. 2). The studied strata are 112 m in thickness. The Yangliujing Formation consists of thick-bedded, cyclic dolomitic limestones to calcitic dolostones of shallow-marine facies. This unit can be more than several hundred metres thick in the region. However, only the uppermost 32 m strata are investigated in detail here. Thin to medium bedded and nodular limestones, representing a deeper, pelagic environment, are characteristic of the overlying Zhuganpo Formation (~74-m-thick in the study section). Only the lowermost part (~6 m) of Wayao Formation is exposed at Yongyue where it consists of basinal facies: marly limestones and finely laminated black shales. The entire succession records rather continuous sedimentation except for the erosional surface, which displays a few centimetres of erosive relief, in the lower part of the Zhuganpo Formation (Fig. 2 C). It marks the sharp juxtaposition of thin-bedded limestones and a massive overlying bed. This sharp lithological junction and abrupt shallowing of facies are suggestive of a sequence boundary.

3. Materials and Methods

The section was logged in detail and a total of 63 samples were collected with a sampling resolution of ~1–2 m. Each sample weighed between 3.4 to 9.7 kg (Table 1). All samples were crushed into ~ 1 cm^3 rock chips and dissolved in 8% acetic acid solution. The residue was wet sieved and dried at room temperature. Heavy liquid (lithium and sodium heteropolytungstates solution, 2.80 g/cm^3, Yuan et al., 2015) was used for heavy liquid fractionation of residuals. A total of 1074 conodont elements are obtained and 446 elements can be used for taxonomic identification. The remaining elements were not sufficiently well preserved for identification (Table 1). The conodonts belong to the genera *Gladigondolella* (*G.*), *Paragondolella* (*P.*) and *Quadralella* (*Q.*).

4. Conodont biostratigraphy

Conodont zones and ranges of taxa are shown in Figure 3. A correlation chart is shown in Figure 4. Note that we have reassigned some *Paragondolella* and *Carnepigondolella* species to *Quadralella* in accordance with the taxonomic studies of Orchard (2013; 2014) and Chen et al. (2015).

4.1 Yangliujing Formation

No elements were recovered from this unit, despite our efforts, probably because the shallow subtidal environments were unsuitable for conodonts. Thus, age constraints of the Yangliujing Formation are poor and can only be assessed via a previous study. Chen and Wang (2009) reported *Neogondolella*-dominated conodont faunas in this unit in the Guanling area, suggesting a late Anisian age (see discussion in Section 5.2)

4.2 Zhuganpo Formation

Four conodont zones are recognised from the 74-m-thick Zhuganpo Formation which straddles the latest Ladinian and the early Carnian. In ascending order, these conodont zones are:

4.2.1 ***Paragondolella foliata*** **Zone**

Lower limit: First occurrence (FO) of *P. foliata*.

Upper limit: FO of *Q. polygnathiformis*.

Associated taxa: *Q.* aff. *acuminatus, Q. intermedius, Q. shijiangjunensis* and *Q*. sp. A.

This zone is less than 2 metre in thickness. This minor thickness is due to the paucity of conodonts in the lowermost 12 metres of Zhuganpo Formation. *P. foliata* Budurov, 1975 is a medium range species known from the late Longobardian to the late Julian (Yang et al., 2002; Sun et al., 2005).

Both *Q. acuminatus* and *Q. intermedius* are present in the *Frankites sutherlandi* ammonoid zone in British Columbia (Orchard, 2007). *Q.* aff. *acuminatus* found at Yongyue shares many common features with *Q. acuminatus* but has a pointed keel end that differs from that seen in the holotype (Orchard, 2007). *Q. shijiangjunensis* was described in the early Carnian *Q. tadpole* Zone (Sun, 2006).

4.2.2 ***Quadralella polygnathiformis*** **Zone**

Lower limit: FO of *Q. polygnathiformis*.

Upper limit: First appearance datum (FAD) of *Q. tadpole.*

Associated taxa: *P. foliata, P. inclinata, Q.* aff. *acuminatus, Q. intermedius, Q.* cf. *langdaiensis, Q. maantangensis, Q.* sp., *Q. shijiangjunensis* and *Q.* aff. *zonneveldi*.

This zone is of early Carnian age and is characterized by a coexistence of several species known from both the Ladinian and Carnian. *Q. polygnathiformis* (Budurov and Stefanov, 1965) is the most characteristic element ranging from the earliest Julian to early Tuvalian. It is globally distributed and has been reported from Canada (Orchard and Tozer, 1997; Orchard, 2007, 2010), Europe (Manco et al., 2004; Hornung et al., 2007; Mietto et al., 2007a; Mietto et al., 2007b; Mietto et al., 2012; Muttoni et al., 2014), Japan (Hayashi, 1968; Igo, 1989), India (Balini et al., 2004; Krystyn et al., 2004) and South China (Wang and Zhong, 1990; Sun et al., 2005; Wang et al., 2005; Sun, 2006; Lehrmann et al., 2015; Sun et al., 2016).

Associated taxa are generally moderately long ranging species. *P. inclinata* Kovács, 1983 is widely distributed and ranges from the earliest Longobardian to late Julian (Kovács, 1983; Rigo et al., 2007; Orchard, 2007; Sun et al., 2016). *Q. maantangensis* (Dai and Tian, 1983) was established in the Tianjingshan Formation of northwestern Sichuan and occurs from the early Julian up to earliest Tuvalian (Yang et al., 1995; Wang, 2000; Yang et al., 2002; Sun et al., 2005; Sun, 2006). In contrast, *Q. zonneveldi* (Orchard, 2007) was short-lived and restricted to the *Q. intermedius* Zone (*Daxatina* ammonite zone) in British Columbia, indicating the earliest Carnian. *Q.* aff. *zonneveldi* from Yongyue is longer than the type *Q. zonneveldi* in the British Columbia and only some of our specimens have the diagnostic sunken carina of the holotype.

4.2.3 ***Quadralella tadpole*** **Zone**

Lower limit: FAD of *Q. tadpole*.

Upper limit: FAD of *Q.* aff. *praelindae.*

Associated taxa: *P. inclinata, Q. intermedius* and *Q. polygnathiformis.*

The *Q. tadpole* Zone is recognized as in the Julian 1 substage at Yongyue and can be recognised regionally in Guizhou (Wang and Zhong, 1990; Yang et al., 1995; 2002; Sun et al., 2005). The base of the zone correlates with the *Trachyceras desatoyense* ammonoid zone and the highest occurrence of *Frankites* in British Columbia, indicating an early Carnian age (Orchard, 2007; Orchard and Balini, 2007).

Q. tadpole is globally distributed. In South China as well as globally, all reported FADs of *Q. tadpole* are stratigraphically higher than the FAD of *Q. polygnathiformis* (e.g., Hayashi, 1968; Metcalfe, 1992; Sun et al., 2005; Hornung et al., 2007; Orchard, 2007; Rigo et al., 2007). *Q. tadpole* is characterised by the tadpole-like platform outline and long free blade. However, it is noteworthy that the majority of *Q. tadpole* specimens reported from eastern Tethys (e.g., Koike, 1991; Sun et al., 2005; Sun et al., 2016) have relatively long but less rounded platform than examples from British Columbia (e.g., Orchard, 2007). This morphotype of *Q. tadpole* with less rounded platform has been long known (e.g., Kovcás, 1983) and might be due to geographic variability.

4.2.4 ***Quadralella* aff. *praelindae* Zone**

Lower limit: FAD of *Q.* aff. *praelindae*.

Upper limit: not defined

Associated taxa: *G. malayensis, P. foliata, P. inclinata, Q. intermedius, Q. jiangyouensis*, *Q. polygnathiformis, Q. maantangensis, Q. tadpole, Q. uniformis, Q. wanlanensis* n. sp. *Q.* aff. *wayaoensis, Q. yongyueensis* n. sp., *Q.* sp. and *Q.* sp. B.

A long-ranging species, *G. malayensis* Nogami, 1968 which is known from Longobardian to latest Julian strata (Hornung et al., 2007; Mietto et al., 2007a; Muttoni et al., 2014; Chen et al., 2015), occurs in this zone and is the only *Gladigondolella* species recovered in this study. The associated *Q. uniformis* was initially described from the *Q. tadpole* Zone (Sun, 2006) and ranges from the earliest Carnian to the late Julian 1 substage.

The associated species *Q. jiangyouensis* (Wang and Dai, 1981) is an endemic species commonly seen in the *Q. polygnathiformis*–*Q. tadpole* and *Q. auriformis* zones (Yang et al., 2002; Sun, 2006). *Q. wayaoensis* (Wang, 2000) was initially described from the Wayao Formation and possibly only occurs in the Julian 2. *Q.* aff. *wayaoensis* obtained from Yongyue has a less constricted posterior platform and less merged middle carina and is likely a predecessor of *Q. wayaoensis* occurring in the middle Julian 1.

4.3 Wayao Formation

Only the lower part of the Wayao Formation is exposed in the study section.

Despite large carbonate samples taken in the field, conodont abundances decrease significantly in this unit.

Due to a lack of age diagnostic conodonts, age constraints for this unit can only be achieved using ammonoid biozones. The Wayao Formation overlies the ammonoid-bearing nodular limestones atop the Zhuganpo Formation. This facies is widespread in the Zhenfeng area and yields *Austrotrachyceras* ex gr. *A. austriacum*, indicating a basal Julian 2 age (Sun et al., 2016). The overlying Wayao Formation is thus of Julian 2 and/or younger age.

5. Discussion

5.1 The age of Zhuganpo Formation

At Yongyue, the Zhuganpo Formation is largely of early Carnian age except for the lowermost 12 m strata which cannot be precisely dated due to the paucity of conodonts. The *P. foliata* Zone contains the oldest conodont assemblage (including *Q.* aff. *acuminatus*, *Q. intermedius* and *Q. shijiangjunensis*) recovered in the study section. The range of *Q. intermedius* are shown to be largely within the upper *Frankites sutherlandi* Zone (Orchard, 2007) where *Daxatina* also occurs, indicating an earliest Carnian age. Adding in the known range of *Q. shijiangjunensis*, the composition of our *P. foliata* Zone supports an early Carnian age.

Though we did not recover any conodonts from the underlying Yangliujing Formation, Chen and Wang (2009) reported *Neogondolella* (*Ng.*) *bulgarica, Ng. cornuta, Ng. postcornuta* and *Ng. pseudobifurcata* in the middle and upper parts of this unit in the Guanling area (~60 km north of Yongyue). This fauna can be correlated with the *Reitziites reitzi* ammonoid zone of the middle Illyrian (late Anisian; Brack et al., 2005). Since Zhuganpo Formation contains a rather complete Julian 1 conodont assemblage which features diverse *Quadralella* species, correlation with Guanling area suggests that only the lower 12 m of this Formation might be of Ladinian age. Many conodont taxa straddling the late Ladinian to the early Carnian (e.g., *Budurovignathus*, *Mosherella* and *Pseudofurnishius*) are not known from the region. Precise Ladinian–Carnian boundary constraints will only become possible with further study of the ammonoid fauna.

5.2 A major hiatus in the Ladinian strata of western Guizhou?

The unusually thin (<12 m) Ladinian strata in western Guizhou suggests there is a sedimentary hiatus, most likely represented by the erosional surface developed in the lower Zhuganpo Formation (Fig. 2 C). The Ladinian is around 5 myr duration and typical pelagic Ladinian successions in western Tethys are ~70-100-m-thick (e.g., Lein et al., 2012). The absence of Ladinian strata over much of South China (e.g., Yin, 1982) probably has led to the loss of several diagnostic conodont taxa. Thus, the late Ladinian *Budurovignathus* does not occur over a large area of Guizhou, except in the Guandao section of the central Nanpanjiang Basin (Wang et al., 2005; Lehrmann et al., 2015) whilst the Ladinian to earliest Carnian genus *Pseudofurnishius* is not known at all from South China. The hiatus in the Ladinian is thus interpreted to be a regional phenomenon and likely represents the manifestation of the GLR (Yin, 1982). The difference in stratigraphic scheme between the Xingyi (Zou et al., 2015) and Zhenfeng areas (this study) probably reflects a large, intra-regional variation and the diachronous nature of the Zhuganpo Formation. Complete Ladinian successions are probably only developed in deep-water settings as found in Luodian and possibly in the Xingyi Basin (Wang et al., 2005; Zou et al., 2015).

5.3 Subdividing Carnian substages in Zhenfeng area

Subdividing Carnian strata in South China to substage levels is difficult due to the absence of many age-diagnostic conodonts that are well known from the western Tethys. The following findings could be used for any future subdivision:

Julian 1–Julian 2 boundary is marked by the deposition of nodular limestones in the uppermost Zhuganpo Formation. This level yields *Austrotrachyceras* ex gr. *A. austriacum*, indicating a basal Julian 2 age (Sun et al., 2016).

Julian–Tuvalian boundary, which is usually defined by the ammonoid *Tropites dilleri* (not yet been found in this region), alternatively can be constrained by the last occurrence of the Julian bivalve *Halobia* cf. *zitteli.*

The last occurrence of *Gladigondolella* was used alternatively as a marker for the Julian/Tuvalian boundary in western Tethys (Kozur, 1989; Kozur, 2003). However, this definition cannot be simply applied in Guizhou and many other regions. *Gladigondolella* is considered to be a pelagic conodont restricted to the Tethyan, part of the Panthalassa, as well as the western margin of North America but it is absent in high latitudes (Kozur et al., 2009). The occurrence of

Gladigondolella in western North America is regarded as arising from the accretion of terranes that were formerly lying within the Panthalassa Ocean (Orchard et al., 2001). Gladigondolellids are very rare in the Ladinian to Carnian strata of Guizhou and therefore may not have any stratigraphic significance in this region. There is only one occurrence of *G.* sp. reported in Julian 1 strata at Long Chang (Sun et al., 2016). Three occurrences of *G. malayensis* at Yongyue, with its last occurrence observed in Julian 1 strata, are reported in this study. Similarly, in the Guri Zi section of northern Albania, the last occurrence of *G. tethydis* is lower than the FAD of *Q. tadpole*, representing an early Julian age whilst in the Aghia Marina section of Greece, the last occurrence of *G. malayensis* is in the Longobardian (Muttoni et al., 2014). As another alternative, Muttoni et al. (2014) used the last occurrence of *P. foliata* to define the base of Tuvalian. However, at Yongyue as well as Long Chang the last occurrences of *P. foliata* lie within the Julian (Sun et al., 2016).

6. Systematic palaeontology

In this section, we describe two new and eleven established species. Amongst the established species, *G. malayensis* and *Q.* aff. *praelindae* are rarely reported from South China whilst *Q. polygnathiformis* is an important boundary marker with large morphological variation. Several species, which are indigenous to South China, are described in detail. Other zonal markers (e.g. *Q. tadpole*) are described in detail by Orchard (2007) and Hornung et al. (2007) and are therefore not listed here. Specimens are housed in the State Key Laboratory of

Biogeology and Environmental Geology, China University of Geosciences (Wuhan).

***Gladigondolella malayensis* Nogami, 1968**

Fig. 5, 12; Fig. 6, 4; Fig. 8, 7

1968 *Gladigondolella malayensis* n. sp. Nogami, Taf. 9. figs. 11-18; Taf. 11. fig. 7.

1980 *Gladigondolella malayensis* Donofrio, Taf. 4. fig. 9.

1993 *Gladigondolella malayensis* Kozur, Pl. 1. fig. 1.

1994 *Gladigondolella malayensis* Senowbari, Taf. 1. figs. 1. 2.

1995 *Gladigondolella malayensis malayensis* Mastandrea, Pl. 1. figs. 1-3.

2001 *Gladigondolella malayensis* De Bono, Pl. 3. figs. 4. 5. 10.

2005 *Gladigondolella malayensis* Goričan et al., Pl. 3. fig. 10.

Description: In upper view, the platform is narrow, ellipsoidal in shape, and gently curved. The widest is found in the middle to two-thirds from the anterior. The platform tapers both anteriorly and posteriorly from the widest point. Intense microreticulation covers the relatively thick platform. There may be a short blade in the anterior. The carina is low and consists of 6-10 discrete denticles. Lateral grooves are moderately deep. The cusp is distinct and close to the posterior end. A small denticle located at the posterior platform brim may develop behind the cusp. In lateral view, the platform is slightly curved before the basal cavity. In lower view, the keel is deeply excavated and extends the entire platform and may be slightly elongated in mature stage. The eye-shaped basal cavity lies near the posterior end.

Comparison: *G. malayensis* differs from *G. tethydis* in its larger platform with a basal cavity closer to the posterior end. *G. budurovi* is morphologically similar to the current species but has a broader platform, a lower carina and an indistinct cusp (Balini et al., 2000) and is only known from the Anisian.

Occurrence: Julian, Zhuganpo Formation, Guizhou, South China.

Quadralella jiangyouensis (Wang and Dai, 1981)

Fig. 9, 4

1981 *Neogondolella jiangyouensis* sp. nov. Wang and Dai, Pl. I, figs. 5-7.

2002 *Paragondolella jiangyouensis* Yang et al., Pl. I, fig. 1.

Description: In upper view, the slender platform extends nearly to the anterior end. A short free blade may develop. Lateral platform margins are parallel and upturned. The posterior platform brim is broad and upturned. The posterior end of the platform is rectangular. The carina consists of 7-10 discrete to moderately fused denticles. Two relatively deep adcarinal grooves develop on both sides of carina. The cusp is moderately big and sub-terminal. In lateral view, the platform is slightly arched or relative straight before the pit. The carina is normally higher than the lateral platform margins anteriorly and gradually decreases in height posteriorly. In lower view, the pit is surrounded by a loop and located sub-terminally. The keel is elevated and the keel end is near rectangular. A narrow furrow extends from the pit to the anterior termination of the platform.

Comparison: *Q. jiangyouensis* and *Q. polygnathiformis* both have relatively broad platforms and sub-terminal cusps. However, *Q. jiangyouensis* is distinguished by having a rectangular platform, a quadrate posterior end and relatively deep adcarinal grooves.

Occurrence: Julian, Tianjingshan Formation, Sichuan; Zhuganpo Formation, Guizhou, South China.

***Quadralella* cf. *langdaiensis* (Yang, 2002)**

Fig. 9, 1

Description: In upper view, the platform is slender and usually upturned. The platform is widest in the posterior quarter. In lateral view, the platform is straight or slightly arched. The carina consists of high and fused denticles in the front and discrete denticles in the posterior. In lower view, the pit is evidently forward shifted and locates at the posterior quarter. The keel is elongated, expanded around the pit and has a pointed end.

Comparison: The current species is very similar to *Q. polygnathiformis* in upper view. However, *Q.* cf. *langdaiensis* is characterized by having a forward shifted pit and a dilated, elongated and pointed keel end. The forward shifted pit location is likely an early morphology character of *Metpolygnathus*. *Q.* cf. *langdaiensis* and *Q. langdaiensis* share characters such as forward shifted pit and pointed keel end. However, *Q. langdaiensis* has a more fused carina and a small cusp. These features are not sufficiently preserved in our specimens.

Occurrence: Julian, Zhuganpo Formation, Guizhou, South China.

***Quadralella maantangensis* (Dai and Tian, 1983)**

Fig. 9, 2

1981 *Neogondolella* sp. Wang and Dai, Pl. I, figs. 23-24.

1983 *Neogondolella maantangensis* sp. nov. Dai and Tian, Pl. 99, figs. 11-12.

2002 *Paragondolella maantangensis* Yang et al., Pl. 1. figs. 3. 7.

2005 *Paragondolella maantangensis* Sun et al., Pl. 2, fig. 6.

Description: In upper view, the platform is triangular and widest at the posterior end. The platform generally extends nearly to the anterior termination. Serration often develops on the anterior platform margins. The platform lateral margins are thick. The posterior end of platform is asymmetrical to subsymmetrial, subrounded or rectangular. Microreticulation covers the entire platform except for the relatively deep adcarinal lateral grooves. The node-like cusp is not prominent and is located sub-terminally. Two or more small denticles may develop on both sides of posterior platform, forming a Y-shaped carina in some specimens. In lateral view, the platform is generally arched. The carina is high and decreases in height posteriorly. Denticles in the middle part of carina are merged together and generally lower than the lateral margins. In lower view, the pit is sub-terminal. The keel end is bifurcated. A furrow extends from the posterior to the anterior end.

Comparison: *Q. polygathiformis magna* and *Q. maantangensis* both have bifurcated keel ends. However, *Q. maantangensis* is characterized by having a triangular platform. *Q. bisecta* differs *Q. maantangensis* by development of a unique bifurcated platform end (i.e. a Y-shaped posterior).

Occurrence: Julian–lower Tuvalian? Tianjingshan Formation, Sichuan; Zhuganpo Formation, Guizhou, South China.

Quadralella polygnathiformis (Budurov and Stefanov, 1965)

Fig. 5, 4; Fig. 6, 2

1965 *Gondolella polygnathiformis* n. sp. Budurov and Stefanov, Pl. 3. fig. 7.

1968 *Paragondolella polygnathiformis* Mosher, Pl. 118. figs. 9-17. 19.

1983 *Gondolella polygnathiformis* Kovács, Pl. II.figs. 5. 6.

1990 *Paragondolella polygnathiformis* Metcalfe, Pl. 2. figs. 7. 8.

2001 *Paragondolella polygnathiformis* Muttoni et al., Pl. 10. fig. 2.

2007 *Metpolygnaththus polygnathiformis* Hornung et al., Pl. 7. figs. e. f.

2007 *Metpolygnaththus polygnathiformis* Orchard, Pl. 1. figs. 22. 23. 24.

2010 *Metpolygnaththus polygnathiformis* Orchard, Pl. 11. figs. 11-13.

2015 *Quadralella polygnathiformis* Lehrmann et al., Fig. 6. 23-25.

Description: In upper view, the platform is posteriorly rounded to slightly sub-quadrate in outline and extends the entire length of element. Platform is gradually tapered to the anterior end. The cusp is large, prominent, well differentiated from denticles, in sub-terminal position and surrounded by a narrow platform brim. In lateral view, at least one anterior lateral margin has a geniculation point or anterior step. The carina is moderately high and may be more or less submerged by upturned platform margins. The partially fused blade is generally well differentiated. In lower view, the pit is sub-terminal with respect to the keel and posterior platform. Medium deep furrow extends from the pit to the anterior end.

Comparison: Compared with *P. foliata* and *P. inclinata, Q. polygnathiformis* has a prominent abrupt step or geniculation on the anterior platform and a wide posterior platform brim. *P. foliata* has a straight basal edge whist *P. inclinata* has a curved one.

Several subspecies of *Q. polygnathiformis* have been identified suggesting that it may display a large intraspecies variability. However, *Q. polygnathiformis noah* and *Q. polygnathiformis magna* are very distinct subspecies. *Q. polygnathiformis noah* differs from *Q. polygnathiformis* for the broader and thicker platform and a more forward shifted pit. *Q. polygnathiformis magna* is characterized by having a broader, quadrate platform (Igo, 1989).

Remark: One illustrated *Q. polygnathiformis* element (Fig. 8.3) has a very high anterior parapet. This might be a stem form or an early example of genus *Parapatella* Orchard, 2013.

Occurrence: lower Julian–upper Julian, Zhuganpo Formation, Guizhou, South China.

Quadralella aff. _praelindae_ (Kozur, 2003)

Fig. 5, 10-11; Fig. 7, 9; Fig. 8, 4 & 14

Description: Element is small. In upper view, a slender platform extends almost the entire length of the element. The widest point is near the middle. A short free blade may develop. A prominent, intense constriction typically occurs at the posterior part of the platform. The lateral platform margins are distinctly upturned and bear no ornamentation except for intense microreticulation. The cusp is large, terminal, and may be followed by a small denticle. In lateral view, the platform is slightly arched. The blade is high and continuously decreases in height toward the carina which consists of 10-12 moderately discrete denticles and is slightly higher than the lateral margins. In lower view, the pit is well-excavated and surrounded by a prominent inflated loop. The basal furrow extends from the pit location to the anterior end.

Comparison: The holotype of *Q. praelindae* has a biconvex platform, broad anterior platform margins that gradually taper to the end of the blade and a strong posterior constriction. In contrast, in upper view, the platform of *Q. lindae* narrows abruptly to the anterior and has a more defined blade. The illustrated specimens of *Q.* aff. *praelindae* have a constriction like *Q. praelindae*, but the anterior morphology is like that of *Q. lindae*. (Orchard, 1991; Kozur, 2003). *Q. lobata* also develops posterior constriction but is ornamented by nodes on platform margins and the posterior constriction is more expanded (e.g., Orchard, 2014, pp. 113, Fig. 80).

Remarks: *Q. praelindae* (Kozur, 2003) has a medium length range and is known from the Julian to Tuvalian (Channell et al., 2003; Kozur, 2003; Rigo et al., 2007; Muttoni et al., 2014). *Q. praelindae* is characterised by its intense constriction in the posterior platform. It is probably the most problematic conodont species within the Carnian, in terms of its description. The holotype of *Q. praelindae* is likely to be a juvenile form because many species resemble *Q. praelindae* in their juvenile stage. Proper revision and establishment of an adult paratype are necessary in order to further validate this species. Caution should be paid to the size of elements and the number of denticles.

Occurrence: lower Julian–lower Tuvalian? Zhuganpo and Wayao formations, Guizhou, South China.

***Quadralella shijiangjunensis* (Sun, 2006)**

Fig. 5, 2; Fig. 8, 9

2006 *Quadralella shijiangjunensis* sp. nov. Sun, Pl. 9, fig. 17.

Description: In upper view, the platform is moderately board and elongated. The lateral platform margins are sub-parallel to parallel. The widest point is near the posterior end of the platform. The cusp is sub-terminal. One or more auxiliary denticle(s) develops beside the cusp and results in an asymmetrical posterior end. In lateral view, the platform is slightly arched. Carina consists of 8 to 12 highly fused denticles. An abrupt step generally develops in the anterior. In lower view, a pit is sub-terminal and slightly forward shifted. The keel end is round, rectangular or pointed but never bifurcated. A narrow furrow extends form the pit to the anterior end.

Comparison: *Q. polygnathiformis and Q. shijiangjunensis* share features of an abrupt anterior step and a relative board and long platform. The latter species has auxiliary denticle(s) by the cusp and an asymmetrical posterior platform.

Occurrence: upper Longobardian–Julian, Zhuganpo Formation, Guizhou, Yunnan, South China.

***Quadralella uniformis* (Sun, 2006)**

Fig. 5, 5; Fig. 8, 13

2006 *Quadralella uniformis* sp. nov. Sun, Pl. 8, fig. 18, Pl. 9, fig. 36

Description: In upper view, the platform is slender. Microreticulation covers the platform except the shallow, adcarinal lateral grooves. The cusp is sub-terminal and erect. The posterior end is rounded. In lateral view, the platform is slightly arched or straight. Denticles composing the carina and the blade are densely arrayed. Tips of all denticles are at a same height, forming a (virtually) straight line. In some cases, the denticles decrease slightly in height towards the end of carina. A geniculation point may occur at the anterior. In lower view, the pit is surrounded by a terminally to sub-terminally located loop. The keel end is rounded to rectangular. A narrow furrow extends to the anterior.

Comparison: *P. foliata* and *Q. uniformis* both have relative straight and slender platforms. However, the latter species has all denticle tips arrayed into a straight line.

Occurrence: Julian, Zhuganpo Formation, Guizhou and Yunnan provinces, South China.

***Quadralella wanlanensis* n. sp. Zhang, Sun and Lai**

Fig. 7, 7-8

Etymology: From the name of the town where the species occurs.

Holotype: Specimen NR-32 157 (Fig. 7. 7) from sample NR-32, Zhuganpo Formation, Yongyue Section, South China.

Paratype: Specimen NR-54 090 (Fig. 7. 8) from sample NR-54, Zhuganpo

Formation, Yongyue Section, South China.

Materials: 5 specimens.

Diagnosis: Platform is broad and relatively flat. Posterior end of the platform is rectangular. No free blade or short free blade developed at the anterior. The blade consists of highly fused denticles, and middle carina is normally merged. Pit is sub-terminal and keel is relatively broad.

Description: In upper view, the species has a broad platform with sub-parallel lateral margins and a sub-rectangular posterior end. The platform extends to the anterior and commonly has no free blade although some specimens may develop a short free blade. The platform tapers anteriorly. The widest point is in the posterior of the platform. Adcarinal lateral grooves are shallow. Intense microreticulation covers the entire platform except for the adcarinal lateral grooves. The cusp is distinct, sub-terminal and followed by a relatively wide posterior platform brim. In lateral view, the platform is slightly arched at the three-quarter point from the anterior end. The carina consists of 12–15 moderately fused denticles which decrease in height posteriorly. The posterior of the platform is relatively flat and not upturned. In lower view, the pit is sub-terminal to terminal. The keel is moderately wide and extends from the pit to the anterior end. The keel end can be slightly bifurcated.

Comparison: Compared with other *Quadralella* species, this species is characterized by having a broad, flat platform and a near-quadrate posterior end.

Compared with the *Q. polygnathiformis magna, Q. wanlanensis* n. sp. has a flat, shorter but broader platform. *Q. polygnathiformis magna* has an evidently bifurcated keel end.

Occurrence: lower Julian–? Zhuganpo Formation, Guizhou, South China.

Quadralella aff. _wayaoensis_ (Wang, 2000)

Fig. 9, 3

Description: In upper view, the platform extends along the entire element. A short free blade may occur at the anterior. Adcarinal lateral grooves are shallow. An obvious constriction may occur in the posterior third. The cusp is not prominent and sub-terminal. The posterior end is round. In lateral view, the platform is straight or slightly arched. The posterior platform is relative flat. An abrupt step occurs anteriorly. Anterior carina decreases in height quickly to the middle and then keeps the same height to the posterior end. In lower view, the pit is sub-terminal. The pit is surrounded by a small loop. The keel end is either rounded, rectangular or weakly bifurcated but not pointed. A furrow extends to the anterior end.

Comparison: The posterior platform of *Q.* aff. *wayaoensis* is not as constricted as seen in *Q. wayaoensis*. The merged middle carina is low but still visible in our specimens, in contrast to the merely visible middle carina of *Q. wayaoensis* (Wang, 2000).

Q. wayaoensis and *Q. praelindae* both have constrictions of their posterior platforms. However, *Q. wayaoensis* is characterized by having a broad and flat platform, a weakly bifurcated or rectangle keel end, weak constriction of the posterior third and a low middle – posterior carina. *Q. parelindae* is slender, constricted strongly near the posterior end and has a rounded keel termination.

Occurrence: Julian–lower Tuvalian? Zhuganpo and Wayao formations, Guizhou, South China.

Quadralella yongyueensis n. sp. Zhang, Sun and Lai

Fig. 7, 3-4

Etymology: From the name of the section where it is found.

Holotype: Specimen NR-67 030 (Fig. 7. 3) from sample NR-67, Zhuganpo Formation, Yongyue Section, South China.

Paratype: Specimen NR-54 085 (Fig. 7. 4) from sample NR-54, Zhuganpo Formation, Yongyue Section, South China.

Materials: 5 specimens.

Diagnosis: Platform is thick and asymmetrical. No free blade or short free blade. Blade and carina are consisted of highly fused denticles. In upper view, accessory denticle(s) follow(s) the cusp on right or left side. Pit is sub-terminal. Keel end is weakly to moderately bifurcated.

Description: In upper view, the platform is moderately broad and long with sub-parallel lateral margins. The platform extends to the anterior and sometimes has a short free blade. The platform tapers from two fifth of entire platform to the anterior end. The lateral margins are moderately upturned. The widest point is in the posterior. Two relatively deep adcarinal lateral grooves are incised on both sides of carina. Intense microreticulation covers the platform except for the adcarinal lateral grooves. The cusp is distinct and nearly terminal and is followed by a narrow platform brim. One or two lateral denticles may develop on one side of the posterior platform and cause an irregular, distorted posterior end. In lateral view, the platform is slightly arched. The carina consists of highly fused denticles. The height of the fused carina is almost the same as the upturned lateral platform margins. In lower view, the furrow always extends from the pit to the anterior end of the platform. The keel may be elongated to the left or right side or bifurcated due to a development of the lateral denticle(s). The pit is sub-terminal and slightly shifted forward.

Remarks: Compared with *Q. polygnathiformis*, *Q. yongyueensis* n. sp. is characterized by the highly fused carina, auxiliary denticles behind the cusp and an irregular posterior end.

Accessory posterior denticles of *Q. yongyueensis* n. sp. are seen in young mature to late growth stages but rarely in juvenile specimens. Therefore, the possibility that accessory denticles are a pathological feature associated with ontogenetic development cannot be completely ruled out and is very difficult to determine from a palaeontological perspective.

Q. yongyueensis n. sp. may be closely affiliated with *Q. maantangensis*, a widely reported species from South China. The latter species is characterized by having a triangular platform, a commonly bifurcated carina and a bifurcated keel end.

Comparison: *Q. shijiangjunensis* and *Q. yongyueensis* n. sp. both have at least one accessary denticle that follows the cusp and irregular posterior ends. However, *Q. yongyueensis* n. sp. has a thicker platform, a weakly bifurcated keel, a highly fused middle carina and shallow adcarinal grooves. In contrast, *Q. shijiangjunensis* has an abrupt step at the geniculation and a rounded, quadrate or pointed keel end.

Occurrence: lower Julian–? Zhuganpo Formation, Guizhou, South China.

***Quadralella* sp. A**

Fig. 6, 1

Materials: 1 complete element.

Description: In upper view, the platform is relatively broad with the widest point in the middle. Intense microreticulation covers the platform except for the adcarinal lateral grooves. The lateral grooves are moderately deep. In lateral view, the platform is slightly curved. Denticles on the blade are highly fused, forming a convex crest. The cusp is distinct and sub-terminal. A smooth slope or geniculation occurs in the middle of platform. The carina consists of highly fused denticles and is generally lower than the lateral platform margins. In lower view, the keel is low and elongated. The pit is slightly shifted forward in respect to the cusp and keel end. A furrow extends from the pit to the platform anterior.

Discussion: Compared with *Q. polygnathiformis*, this species has a slightly forward shifted pit, an elongated keel and a high anterior blade.

Occurrence: upper Longobardian–? Zhuganpo Formation, Yongyue section, Guizhou, South China.

***Quadralella* sp. B**

Fig. 8, 11

2016 *Quadralella* sp. Sun et al., Fig. 6. fig.14

Materials: 1 complete element and 4 broken elements.

Description: In upper view, the platform is relatively broad with sub-parallel lateral margins that extend to the anterior end. No free blade. Intense microreticulation covers the entire platform except the shallow adcarinal lateral grooves. Maximum width is in the middle or posterior. Lateral platform margins are not upturned. The posterior end is nearly rectangular. In lateral view, the platform is slightly curved. A prominent robust cusp is located at the terminal platform and is followed by a narrow posterior brim. Denticles in the carina are highly fused and of almost the same height, forming a ridge extending along the entire platform. Compared with the height of carina, the lateral margins are lower. This species has no geniculation point. In lower view, the pit is terminal. The furrow extends from the pit to the anterior end of platform.

Discussion: Compared with others *Quadralella* species, the current species has an extremely robust cusp in the posterior end and the platform covers all the element.

Occurrence: upper Julian–? upper Zhuganpo to lower Wayao formations., Guizhou, South China.

7. Conclusions

A detail conodont biostratigraphic study has been carried out in the Middle–Late Triassic Yongyue section, Zhenfeng area, South China in order to clarify the long disputed age. Twenty conodont species are recognized and four conodont zones are established. Based on the new conodont dating, the following conclusions are drawn:

1. Most of the Zhuganpo Formation in the study section is of Julian 1 age, except the lower 12 m strata are possibly of Ladinian age while the topmost 2 m nodular limestones are of early Julian 2 age.
2. A substantial part of the Ladinian in the study region is likely to be missing due to erosion/sequence boundary development in the lower Zhuganpo Formation.
3. The last occurrence of *Gladigondolella* falls in the Julian 1 and cannot be used as a marker of the Julian–Tuvalian boundary in Guizhou and is most probably not a good Julian–Tuvalian marker in general.

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Figure and table captions

Fig. 1 Location map of the study section at Yongyue village, Zhenfeng area, Guizhou Province, South China.

Fig. 2 Field photographs of the study section. A. Overview of the section, showing three distinctive lithological units: Yangliujing, Zhuganpo and Wayao formations. B., Photograph showing the lower part of Zhuganpo Formation. C., The erosional surface in the lower part of the Zhuganpo Formation D., Photograph showing the boundary between the Zhuganpo and Wayao Formations.

Fig. 3 Log of the study section, showing sampling horizons and conodont ranges.

Fig.4 Correlation of the Ladinian-Carnian conodont zones amongst different areas (*P.* = *Paragondolella*, *B.* = *Budurovignathus*, *C.* = *Carnepigondolella*, *M.* = *Metapolygnathus*, *Ma.* = *Mazzaella*, *G.* = *Gladigondolella, Q.* = *Quadralella, K.* = *Kraussodontus, A.* = *Acuminatella*)

Fig. 5 SEM photos of conodonts from the Ladinian-Carnian strata of Yongyue Section-I. Scale bar=300μm. “a” for upper view, “b” for lateral view, “c” for lower view.

1. *Paragondolella foliata* Budurov, 1975 NR-95 006;

2. *Quadralella shijiangjunensis* (Sun, 2006) NR-95 005;

3. *Quadralella* aff. *acuminatus* (Orchard, 2007) NR-93 023;

4. *Quadralella polygnathiformis* (Budurov and Stefanov, 1965) NR-93 030;

5. *Quadralella uniformis* (Sun, 2006) NR-66 050;

6. *Quadralella tadpole* (Hayashi, 1968) NR-23 008;

7. *Quadralella* sp. NR-92 080;

8. *Quadralella* sp. NR-92 079;

9. *Quadralella* sp. NR-81 088;

10. *Quadralella* sp. NR-67 015;

11. *Quadralella* aff. *praelindae* (Kozur, 2003) NR-66 052;

12. *Gladigondolella malayensis* Nogami, 1968 NR-66 067;

13. *Quadralella* sp. NR-54 098;

Fig. 6 SEM photos of conodonts from the Ladinian-Carnian strata of Yongyue Section-II. Scale bar=300μm. “a” for upper view, “b” for lateral view, “c” for lower view.

1. *Quadralella* sp. A NR-95 012;

2. *Quadralella polygnathiformis* (Budurov and Stefanov, 1965) NR-93 016;

3. *Quadralella* aff. *zonneveldi* (Orchard, 2007) NR-93 017;

4. *Gladigondolella malayensis* Nogami, 1968 NR-51 109;

5. *Quadralella* aff. *zonneveldi* (Orchard, 2007) NR-93 031;

6. *Quadralella* aff. *acuminatus* (Orchard, 2007) NR-92 070;

7. *Quadralella* sp. NR-92 071;

8. *Quadralella* sp. NR-92 076;

9. *Quadralella* sp. NR-92 085;

10. *Quadralella intermedius* (Orchard, 2007) NR-81 093;

11. *Quadralella tadpole* (Hayashi, 1968) NR-67 012;

12. *Quadralella tadpole* (Hayashi, 1968) NR-67 028;

13. *Paragondolella inclinata* Kovács, 1983, NR-67 035;

Fig. 7 SEM photos of conodonts from the Ladinian-Carnian strata of Yongyue Section-III. Scale bar=300μm. "a" for upper view, "b" for lateral view, "c" for lower view.

1. *Quadralella* sp. NR-70 147;

2. *Paragondolella inclinata* Kovács, 1983 NR-70 151;

3. *Quadralella yongyueensis* n. sp. NR-67 030;

4. *Quadralella yongyueensis* n. sp. NR-54 085;

5. *Quadralella* sp. NR-54 106；

6. *Quadralella* sp. NR-36 129;

7. *Quadralella wanlanensis* n. sp. NR-32 157;

8. *Quadralella wanlanensis* n. sp. NR-54 090;

9. *Quadralella* sp. NR-46 126;

Fig. 8 SEM photos of conodonts from the Ladinian-Carnian strata of Yongyue Section-IV. Scale bar=300μm. "a" for upper view, "b" for lateral view, "c" for lower view.

1. *Paragondolella inclinata* Kovács, 1983 NR-29 166;

2. *Quadralella polygnathiformis* (Budurov and Stefanov, 1965) NR-20 022；

3. *Quadralella polygnathiformis* (Budurov and Stefanov, 1965) NR-20 029;

4. *Quadralella* aff. *praelindae* (Kozur, 2003) NR-11 129;

5. *Quadralella tadpole* (Hayashi, 1968) NR-11 130;

6. *Quadralella polygnathiformis* (Budurov and Stefanov, 1965) NR-4 054;

7. *Gladigondolella malayensis* Nogami, 1968 NR-66 068;

8. *Quadralella intermedius* (Orchard, 2007) NR-95 003;

9. *Quadralella shijiangjunensis* (Sun, 2006) NR-92 065;

10. *Quadralella* sp. NR 72 144;

11. *Quadralella* sp. B NR-7 061;

12. *Quadralella* sp. NR-29 160;

13. *Quadralella uniformis* (Sun, 2006) NR-54 082;

14. *Quadralella* aff. *praelindae* (Kozur, 2003) NR-9 079;

Fig. 9 SEM photos of conodonts from the Ladinian-Carnian strata of Yongyue Section-V. “a” for upper view, “b” for lateral view, “c” for lower view.

1. *Quadralella* cf. *langdaiensis* (Yang et al., 2002) NR-92 064;

2. *Quadralella maantangensis* (Dai and Tian, 1983) NR-72 127;

3. *Quadralella* aff. *wayaoensis* (Wang, 2000) NR-46 125;

4. *Quadralella jiangyouensis* (Wang and Dai, 1981) NR-32 147.

Table. 1 Conodont yields from the Yongyue samples, Zhenfeng area. Only samples that yielded conodonts are listed.

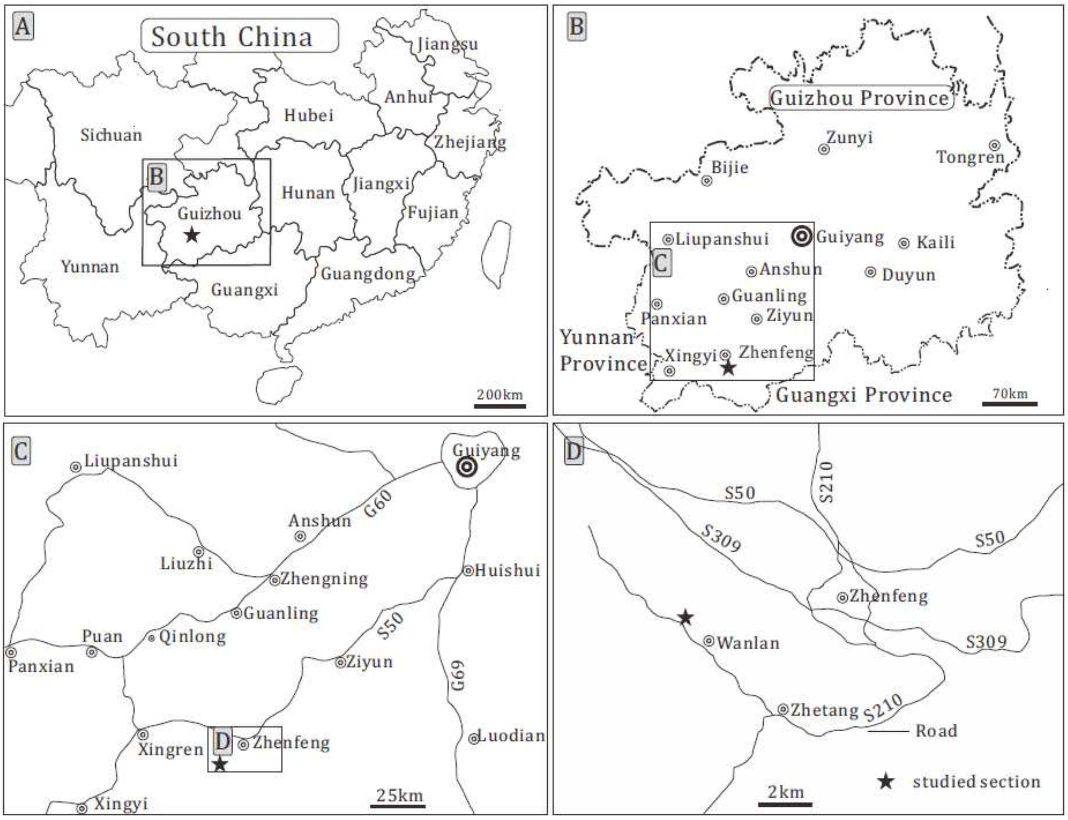
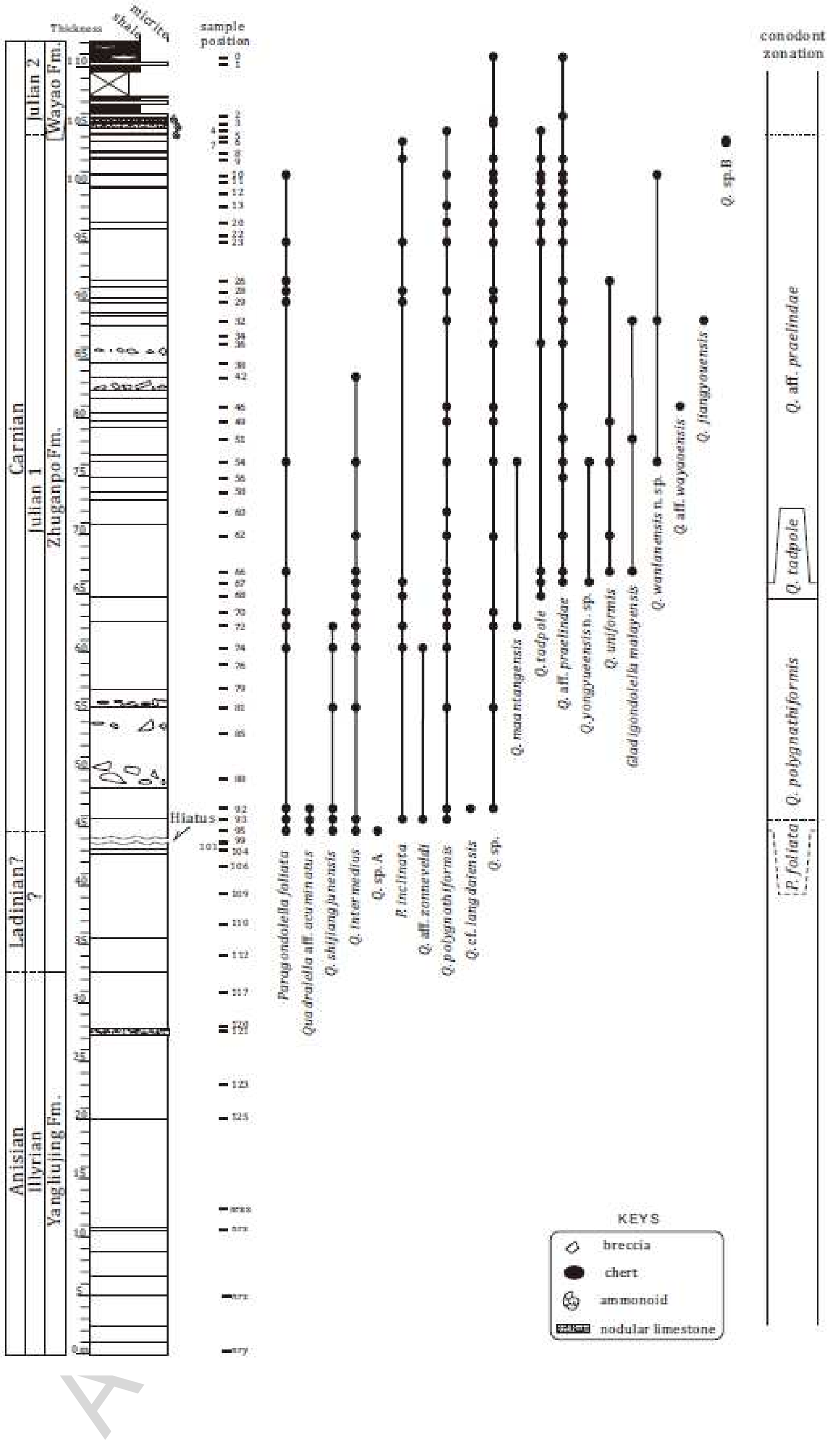

A
South China
Jiangsu
Anhui
Hubei
Sichuan
Zhejiang
B
Guizhou
Hunan
Jiangxi
Fujian
Yunnan
Guangxi
Guangdong
200km
B
Guizhou Province
Zunyi
Tongren
Bijie
Liupanshui
Guiyang
Kaili
C
Anshun
Duyun
Guanling
Panxian
Ziyun
Yunnan Province
Xingyi
Zhenfeng
Guangxi Province
70km
C
Liupanshui
Guiyang
Anshun
G60
Liuzhi
Huishui
Zhengning
Guanling
S50
Puan
Qinlong
Panxian
Ziyun
G69
Xingren
D
Zhenfeng
Luodian
25km
Xingyi
D
S50
S210
S309
S50
Zhenfeng
Wanlan
S309
Zhetang
S210
Road
2km
studied section

Fig. 1


Yangliujing Fm.
Zhuganpo Fm.
Wayao Fm.
A
Zhuganpo Fm.
C
B
C
Zhuganpo Fm.
Wayao Fm.
D

Fig. 2



Thickness
shale
micrite
sample position
conodont zonation
Carnian
Julian 2
Wayao Fm.
Julian 1
Zhuganpo Fm.
Ladinian?
?
Anisian
Illyrian
Yangliujing Fm.
Hiatus
Paragondolella foliata
Quadralella aff. acuminatus
Q. shijiangjunensis
Q. intermedius
Q. sp. A
P. inclinata
Q. aff. zoneveldi
Q. polygnathiformis
Q. cf. langdaiensis
Q. sp.
Q. maantangensis
Q. tadpole
Q. aff. praelindae
Q. yongyueensis n. sp.
Q. uniformis
Gladigondolella malayensis
Q. wanlanensis n. sp.
Q. aff. wayaoensis
Q. jiangyouensis
Q. sp. B
Q. aff. praelindae
Q. tadpole
Q. polygnathiformis
P. foliata
KEYS
breccia
chert
ammonoid
nodular limestone

Fig. 3

<table>
<tr><th rowspan="2">Stage</th><th rowspan="2">Substage</th><th>This study</th><th>Yang et al.,1995</th><th>Koike,1981</th><th>Gallet et al.,1994</th><th colspan="2">Orchard and Tozer,1997</th><th colspan="2">Kozur, 2003</th></tr>
<tr><th>Yongyue</th><th>SW Guizhou</th><th>Japan</th><th>Alps and Turkey</th><th>Tethys</th><th>Western Canada</th><th>Tethys</th><th>North America</th></tr>
<tr><td rowspan="11">Carnian</td><td rowspan="5">Tuvalian</td><td rowspan="5"></td><td rowspan="5">Q. polygnathiformis</td><td rowspan="3">Q. nodosa</td><td>M. communisti</td><td>M. communisti</td><td>C. pesudoechinata</td><td>C. pseudodiebeli</td><td>A. angusta-M. communisti</td></tr>
<tr><td rowspan="2">Q. nodosa</td><td rowspan="2">Q. nodosa</td><td>C. samueli</td><td rowspan="2">C. zoae</td><td rowspan="2">C. zoae</td></tr>
<tr><td>C. zoae</td></tr>
<tr><td rowspan="8">Q. polygnathiformis</td><td>Q. carpathica</td><td rowspan="8">Q. polygnathiformis</td><td>Q. lindae</td><td>Q. carpathica</td><td>Q. lindae</td></tr>
<tr><td>Q. polygnathiformis</td><td rowspan="7">P. inclinata-Mosherella</td><td>K. postinclinata-Q. polygnathiformis</td><td rowspan="7">Q. polygnathiformis</td></tr>
<tr><td rowspan="6">Julian</td><td rowspan="2"></td><td rowspan="5">Q. polygnathiformis-tadpole</td><td>G. tethydis</td><td rowspan="4">G. tethydis-Q. polygnathiformis</td></tr>
<tr><td>Ma. carnicus</td></tr>
<tr><td rowspan="2">Q. aff. praelindae</td><td>Q. auriformis</td></tr>
<tr><td rowspan="2">Q. tadpole</td></tr>
<tr><td>Q. tadpole</td><td rowspan="2">B. diebeli-Q. polygnathiformis</td></tr>
<tr><td>Q. polygnathiformis</td><td>Q. polygnathiformis-maantangensis</td><td>B. mostleri</td></tr>
<tr><td>Ladinian</td><td>Longob.</td><td>P. foliata</td><td>P. foliata inclinata</td><td>P. foliata</td><td></td><td></td><td></td><td></td><td></td></tr>
</table>

Fig. 4


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
8a
8b
8c
9a
9b
9c
10a
10b
10c
300μm
11a
11b
11c
12a
12b
12c
13a
13b
13c

Fig. 5

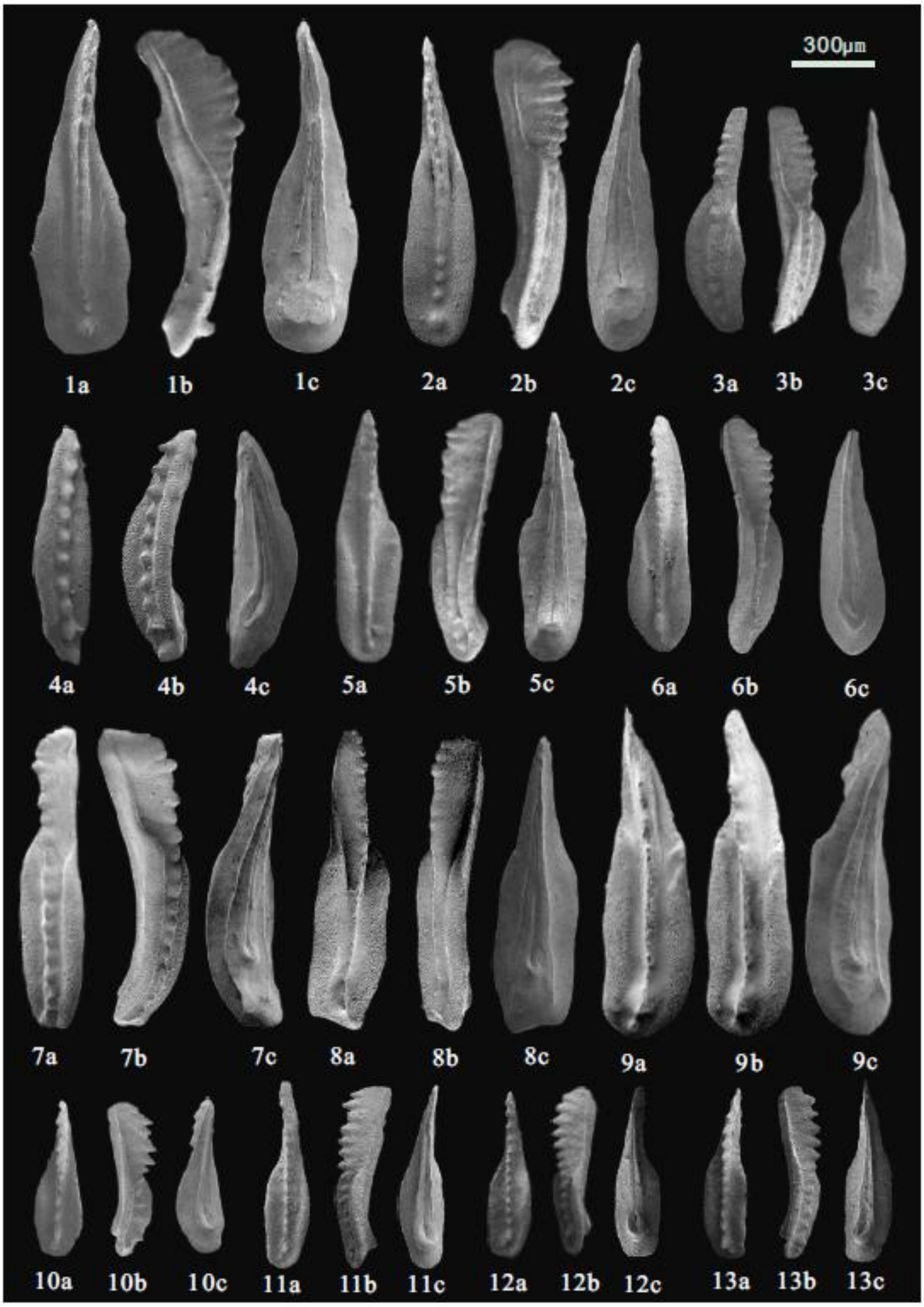

300μm
1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
8a
8b
8c
9a
9b
9c
10a
10b
10c
11a
11b
11c
12a
12b
12c
13a
13b
13c

Fig. 6


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
8a
8b
8c
9a
9b
9c
300μm

Fig. 7


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
8a
8b
8c
9a
9b
9c
10a
10b
10c
11a
11b
11c
12a
12b
12c
13a
13b
13c
14a
14b
14c
300 μm

Fig. 8

Table 1

Sample No.	Weight/ Kg	P1 complete	P1 broken	Ramiform	Total
NR 0	9.2	4	2	2	8
NR 1	4.4	0	0	1	1
NR 2	4.6	7	7	5	19
NR 3	8.3	1	1	0	2
NR 4	3.7	5	1	1	7
NR 6	7.1	2	6	4	12
NR 7	4.0	4	7	4	15
NR 8	8.4	2	5	3	10
NR 9	4.3	25	12	41	78
NR 10	4.9	8	28	32	68
NR 11	4.0	10	16	3	29
NR 12	4.1	4	8	10	22
NR 13	4.7	4	7	2	13
NR 14	9.6	25	31	22	78
NR 23	3.9	14	3	12	29
NR 26	4.6	10	7	3	20
NR 28	4.8	8	9	6	23
NR 29	4.4	25	8	37	70
NR 32	4.7	17	9	20	46

NR 34	4.1	0	4	0	4
NR 36	3.9	8	8	4	20
NR 42	4.7	1	0	0	1
NR 46	5.1	8	1	5	14
NR 49	5.1	30	12	11	53
NR 51	4.7	4	1	0	5
NR 54	9.7	31	19	17	67
NR 56	4.8	1	1	0	2
NR 62	4.4	7	2	1	10
NR 66	4.8	14	7	18	39
NR 67	4.1	30	12	11	53
NR 68	5.0	12	4	1	17
NR 70	4.8	6	6	1	13
NR 72	3.9	34	14	14	62
NR 74	4.9	8	6	1	15
NR 76	5.2	1	2	1	4
NR 79	5.7	0	0	1	1
NR 81	4.5	9	3	3	15
NR 85	4.4	0	0	2	2
NR 88	3.9	1	1	0	2
NR 92	4.0	16	11	6	33

NR 93	3.4	41	26	8	75
NR 95	4.6	9	6	2	17
Total	213.4	446	313	315	1074