A MULTI-METHOD STUDY ON TRIASSIC CONODONTS

Dissertation

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CONTENTS

GEOMETRIC MORPHOMETRIC ANALYSIS REVEALS THE ALLOMETRY OF ANISIAN (MIDDLE TRIASSIC) SEGMINIPLANATE CONODONTS

A REVIEW OF THE EVOLUTION, BIOSTRATIGRAPHY, PROVINCIALISM AND DIVERSITY OF MIDDLE AND EARLY LATE TRIASSIC CONODONTS

PREFACE

This thesis focuses on conodonts from the Early Triassic to early Late Triassic. The PhD project started at September, 2011 and Yanlong Chen was personally supported by the China Scholarship Council for his stay in Austria. The studied material of Jiarong section was obtained by himself during his master's program, but the conodonts size measurements and the writing of the manuscript were conducted at the University of Graz. Parts of Slovenian conodonts were donated by Tea Kolar-Jurkovšek of the Geological Survey of Slovenia and part was obtained by Yanlong Chen after field sampling and laboratory work. Conodonts of Austria (Öfenbachgraben Section and Mendlingbach Section) were donated by Prof. Leopold Krystyn of Vienna University. The integrated study of these conodonts in the present thesis has a profound meaning for biostratigraphy, paleo-environment, biogeography, taxonomy and evolution of Triassic conodonts. And it is a contribution to both the scientific world and the mining and petroleum industry.

The PhD candidate (Yanlong Chen) has performed paleontological, biostratigraphical and morphological analyses focusing on the Triassic conodonts. The present thesis is a summary of the work during his doctoral program. Chapter 1 provides a summary and introduction of the paleogeography of the studied areas, the terminology of conodonts shape categories and the state of the art of the research in Triassic conodonts. Chapter 2–5 are papers which have been published, submitted or are ready for submission to a peer reviewed scientific journal. The supplementary information contains the publications following the master thesis in Wuhan (China) and the eight articles co-authored by Yanlong Chen during his PhD programme.

Chapter 2 Chen, Y.L., Twitchett, R.J., Jiang, H.S., Richoz, S., Lai, X.L., Yan, C.B., Sun, Y.D., Liu, X.D., Wang, L.N., 2013. Size variation of conodonts during the Smithian-Spathian (Early Triassic) global warming event. *Geology*, 41(8), 823–826.

Chapter 3 Chen, Y.L., Kolar-Jurkovšek, T., Jurkovšek, B., Aljinović, D., Richoz, S. Early Triassic conodonts and carbonate carbon isotope record of Idrija–Žiri area, Slovenia. (Submitted to *Palaeogeography Palaeoclimatology Palaeoecology*)

Chapter 4 Chen, Y.L., Neubauer T.A., Krystyn L., Richoz S. Geometric morphometric analysis reveals the allometry of Anisian (Middle Triassic) segminiplanate conodonts. (Ready for Submission)

Chapter 5 Chen, Y.L., Krystyn, L., Orchard, M.J., Lai, X.L., Richoz, S. A review of the evolution, biostratigraphy, provincialism and diversity of Middle and early Late Triassic conodonts. (*Papers in Palaeontology*, in press)

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ABSTRACT

Conodonts are an extinct group of marine chordates with a feeding apparatus composed of microscopic “tooth-like” elements. They are one of the fastest-evolving fossil groups, sensitive to environmental stress, and are thus an ideal organism group for biostratigraphic studies, to test ecological responses to past episodes of climatic change and to reveal evolutionary patterns. Final recovery of marine ecosystems after the end-Permian mass extinction took several million years, partly due to persistent inhospitable environments and partly due to (at least) three episodes of further extinction that occurred during the Early Triassic: in the late Griesbachian, near the Smithian-Spathian boundary (SSB), and in the late Spathian. The Middle Triassic represents an interval of full recovery from the end-Permian mass extinction.

I studied the conodonts of these peculiar time intervals following different periods, methods and point of view. In the first study (Chapter 2), a comprehensive, high-resolution stratigraphic framework of a section in South China comprising six Lower Triassic conodont zones is provided. Detailed size measurements of 441 conodont elements of the closely related genera *Neospathodus*, *Triassospathodus*, and *Novispathodus* show for the first time that these clades suffered a temporary, but significant, size reduction during the SSB crisis, followed by gradual and steady size increase during the early Spathian. Size reduction of conodonts was caused by an episode of global warming, further strengthening the link between morphological and climatic changes recorded in the fossil record.

The Early Triassic of the eastern marginal Tethys (South China) has been well documented for conodont biostratigraphy, while the contemporaneous western marginal Tethys still lacks of detailed conodont biostratigraphical framework. Meanwhile, the size reduction of conodonts during the Smithian-Spathian transitional interval is only restricted to South China. To be sure that this is a global effect, it is now necessary to carry studies on other Early Triassic locations. Central Europe was located at this time on the western margin of the Tethys and thus presents an interesting alternative to South China. Systematic sampling of five sections in the Idrija–Žiri area has resulted in the discovery of new species: *Platyvillosus corniger* sp. nov. and *Neospathodus planus* sp. nov. Based on these new species and other conodont elements obtained from these sections, nine discrete conodont Unitary Association (UA) zones are proposed for this area. In ascending order they are: *Eurygnathodus hamadai* Zone (UA 1), *Eurygnathodus costatus* Zone (UA 2), *Foliella*

gardenae Zone (UA 3), *Neospathodus robustus* Zone (UA 4), *Platyvillosus corniger* Zone (UA 5), *Platyvillosus regularis* Zone (UA 6), *Triassospathodus hungaricus* Zone (UA 7), *Triassospathodus symmetricus* Zone (UA 8), and *Neospathodus robustispinus* Zone (UA 9). The conodonts and $\delta^{13}C$ data indicate that these conodont zones span the Dienerian/Smithian (i.e. Induan/Olenekian) boundary interval to the Spathian, and they also indicate that *Triassospathodus hungaricus* Zone (UA 7) does not occur at the base of the Spathian. These conodont zones are valuable for stratigraphic correlation within Central and South Europe, and they also promote a better correlation worldwide. Conodonts in the Idrija–Žiri area are adapted to a shallow water environment on an epeiric ramp. However, the Lilliput effect recorded here is in younger strata than in South China (early Spathian) and demonstrates that further research is needed to better understand this phenomenon.

Early Triassic conodonts evolved faster and were more diversified than Middle and Late Triassic conodonts, which contain species very similar to each other. The segminiplanate conodonts represent an important morphological group ranging from the Upper Carboniferous to the Upper Triassic. However, the morphological similarity of segminiplanate P_1 elements generates problems for taxonomy, especially in Permian and Triassic clades. Chapter 4 represents the first study of morphological variation in Triassic segminiplanate conodonts using geometric morphometrics. Using linear regressions between relative warp scores from both upper and lateral views and conodont length, we demonstrate strong allometric growth patterns for the species *Paragondolella bifurcata* Budurov & Stefanov, 1972. Based on our results, we synonymize the species-group taxa *Gondolella praeszaboi bystrickyi* Kovacs, Papsova & Perri, 1996, and *Paragondolella unilobata* (Gedik, 1975), all of which were introduced for juvenile specimens. We suggest using only larger sized conodonts in the population of a rock sample for the definition of new species in future studies.

The demonstration of allometry of Middle Triassic conodonts reveals that some conodonts species were defined based on different growth stages of one natural species. These synonyms need to be ruled identified by upcoming revisions (Chapter 5). Meanwhile, Middle and early Late Triassic (Anisian, Ladinian and Carnian) conodonts have been studied for nearly 60 years and until now about 195 species were recognized during this time interval, but so far no recent summary of their evolution and stratigraphic distributions is available. In Chapter 5, a review of the literature on all Middle and early Late Triassic conodonts is presented. The evolutionary lineages, stratigraphic distributions as well as their taxonomic systems have been re-evaluated, and synonymous species have been identified. Conodont provincialism and diversity have been briefly discussed. Based on the lineages, 27 genera are recognized in the Middle and early Late Triassic, including a newly recognized genus which is left in open nomenclature. Conodont provincialism is low in the Anisian. From the late Anisian faunistic differences start to increase and get stronger during the early Ladinian to reach a peak around the middle Ladinian. Provincialism remains strong till the lowermost Carnian to change to an all-Triassic low in the early Tuvalian. The provincialism between North America and Tethys rebounds on the specific level during the late Tuvalian. Diversities on generic and specific levels have been achieved and three major conodont diversity cycles are recognized. The first cycle ranges from Aegean to the early Fassanian, the second cycle from the late Fassanian to the earliest Julian, and the third cycle from the middle Julian to the latest Tuvalian.

CHAPTER 1

INTRODUCTION TO THE END-PERMIAN MASS EXTINCTION AND THE FOLLOWING RECOVERY, THE TRIASSIC PALEOGEOGRAPHY AND THE STATUS OF TRIASSIC CONODONT STUDIES

1.1 The end-Permian mass extinction and the following recovery

The Permian/Triassic transitional interval is a time of crisis and profound changes in the Earth ecosystem. It is known as the greatest mass extinction of life on Earth and has removed more than 80% of marine genera (Erwin, 2001; Brayard et al., 2009). Life was not fully recovered from the mass extinction until the Middle Triassic. The Early Triassic which lasted for 5 million years (Ma) was characterized by a slow recovery process from the end Permian mass extinction (Galfetti et al., 2007), large-scale fluctuations of the global carbon cycle (Payne et al., 2004; Richoz, 2006), several small scaled extinction events (Stanley, 2009), changes in water temperature (Sun et al., 2012; Romano et al., 2013), ocean acidification (Payne et al., 2010; Hinojosa et al., 2012; Clarkson et al., 2015), anoxia events (Isozaki, 1997; Grasby et al., 2013; Sun et al., 2015), euxinia (Grice et al., 2005), and fluctuating productivity (Suzuki et al., 1998; Payne and Kump, 2007).

The pronounced stable carbon isotopic ($\delta^{13}C_{carb}$‰) excursion at the Permian-Triassic boundary was not an isolated event but the first in a series of large fluctuations that continued throughout the Early Triassic before ending abruptly early in the Middle Triassic (Payne et al., 2004; Sun et al., 2015). The Middle and early Late Triassic was a time interval with relatively uniform carbonate stable carbon isotope values (Muttoni et al., 2014; Lehrmann et al., 2015; Fig. 1.1). The proposed Early Triassic sea surface temperatures (SSTs) have a strong correlation with the contemporaneous carbonate carbon isotope curve (e.g., Sun et al., 2012, fig. 2; Figure 1.1) which probably indicates that the SSTs were controlled by the concentration of CO_2 of the atmosphere. Compared to the high SSTs during the Early Triassic, the Middle and early Late Triassic was cooler (Trotter et al., 2015; Fig. 1.1). The Middle Triassic shows still variations, but the Carnian is quite stable. Despite their fluctuations, the Early to early Late Triassic SSTs never reached again the early Changhsingian (latest Permian) cooler condition.

The Lilliput effect is the temporary post extinction size reduction of surviving taxa (Urbanek, 1993). The reduction in body size (Lilliput effect) has been reported for many marine organisms, e.g., conodonts, brachiopods, bivalves and gastropods, during the recovery

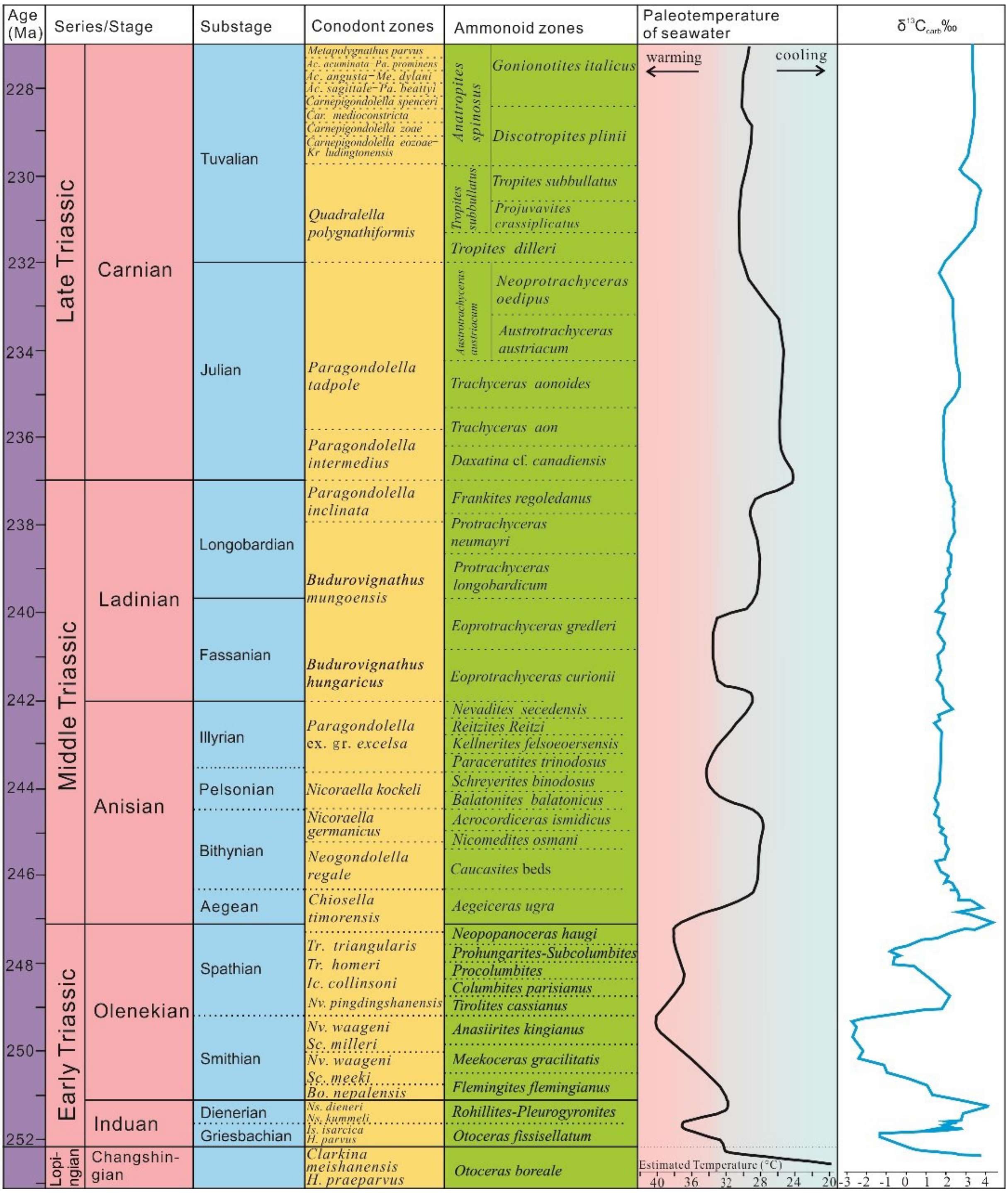

Figure 1.1. Summary of numerical ages of series, stages, and substages of the Early, Middle and early Late Triassic with selected marine biostratigraphic zonations. Conodont zones are defined after Orchard and Tozer (1997), Kozur (2003) and Orchard (2014). This is a global composite zonation and the local zonation can be quite different (see Chapters 2 and 3). Ammonoid zones are defined after Gallet et al. (1994), Krystyn et al. (2004), and Ogg (2012). Absolute age constraints after Cohen et al. (2013). Paleotemperature based on Trotter et al (2015). Carbonate carbon isotope based on Muttoni et al. (2014) and Lehrmann et al. (2015). Abbreviations: *Ac.=Acuminatella*; *Bo.=Borinella*; *C.=Clarkina*; *Ds.=Discretella*; *Eu.=*

Eurygnathodus; *H.=Hindeodus*; *Ic.=Icriospathodus*; *Is.=Isarcicella*; *Me.=Metapolygnathus*; *Nc.=Neoclarkina*; *Ns.=Neospathodus*; *Nv.=Novispathodus*; *Pau.=Paullella*; *Pa.=Parapetella*; *Sc.=Scythogondolella*; *Tr.=Triassospathodus*.

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from the Permian-Triassic mass extinction (Fraiser and Bottjer, 2004; He et al., 2010; Brayard et al., 2010; 2015; Metcalfe et al., 2011; Fraiser et al., 2011; Chen et al., 2013). A significant reduction in burrow diameters demonstrates that infaunal organisms were also affected by the Lilliput effect (e.g., Twitchett, 2007). Although a general decrease in body size is recorded in many groups through most of the Early Triassic, Brayard et al. (2010, 2011) documented numerous large-sized gastropods and thus questioned the Lilliput hypothesis (Brayard et al., 2015). The controversy on the Early Triassic Lilliput effect urges more documentation of sizes of Permian and Triassic organisms. For the conodonts, the effect was until my studies confined to the first or second conodont zone of the Induan (Twitchett, 2007; Luo et al., 2008; Metcalfe et al., 2011). In Chapter 2, we documented a conodont size reduction during the Smithian-Spathian transitional interval in South China. But in Chapter 3 we documented that the Lilliput effect occurs in Slovenia later, during the third conodonts zone of the Spathian. Several questions are still to be answered: was the Lilliput effect ubiquitous during the early Triassic or only restricted to short intervals and specific geographical localities? Was the Lilliput effect restricted to few clades of the survivors or it was a general phenomenon of all the survivors? What was the cause for these small sized organisms which have been already repeatedly observed?

Marine ecosystems had recovered substantially in the early to middle Anisian which is characterized by the end of the coral and coal gaps (Chen & Benton, 2012). The middle to late Middle Triassic was a time interval of full recovery from the end Permian mass extinction. Then the Carnial Pluvial Event indicates an episode of increased rainfall and had a well recognizable and widespread influence on Carnian marine and continental sedimentary systems (Simms and Ruffell, 1989; Breda et al., 2009, Dal Corso et al., 2015). It has been documented by a demise of carbonate platforms and reefs, a major faunal and floral turnover in the late Julian and a significant extinction event affecting conodonts and ammonoids at the Julian/Tuvalian boundary (Hornung et al., 2007). The diversity of Carnian conodonts has been summarized in Chapter 5. Conodont diversity shows a gradual decrease trend in the Julian and reached the minimum value at the base of the Tuvalian. Following this minimum diversity, the middle and late Tuvalian show a higher diversification rate of conodonts and witnessed a dramatical increase of conodont species.

1.2 Paleogeography of the study areas

The Early and Middle Triassic world was characterized by two major distinct longitudinal hemispheres: the Panthalassan Ocean on one side and the continental-influenced hemisphere which was composed of Pangea and the Tethyan Ocean (Fig. 1.2). Except the review paper (Chapter 5), my study concentrates on two distinct zones on the scheme: the Dinaridic-Alpine-Carpathian area and South China. During the Early and Middle Triassic, South China was located on the eastern margin of Tethys, while the Dinaridic-Alpine-Carpathian area was located on the western margin of the Tethys (Michalik, 1994; Mandl, 2000).

The Yangtze platform in South China formed a stable shallow-water carbonates deposition centre from the Late Proterozoic to the end of the Middle Triassic. The Yangtze platform was dominated by shallow water carbonates with intermittent terrigenous influx (Enos et al., 1998). This carbonate platform demised at the transition from the Ladinian to the Carnian due to drowning and covering by dark lime mudstones (Enos et al., 1998; 2006). However, a part of the Yangtze Platform was already drowned during the Permian-Triassic transition producing an enlargement of the adjacent Nanpanjiang basin by 100 km northward (Enos, 1995; Enos et al., 1998). In the Nanpanjiang basin, isolated platforms occurred from the Middle Devonian through the Middle Triassic. South China presents thus Upper Permian to Early Triassic sediments in basinal or slope settings, ranging from the huge Yangtze carbonate platform or from isolated carbonate platforms within the Nanpanjiang basin to basinal environments, and is therefore an ideal region for the study of the end Permian mass extinction and Triassic recovery.

The Early Triassic of the Dinaridic-Alpine-Carpathian area is completely different from the Yangtze platform and thus studies in both regions allow us to compare conodont evolution in two different paleoenvironments. The Dinaridic-Alpine-Carpathian area is characterized by widespread deposition of shallow shelf siliciclastics, containing carbonates in its lowermost and upper parts (Hips & Pelikan, 2002; Ogorelec, 2011). Dinaridic Early Triassic sediments are characterized by terrigenous influx, represented mostly by oolitic and sandy limestones, sandstones and shales (cf. Budurov & Pantić, 1974; Kolar-Jurkovšek, 1990; Kolar-Jurkovšek & Jurkovšek, 1996; Aljinović, 1995; Jelaska et al., 2003). The sedimentary environment was explained as an epeiric ramp (Aljinović et al., in prep.; Chapter 3). Early Triassic conodont and carbonate carbon isotope studies of this specific region and sedimentary environment has been provided in Chapter 3.

During the Middle and early Late Triassic, carbonate sedimentation was prevalent in the area of the Dinaridic-Alpine-Carpathian area, and several successive large carbonate platforms (Gutenstein, Steinalm, Wetterstein) developed (Mandl, 2000). Block faulting and deepening was responsible for the drowning of a part of the Steinalm carbonate platform during the late Pelsonian and early Illyrian. This is the so-called Reifling event which differentiated shallow platforms and basinal areas in the Northern Calcareous Alps (Mandl, 2000). The south-eastern part of the region reached greater depth indicated by the development of basinal facies much earlier in the East. At the western Öfenbachgraben Section (Austria), the platform facies passed into basinal facies during the Pelsonian-Illyrian transitional time, while at the eastern Mendlingbach Section (Austria), the platform facies transform into basinal facies already during the late Pelsonian (see Chapter 4).

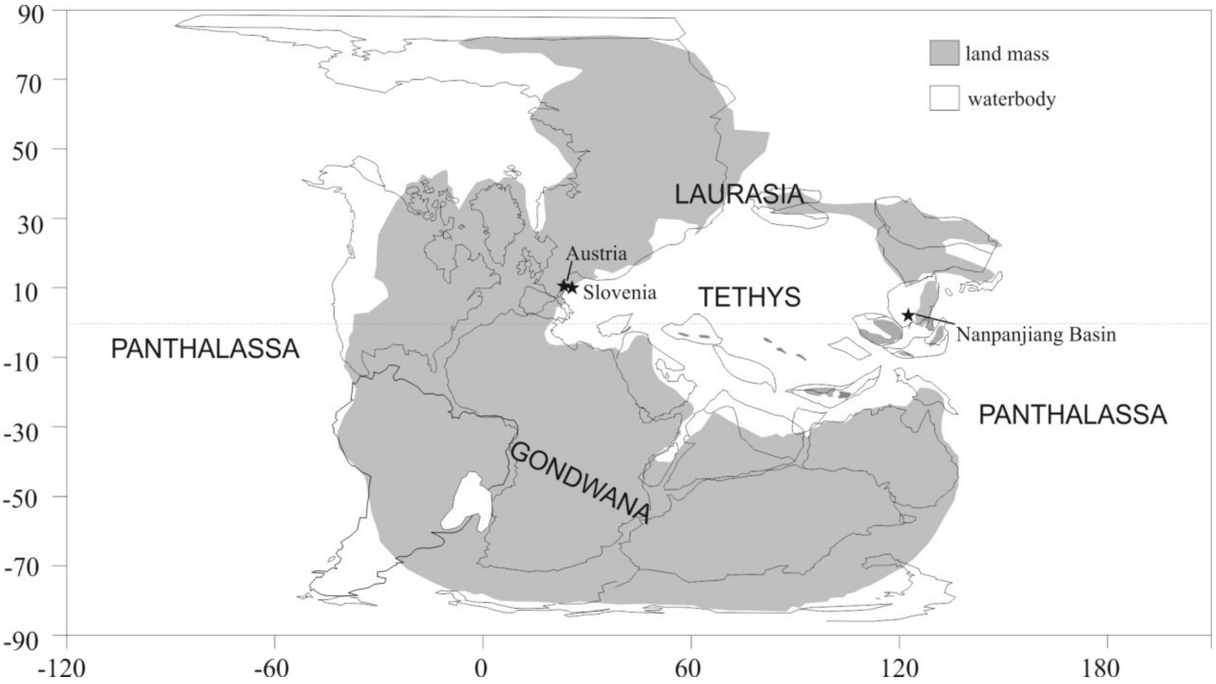

Figure 1.2. Paleogeography of the Olenekian (late Early Triassic) world (after Peron et al., 2005). Asterisks indicate important localities mentioned in the text.

1.3 Introduction to Triassic conodonts

Conodonts are an extinct group of marine eel-like chordates with a feeding apparatus composed of microscopic 'tooth-like' elements (Fig. 1.3), which are probably the known earliest venomous animals on earth (Szaniawski, 2009). Their phosphatic feeding apparatus, which is usually 0.1mm – 4mm in size, can be found in marine sediments with a range from Cambrian to Triassic. Conodonts have proven to be one of the most useful biostratigraphic groups for the Paleozoic to the early Mesozoic: conodonts are one of the fastest evolving fossil groups, are sensitive to environmental stress, and are thus an ideal organism to test ecological responses to past episodes of extinction and climatic change. They possess different advantages: (1) they can be found in marine strata without macrofossils; (2) they bear information for biodiversity and extinction rates (e.g., Orchard, 2007; Stanley, 2009); (3) they are especially suitable for assessing the neodymium isotope ratios, which can serve as indicator of oceanic circulation and continental weathering inputs (Wright et al., 2002); (4) their oxygen stable isotope ratio in apatite can serve as thermometer for paleoseawater, and enables to reconstruct the paleoclimate (e.g., Joachimski & Buggish, 2003; Sun et al., 2012; Romano et al., 2013; Trotter et al., 2015); (5) the colour of conodonts is an indicator for the estimation of the maximum temperature reached by its host rock. Condonts are thus excellent and important for both mining and scientific research.

1.3.1 Shape categories of conodonts

Conodonts can be divided into three main groups which are coniform (simple cones), ramiform (bars) and pectiniform (blades, plates, platforms) (Sweet, 1988), and all these groups are present in the Triassic. A conodont apparatus composed of these conodonts forms is located in the mouth and throat of the conodont animal (e.g., Purnell et al., 2000). Pectiniform (P_1 and P_2) elements occupy a position in the throat of the conodont animal, while the M and S elements occupy a position in the mouth (Purnell et al., 2000). There have only been four types of conodont apparatuses throughout the Earth's history and consist of either 14, 15, 17 or 19 elements (Agematsu et al., 2008; Aldridge et al., 2013). Most of the known Triassic apparatuses consisted of 15 elements (e.g. Orchard and Rieber, 1999; Koike, 2004; Orchard, 2005; Goudemand et al., 2012; Agematsu et al., 2014): paired P_1, P_2, S_1, S_2, S_3, S_4, M and unpaired S_0. One single known exception is the apparatus of the Spathian genus *Neostrachanognathus* which is suggested to be composed of only 14 elements: paired P_1, P_2, P_3, S_1, S_2, S_3, and S_4 (Agematsu et al., 2008).

The conodont taxonomy system was largely based on P_1 elements, due to both taphonomic and historical reasons. P_1 elements are normally the most robust elements of an apparatus and are thus the most easily preserved and recovered elements in sediments. For a long time, conodont workers did not realize that a single conodont animal can bear many elements, and each element morphotype was believed to belong to a different individual and was thus named as different species (Lai and Swift 2002). Since the recognition of a conodont apparatus composed of multi-elements, species defined by S and M elements were abandoned and only the one based on P_1 elements was kept.

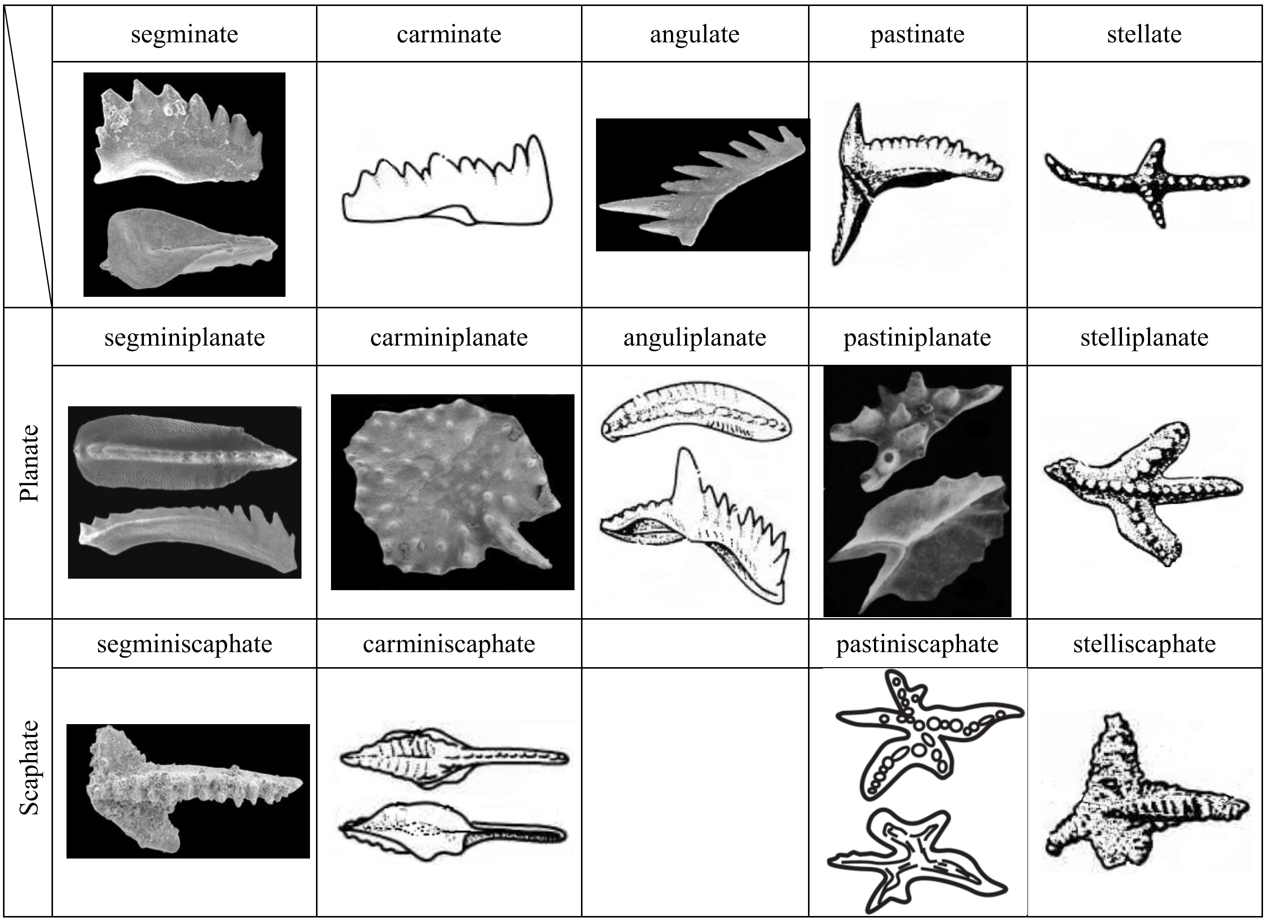

Figure 1.3. Shape categories of pectiniform conodonts (after Sweet, 1988). Figures with black background are Triassic conodonts. Pastiniplanate conodonts are re-illustrated from Solien (1979); the angulate conodont was obtained from Troistedt section, Germany; the carminiplanate conodont from Plavno Section, Croatia; the segminate and segminiscaphate conodonts from Guizhou Province, South China; the segminiplanate conodont from Mendlingbach Section, Austria.

Based on the number of primary processes, the development of lateral platform, the position and size of basal cavity, pectiniform elements can be divided into 7 catogries: segminate, carminate, angulate, pastinate, stellate, planate, scaphate (Sweet, 1988). The first five categories can be then combined with the last two catogries and form sub-categories such as: segminiplanate, segminiscaphate, carminiplanate, carminiscaphate, anguliplanate, pastiniplanate, pastiniscaphate, stelliplanate and stelliscaphate (Fig. 1.3).

1) Segminate elements are characterized by a well-developed anterior process and a badly developed posterior process. Those elements were usually located in the posterior part of the throat which has been noted now as P_1 position;

2) Carminate elements have both well-developed anterior and posterior processes, and has a basal cavity or basal pit located on the middle part of the unit. These elements were usually located in the posterior part of the throat and noted as P_1 position;

3) Angulate elements is arched and have well developed anterior processes and a less well-developed posterior process. Well-developed elements of his category has a very narrow furrow on the lower side of the unit; the basal pit is not prominent and sometimes cannot even be observed. These elements were usually located in the anterior part of the throat and noted as P_2 position.

4) Pastinate has two anterior processes and one posterior process. These elements were usually located in the posterior part of the throat and noted as P_1 position.

5) Stellate has four processes, including anterior, posterior and two lateral processes. These elements were usually located in the posterior part of the throat and noted as P_1 position.

6) Planate has relatively well-developed platform and its basal cavity reduced to a narrow keel and groove. The basal pit is usually small and deep and sometimes can not even be observed.

7) Scaphate elements also have well-developed platform. Its basal cavity is not reduced but is capacious.

1.3.2 Conodont biostratigraphy of the Triassic

Historically, ammonoids are the main tool for worldwide Triassic stratigraphic correlations, but nowadays, due to its high abundance in marine sediments, conodonts become the major fossil group for global correlation. The Early Triassic conodont biostratigraphy has been well documented from the middle-eastern Tethys and Panthalassa, and most reviews on Early Triassic conodont biostratigraphy neglect the European fauna (e.g., Sweet et al., 1971; Lai & Mei, 2000; Kozur, 2003; Fig. 1.1). Kozur (1973) already noticed that provincialism during the early Triassic raised major difficulties to propose a standard conodont zonation for the Early Triassic globally. Sections in the Idrija–Žiri area (Chapter 3) contain unusual high numbers of conodont elements for the Early Triassic western Tethys. This allowed for the first time to establish a detailed conodont biostratigraphy for the late Induan-Olenekian in the Idrija–Žiri area. This new zonation allows correlation within central and southern Europe.

The Induan-Olenekian transitional interval is characterized by a worldwide recognizable peak value of $\delta^{13}C$ (e.g., Payne et al., 2004; Richoz, 2006; Horacek et al., 2007). And the Smithian-Spathian transitional interval is characterized by a drastic positive excursion of $\delta^{13}C$ values documented worldwide, followed by a peak value and a subsequent gradual decreasing trend in the early Spathian (e.g., Payne et al., 2004; Richoz, 2006; Horacek et al., 2007). Due to lack of Early Triassic ammonoids in the Idrija–Žiri area, the carbonate stable carbon isotopes (Fig. 1.1) have been a useful tool for the recognition of substage and allow a rough correlation with South China, which is one of the regions with the best documented Early Triassic conodont biostratigraphy in the world.

The Early Triassic conodont diversity and evolutionary lineages have been well summarized by Orchard (2007). This time interval was characterized by a highly diversified conodont fauna and fast evolution rates which makes conodonts favourable for high resolution biostratigraphy. On the contrary, the Middle Triassic conodonts present a period of slow evolutionary rates and domination of similar segminiplanate conodonts (Fig. 1.1; Fig. 1.3). Many conodont morpho-species were recognized for these segminiplanate forms but as they are very similar to each other, their validity has been questioned. Moreover, the population variability has never been statistically tested. To provide basis for the revision of the taxonomic system of the Middle Triassic segminiplanate conodonts and to promote a better understanding of the Middle and early Late Triassic conodont biostratigraphy, a geometric morphometric analysis has been carried out (Chapter 4) to analyse the allometry of segminiplanate conodont P_1 elements. This lead us to synonymise three species. Based on the taxonomic revision, and due to new statistic methods and multi-elements apparatus reconstruction, a review of all the Middle and early Late Triassic conodonts (Chapter 5) has been carried out.

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CHAPTER 2

SIZE VARIATION OF CONODONTS DURING THE SMITHIAN–SPATHIAN (EARLY TRIASSIC) GLOBAL WARMING EVENT

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Abstract

Final recovery of marine ecosystems after the end-Permian mass extinction took several million years, partly due to inhospitable environments and three episodes of further extinction that occurred during the Early Triassic: in the late Griesbachian, near the Smithian-Spathian boundary (SSB), and in the late Spathian. The SSB crisis coincides with an episode of extreme warmth, but has been little studied. This study represents the first stratigraphic and paleoecological analysis of the SSB crisis in the Nanpanjiang Basin, south China, which is a key area for Permian–Triassic studies. A comprehensive, high-resolution stratigraphic framework comprising six conodont zones is provided. Conodonts are an extinct group of marine chordates with a feeding apparatus composed of microscopic “tooth-like” elements. They are one of the fastest-evolving fossil groups, sensitive to environment stress, and are thus an ideal organism to test ecological responses to past episodes of climatic change. Detailed size measurements of 441 conodont elements of the closely related genera Neospathodus, Triassospathodus, and Novispathodus show for the first time that this clade suffered a temporary, but significant, size reduction during the SSB crisis, followed by gradual and steady size increase during the early Spathian. Size reduction of conodonts was caused by an episode of global warming, further strengthening the link between morphological and climatic changes recorded in the fossil record.

2.1. Introduction

The end-Permian mass extinction is believed to be the most severe biodiversity crisis in the history of life (Erwin, 2006). Immediately after the extinction, many marine taxa suffered a temporary but dramatic size reduction (i.e., the "Lilliput Effect"), and a significant reduction in burrow diameters demonstrates that infaunal organisms were also affected (e.g., Twitchett, 2007). Compiled data show that recovery from the end-Permian mass extinction was not a smooth process, but included several episodes of environmental disturbance (Payne et al., 2004), and three further episodes of extinction affected conodonts and ammonoids: (1) in the late Griesbachian, ~0.5 m.y. after the Permian-Triassic boundary (PTB); (2) near the Smithian-Spathian boundary (SSB), ~1.8 m.y. post-PTB; and (3) in the late Spathian, ~5 m.y. post-PTB (Stanley, 2009; Brayard et al., 2009). These events are associated with extreme hothouse conditions (Sun et al., 2012). However, the body size changes associated with these climatic events, and the subsequent biotic recovery, have received little study. Furthermore, although many studies of the Permian and Triassic strata in the Nanpanjiang Basin, south China (Fig. 2.1), have shown that area to be critical in understanding the end-Permian mass extinction and recovery (e.g., Lehrmann, 1999; Payne et al., 2004; Sun et al., 2012), no studies have defined the SSB in that region or documented the associated SSB crisis in detail.

To address these issues, we provide the first quantitative assessment of conodont size variation through this interval, based on the study of the Jiarong section in the Nanpanjiang Basin. Size is a key paleoecological criterion in understanding the ecological, environmental, and biological change during the extinction (Twitchett, 2006), and conodonts are one of the fastestevolving fossil groups, sensitive to environment stress (Stanley, 2009). Our statistical analyses, which are supported by a novel, high-resolution biostratigraphic framework, reveal new paleoecological information on the SSB event and advance our understanding of why the recovery from the PTB crisis took so long.

2.2. Geological setting

The Nanpanjiang Basin was situated on the southern margin of the carbonate Yangtze Platform, a vast area of shallow-marine deposits that stretches across much of the South China Block (Lehrmann, 1999). The Great Bank of Guizhou is the northernmost isolated platform in the Nanpanjiang Basin. Lower Triassic strata are well developed and well exposed throughout the basin, including at the study site at Jiarong (Fig. 2.1). The Jiarong section is situated a few hundred meters away from the center of Jiarong town, next to the asphalt road from Guiyang to Luodian County. During the Early Triassic, it was located in the north of the Nanpanjiang

Basin embayment, approximately midway between the Yangtze Platform and the Great Bank of Guizhou (Fig. 2.1). The Jiarong succession includes, in ascending order, the Upper Permian Dalong Formation, the Lower Triassic Luolou and Ziyun Formations, and the Middle Triassic Xinyuan and Bianyang Formations. The Luolou Formation is ~230 m thick locally. Microfacies analyses of thin sections indicate that the depositional environments of the Smithian and Spathian range from foreslope to basin. The SSB transitional beds belong to a basinal facies, suggesting a low-energy depositional environment.

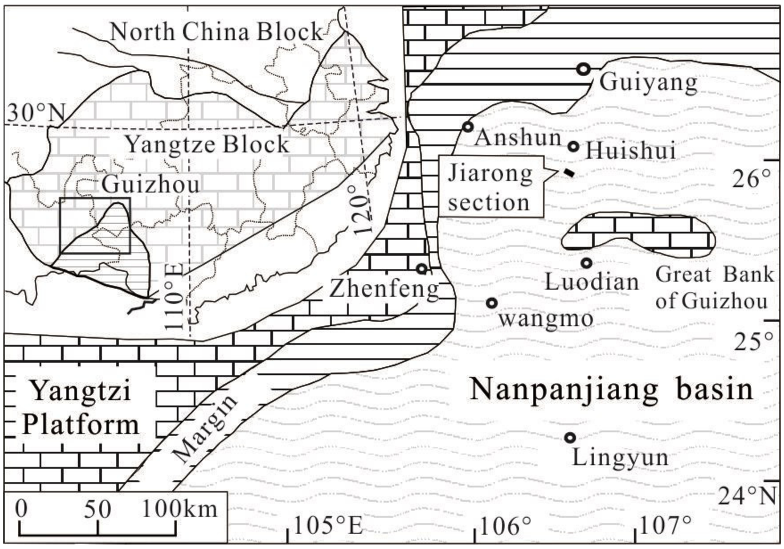
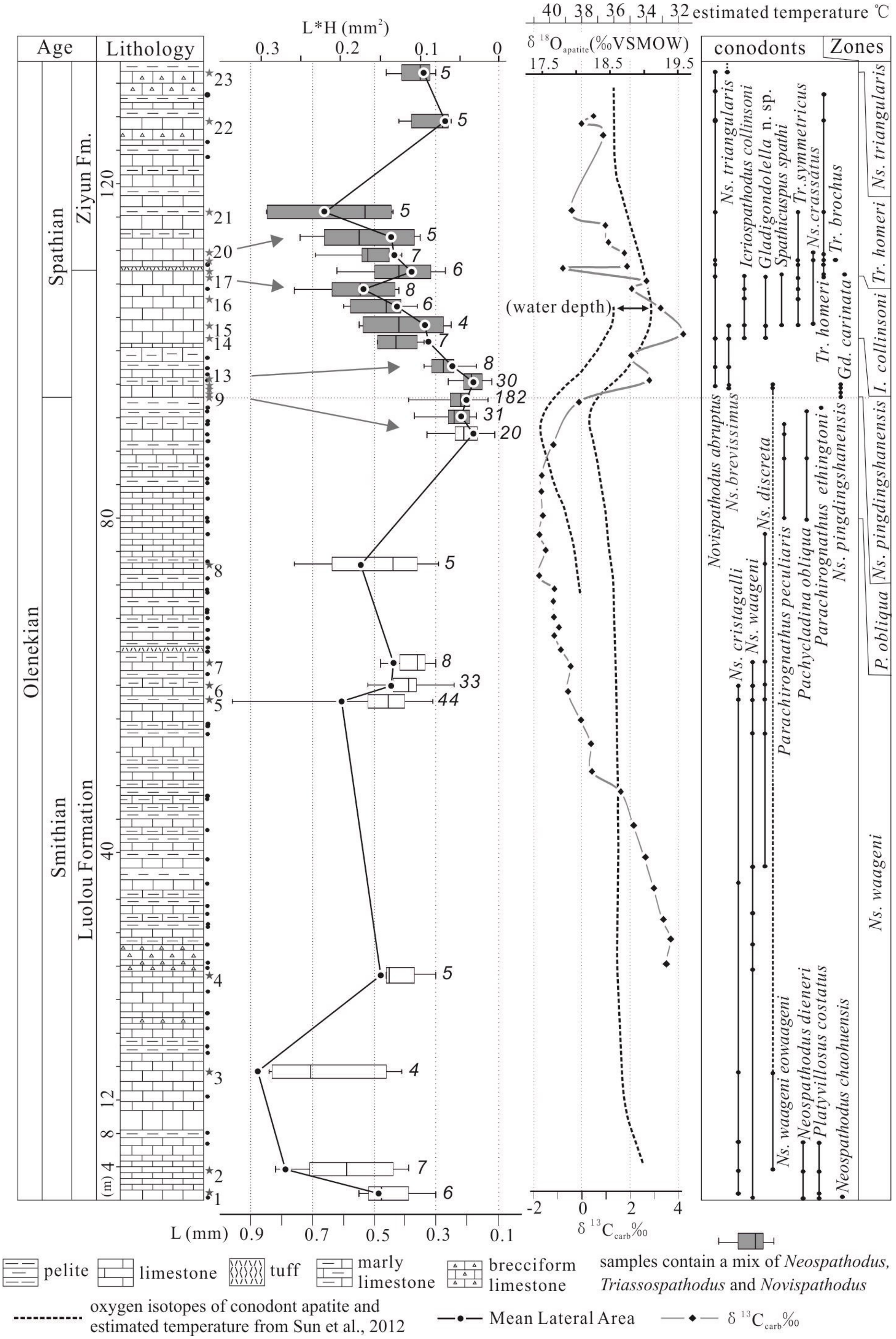


Figure 2.1. Early Triassic paleogeographic reconstruction and the location of the Jiarong section, south China (after Payne et al., 2004).

2.3. Method and materials

A well-exposed and easily accessible section was measured; this section spans the Smithian to Spathian substages (Olenekian, Lower Triassic). A total of 81 rock samples, of ~3–5 kg each, were collected and processed by acetic acid dissolution. The residues were picked for conodont elements, and 1057 were obtained. Most samples comprise *Neospathodus*, *Triassospathodus*, and *Novispathodus*, with a small quantity of *Neogondolella*, *Gladigondolella*, *Pachycladina*, and *Parachirognathus* elements. The 23 samples with the most abundant *Neospathodus*, *Triassospathodus*, and *Novispathodus* P1 elements were selected for conodont size analysis (Fig. 2.2). These genera are combined together because *Triassospathodus* and *Novispathodus* are thought to have originated from *Neospathodus pingdingshanensis* during the early Spathian (Orchard, 2007). The remaining samples, containing fewer than four P1 elements of these genera, were not included in the statistical analysis in order to minimize potential error. In this study, the length (L) of the basal part of



Age
Lithology
Olenekian
Spathian
Smithian
Ziyun Fm.
Luolou Formation
(m)
4
8
12
40
80
120
L*H (mm²)
0.3
0.2
0.1
0
L (mm)
0.9
0.7
0.5
0.3
0.1
1
2
3
4
5
6
7
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13
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21
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23
6
7
4
5
44
33
8
5
20
31
182
30
8
7
4
6
8
6
7
5
5
5
5
(water depth)
estimated temperature ℃
40
38
36
34
32
δ ¹⁸O apatite (‰VSMOW)
17.5
18.5
19.5
δ ¹³C carb ‰
-2
0
2
4
conodonts
Zones
Novispathodus abruptus
Ns. triangularis
Ns. brevissimus
Icriospathodus collinsoni
Gladigondolella n. sp.
Spathicuspus spathi
Tr. symmetricus
Ns. crassatus
Tr. brochus
Tr. homeri
Gd. carinata
Ns. pingdingshanensis
Parachirognathus ethingtoni
Pachycladina obliqua
Parachirognathus peculiaris
Ns. discreta
Ns. waageni
Ns. cristagalli
Ns. waageni eowaageni
Neospathodus dieneri
Platyvillosus costatus
Neospathodus chaohuensis
Ns. triangularis
Tr. homeri
I. collinsoni
Ns. pingdingshanensis
P. obliqua
Ns. waageni
pelite
limestone
tuff
marly limestone
brecciform limestone
samples contain a mix of Neospathodus, Triassospathodus and Novispathodus
oxygen isotopes of conodont apatite and estimated temperature from Sun et al., 2012
Mean Lateral Area
δ ¹³C carb ‰

← **Figure 2.2**. Stratigraphy, sample horizons, conodont ranges, size variation of conodont P1 elements, and carbonate isotope data at the Jiarong section, south China. A black dot or a star indicates a sampled horizon; 23 numbered stars show the samples chosen for statistical size analysis; the first nine samples only contain *Neospathodus*. For each sample, the 25%–75% quartiles of length (L) are shown by a box; the vertical line inside each box shows the median value; and the maximum and minimum values are shown as short vertical lines to the left or right of the box, respectively. The number on the right side of the box indicates the amount of conodont P1 elements. Isotope data δ13Ccarb, δ18Oapatite (‰ VSMOW, Vienna standard mean ocean water), and estimated temperatures are from Sun et al. (2012). *Gd.* = *Gladigondolella*; *I.* = *Icriospathodus*; *Ns.* = *Neospathodus*; *P.* = *Pachycladina*; *Tr.* = *Triassospathodus*.

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these P1 elements was used as a size proxy (Fig. 2.3). We also measured the height (H) of each conodont, which was combined with the length to estimate an approximate lateral area (LA ≈ L × H) of each conodont.

2.4. Results

Six conodont zones were newly established at the Jiarong section, each zone defined by a first-occurrence datum (FOD). *Ns. pingdingshanensis* was used as a guide fossil for the SSB in Chaohu (Liang et al., 2011), and so we define the SSB by the FOD of *Ns. pingdingshanensis* at the Jiarong section (Fig. 2.2). In the individual samples from the *Ns. waageni* zone, the median size (L) of *Neospathodus* P1 elements ranges from 0.36 mm to 0.70 mm (Fig. 2.2, samples 1–8). In the *Ns. pingdingshanensis* zone samples, however, the median size of *Neospathodus*, *Triassospathodus*, and *Novispathodus* P1 elements declined to 0.21–0.27 mm (Fig. 2.2, samples 9–13). In the *I. collinsoni*, *Tr. homeri*, and *Ns. triangularis* zones, the median size is 0.35–0.55 mm (Fig. 2.2, samples 14–23). The smallest sizes are restricted to the *Ns. pingdingshanensis* zone. It appears that conodont size fluctuates through the study interval, with relatively small sizes recorded in other samples also (e.g., samples 4, 7, 22, and 23). It should be noted, however, that these data are from samples with relatively few specimens, and absolute sizes are not as small as those of the *Ns. pingdingshanensis* zone (for a more detailed data set, see the GSA Data Repository1).

Taphonomic biases, such as hydrodynamic sorting during transportation, might lead to micromorphic fossil assemblages. In the present study, transportation can be ruled out for the following reasons: (1) there are no fragments of larger-sized elements in any of the *Ns.*

pingdingshanensis zone samples, (2) the sedimentological facies indicate a low-energy depositional setting, and (3) small-sized *Ns. pingdingshanensis* were also recognized from the Chaohu section of the Yangtze Platform (Liang et al., 2011), indicating that the size reduction probably represents at least a regional phenomenon.

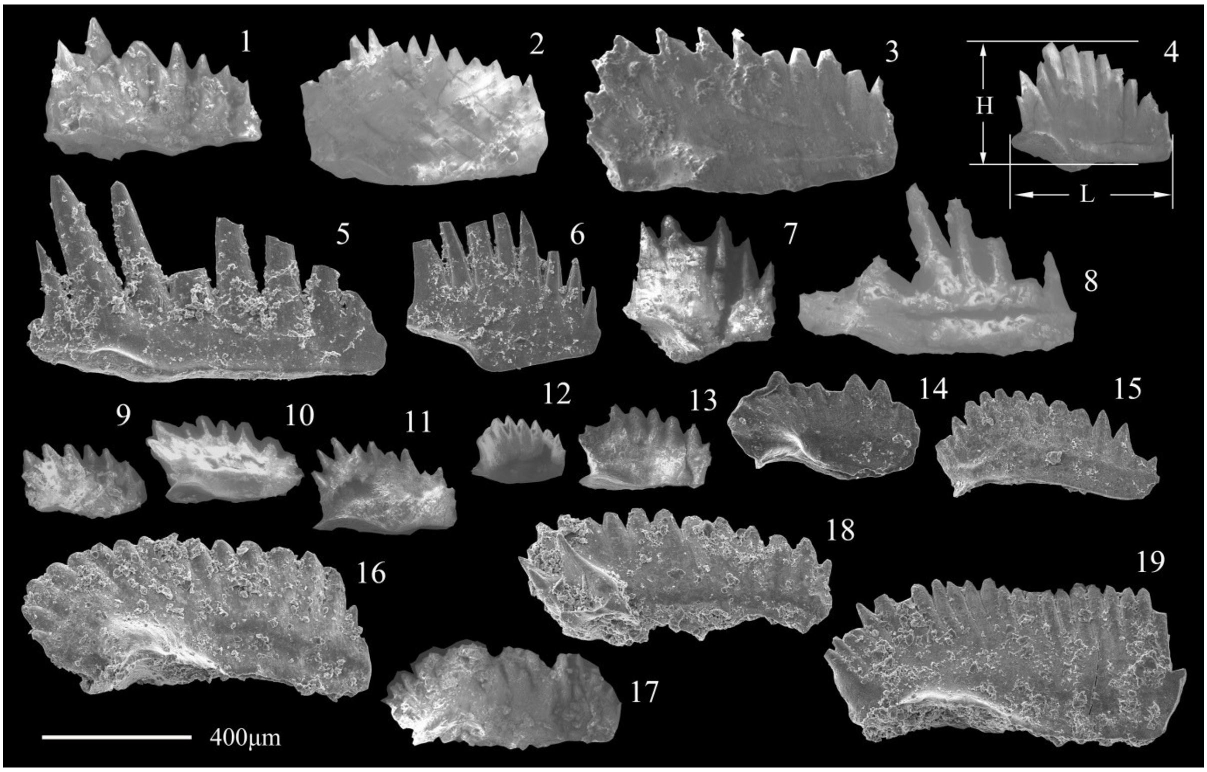

Figure 2.3. Conodont P1 elements recovered from Jiarong section, south China. Note: Specimens 9–13 represent the largest individual specimens from samples 9–13, respectively (Fig. 2.2). 1 and 6—*Neospathodus cristagalli* (Huckriede, 1958), 1, sample 1 (n-1); 6—n-6; 2 and 11—*Neospathodus waageni eowaageni* Zhao and Orchard 2007, 2, n-2; 3—*Neospathodus posterolongatus* Zhao and Orchard 2007, 3, n-3; 4 and 7—*Neospathodus waageni* Sweet 1970, 4, n-4; 7—n-7; 5 and 8—*Neospathodus discreta* (Müller, 1956), 5, n-5; 8—n-8; 9–10 and 12–13—*Neospathodus pingdingshanensis* Zhao and Orchard 2007; 14, 16, and 19—*Novispathodus abruptus* (Orchard, 1995), 14, n-14; 16—n-17; 19—n-21; 15 and 18—*Neospathodus crassatus* (Orchard, 1995), 15, n-15; 18—n-20; 17—*Triassospathodus homeri* (Bender, 1970), n-18. L and H are length and height of conodonts, respectively.

No *Neospathodus* P1 elements were discovered from the uppermost Smithian (Fig. 2.2), confirming results from the Chaohu section (Zhao et al., 2007, their figures 1 and 2). The absence of *Neospathodus* below the SSB coincides with the largest conodont extinction event of the Triassic (Orchard, 2007) and the late Smithian ammonoid extinction (Brayard et al., 2009). These extinctions are likely a response to the Late Smithian Thermal Maximum (e.g., Sun et al., 2012).

The abundance of conodont P1 elements varies considerably between samples. Highest abundance is recorded in a sample from the *Ns. pingdingshanensis* zone, which also records size reduction (Fig. 2.2, sample 11). As first noted by Urbanek (1993), one characteristic of Lilliput taxa is that they typically occur in high abundance during the immediate postextinction interval. *Ns. pingdingshanensis* are characterized in Jiarong, as well as in Chaohu (Zhao et al., 2007), by large populations and short stratigraphic range and can be thus considered as opportunistic species (Levinton, 1970). Blooms of opportunists characterize the immediate aftermaths of small-scale biotic crises and of mass extinction events (e.g., Twitchett, 2007), and indicate that communities were controlled by physical, rather than biotic, factors (Levinton, 1970).

2.5. Discussion

A number of previous studies have recorded size change in marine groups following the end-Permian mass extinction, including in fish (Mutter and Neuman, 2009), conodonts (Luo et al., 2008), brachiopods (He et al., 2010; Metcalfe et al., 2011), and gastropods (Metcalfe et al., 2011). The temporary postextinction size reduction of surviving taxa (i.e., the Lilliput Effect; Urbanek, 1993) is confined to the first conodont zone or two of the Induan (Twitchett, 2007; Metcalfe et al., 2011), although a general depression of body size is recorded in many groups through most of the Early Triassic.

One group that suffered size reduction through the Permian–Triassic transition was the *Hindeodus-Isarcicella* conodont clade (Luo et al., 2008). The fluctuations in element size recorded by those taxa at that time are, however, of much smaller magnitude than those recorded by *Neospathodus* during the SSB crisis. This may reflect differences in the conodont taxa involved, but most probably reflects the relative importance of the two extinction intervals for conodonts given that the late Smithian represents the most severe conodont extinction of the Triassic (Orchard, 2007). Conodont elements formed the feeding apparatus of an otherwise soft-bodied marine chordate (Sweet and Donoghue, 2001), and the relationship between element size and total body size is not known. The assumption is that larger elements derive from larger conodont animals. In marine organisms, small size can be linked to biotic factors such as decrease of primary production, loss of symbiotic associations, or general biotic stress (Wade and Twitchett, 2009). On the other hand, it can also be linked to physical factors, including oceanic anoxia, global warming, sea-level changes, salinity changes, and oxygen levels (e.g., Twitchett, 2007; Luo et al., 2008; Wade and Twitchett, 2009).

The SSB transition is characterized by a short-lived climatic warming event during the latest Smithian, as inferred from ammonoid distribution patterns, which suggest a flat seasurface temperature gradient from pole to equator (Galfetti et al., 2007), and from oxygen isotope data from conodont apatite (Sun et al., 2012). This inferred warming episode occurs as δ^{13}Ccarb values are rising rapidly from their low in the Smithian to a peak in the earliest Spathian (Fig. 2.2) (Payne et al., 2004; Richoz, 2006; Sun et al., 2012).

Small-sized conodonts appear after the peak warming (Fig. 2.2), which potentially indicates that the temperature had dropped just below the upper thermal tolerances of *Neospathodus*, *Triassospathodus*, and *Novispathodus*. It appears that global warming, or associated physical effects, were probably the main cause of the latest Smithian absence of *Neospathodus* and the earliest Spathian size reduction. There are two possible ways that global warming, directly or indirectly, could result in a size reduction in conodont animals. First, being ectothermic organisms, they would have had relatively low metabolic rates in colder conditions. When temperatures increased, their metabolic and ontogenetic rates would have increased (cf. Clarke and Fraser, 2004), and if all other factors (e.g., oxygen, food) remained equal, they would tend to be smaller (Sheridan and Bickford, 2011). Second, a warm climate during the SSB transition would have caused a reduction in the amount of oxygen dissolved in seawater (cf. Sheridan and Bickford, 2011), which would have been exacerbated by stratified oceans (e.g., Isozaki, 1997). Lack of oxygen would have reduced individual growth and development directly linked to body size (Sheridan and Bickford, 2011).

2.6. Implications

This study has implications for predicting the ecological responses of organisms to other climate-related crises, past and present. It provides further evidence that those marine organisms that survive episodes of global warming typically record a temporary decrease in body size in the aftermath of the event, coincident with high temperatures and associated environmental changes such as the expansion of hypoxic conditions discussed above. This ecological response appears to be independent of skeletal mineralogy and is recorded in chordates, such as conodonts (this study) and fish (Mutter and Neuman, 2009), invertebrates with phosphatic or calcium carbonate skeletons (e.g., He et al., 2010; Metcalfe et al., 2011), and lightly skeletonized or soft-bodied benthos (Twitchett, 2007). In contrast, climatic cooling is associated with larger body sizes in many marine organisms, for example in Cenozoic planktonic foraminifera (Schmidt et al., 2004). The size increase of the conodonts during the early Spathian recorded at Jiarong may thus reflect a cooler, better-oxygenated ocean as conditions returned to normal following the SSB biotic crisis. Reversals in this general trend, such as the sudden size decrease in the upper *Tr. homeri* zone (Fig. 2.2), may indicate other transient warming events in the later Early Triassic, but these data need to be confirmed with more specimens and studies from other localities. While it may be possible to predict the direction of climate-related size change in marine organisms, predicting the magnitude of change in any one group is currently more problematic.

2.7. Acknowledgments

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Note:

Appendix 2.1 Length of conodonts (mm)

Appendix 2.2 Height of conodonts (mm)

*Appendix 2.3 Lateral Area of conodonts (LA≈L*H, square of mm)*

Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length of conodonts (mm)	0,44	0,56	0,84	0,3	0,42	0,34	0,36	0,44	0,14	0,32	0,22	0,19	0,27	0,34	0,49	0,43	0,64	0,43	0,69	0,55	0,84	0,34	0,34
	0,42	0,82	0,8	0,45	0,42	0,38	0,3	0,43	0,21	0,17	0,2	0,2	0,34	0,49	0,35	0,57	0,43	0,62	0,45	0,58	0,44	0,42	0,36
	0,55	0,44	0,61	0,46	0,37	0,35	0,36	0,76	0,2	0,19	0,36	0,14	0,25	0,36	0,55	0,36	0,62	0,27	0,52	0,74	0,45	0,25	0,46
	0,3	0,39	0,41	0,44	0,41	0,49	0,48	0,29	0,27	0,25	0,2	0,12	0,32	0,43	0,25	0,48	0,54	0,33	0,53	0,39	0,85	0,28	0,3
	0,5	0,59		0,46	0,49	0,24	0,43	0,51	0,23	0,25	0,2	0,14	0,17	0,49		0,44	0,43	0,41	0,41	0,35	0,53	0,27	0,35
	0,51	0,63			0,51	0,45	0,33		0,21	0,26	0,24	0,21	0,29	0,45		0,6	0,55	0,46	0,46				
		0,71			0,42	0,46	0,38		0,21	0,25	0,19	0,19	0,24	0,36			0,44		0,54				
					0,38	0,4	0,35		0,15	0,19	0,17	0,25	0,28				0,76						
					0,41	0,37			0,33	0,29	0,14	0,21											
					0,46	0,35			0,19	0,24	0,16	0,26											
					0,46	0,48			0,27	0,25	0,18	0,24											
					0,35	0,51			0,18	0,22	0,26	0,19											
					0,54	0,46			0,25	0,37	0,27	0,26											
					0,54	0,39			0,24	0,29	0,23	0,22											
					0,37	0,42			0,18	0,34	0,21	0,21											
					0,42	0,5			0,14	0,24	0,25	0,16											
					0,46	0,37			0,16	0,26	0,16	0,15											
					0,35	0,38			0,11	0,27	0,23	0,17											
					0,4	0,38			0,21	0,23	0,26	0,22											
					0,54	0,39			0,23	0,2	0,2	0,19											
					0,33	0,36				0,23	0,28	0,14											
					0,48	0,4				0,24	0,18	0,21											
					0,46	0,39				0,17	0,23	0,14											
					0,55	0,4				0,18	0,19	0,15											
					0,85	0,36				0,24	0,16	0,18											
					0,59	0,38				0,18	0,19	0,16											
					0,41	0,34				0,19	0,17	0,15											
					0,52	0,38				0,23	0,25	0,16											
					0,4	0,43				0,19	0,15	0,17											
					0,44	0,52				0,2	0,16	0,18											
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					0,44	0,4					0,21												
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Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length of conodonts (mm)					0,96						0,27												
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Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length of conodonts (mm)											0,21												
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Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length of conodonts (mm)											0,25												
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Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Length of conodonts (mm)											0,18												
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Appendix 2.1 Length of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
N	6	7	4	5	44	33	8	5	20	31	182	30	8	7	4	6	8	6	7	5	5	5	5
Min	0,3	0,39	0,41	0,3	0,31	0,24	0,3	0,29	0,11	0,17	0,13	0,12	0,17	0,34	0,25	0,36	0,43	0,27	0,41	0,35	0,44	0,25	0,3
Max	0,55	0,82	0,84	0,46	0,96	0,52	0,48	0,76	0,33	0,37	0,39	0,26	0,34	0,49	0,55	0,6	0,76	0,62	0,69	0,74	0,85	0,42	0,46
Sum	2,72	4,14	2,66	2,11	20,7	13,24	2,99	2,43	4,11	7,33	40,8	5,56	2,16	2,92	1,64	2,88	4,41	2,52	3,6	2,61	3,11	1,56	1,81
Mean	0,45	0,59	0,67	0,42	0,47	0,401	0,37	0,49	0,21	0,24	0,22	0,185	0,27	0,42	0,41	0,48	0,55	0,42	0,514	0,52	0,62	0,31	0,36
Std. error	0,04	0,06	0,1	0,03	0,02	0,01	0,02	0,08	0,01	0,01	0	0,007	0,02	0,02	0,07	0,04	0,04	0,05	0,034	0,07	0,09	0,03	0,03
Variance	0,01	0,02	0,04	0	0,01	0,003	0	0,03	0	0	0	0,001	0	0	0,02	0,01	0,01	0,01	0,008	0,02	0,04	0	0
Stand. dev	0,09	0,15	0,2	0,07	0,12	0,058	0,06	0,17	0,05	0,05	0,05	0,038	0,05	0,06	0,14	0,09	0,12	0,12	0,091	0,16	0,21	0,07	0,06
Median	0,47	0,59	0,71	0,45	0,46	0,39	0,36	0,44	0,21	0,24	0,22	0,185	0,28	0,43	0,42	0,46	0,55	0,42	0,52	0,55	0,53	0,28	0,35
25 prcntil	0,39	0,44	0,46	0,37	0,4	0,365	0,34	0,36	0,17	0,19	0,19	0,15	0,24	0,36	0,28	0,41	0,43	0,32	0,45	0,37	0,45	0,26	0,32
75 prcntil	0,52	0,71	0,83	0,46	0,52	0,44	0,42	0,64	0,24	0,26	0,25	0,21	0,31	0,49	0,54	0,58	0,64	0,5	0,54	0,66	0,85	0,38	0,41
Skewness	-1,05	0,14	-0,77	-2,16	2,31	0,072	0,9	1,03	0,36	0,89	0,42	0,382	-0,74	-0,02	-0,28	0,22	0,59	0,68	1,2	0,34	0,49	1,18	1,38
Kurtosis	1,1	-0,5	-1,41	4,7	7,58	0,922	0,64	2,01	0,36	0,74	0,36	-0,64	1,09	-2,16	-2,73	-1,16	-0,41	1,01	2,045	-0,92	-3,19	0,55	2,82
Geom. mean	0,45	0,58	0,64	0,42	0,46	0,397	0,37	0,46	0,2	0,23	0,22	0,182	0,27	0,41	0,39	0,47	0,54	0,41	0,508	0,5	0,6	0,31	0,36

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of	0,31	0,38	0,48	0,3	0,38	0,26	0,36	0,34	0,15	0,21	0,19	0,17	0,22	0,17	0,26	0,24	0,39	0,26	0,22	0,25	0,4	0,23	0,23
conodonts	0,31	0,57	0,44	0,37	0,38	0,34	0,34	0,36	0,14	0,19	0,17	0,16	0,23	0,21	0,16	0,31	0,26	0,29	0,24	0,27	0,34	0,27	0,24
(mm)	0,33	0,34	0,53	0,35	0,31	0,24	0,34	0,45	0,15	0,18	0,24	0,14	0,19	0,18	0,25	0,17	0,32	0,24	0,26	0,32	0,24	0,19	0,33
	0,26	0,31	0,34	0,37	0,41	0,31	0,4	0,27	0,16	0,2	0,18	0,12	0,26	0,2	0,21	0,26	0,29	0,25	0,25	0,21	0,41	0,18	0,22
	0,36	0,42		0,36	0,46	0,24	0,38	0,29	0,15	0,18	0,15	0,14	0,15	0,18		0,25	0,24	0,21	0,23	0,22	0,3	0,2	0,28
	0,34	0,51			0,43	0,45	0,33		0,18	0,18	0,17	0,2	0,2	0,27		0,33	0,29	0,31	0,24				
		0,44			0,4	0,42	0,37		0,17	0,23	0,14	0,18	0,2	0,3			0,27		0,36				
					0,34	0,49	0,33		0,16	0,22	0,17	0,25	0,28				0,37						
					0,43	0,27			0,2	0,19	0,16	0,19											
					0,49	0,23			0,18	0,2	0,15	0,21											
					0,45	0,39			0,19	0,23	0,17	0,21											
					0,35	0,54			0,16	0,19	0,19	0,19											
					0,57	0,42			0,19	0,24	0,16	0,22											
					0,44	0,32			0,16	0,22	0,18	0,18											
					0,32	0,36			0,14	0,19	0,2	0,2											
					0,38	0,29			0,13	0,23	0,19	0,17											
					0,44	0,32			0,15	0,24	0,14	0,15											
					0,35	0,31			0,11	0,25	0,2	0,18											
					0,38	0,41			0,13	0,22	0,24	0,18											
					0,44	0,27			0,17	0,18	0,16	0,17											
					0,42	0,38				0,23	0,21	0,14											
					0,49	0,33				0,21	0,15	0,22											
					0,45	0,24				0,19	0,16	0,1											
					0,56	0,35				0,18	0,15	0,14											
					0,49	0,31				0,19	0,18	0,18											
					0,39	0,27				0,21	0,15	0,16											
					0,21	0,2				0,18	0,14	0,16											
					0,48	0,34				0,22	0,21	0,17											
					0,32	0,39				0,19	0,13	0,17											
					0,38	0,43				0,17	0,13	0,16											
					0,31	0,27				0,19	0,16												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of conodonts (mm)					0,36	0,27					0,16												
					0,45	0,37					0,17												
					0,26						0,16												
					0,37						0,19												
					0,39						0,17												
					0,48						0,19												
					0,56						0,19												
					0,39						0,16												
					0,5						0,19												
					0,37						0,15												
					0,31						0,2												
					0,51						0,15												
					0,43						0,2												
											0,19												
											0,19												
											0,23												
											0,2												
											0,23												
											0,18												
											0,2												
											0,17												
											0,19												
											0,21												
											0,15												
											0,17												
											0,16												
											0,21												
											0,19												
											0,14												
											0,2												
											0,19												
											0,15												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of conodonts (mm)											0,19												
											0,22												
											0,17												
											0,22												
											0,2												
											0,16												
											0,17												
											0,29												
											0,17												
											0,17												
											0,23												
											0,21												
											0,15												
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											0,19												
											0,16												
											0,21												
											0,21												
											0,16												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of conodonts (mm)											0,2												
											0,19												
											0,17												
											0,22												
											0,21												
											0,14												
											0,21												
											0,2												
											0,21												
											0,23												
											0,23												
											0,16												
											0,13												
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											0,18												
											0,2												
											0,16												
											0,18												
											0,17												
											0,21												
											0,18												
											0,17												
											0,18												
											0,15												
											0,14												
											0,18												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of conodonts (mm)											0,18												
											0,2												
											0,19												
											0,17												
											0,17												
											0,14												
											0,2												
											0,22												
											0,19												
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											0,18												
											0,16												
											0,2												
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											0,2												
											0,17												
											0,21												
											0,17												
											0,19												
											0,2												
											0,15												
											0,19												
											0,19												
											0,18												
											0,2												
											0,13												
											0,15												
											0,15												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Highness of conodonts (mm)											0,18												
											0,2												
											0,15												
											0,17												
											0,2												
											0,17												
											0,11												
											0,17												
											0,2												
											0,2												
											0,19												
											0,16												
											0,21												
											0,23												
											0,13												
											0,18												
											0,25												
											0,25												
											0,23												
											0,2												
											0,18												
											0,18												
											0,18												

Appendix 2.2 Height of conodonts (mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
N	6	7	4	5	44	33	8	5	20	31	182	30	8	7	4	6	8	6	7	5	5	5	5
Min	0,26	0,31	0,34	0,3	0,21	0,2	0,33	0,27	0,11	0,17	0,11	0,1	0,15	0,17	0,16	0,17	0,24	0,21	0,22	0,21	0,24	0,18	0,22
Max	0,36	0,57	0,53	0,37	0,57	0,54	0,4	0,45	0,2	0,25	0,29	0,25	0,28	0,3	0,26	0,33	0,39	0,31	0,36	0,32	0,41	0,27	0,33
Sum	1,9	2,96	1,79	1,75	18	11	2,83	1,71	3,15	6,27	33,2	5,19	1,72	1,51	0,88	1,56	2,42	1,55	1,8	1,26	1,68	1,07	1,29
Mean	0,32	0,42	0,45	0,35	0,41	0,33	0,35	0,34	0,16	0,2	0,18	0,17	0,22	0,22	0,22	0,26	0,3	0,26	0,26	0,25	0,34	0,21	0,26
Std. error	0,01	0,03	0,04	0,01	0,01	0,01	0,01	0,03	0	0	0	0,01	0,01	0,02	0,02	0,02	0,02	0,01	0,02	0,02	0,03	0,02	0,02
Variance	0	0,01	0,01	0	0,01	0,01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stand. dev	0,04	0,09	0,08	0,03	0,08	0,08	0,03	0,07	0,02	0,02	0,03	0,03	0,04	0,05	0,04	0,06	0,05	0,04	0,05	0,04	0,07	0,04	0,05
Median	0,32	0,42	0,46	0,36	0,41	0,32	0,35	0,34	0,16	0,2	0,18	0,17	0,21	0,2	0,23	0,25	0,29	0,25	0,24	0,25	0,34	0,2	0,24
25 prcntil	0,29	0,34	0,37	0,32	0,36	0,27	0,33	0,28	0,14	0,19	0,16	0,15	0,19	0,18	0,18	0,22	0,26	0,23	0,23	0,21	0,27	0,19	0,22
75 prcntil	0,34	0,51	0,51	0,37	0,46	0,39	0,38	0,4	0,18	0,22	0,2	0,19	0,25	0,27	0,26	0,32	0,36	0,29	0,26	0,29	0,4	0,25	0,3
Skewness	-0,8	0,51	-0,9	-1,66	-0,1	0,6	0,57	0,75	-0,06	0,28	0,41	0,09	-0	1,1	-0,82	-0,5	0,64	0,05	2,26	0,95	-0,4	1,34	1,33
Kurtosis	1,17	-0,53	0,89	2,8	0,09	0,01	-1	0,34	0,14	-1,3	0,71	0,6	0,4	-0,12	-1,09	0,31	-0,6	-0,1	5,49	0,43	-1,2	1,05	0,87
Geom. mea	0,31	0,41	0,44	0,35	0,4	0,32	0,35	0,34	0,16	0,2	0,18	0,17	0,21	0,21	0,22	0,25	0,3	0,26	0,25	0,25	0,33	0,21	0,26

Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lateral Area	0,14	0,21	0,4	0,09	0,16	0,09	0,13	0,15	0,02	0,07	0,04	0,03	0,06	0,06	0,13	0,1	0,25	0,11	0,15	0,14	0,33	0,08	0,08
of	0,13	0,52	0,35	0,17	0,16	0,13	0,1	0,15	0,03	0,03	0,03	0,03	0,08	0,1	0,06	0,18	0,11	0,18	0,11	0,15	0,15	0,11	0,08
conodonts	0,18	0,15	0,32	0,16	0,12	0,08	0,12	0,34	0,03	0,03	0,09	0,02	0,05	0,06	0,14	0,06	0,2	0,06	0,14	0,23	0,11	0,05	0,15
(square of	0,08	0,12	0,14	0,16	0,17	0,15	0,19	0,08	0,04	0,05	0,04	0,01	0,08	0,09	0,05	0,12	0,16	0,08	0,13	0,08	0,35	0,05	0,07
	0,22	0,25		0,17	0,23	0,06	0,16	0,15	0,04	0,05	0,03	0,02	0,02	0,09		0,11	0,1	0,08	0,09	0,08	0,16	0,05	0,1
	0,17	0,32			0,22	0,2	0,11		0,04	0,05	0,04	0,04	0,06	0,12		0,2	0,16	0,14	0,11				
		0,31			0,17	0,19	0,14		0,03	0,06	0,03	0,03	0,05	0,11			0,12		0,19				
					0,13	0,2	0,12		0,02	0,04	0,03	0,06	0,08				0,28						
					0,18	0,1			0,07	0,05	0,02	0,04											
					0,23	0,08			0,03	0,05	0,02	0,05											
					0,21	0,19			0,05	0,06	0,03	0,05											
					0,12	0,28			0,03	0,04	0,05	0,04											
					0,31	0,19			0,05	0,09	0,04	0,06											
					0,24	0,12			0,04	0,06	0,04	0,04											
					0,12	0,15			0,03	0,06	0,04	0,04											
					0,16	0,15			0,02	0,06	0,05	0,03											
					0,2	0,12			0,02	0,06	0,02	0,02											
					0,12	0,12			0,01	0,07	0,05	0,03											
					0,15	0,15			0,03	0,05	0,06	0,04											
					0,24	0,11			0,04	0,04	0,03	0,03											
					0,14	0,14				0,05	0,06	0,02											
					0,24	0,13				0,05	0,03	0,05											
					0,21	0,09				0,03	0,04	0,01											
					0,31	0,14				0,03	0,03	0,02											
					0,42	0,11				0,04	0,03	0,03											
					0,23	0,1				0,04	0,03	0,02											
					0,09	0,07				0,03	0,02	0,02											
					0,25	0,13				0,05	0,05	0,03											
					0,13	0,17				0,04	0,02	0,03											
					0,17	0,22				0,03	0,02	0,03											
					0,11	0,11				0,04	0,03												
					0,16	0,1					0,03												

Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lateral Area					0,2	0,15					0,04												
of					0,08						0,02												
conodonts					0,19						0,04												
(square of					0,2						0,04												
					0,25						0,05												
					0,54						0,05												
					0,14						0,03												
					0,27						0,05												
					0,21						0,03												
					0,13						0,04												
					0,28						0,03												
					0,2						0,05												
											0,05												
											0,04												
											0,06												
											0,05												
											0,06												
											0,05												
											0,04												
											0,04												
											0,05												
											0,05												
											0,02												
											0,03												
											0,03												
											0,05												
											0,04												
											0,02												
											0,06												
											0,05												
											0,03												
											0,05												

Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lateral Area of conodonts (square of											0,04												
											0,04												
											0,07												
											0,05												
											0,02												
											0,03												
											0,11												
											0,03												
											0,04												
											0,05												
											0,04												
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Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

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Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

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Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

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Appendix 2.3 Lateral Area of conodonts (L*A≈LH, square of mm)

sample no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
N	6	7	4	5	44	33	8	5	20	31	182	30	8	7	4	6	8	6	7	5	5	5	0,07
Min	0,08	0,12	0,14	0,09	0,08	0,06	0,1	0,08	0,01	0,03	0,01	0,01	0,02	0,06	0,05	0,06	0,1	0,06	0,09	0,08	0,11	0,05	0,15
Max	0,22	0,52	0,4	0,17	0,54	0,28	0,19	0,34	0,07	0,09	0,11	0,06	0,08	0,12	0,14	0,2	0,28	0,18	0,19	0,23	0,35	0,11	0,48
Sum	0,91	1,88	1,21	0,75	8,73	4,5	1,07	0,87	0,66	1,5	7,61	0,99	0,48	0,63	0,37	0,77	1,37	0,66	0,93	0,68	1,1	0,34	0,1
Mean	0,15	0,27	0,3	0,15	0,2	0,14	0,13	0,17	0,03	0,05	0,04	0,03	0,06	0,09	0,09	0,13	0,17	0,11	0,13	0,14	0,22	0,07	0,02
Std. error	0,02	0,05	0,06	0,01	0,01	0,01	0,01	0,04	0	0	0	0	0,01	0,01	0,02	0,02	0,02	0,02	0,01	0,03	0,05	0,01	0
Variance	0	0,02	0,01	0	0,01	0	0	0,01	0	0	0	0	0	0	0	0	0	0	0	0	0,01	0	0,03
Stand. dev	0,05	0,13	0,11	0,03	0,08	0,05	0,03	0,1	0,01	0,01	0,01	0,01	0,02	0,02	0,04	0,05	0,07	0,04	0,03	0,06	0,11	0,03	0,08
Median	0,15	0,25	0,34	0,16	0,19	0,13	0,12	0,15	0,03	0,05	0,04	0,03	0,06	0,09	0,09	0,12	0,16	0,1	0,13	0,14	0,16	0,05	0,07
25 prcntil	0,12	0,15	0,18	0,13	0,14	0,1	0,11	0,11	0,02	0,04	0,03	0,02	0,05	0,06	0,05	0,09	0,11	0,08	0,11	0,08	0,13	0,05	0,12
75 prcntil	0,19	0,32	0,39	0,17	0,23	0,16	0,16	0,25	0,04	0,06	0,05	0,04	0,08	0,11	0,13	0,18	0,23	0,15	0,15	0,19	0,34	0,1	1,7
Skewness	-0,36	1,11	-1,5	-2,2	1,92	0,83	1,08	1,59	0,84	0,87	1,04	0,64	-0,6	-0,3	0,03	0,22	0,68	0,78	1,05	0,9	0,49	1,47	3,09
Kurtosis	-0,02	1,58	2,5	4,83	5,81	0,81	0,44	3,4	1,46	1,12	3,41	0,01	-0,2	-1,2	-5,7	-0,9	-0,8	-0,5	1,14	0,41	-3	1,52	0,09
Geom. mean	0,14	0,24	0,28	0,15	0,18	0,13	0,13	0,16	0,03	0,05	0,04	0,03	0,06	0,09	0,09	0,12	0,16	0,1	0,13	0,12	0,2	0,06	

CHAPTER 3

EARLY TRIASSIC CONODONTS AND CARBONATE CARBON ISOTOPE RECORD OF THE IDRIJA-ŽIRI AREA, SLOVENIA

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Abstract

The first recovery of the conodont *Hindeodus parvus* from Žiri area (Slovenia) a few years ago highlights the area for Early Triassic biostratigraphical study. Systematic sampling of five sections in Idrija–Žiri area has resulted in the discovery of new species: *Platyvillosus corniger* sp. nov. and *Neospathodus planus* sp. nov. Based on these new species and other conodont elements obtained from these sections, nine discrete conodont Unitary Association (UA) zones are proposed for this area. In ascending order they are: *Eurygnathodus hamadai* Zone (UA 1), *Eurygnathodus costatus* Zone (UA 2), *Foliella gardenae* Zone (UA 3), *Neospathodus robustus* Zone (UA 4), *Platyvillosus corniger* Zone (UA 5), *Platyvillosus regularis* Zone (UA 6), *Triassospathodus hungaricus* Zone (UA 7), *Triassospathodus symmetricus* Zone (UA 8), and *Neospathodus robustispinus* Zone (UA 9). The conodont and $\delta^{13}C$ data indicate that these conodonts span the Dienerian/Smithian (i.e. Induan/Olenekian) boundary interval to Spathian, and they also indicate that *Triassospathodus hungaricus* Zone (UA 7) does not occur on the base of the Spathian. These conodont zones are valuable for stratigraphic correlation within Central and South Europe, and they also promote a better correlation worldwide. Conodonts in the Idrija–Žiri area adapted to a shallow water environment in an epeiric ramp.

3.1. Introduction

The Early Triassic was a prolonged interval of recovery from the Late Permian mass extinction (e.g., Twitchett, 1999; Erwin et al., 2002) due to inhospitable marine environments (Payne et al., 2004; Sun et al., 2012) along with at least three smaller-scale extinction events (Stanley, 2009; Brayard et al., 2009). These small-scale extinction events have been documented based on both the ammonoid and conodont faunas: in the late Griesbachian, late Smithian, and late Spathian (Stanley, 2009; Brayard et al., 2009). The Smithian-Spathian transition was characterized by a climatic warming event (Galfetti et al., 2007; Sun et al., 2012; Romano et al., 2013), coupled with a rapid positive shift of $\delta^{13}C_{carb}$ values (Payne et al., 2004; Richoz, 2006) and a reduction in conodont element size in South China and northeastern Vietnam (Chen et al., 2013; Maekawa & Komatsu, 2014).

Conodonts are an excellent group for stratigraphic purposes because they exhibit several advantages: (1) they can be found from marine strata without macrofossils; (2) they bear information on biodiversity and extinction rates (e.g., Orchard, 2007; Stanley, 2009); (3) and their oxygen isotope ratio in apatite can serve as a thermometer for paleoseawater (e.g., Sun et al., 2012; Romano et al., 2013).

The earliest report on upper Induan and Olenekian (Early Triassic) conodonts was in 1956 in Nevada (USA), and the new species *Scythogondolella milleri* (Müller); *Discretella discreta* (Müller); *Conservatella conservativa* (Müller) were described for the first time (Müller, 1956). Then, in 1964, Olenekian conodonts were first reported from Central Europe; new species such as *Eurygnathodus costatus* Staesche, *Pachycladina obliqua* Staesche, *Pachycladina lata* Staesche were described from Werfen Formation, northern Italy (Staesche, 1964). With further study, *Triassospathodus symmetricus* (Orchard) (see Perri, 1986, pl.1, fig. 1a-e) and *Icriospathodus crassatus* (Orchard) (see Perri & Andraghetti, 1987, pl. 33, figs. 1-5) were also reported from the same area. Some European conodonts differ considerably from those in North America, western Pakistan (Sweet, 1970a), Kashmir (Sweet, 1970b) and South China (e.g., Zhao et al., 2008; Wang et al., 2005). The difference is reflected in species such as *Novispathodus waageni* (Sweet), *Scythogondolella milleri*, and *Icriospathodus collinsoni* (Solien), which have never been reported in Central-South Europe, although they are markers for Early Triassic conodont zones (Solien, 1979; Sweet et al., 1971; Kozur, 2003). *Triassospathodus hungaricus* (Kozur & Mostler) is the only species that was first discovered from Central Europe (Kozur & Mostler, 1970) and has featured in a global conodont zonation of the Triassic (Kozur, 2003). In the type locality in Felsöörs, Hungary, this species co-occurs with the lowermost Spathian ammonoid *Tirolites* (Kozur & Mostler, 1970). *Tr. hungaricus* has been further documented only from Sichuan Province, South China (Tian et al., 1983), western USA (Lucas & Orchard, 2007), and the Dinarides (Kolar-Jurkovšek et al. 2013; 2014).

In the last decade, Triassic stratigraphers and paleontologists have devoted great efforts to establish the Global Stratotype Section and Point (GSSP) for the base of the Olenekian Stage. The M04 section near Mud in northern India and the Chaohu Section in South China are proposed as the candidates for this GSSP (Krystyn et al., 2007; Tong et al., 2004), and these two sections are intensively studied and well documented for upper Induan and Olenekian conodont biostratigraphy. Comparatively, the Central European sections are less studied for the upper Induan and Olenekian interval. The recent discovery of *Hindeodus parvus* (Kozur & Pjatakova) from the Permian-Triassic interval beds in the Žiri area, Slovenia (Kolar-Jurkovšek & Jurkovšek, 2007), highlights this area for Early Triassic conodont biostratigraphical studies. Compared to other sections of the Dinaridic-Alpine-Carpathian area, the Idrija-Žiri area is relatively abundant in conodonts. The Induan has been previously described in detail (Kolar-Jurkovšek et al. 2011a, b), and here we document the younger conodonts from the Dienerian/Smithian (i.e. Induan/Olenekian) transitional interval to the Spathian (Olenekian). The present data indicate that the Idrija-Žiri area could serve as a key area for Early Triassic paleontological and biostratigraphical studies in the western Tethyan margin and provide a better understanding of Early Triassic conodonts in Europe.

3.2. Geological settings

In a wider geotectonic sense, the Idrija-Žiri area is part of the External Dinarides (Fig. 3.1A). All Lower Triassic sections presented in this work are situated in the Trnovo Nappe, which represents the highest nappe unit in this region (Placer, 1981). Carboniferous, Permian and Triassic rocks predominate. The Upper Permian strata belong to the Bellerophon Formation with the Bellerophon Limestone Member in the lower part and the Evaporite-Dolomite Member in the upper part. Evaporite and dolomite are concordantly overlain by different carbonate lithofacies of the Transitional Beds, which contain the first appearance of *Hindeodus parvus* marking the base of the Triassic System (Kolar-Jurkovšek & Jurkovšek, 2007). In Žiri, the Transitional Beds pass into the Streaky Limestone Member and the Carbonate-clastic Member of the Lukač Formation (Kolar-Jurkovšek et al., 2011a, b). The youngest proven conodont zone in this succession is the Induan *Hadrodontina anceps* Zone (Kolar-Jurkovšek et al., 2011a). In the wider Idrija-Žiri area, the uppermost Permian and lowermost Triassic strata can show a slightly different development. The Bellerophon

Limestone Member can lie directly below the Lower Triassic succession, while the Evaporite-dolomite Member is missing. In some other places, the entire succession around the Permian-Triassic boundary is dolomitic (Ogorelec, 2011).

The presence of upper Induan strata has not yet been paleontologically proven. In Slovenia, an interval that comprises reddish shale and sandstone with oolite limestones has been erroneously considered as equivalent to the Induan Seis beds of the Dolomites, but most of this interval actually belongs to the lower Olenekian (Kolar-Jurkovšek, 1990). In a wider area, these Slovenian strata are overlain with limestone and marls that are traditionally compared with the Campil beds of the Dolomites. In their higher part, they contain characteristic Olenekian fauna with prevailing ammonoids belonging to the genera *Tirolites* and *Dinarites* as well as frequent gastropods (*Natiria* and *Turbo*) in association with the foraminifera *Meandrospira pussila* (Ho) (Premoli Silva). Development of the Olenekian strata in the studied sections near Žiri differs significantly from the typical Campil beds and we have therefore assigned them to the informal lithostratigraphic unit, the "Žiri Formation"; this passes upwards into Anisian dolomite.

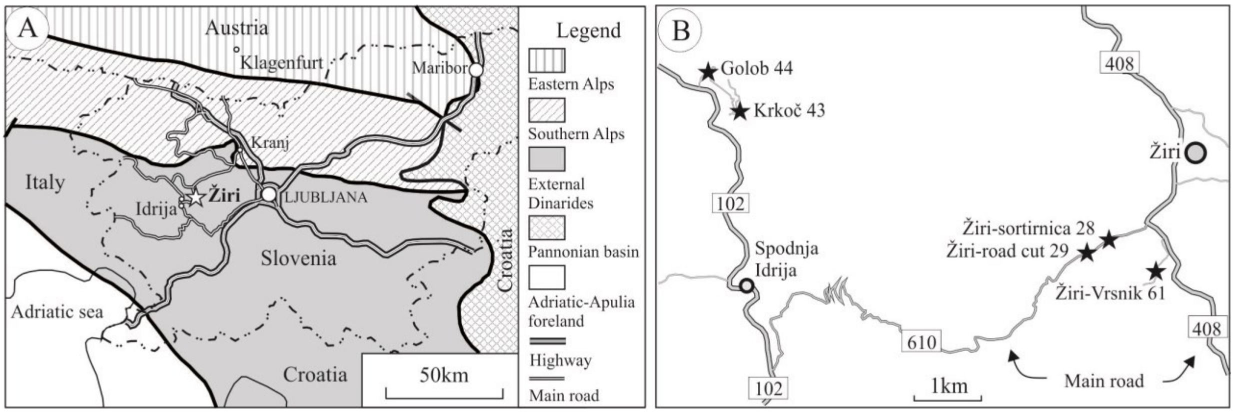


Figure 3.1. Geographic position of the Idrija–Žiri area. A, Geotectonic units in Idrija–Žiri and its adjacent area (after Kolar-Jurkovšek et al., 2011a); B, Locations (asterisks) of studied sections.

In the investigated sections Golob, Žiri road cut 29 and in the lower part of Žiri-Vrsnik 61 (up to the sample 61/10, Fig. 3.1B and 3.2), the "Žiri Formation" is composed of bioclastic packstones or bioclastic/oolitic grainstones which alternate with lime mudstones or silty lime mudstones. Among bioclasts, microgastropods dominate. Ooids are small or middle sized and usually have a very simple fabric (with only one superficial cortex, whereas nuclei are often late diagenetically dolomitized). The only exception is oolitic grainstones in the Žiri-road cut

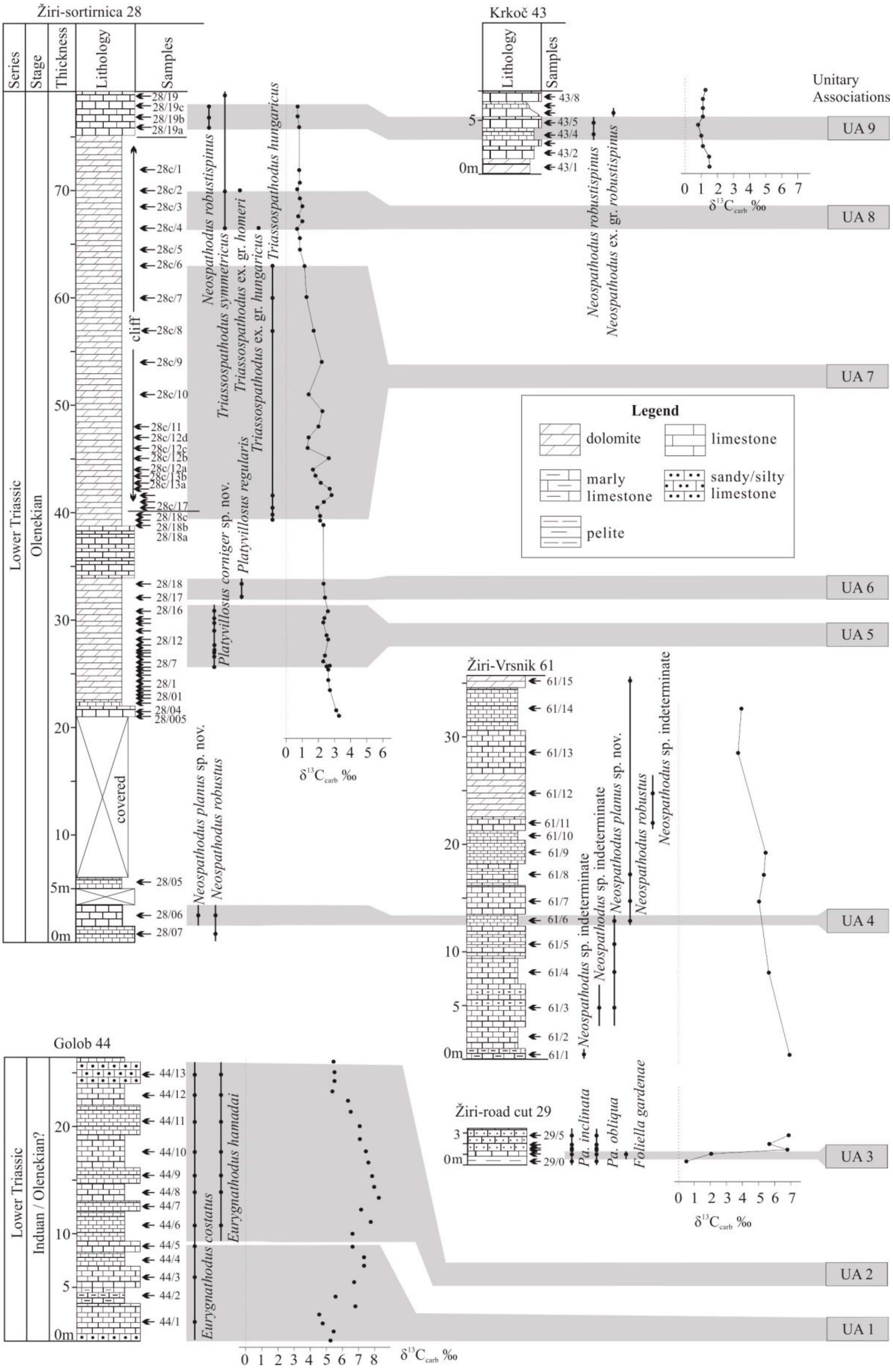


Figure 3.2. Stratigraphic columns, conodont ranges and Unitary Association zones at the sections in the Idrija–Žiri area, Slovenia.

section, which are composed of coarse-grained ooids with well-preserved primary fabric. structure. Various amounts of silty siliciclastic detritus are preserved in laminated varieties. The siliciclastic component consists of well-sorted and poorly rounded quartz and feldspar grains. Hummocky cross stratification, which is a typical storm structure, has been observed in the Golob 44 section. Sandy limestone and pelitic sediments are present in the Žiri-road cut 29 section (Fig. 3.2). These features indicate shallow-water conditions in which the sediments can be disturbed by storms.

In the sections Žiri-Vrisnik (from sample 61/11 to 61/15), Žiri-sortirnica, and Krkoč 43, subhedral planar macro-crystalline dolomite alternate mainly with layers of lime mudstones or dolomitized mudstones. Textural characteristics of dolomite suggest dolomitization in the burial phase. In the homogeneous lime mudstones, numerous foraminifera tests can be preserved. Only at the beginning of the Žiri-sortirnica 28 section (samples 28/05, 28/06 and 28/07) and at the topmost part of Krkoč 43 section, grainy limestone varieties occur. Middle-grain-sized oolitic detritus is poorly preserved due to intensive recrystallization. Micrite preserved in the oolitic packstones suggests reworking of primary detritus. During the Dienerian-Smithian, this area is recognized as having been a sedimentary environment similar to an epeiric ramp (Aljinović et al., in preparation). The epeiric ramp model is characterized by hundreds of kilometers of lateral extension, very low slope angles (< 1°), water depths of a few tens of meters, storm influences and nearshore currents (Lukasik et al., 2000; Aljinović et al., in preparation).

3.3. Materials and methods

3.3.1. Conodont sampling and extraction

Five sections were investigated (Fig. 3.1B), and 94 carbonate samples weighing *ca.* 2.5 kg were collected, as shown in Figure 3.2. The lower part of Žiri-sortirnica 28 section begins with coordinates 46° 2'22.03"N; 14° 5'47.42"E, is located on a stream and 3 samples were collected; the upper part of this section begins with coordinates 46° 2'20.17"N; 14° 5'47.94"E, is located in an abandoned quarry and 51 samples were collected. Strata between these two parts are covered by waste separation facilities. 15 samples were collected from the Žiri-Vrsnik 61 section (46° 2'8.89"N; 14° 6'23.09"E); 5 samples from the Žiri-road cut 29 section (46° 2'11.98"N; 14° 5'24.05"E); 8 samples from the Krkoč 43 section (46° 3'40.16"N; 14° 1'24.17"E); and 15 samples from the Golob 44 section (46° 3'47.21"N; 14° 0'59.29"E).

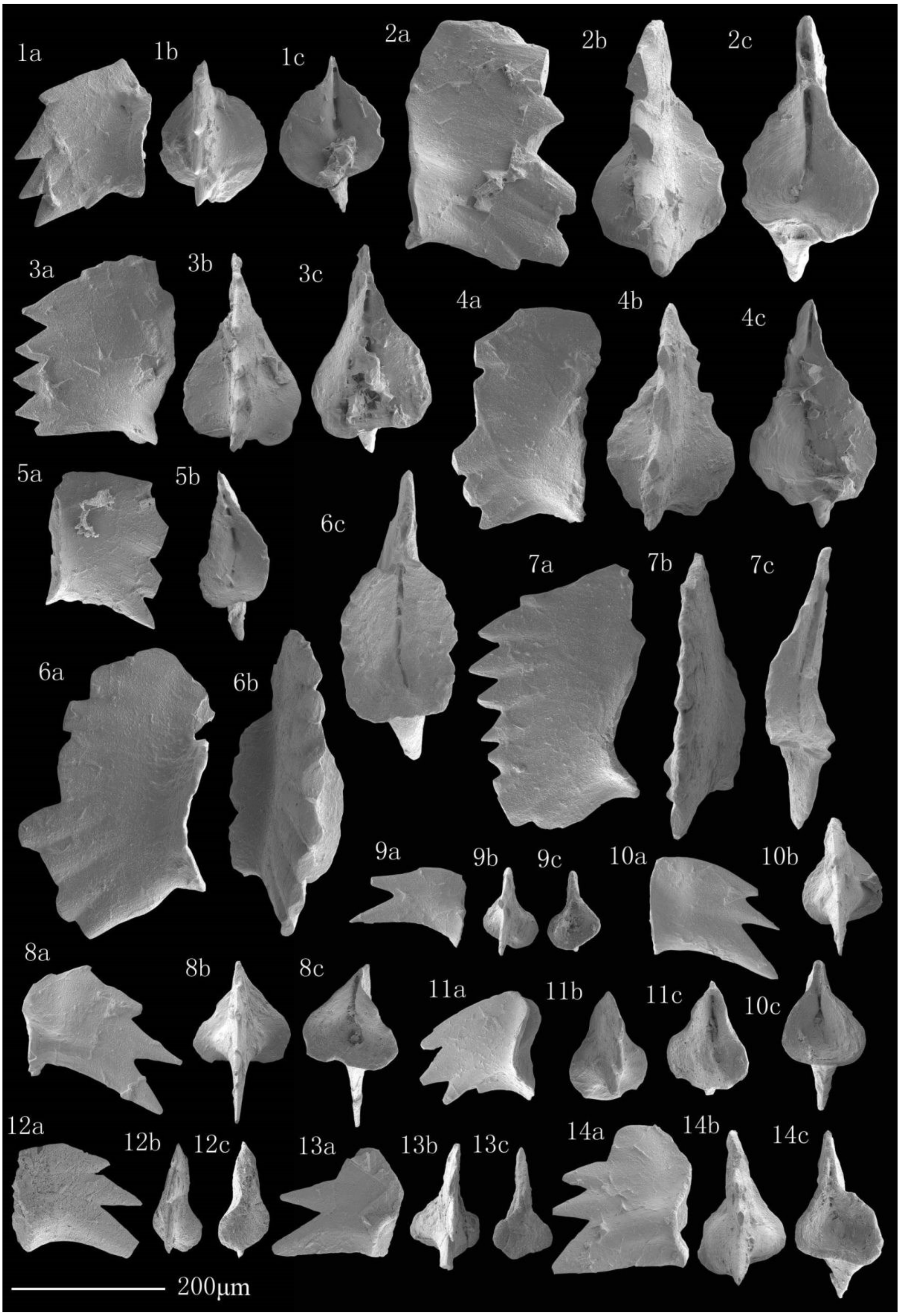


Figure 3.3. SEM photos of conodonts obtained from the Žiri-sortirnica 28 section. 1–5, *Neospathodus robustispinus* Zhao and Orchard, 1–4 from sample 28/19c, 5 sample 28/19b. 6–7 *Triassospathodus symmetricus* (Orchard), sample 28/19. 8–10, 12–14, *Triassospathodus hungaricus* (Kozur & Mostler), sample 28/18c. 11, *Neospathodus* ex. gr. *curtus* (Dagis), sample 28/18c. Scale bar = 200μm; a, lateral view; b, upper view; c, lower view.

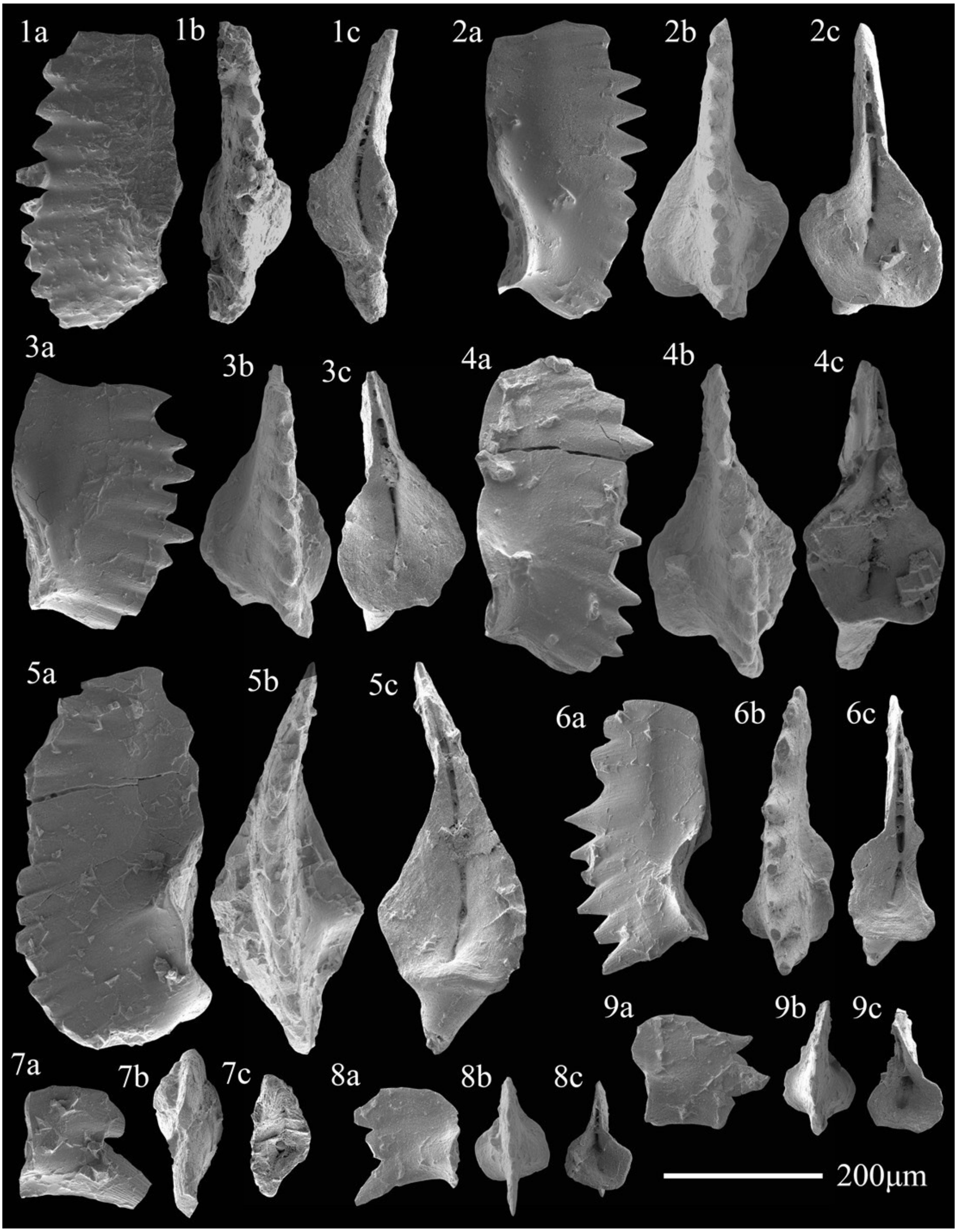


Figure 3.4. SEM photos of conodonts obtained from the Žiri-sortirnica 28 section. 1, *Triassospathodus* ex. gr. *homeri* (Bender), sample 28c/2. 2–6, *Triassospathodus symmetricus* (Orchard), sample 28c/4. 7, *Triassospathodus* ex. gr. *hungaricus* (Kozur & Mostler), sample 28c/4. 8–9, *Triassospathodus hungaricus* (Kozur & Mostler), sample 28c/6. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

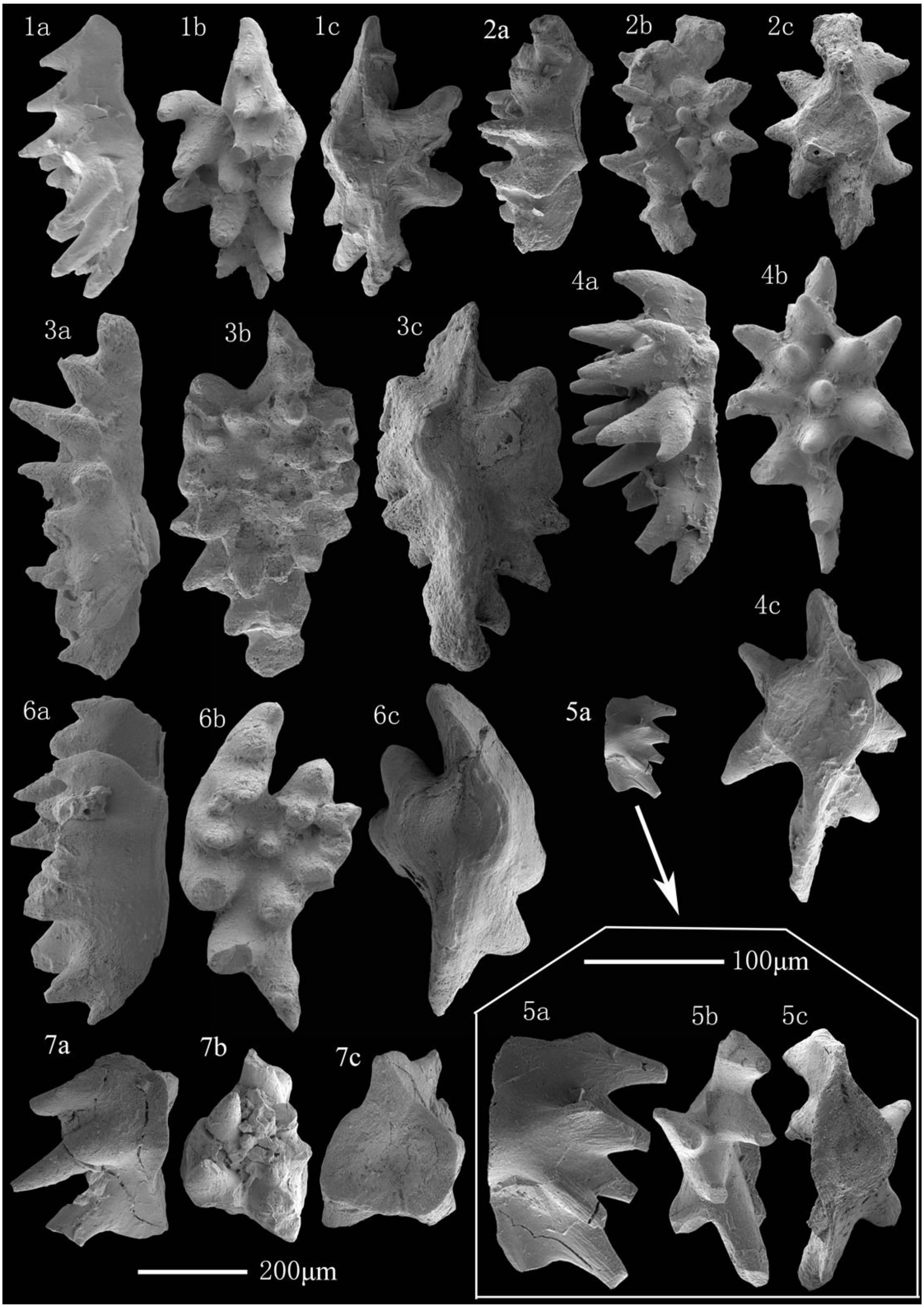


Figure 3.5. SEM photos of conodonts obtained from the Žiri-sortirnica 28 section. 1–4, *Platyvillosus regularis* (Budurov & Pantić), 1–3 sample 28/18, 4 sample 28/17. 5–7, *Platyvillosus corniger* sp. nov. Kolar-Jurkovšek & Chen, 5–6 sample 28/15, 7 sample 28/9. Scale bar of left side = 200μm; scale bar of right side = 100μm; a, lateral view; b, upper view; c, lower view.

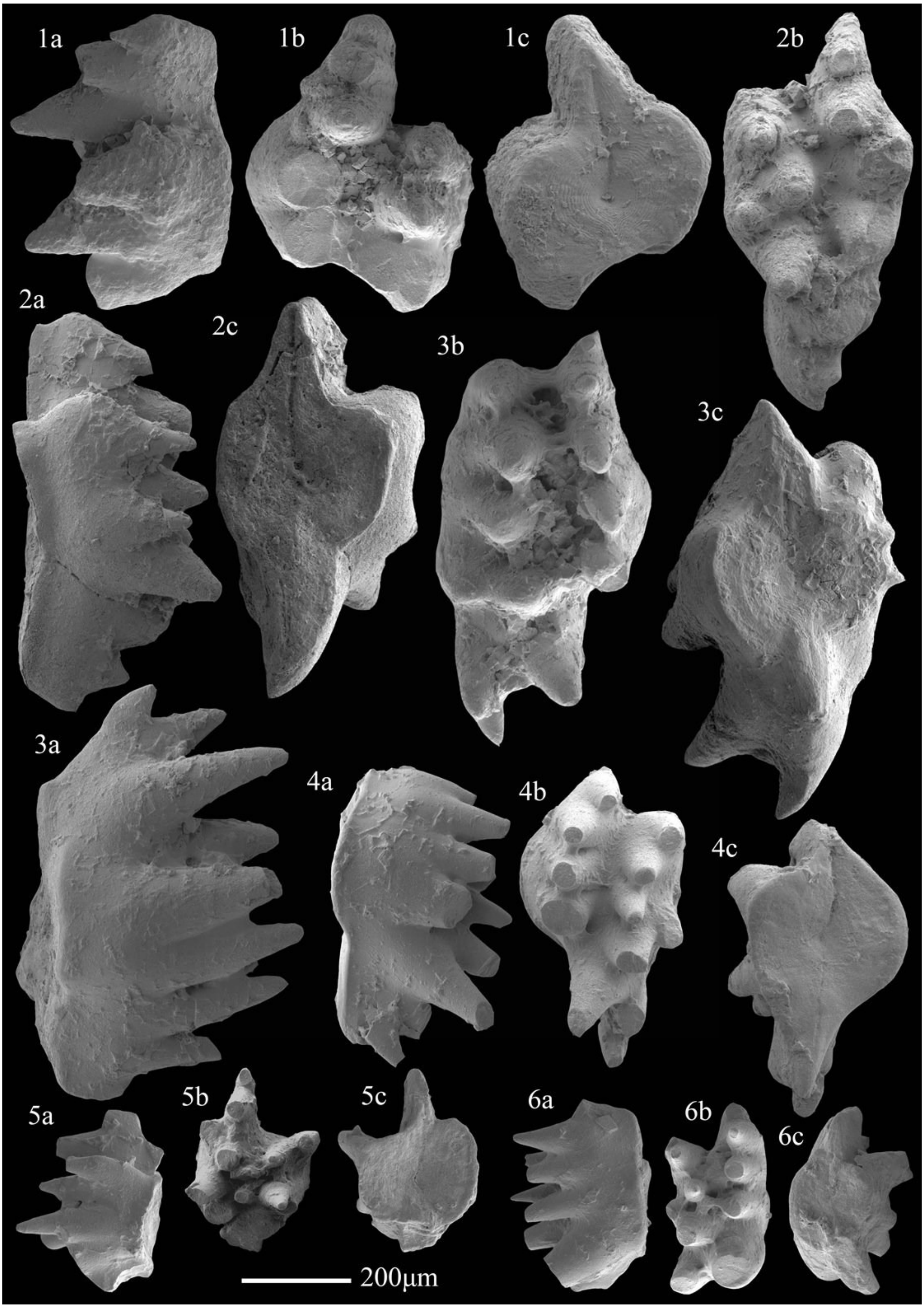


Figure 3.6. SEM photos of conodonts obtained from the Žiri-sortirnica 28 section. 1–6, *Platyvillosus corniger* sp. nov. Kolar-Jurkovšek & Chen, 1 sample 28/10, 2 sample 28/9, 3 sample 28/10, 4 holotype and sample 28/8, 5–6 sample 28/6. Scale bar = 200μm; a, lateral view; b, upper view; c, lower view.

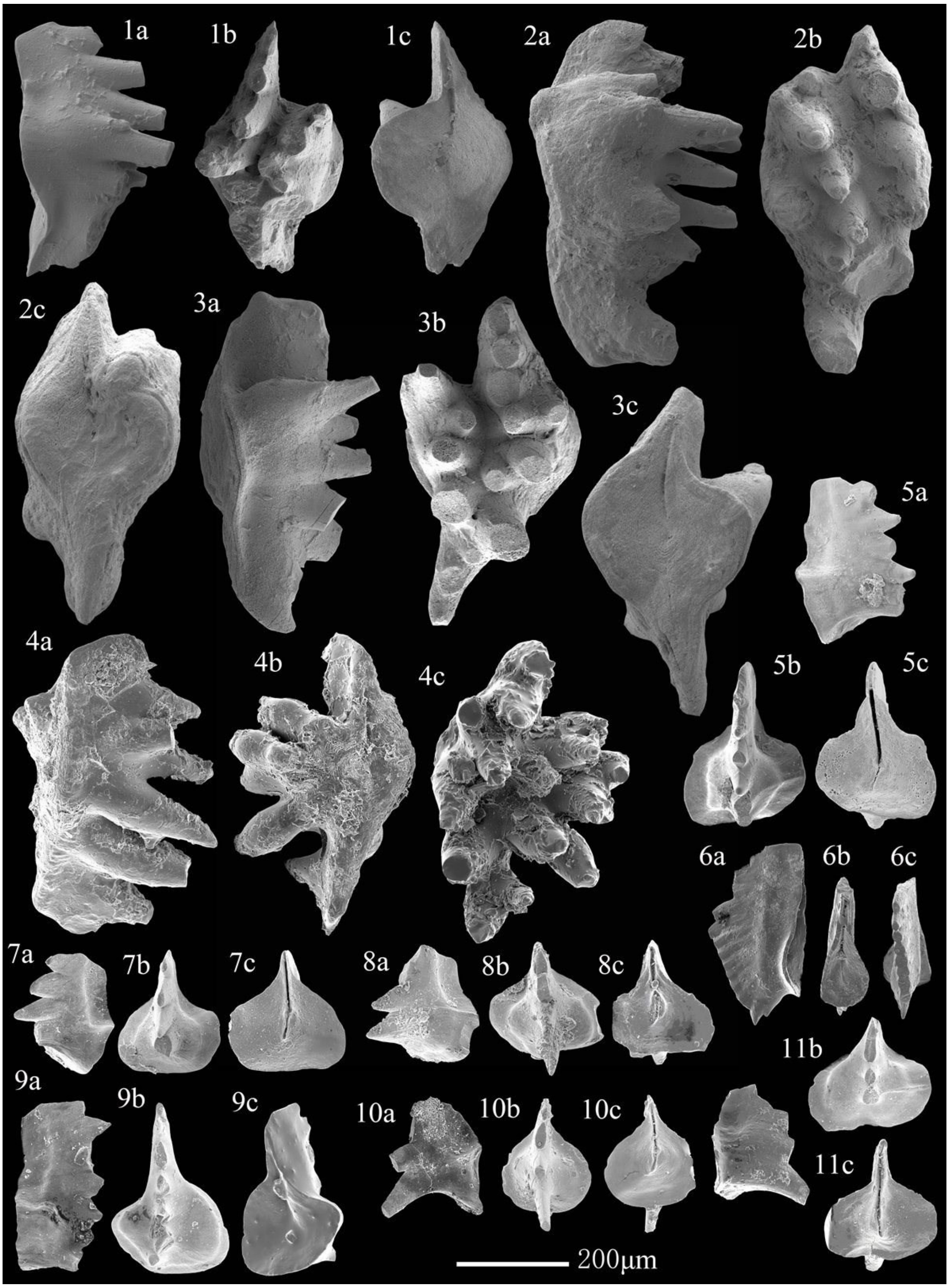


Figure 3.7. SEM photos of conodonts obtained from the Žiri-sortirnica 28 and Žiri-Vrsnik 61 sections. 1–3, *Platyvillosus corniger* sp. nov. Kolar-Jurkovšek & Chen, sample Žiri-sortirnica 28/8. 4, *Platyvillosus regularis* (Budurov & Pantić), sample Žiri-sortirnica 28/17. 5, *Neospathodus planus* sp. nov. Chen & Kolar-Jurkovšek, sample Žiri-sortirnica 28/06. 6 *Neospathodus* sp. indeterminate, sample Žiri-Vrsnik 61/1. 7–11, *Neospathodus planus* sp. nov. Chen & Kolar-Jurkovšek, 7–9 sample Žiri-Vrsnik 61/3, 10 and 11 sample Žiri-Vrsnik 61/4. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

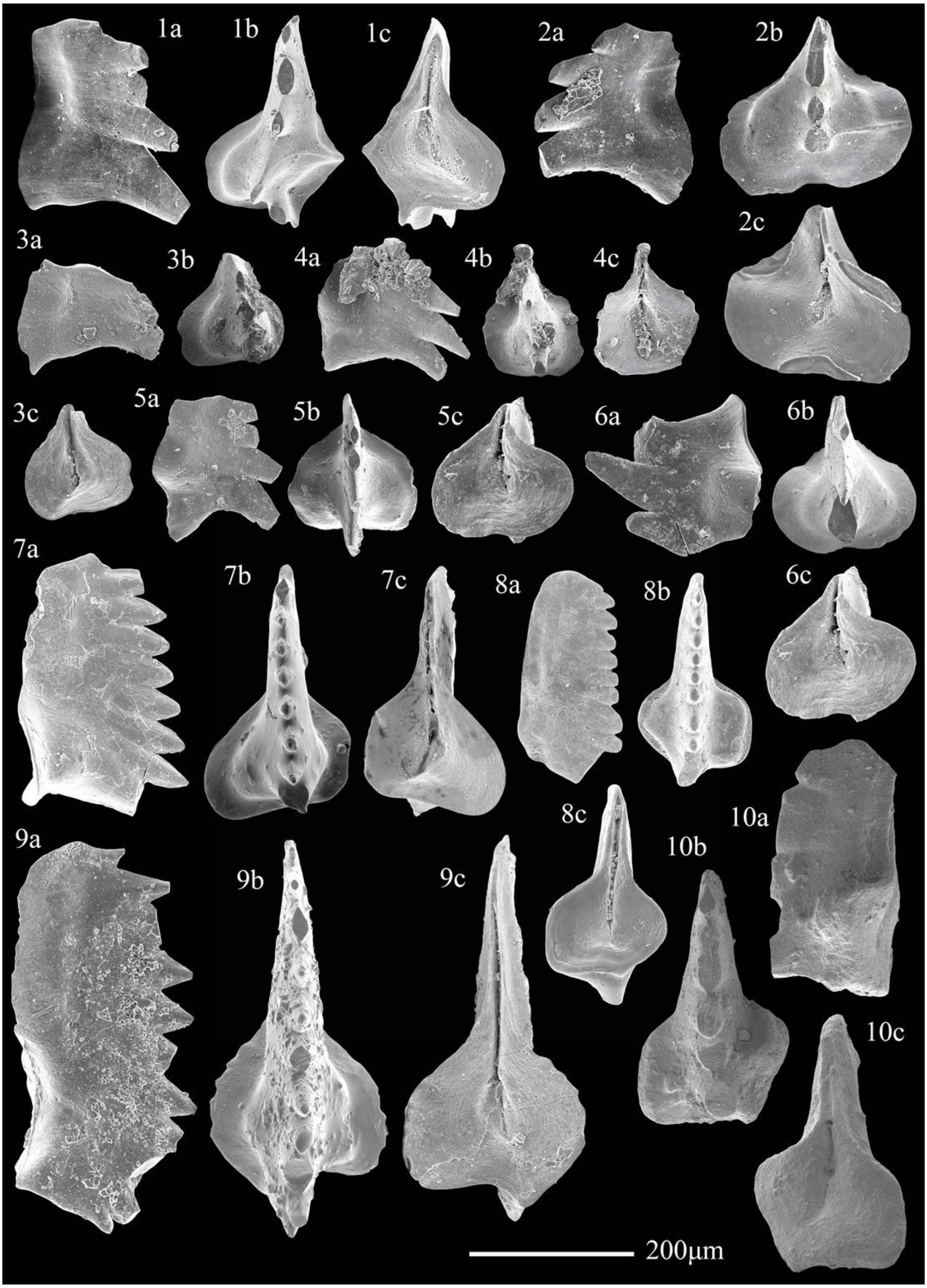


Figure 3.8. SEM photos of conodonts obtained from the Žiri-Vrsnik 61 section. 1–6 and 10, *Neospathodus planus* sp. nov. Chen & Kolar-Jurkovšek, 5 holotype, 1–6 sample 61/4, 10 sample 61/3. 7 and 8, *Neospathodus robustus* Koike, sample 61/6. 9, *Neospathodus* ex. gr. *robustus* Koike, sample 61/7. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

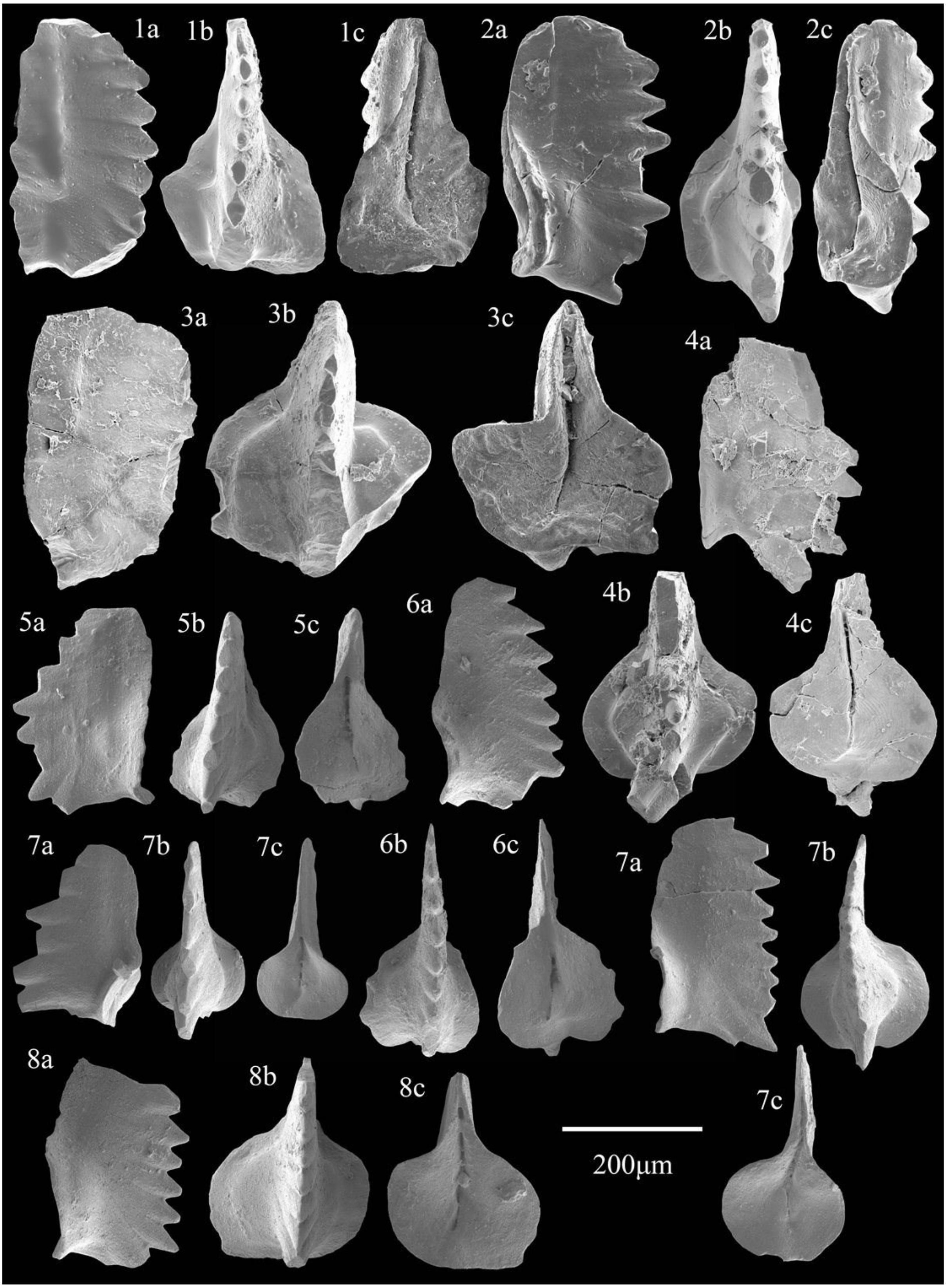


Figure 3.9. SEM photos of conodonts obtained from the Žiri-Vrsnik 61 section. 1–9, *Neospathodus robustus* Koike, 1 sample 61/8, 2–4 sample 61/15, 5 sample 61/3, 6–7 and 9 sample 61/5, 8 sample 61/6. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

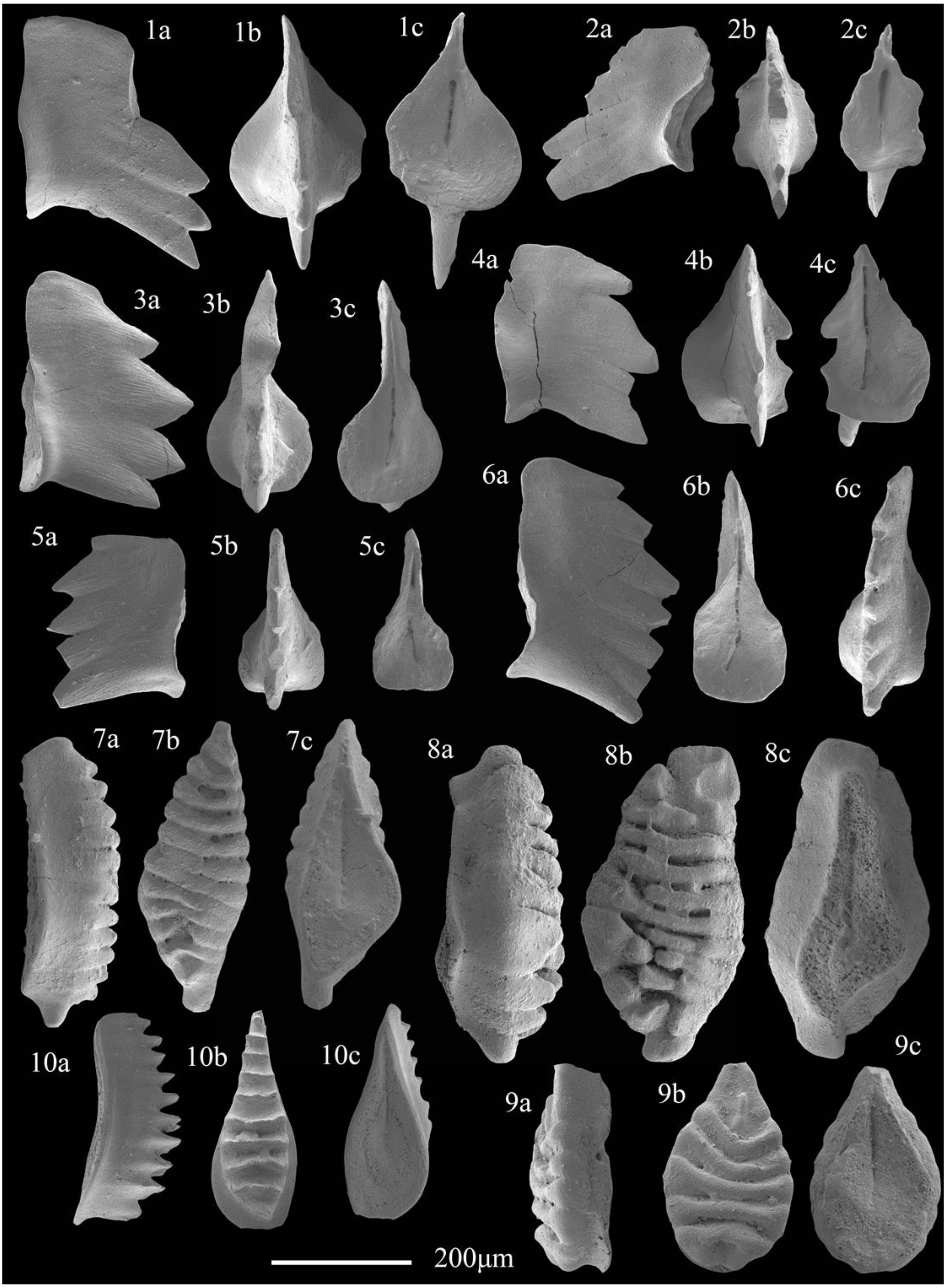


Figure 3.10. SEM photos of conodonts obtained from the Krkoč 43 and Golob 44 sections. 1–5, *Neospathodus robustispinus* Zhao and Orchard, 1 sample Krkoč 43/4, 2–5 sample Krkoč 43/5. 6, *Neospathodus* ex. gr. *robustispinus* Zhao and Orchard, sample Krkoč 43/6. 7–10, *Eurygnathodus costatus* Staesche, 7–8 sample Golob 44/1, 9 sample Golob 44/3, 10 sample Golob 44/5. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

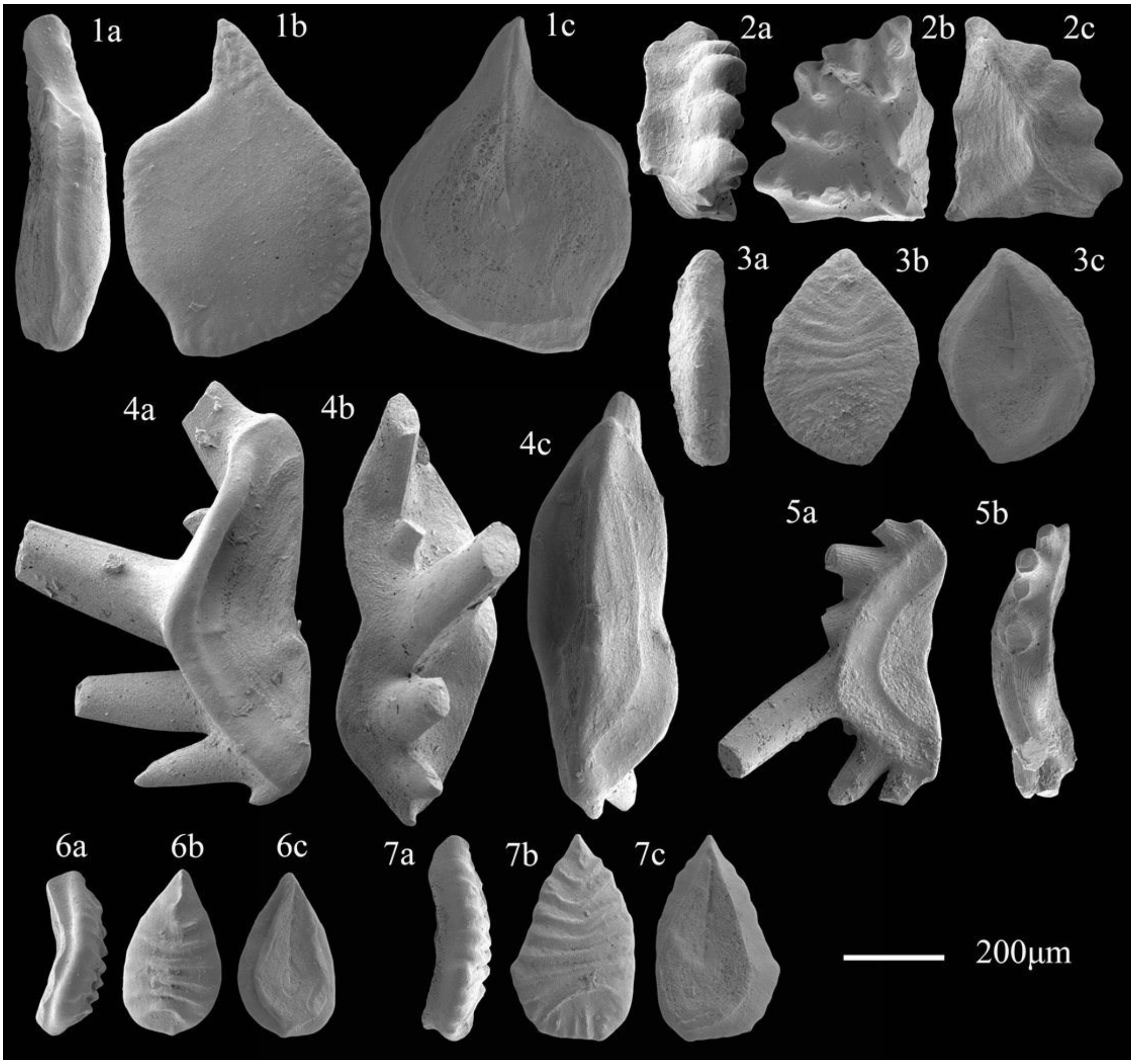


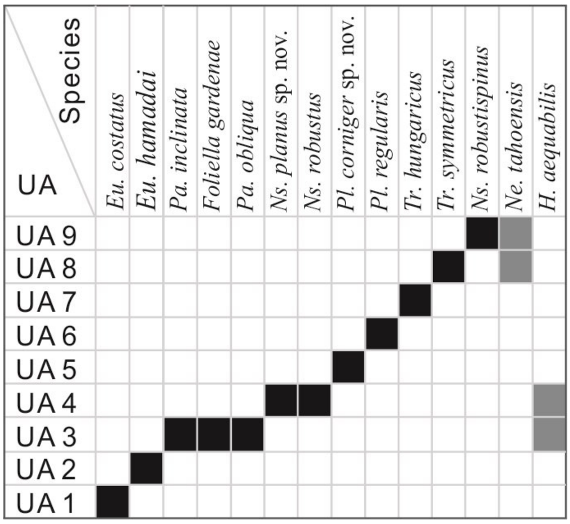
Figure 3.11. SEM photos of conodonts obtained from the Golob 44 and Žiri-road cut 29 sections. 1, *Eurygnathodus hamadai* (Koike), sample Golob 44/8. 2, fragment of *Foliella gardenae* (Staesche), sample Žiri-road cut 29/1. 3, 6 and 7, *Eurygnathodus costatus* Staesche, 3 sample Golob 44/8, 6 and 7 sample Golob 44/5. 4, *Pachycladina obliqua* Staesche, sample Žiri-road cut, composite sample. 5, *Pachycladina inclinata* morphotype A Staesche, sample Žiri-road cut 29/1. Scale bar = 200µm; a, lateral view; b, upper view; c, lower view.

The laboratory preparation was carried out partly at the Geological Survey of Slovenia and partly at the University of Graz. All micropaleontological materials are stored and inventoried under the repository numbers 3316-3318, 3326-3332, 3361-3382, 3393-3395, 3604-3611, 3613-3626, 3693-3705, 3726-3731, 3734-3740, 3979-3983, 5295-5308 and abbreviated GeoZS at the Geological Survey of Slovenia.

Rock samples were dissolved in diluted formic acid (10-12%) and acetic acid (*ca*. 8%), and after dissolution, the residues were collected, sieved and dried. Conodonts were picked under a binocular microscope. SEM photos were taken partly at Graz University (Zeiss DSM 982 Gemini) and partly at the Geological Survey of Slovenia (JEOL JSM 6490LV Scanning Electron Microscope) and they are illustrated in Figures 3.3 – 3.11.

3.3.2. Unitary Association analysis

The Unitary Association (UA) analysis (Guex 1991) was conducted for recognizing conodont zones and biostratigraphical correlations because of its solid theoretical basis and minimum of statistical assumptions. The published data from Sudar et al., (2014), as well as the data from Mokrice section, Slovenia (Kolar-Jurkovšek et al., submitted), were included in this analysis (see supplementary material S1) using the software PAST (Hammer et al., 2001). Species with uncertain taxonomic positions (e.g., *Triassospathodus* ex. gr. *homeri* and *Triassospathodus* ex. gr. *hungaricus*) are not included in this analysis. The Golob 44 section was analyzed separately because it lacks of overlap with other sections. The results of these analyses are combined and shown in Figure 3.12.



UA	*Eu. costatus*	*Eu. hamadai*	*Pa. inclinata*	*Foliella gardenae*	*Pa. obliqua*	*Ns. planus* sp. nov.	*Ns. robustus*	*Pl. corniger* sp. nov.	*Pl. regularis*	*Tr. hungaricus*	*Tr. symmetricus*	*Ns. robustispinus*	*Ne. tahoensis*	*H. aequabilis*
UA 9												■	▨	
UA 8											■		▨	
UA 7										■				
UA 6									■					
UA 5								■						
UA 4						■	■							▨
UA 3			■	■	■									▨
UA 2		■												
UA 1	■													

Figure 3.12. The results of the Unitary Association analysis showing the sequence of conodont zones.

3.3.3. Carbonate carbon isotope

Ninety-six carbonate samples were collected for $\delta^{13}C_{carb}$ analyses. Carbonate powders were drilled on fresh-cut rock surface using a diamond-tipped drill for 0.5–1.0 mg sub-samples. Cracks, veins and fossil shells are avoided for drilling. The carbonate powder was reacted with 100% orthophosphoric acid at 70 °C in a Kiel II automated carbonate preparation system. The resulting CO_2 was then analyzed on a DeltaplusXL mass spectrometer at University of Graz. Reproducibility of replicate analyses for standards (in-house and NBS 19) and sediment samples was better than ±0.1‰ for $\delta^{13}C$. All carbonate carbon isotopic values are reported in per mil relative to V-PDB (see supplementary material S2).

3.4. Conodont biostratigraphy

In total, *ca*. 1100 conodont elements were recovered, including *ca*. 400 P_1 elements and *ca*. 600 other elements. The most abundant samples are Žiri-sortirnica 28/18c, Golob 44/13 and Golob 44/5, from which, respectively, 137, 110 and 65 elements were obtained. All studied conodonts have Conodont Alteration Index (CAI) around 5, i.e., black in color. Most of rock samples yield only one or two species (Fig. 3.2). The smallest sized conodonts are observed from the *Triassospathodus hungaricus* Zone (UA7; Fig. 3.3 and 3.4).

Nine discrete Unitary Association (UA) zones were recognized and shown in Figure 3.12. The gray squares in the Figure 3.12 indicate species (*Neostrachanognathus tahoensis* and *Hadrodontina aequabilis*) which are problematic for correlations, because they were only found from one section. These UA zones are discussed below in ascending stratigraphic order.

3.4.1. *Eurygnathodus costatus* Zone (UA 1)

Locality: section Golob 44; Recognized from the base of the Golob 44 section to the First Occurrence (FO) of *Eurygnathodus hamadai* (Fig. 3.12).

Content: *Eurygnathodus costatus*.

Eurygnathodus costatus has a very large geographical distribution. *Eu. costatus* has been reported from North Italy (Staesche 1964), Croatia (Aljinović et al., 2006), Western Serbia (Budurov & Pantić, 1973), Kashmir and Spiti, India (Krystyn et al., 2007), South Primorye, Northeastern Asia (Igo, 2009), Southwest Japan (Koike, 1988), Northeastern Vietnam (Maekawa & Komatsu, 2014), Northwest and Western Malaysia (Koike, 1982); Nevada, USA (Sweet et al., 1971); British Columbia, Canada (Beyers & Orchard, 1991). In South China, it was reported from western Hubei Province (Wang & Cao, 1981; Zhao et al., 2013), Chaohu of Anhui Province (Zhao et al., 2008), Sichuan Province (Tian et al., 1983), Guizhou Province (Wang et al., 2005; Chen et al., 2015), Guangxi Province (Yang et al., 1986; Zhang, 1990).

3.4.2. *Eurygnathodus hamadai* Zone (UA 2)

Locality: section Golob 44; recognized from the stratigraphic interval between FO and Last Occurrence (LO) of *Eurygnathodus hamadai*.

Content: *Eurygnathodus costatus* and *Eu. hamadai*.

The *Eurygnathodus hamadai* Zone here equivalent to the *Eu. costatus* and *Eu. hamadai* assemblage zone which can be recognized from Northwest and Western Malaysia (Koike, 1982), Japan (Koike, 1988), western Hubei Province, South China (Wang & Cao, 1981; Zhao et al., 2013), Anhui Province, South China (Zhao et al., 2008).

3.4.3. *Foliella gardenae* Zone (UA 3)

Locality: the Žiri-road cut 29 section; recognized from rock sample 29/1.

Content: *Foliella gardenae*, *Pachycladina obliqua* and *Pa. inclinata*.

Foliella gardenae was originally reported form northern Italy (Staesche 1964), then from Serbia (Budurov & Pantić, 1973; Sudar et al., 2014), Slovenia (Kolar-Jurkovšek, 1990; Kolar-Jurkovšek & Jurkovšek, 1995), and Croatia (Aljinović et al., 2006). This species has so far been reported from Europe only (Kolar-Jurkovšek & Jurkovšek, 1996) and it is therefore apparently geographically restricted. It is unclear whether the species reported from South Primorye of Northeastern Asia (Igo, 2009) as *F. gardenae* is related to *F. gardenae* or *Furnishius triserratus* Clark. The correlation between the present study and the eastern Russian section is thus difficult.

Pachycladina obliqua has been reported from northern Italy (Perri & Andraghetti 1987; Perri 1991), central Slovenia (Kolar-Jurkovšek & Jurkovšek 1995, 1996, Jurkovšek et al. 1999, Kolar-Jurkovšek & Jurkovšek 2001, Dozet & Kolar-Jurkovšek, 2007), Croatia (Jelaska et al. 2003; Aljinović et al., 2006), Bosnia and Herzegovina (Aljinović et al., 2011), South China (Wang & Cao, 1981; Yang et al., 1986; Yan et al., 2013) and North America (Beyers & Orchard, 1991). In northern Italy, the *Pa. obliqua* multi-element apparatus was first reported by Perri and Andraghetti (1987) and Perri (1991).

3.4.4. *Neospathodus planus-Neospathodus robustus* Zone (UA 4)

Locality: the Žiri-Vrsnik 61 section and Žiri-sortirnica 28 section; recognized from rock sample 61/15 and 28/06.

Content: *Neospathodus planus* sp. nov. (see taxonomic notes below) and *Neospathodus robustus*.

Neospathodus planus sp. nov. has been repored from Serbia, where it lies immediately above the *Pachycladina obliqua-Foliella gardenae* Assemblage Zone (Sudar et al., 2014). *Ns. robustus* was originally reported from Western Malaysia (Koike, 1982), but it was rarely reported from other places.

3.4.5. *Platyvillosus corniger* Zone (UA 5)

Locality: the Žiri-sortirnica 28 section; recognized from strata between FO and LO of *Platyvillosus corniger* sp. nov (Fig. 3.2).

Content: *Platyvillosus corniger* sp. nov. (see taxonomic notes below).

Platyvillosus corniger sp. nov. has also been recognized from Mokrice section, Western Slovenia (Kolar-Jurkovšek et al., submitted), where it is also mono-species in its stratigraphic range.

3.4.6. *Platyvillosus regularis* Zone (UA 6)

Locality: the Žiri-sortirnica 28 section; recognized from strata between FO and LO of *Platyvillosus regularis* (Fig. 3.2).

Content: *Platyvillosus regularis*.

Platyvillosus regularis (see taxonomic notes below) has also been recognized among other places, from Mokrice section, Western Slovenia (Kolar-Jurkovšek et al., submitted) and western Serbia (Budurov and Pantić, 1973).

3.4.7. *Triassospathodus hungaricus* Zone (UA 7)

Locality: the Žiri-sortirnica 28 section; recognized from strata between FO and LO of *Triassospathodus hungaricus*.

Content: *Triassospathodus hungaricus.*

Tr. hungaricus was originally reported from Hungary (Kozur & Mostler, 1970), later from Sichuan province (Southwest China; Tian et al., 1983), and more recently from Studorski Preval, northwest Slovenia (Kolar-Jurkovšek et al., 2013), and Bosnia and Herzegovina (Kolar-Jurkovšek et al., 2014). Meanwhile, a similar species has been reported from Nevada (North America) as "*Neospathodus*" cf. *hungaricus* (Lucas & Orchard, 2007).

3.4.8. *Triassospathodus symmetricus* Zone (UA 8)

Locality: the Žiri-sortirnica 28 section; Recognized from rock sample 28c/2 and 28c/4**.**

Content: *Triassospathodus symmetricus*.

Tr. symmetricus was first reported from Oman and North America, where it co-occurs with *Icriospathodus collinsoni* and *Tr. homeri* (Mosher, 1968; Orchard, 1995). Elsewhere, this species was also reported from Italy (Perri, 1986), Greece (Dürkoop et al., 1986), West Pakistan (Sweet, 1970a), Kashmir and Kumaun Himalayas (Chhabra & Sahni, 1981), Nepal (Hatleberg & Clark, 1984), Guizhou province, South China (Wang et al., 2005; Yan et al., 2013; Chen et al., 2015), North Vietnam (Maekawa & Komatsu, 2014), Southwest Japan (Koike, 2004) and North America (e.g., Mosher, 1973).

3.4.9. *Neospathodus robustispinus* Zone (UA 9)

Locality: the Žiri-sortirnica 28 section and Krkoč 43 section; recognized from strata between FO and LO of *Neospathodus robustispinus*.

Content: *Neospathodus robustispinus*.

Ns. robustispinus was first reported from Chaohu, Anhui province (South China), and it occurs with ammonoids of the lower Spathian *Columbites*-*Tirolites* Zone (Zhao et al., 2008). *Ns. robustispinus* occurs higher than the FO of *Triassospathodus symmetricus* in the Idrija–Žiri area.

3.5. Carbonate carbon isotopes

Two major positive excursions of $\delta^{13}C$ can be observed from the Idrija–Žiri area (Fig. 3.2 and 3.13). The first positive excursion was documented from the Golob 44 section, where the lowest value (4.6‰) was seen in the lower part of the section (Fig. 3.2; Fig. 3.13). These values were followed by a steady rise to a peak (8.3‰) at the lower part of UA 2. After the peak value, a steady decrease can be seen from the middle to upper part of the UA 2. The second positive excursion was documented from Žiri-road cut 29, where a drastic positive excursion of $\delta^{13}C$ values from 0.5‰ to 6.7‰ can be seen. The stratigraphically higher sections (Žiri-Vrsnik 61 and Žiri-sortirnica 28) show a gradual decrease trend with $\delta^{13}C$ values from 6.9‰ to 3.7‰. A cross-diagramm $\delta^{13}C$ - $\delta^{18}O$ (see supplementary material) do not display any trend to diagenetic alteration. Moreover the good correlation between Žiri carbon isotopic curve with other curve around the world (e.g., Payne et al., 2004; Richoz, 2006; Horacek et al., 2007; Clarkson et al., 2013) give evidence that there is no significant diagenetical influence on the carbon isotopic composition.

3.6. Discussion

3.6.1. The Substage Boundaries

3.6.1.1. The Dienerian/Smithian boundary

The FO of *Novispathodus waageni* has been proposed as a marker for the base of the Global Stratotype Section and Point (GSSP) of the Olenekian Stage (i.e., base of Smithian Substage) (Krystyn et al., 2007; Zhao et al., 2008). Reports show that the FOs of both *Eurygnathodus hamadai* and *Eu. costatus* are in the lowermost part of the Smithian in both GSSP candidates:

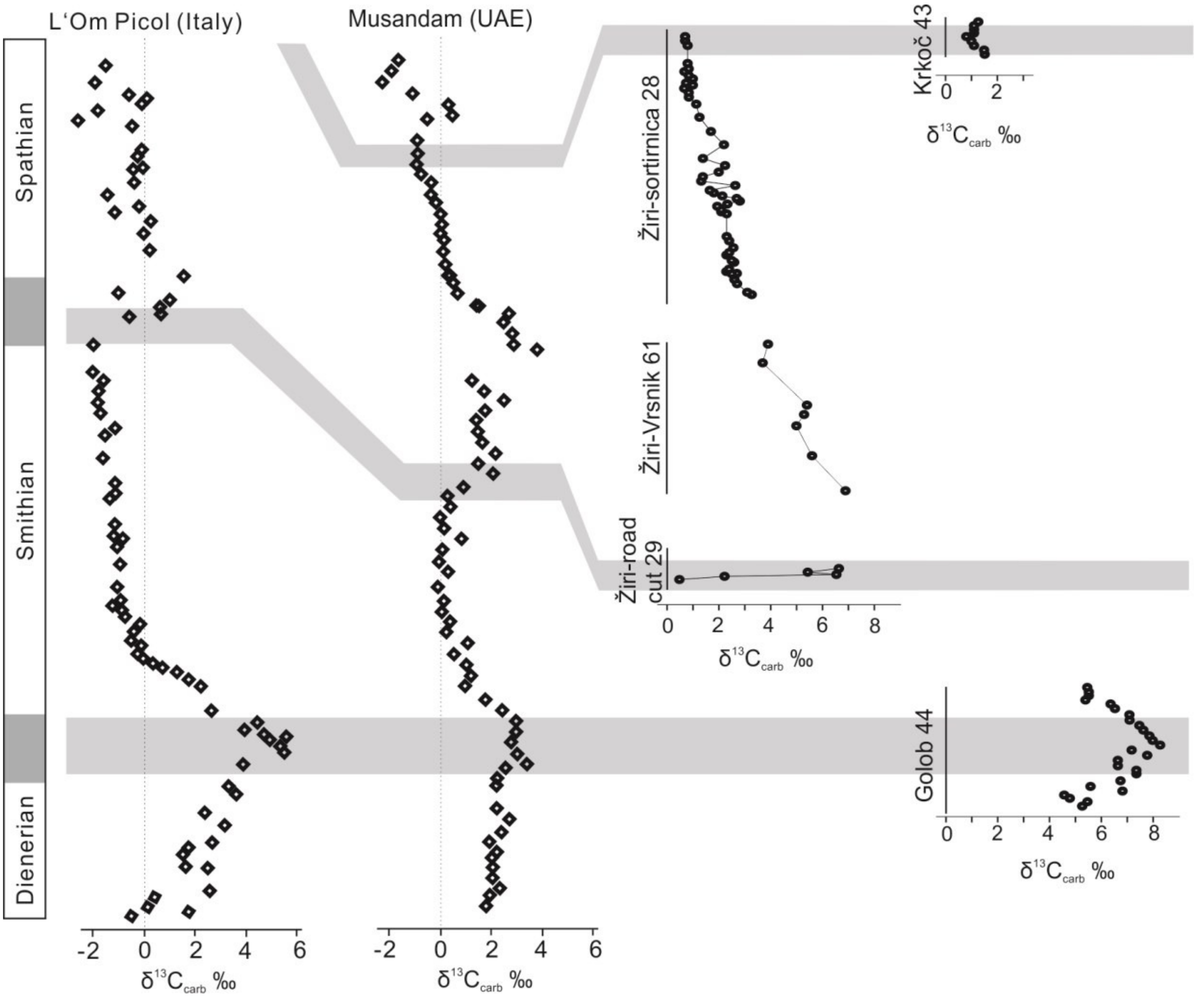


Figure 3.13. Correlation diagram of Early Triassic carbon isotope curves. Isotope data of Italy from Horacek et al., (2007); Musandam, United Arab Emirates (UAE) from Clarkson et al., (2013).

Spiti, India (Krystyn et al., 2007), and Chaohu, Anhui Province (Zhao et al., 2008). However, *Eu. costatus* cannot be used to define the boundary presently because it has also been reported from the latest Induan (i.e., latest Dienerian), e.g., southern Primorye, northeastern Asia (Igo, 2009), western Guangxi, South China (Zhang, 1990). It was also reported from probably middle or upper Smithian strata in western Hubei Province (Zhao et al., 2013), which suggests a longer upper range. Further studies on *Eurygnathodus* species are needed because either the FO of *Eu. costatus* is diachronous, or the Induan records are in error. The absence of *Nv. waageni*, and the uncertainty of the FO of *Eu. costatus*, which moreover appear in the first sample of the section, precludes the exact position of the Induan-Olenekian boundary being determined by conodonts in Idrija-Žiri area.

The Induan-Olenekian transitional interval is characterized by a worldwide recognizable peak value of $\delta^{13}C$ (e.g., Payne et al., 2004; Richoz, 2006; Horacek et al., 2007; Krystyn et al., 2007; Clarkson et al., 2013). This peak is actually double, with the highest values for the second one, which occur just after the FO of *N. waageni* in Spiti (Richoz et al., 2007). This double positive peak in $\delta^{13}C$ values has also been recognized at Golob 44 section (Fig. 3.2; Fig. 3.13). Based on the C-isotope data of the Idrija-Žiri area, the Induan-Olenekian boundary probably lies within the Golob 44 section, between the samples 44/4 and 44/6.

3.6.1.2. The Smithian/Spathian boundary

Triassospathodus hungaricus co-occurs with the ammonoid *Tirolites* in Hungary (Kozur & Mostler, 1970), which is widely accepted by stratigraphers as a marker for the Smithian-Spathian boundary (e.g., Kozur, 2003). And the *Tr. hungaricus* Zone was suggested to be the first conodont zone of the Spathian, lying below *Icriospathodus collinsoni* (Kozur, 2003). According to Kozur, in the shallow western Tethys, the *Tr. hungaricus* Zone lies in the lower Spathian, where *Icriospathodus collinsoni* is missing (Kolar-Jurkovšek et al. 2013).

Our C-isotope data, however, do not support the suggestion of Kozur (2003), but indicate that *Triassospathodus hungaricus* lies above several early Spathian conodont zones recognized in this study. The Smithian-Spathian transitional interval is characterized by a drastic positive excursion of $\delta^{13}C$ values documented worldwide, followed by a peak value and a subsequent gradual decreasing trend in the lower Spathian (e.g., Payne et al., 2004; Richoz, 2006; Horacek et al., 2007; Clarkson et al., 2013). We observed the major positive excursion at Žiri-road cut 29 and the gradual decrease trend of $\delta^{13}C$ values at Žiri-Vrsnik 61 and Žiri-sortirnica 28 sections. The maximum of the positive excursion is evident just above the occurrence of *Fo. gardenae* (UA3). The decrease trend indicates that conodont Unitary Association 4 (UA 4) to UA 7 are probably lower Spathian in age (Fig. 3.2; Fig. 3.13). The Smithian/Spathian boundary is thus located between UA3 characterized by the presence of *Fo. Gardenae* and UA 4 signalized by the co-occurrence of *Neospathodus planus* and *Neospathodus robustus.*

3.6.2. Conodont paleoecology

In general, conodonts of the Idrija-Žiri area show a very low diversity, as most of samples yielded only one or two species (Fig. 3.2). Some of these species (e.g., *Platyvillosus regularis* and *Pl. corniger* sp. nov.) have been reported only from the Dinarids. In contrast, *Novispathodus waageni*, *Icriospathodus collinsoni* and *Nv. pingdingshanensis* are typical

Tethyan and Panthalassan conodont species, and they have not been found in the Dinarides. This underlines that *Eurygnathodus*, *Foliella* and *Platyvillosus* species have ecologically other needs or geographically other repartition than *Neospathodus*, *Triassospathodus* and *Novispathodus* species. A better understanding of the mechanisms behind this particular paleontological record can provide insights into conodont ecology, provincialism and the recovery from the end-Permian mass extinction.

During the Early Triassic, central-south Europe was located on the western margin of Tethys (Mandl, 2000, fig. 2). The Lower Triassic paleogeographic scheme indicates that the Western and Middle-eastern Tethys were connected (Mandl, 2000, fig. 2). This is supported by the presence of common conodont species (e.g., *Eurygnathodus costatus*, *Pachycladina obliqua*, *Neospathodus robustispinus*, *Triassospathodus hungaricus* and *Triassospathodus symmetricus*) and ammonoids (e.g., *Tirolites*) in both regions (c.f. Koike, 1982; Tian et al., 1983; Wang et al., 2005; Brayard et al., 2006; Igo, 2009; Yan et al., 2013; Maekawa & Komatsu, 2014; Chen et al., 2015). Among the conodont species obtained during this study, and according to available data, *Eurygnathodus costatus* has the widest geographic distribution. It extends from the western marginal Tethys to eastern Panthalassa. It has been reported from ooid shoal facies (Aljinović et al., 2006), platform interior (Yang et al., 1999), platform margin (Wang et al., 2005), carbonate slope (Komatsu et al., 2014), middle or outer ramp (Zhao et al., 2008), basin-floor facies (Igo, 2009), and shallow and low-energy environments (Yang et al., 1986; Koike, 1988).

The similarities within the Early Triassic marine deposits in the Dinaridic-Alpine-Carpathian area indicates a large and similar sedimentary environment stretching from northern Italy, Austria, Hungary, to former Yugoslavia (Hips & Pelikan, 2002; Ogorelec, 2011). During the Dienerian-Smithian, this area has been recognized as a sedimentary environment similar to an epeiric shelf (Hips & Pelikan, 2002) or epeiric ramp (Aljinović et al., in preparation). The epeiric ramp model is characterized by hundreds of kilometers of lateral extension, very low slope angles (< 1°), water depths of a few tens of meters, storm influences and nearshore currents (Lukasik et al., 2000; Aljinović et al., in preparation). Contemporaneous differences of sediment deposition within the Dinaridic-Alpine-Carpathian area are common in Early Triassic, and these differences are suggested to be controlled by local environmental factors (Hips & Pelikan, 2002).

In the External Dinarides of Croatia, *Eurygnathodus costatus* and *Eu. hamadai* have been reported from dolomitized ooid grainstones (Aljinović et al., 2006) or in sediment presenting hummocky cross stratification, a typical storm structure (this study). In several locations of Slovenia (central and NW part), Croatia and in western and northwestern Serbia, *Pa. obliqua* and *F. gardenae* are reported from oolitic limestones, which are interlayered with sandy and silty claystones and marls (Budurov & Pantić, 1974; Kolar-Jurkovšek & Jurkovšek, 1995; 1996; Aljinović et al., 2006; 2011; Sudar et al., 2014; this study). In Gučevo, NW Serbia, *Neospathodus planus* sp. nov. was found in bioturbated and thick-bedded limestones, which have been suggested to be deposited in a subtidal zone (Sudar et al., 2014). *Triassospathodus hungaricus* has been reported from Julian Alps, northwestern Slovenia, in sediments characterized by tempestite, bioturbated mudstones and claystones. They have been interpreted to be deposited below fair-weather wave base but shallower than storm wave base (Kolar-Jurkovšek et al., 2013). *Tr. hungaricus* of the Jajce area in Bosnia and Herzegovina was reported from a shallow ramp environment (Kolar-Jurkovšek et al., 2014).

Most of the shallow-water conodont assemblages in the Alps-Carpathian-Dinarids system are thus deposited in a high-energy (e.g., oolite) or at least storm-influenced environment, directly connected to the open ocean. The salinity was probably related to the oceanic one and would not have shown large variability. The situation in the other Tethyan area where the shallow-water conodont association is described, South China, is remarkably different. The platform there presents quieter conditions than in the western Tethys, perhaps elevated salinity, and the platform margin is deeper (Yang et al., 1999; Enos et al., 2006).

In South China, the Olenekian shallow conditions are identified as two conodont biofacies: 1) the platform facies and 2) the platform-margin facies (Yang et al., 1999). The platform facies is characterized by the species, in ascending order: *Eurygnathodus costatus*, *Neospathodus cristagalli* Huckriede, *Pachycladina* species, *Icriospathodus collinsoni* and *Triassospathodus homeri.* The platform-margin facies is characterized by the following taxa: *Ns. pakistanensis*, *Novispathodus waageni* and *Tr. homeri* (Yang et al., 1999).

In contrast, in western USA, the nearshore outer shelf (sensu Clark and Carr 1984) presents environmental conditions similar to those in the western Tethys, with higher-energy, constantly agitated sediments and water masses open to the ocean. This facies is characterized by the species, in ascending order: *Furnishius* sp., *Ellisonia triassica, Pachycladina* sp., *Neospathodus bicuspidatus, Novispathodus waageni, Scythogondolella milleri, Neogondolella jubata, Triassospathodus triangularis*?, *Platyvillosus asperatus* Clark, Sincavage & Stone, *Icriospathodus collinsoni*, *Triassospathodus symmetricus*? and *Triassospathodus homeri* (c.f. Solien, 1979; Clark & Carr, 1984, Carr et al., 1984). Thus, some paleoenvironmental factors such as bathimetry, water energy, and salinity are similar between the nearshore outer shelf in the USA and the western Tethys settings, but conodont assemblages still present an important disparity. This could be explained by further paleonvironmental factors that are less well constrained such as nutrient availibilty, warm-cold current or by a limited provincialism, with certain species being ubiquist, like *Eurygnathodus costatus* or *Triassospathodus homeri*.

3.6.3. Extinction, recovery and conodonts size

Multiple extinctions occurred during the Early Triassic (Stanley, 2009), and one of them took place during the late Smithian (Stanley, 2009; Sun et al., 2012; Romano et al. 2013). In South China and northern Vietnam, conodont size was reduced immediately after the late Smithian extinction event (Chen et al., 2013; Maekawa & Komatsu, 2014). *Triassospathodus hungaricus* is the smallest conodont found in the Idrija-Žiri area (Fig. 3.3 and 3.4), but our isotope data do not support that these small-sized conodonts occurred in the latest Smithian and/or the earliest Spathian. Thus, the geographical amplitude of size reduction around the Smithian/Spathian boundary and the mechanisms of these small-sized conodonts in Idrija-Žiri area remain to be answered. The relatively low diversity in the Idrija-Žiri area compared to the middle-eastern Tethys is probably related on one hand to the local ecological conditions and on the other to the repeatedly disturbed recovery process from the end-Permian mass extinction (Payne et al., 2004; Richoz, 2006; Stanley, 2009; Brayard et al., 2009).

3.7. Conclusions

Nine discrete Unitary Association zones from the Idrija-Žiri area promote a better correlation with Early Triassic strata of Europe. *Neospathodus planus* sp. nov., *Platyvillosus corniger* sp. nov. and *Pl. regularis* have been reported only from Slovenia and Serbia, and they highlight these areas for studies of conodont biostratigraphy and paleoecology.

Generally, the species of the Idrija-Žiri area are adapted to a shallow-water environment in an epeiric ramp. Nonetheless, the discrepancy with the fauna in North America in a similar setting argues for provincialism or for controlling factors other than water energy, bathimetry and salinity. The wide geographic distribution of *Eu. costatus* and its presence in diverse paleoenvironments indicate that this species could adapt to different ecological settings ranging from high- to low-energy conditions. Our data support a first appearance of *Eu. costatus* already in the Induan.

Based on both conodont and isotope data, the Dienerian/Smithian boundary probably lies within the Golob 44 section, between samples 44/4 to 44/6. Our $\delta^{13}C$ data do not support the suggestion of Kozur (2003) that the *Triassospathodus hungaricus* Zone lies at the base of the Spathian, but the *Foliella gardenae* Zone (UA 3) may characterize the Smithian-Spathian transitional interval.

3.8. Taxonomic notes (Chen Y.L. & Kolar-Jurkovšek T.)

Two new species and *Platyvillosus regularis* (Budurov & Pantić, 1973) obtained from the Idrija–Žiri area are described and discussed here. All these species are assigned to order Ozarkodinida Dzik, 1976, family Gondolellidae Lindström, 1970.

Neospathodus planus sp. nov. Chen Y.L. & Kolar-Jurkovšek T.
Figure 3.7.7–11; Figure 3.8.1–6, 10

Etymology: Latin, *planus*, means flat or plane; P_1 element of this species has low angle slope on each side of the posterior part of the unit (e.g., Fig. 3.14.3–5), sometimes it can be flat at the outer upper side of the basal cavity (e.g., Fig. 3.14.3).

Holotype: specimen illustrated in the Figure 3.8.5

Paratype: specimen illustrated in the Figure 3.7.7–11; Figure 3.8.1–4, 6, 10

Type locality: Žiri-Vrsnik 61 section, Žiri, Slovenia.

Type level: from 7 m to 9.4 m of Žiri-Vrsnik 61 section, Olenekian, Lower Triassic.

Diagnosis: P_1 element is a bladelike form with 3–6 denticles and a height: length: width ratio of about 1:1:1. It has a strongly expanded basal cavity.

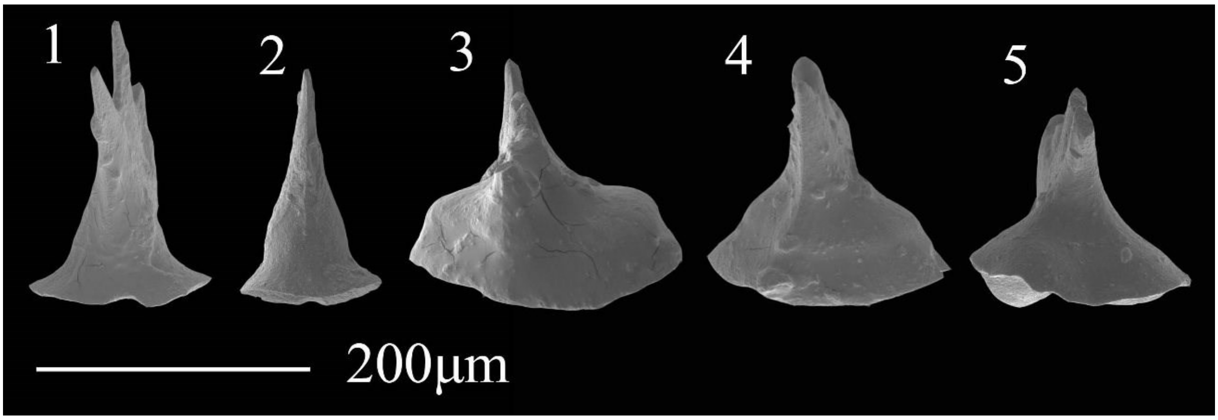


Figure 3.14. SEM photos of conodonts from the Idrija–Žiri area, Slovenia. 1–2, *Triassospathodus hungaricus* (Kozur & Mostler); 3–5, *Neospathodus planus* sp. nov. Chen & Kolar-Jurkovšek. Scale bar = 200μm; all these photos are posterior views. Lateral, upper and lower views have been illustrated: 1 in Figure 3.3.8; 2 in Figure 3.3.10; 3 in Figure 3.7.9; 4 in Figure 3.7.8; 5 in Figure 3.8.5.

Description: In lateral view, denticles are lowest at the anterior end and increasingly higher toward the posterior end where the cusp is located. The basal margin is straight throughout the unit or slightly upturned in the posterior part. In upper view, some specimens are flat with the outer upper side of the basal cavity on both sides of the posterior part of the unit; others show a very low angle slope. In lower view, the basal cavity is deep, round or sub-triangular in outline, truncated or roundish in the posterior end, and occupies about a minimum of two-thirds of the total length of the element. A small pit is located in the center of the basal cavity, and a deep basal furrow runs from the basal pit to the anterior end of the unit.

Comparisons: The present species resembles *Ns. novaehollandiae* and *Ns. robustus* in the extreme dilation of the basal cavity and its two horizontal to low angle sloping upper surface on each side of the posterior part of the unit. However, the latter two species are relatively longer and have more denticles, commonly 6–13 (McTavish, 1973; Koike, 1982). *Neospathodus planus* sp. nov. can be differentiated from *Tr. hungaricus* by its inflated basal cavity and relatively robust unit (Fig. 3.14). Moreover, the species does not show a downturned basal margin of the posterior part. The extreme dilation of the basal cavity resembles that of the lowermost Triassic species *Isarciella inflata* which was first described by Perri and Farabegoli (2003).

The stratigraphic distribution of *Ns. planus* is lower than that of *Ns. robustus* (this study; Sudar et al., 2014), this suggests that *Ns. planus* can not be a juvenile synonym of *Ns. robustus*. *Ns. planus* resembles *Ns. robustus*, thus it is probably the forebear of *Ns. robustus*.

Stratigraphic distribution: Olenekian, higher than UA 3, in and lower than UA 4.

Material: 40 well preserved specimens obtained from the Žiri-Vrsnik 61 section, sample 61/3, 61/4 and 61/5, 61/6. 1 specimen obtained from the Žiri-sortirnica 28, sample 28/06.

Genus *Platyvillosus* Clark, Sincavage & Stone, 1964

Type species: *Platyvillosus asperatus* Clark, Sincavage & Stone, 1964

Diagnosis: the P_1 element is a platform with a large and concave basal cavity. The basal pit is located in the center of the basal cavity, and a basal furrow can be clearly observed from the basal pit to the anterior end. Protrusions on the upper surface are either low nodes or high denticles, which are either randomly arranged or in a definite pattern.

Comparison: This genus resembles the genera *Foliella* Budurov & Pantić, 1973, *Furnishius* Clark, 1959 and *Eurygnathodus* Staesche, 1964. The type species of the genus *Foliella*,

Foliella gardenae, differs in having a basal keel that extends beneath the entire P_1 element and without a basal furrow in the adult form. Species of *Furnishius* differs in having a Y-shape keel. *Eurygnathodus,* which has been reported from the upper Dienerian and lower Smithian, has either ridge like denticles on the upper surface or no denticulation, whereas *Platyvillosus* has nodes or horn-like denticles, and is restricted to late Smithian and early Spathian. The present genus also resembles the early Triassic genus *Radiatignathus* Tian, 1983, but the P_1 element of that genus has two denticulate lateral processes, each of which forms an acute angle with the anterior process (Tian et al., 1983).

Remarks: It was believed that the genus *Eurygnathodus* Staesche 1964 is a junior synonym of *Platyvillosus* Clark, Sincavage & Stone 1964 (e.g., Kozur and Mostler, 1973). However, Orchard (2007) suggested that they are not synonymous, and he believes *Eurygnathodus* developed from segminate-bearing conodonts, probably during the Dienerian-Smithian transition, whereas *Platyvillosus* also evolved from *Neospathodus* species but later. Our materials obtained from the present zone support Orchard's (2007) suggestion. In juvenile stage of *Pl. corniger* (e.g., Fig. 3.5.5), the P_1 element shows a transitional character between blade-like (i.e. segminate) conodonts (e.g., species of genera *Neospathodus*, *Discretella* and *Novispathodus*) and platform conodonts. This indicates that *Pl. corniger* was probably derived from a blade-like conodont and not from *Eurygnathodus*. Moreover, in the Idrija–Žiri area, species of *Eurygnathodus* and *Platyvillosus* do not co-occur, and there is a stratigraphic gap between occurrences of these two genera.

Stratigraphic range: Known from Olenekian.

Platyvillosus corniger sp. nov. Kolar-Jurkovšek T. & Chen Y.L.

Figure 3.5.5–7; Figure 3.6.1–6; Figure 3.7.1–3

Etymology: Latin, *corniger*, means horned, having horn; for denticles of the holotype that resemble horns.

Holotype: specimen illustrated in the Figure 3.6.4

Paratype: specimen illustrated in the Figure 3.5.5–7; Figure 3.6.1–3, 5–6; Figure 3.7.1–3

Type locality: Žiri-sortirnica 28 section, Žiri, Slovenia.

Type level: at 26.6 m of Žiri-sortirnica 28 section, Olenekian, Lower Triassic.

Diagnosis: P_1 element is platform-like in adult stage, with a width: length ratio of about 1:2, and commonly bearing 9–13 denticles on the upper surface, a large concave basal cavity.

Description: in upper view, denticles are in a roughly arranged pattern: one or two rows can be observed in the anterior part of the unit, and a sinus can be clearly observed between these two rows. In some specimens these two rows converge in the posterior part of the unit (e.g., Fig. 3.7.1–3), while others do not show a clearly joined carina on the posterior process (e.g., Fig. 3.6.3). In lateral view, denticles are generally erect and high, sometimes slightly posteriorly inclined in the posterior part of the unit; they occupy about half of the total depth of the element. In lower view, there is a large concave basal cavity that occupies about two-thirds of the total length of the unit, a basal pit located in the center of the cavity, a basal furrow extending from the basal pit to the anterior end, and sometimes a very weak furrow running through the basal pit to the posterior end.

In juvenile stage (e.g., Fig. 3.5.5), P_1 elements show a transitional character between blade-like (segminate) conodonts (e.g., species of genera *Neospathodus*, *Discretella, Spathicuspus* and *Novispathodus*) and platform conodonts. The juvenile unit is narrower than the adult stage, has a width: length ratio of about 1:3, with denticles that are slightly laterally compressed, and an indistinct cusp. A large and deep, elliptical basal cavity occupies about two-thirds of the total length of the basal margin. A small pit is located in the center of the basal cavity and a basal furrow runs from the pit to the anterior end.

Comparisons: the present species can be distinguished from *Platyvillosus regularis* by its two rows of denticles in the anterior part of the unit, and a clear sinus between these two rows. It can be differentiated from *Pl. asperatus* by larger and higher denticles on the upper surface. *Pl. corniger* can be differentiated from *Radiatignathus radiatus* (Tian, 1983) by the lack of distinct lateral processes. Another similar species *Parafurnishius xuanhanensis* Yang, Yuan, Henderson, and Shen has also been reported from Sichuan Province (Yang et al., 2014), but is Griesbachian in age. *Pa. xuanhanensis* commonly has a triangular platform in posterior part of the unit that is not observed in the group of *Pl. corniger* sp. nov. Moreover, the Chinese species has an anterior carina that commonly fades in the middle part of the unit (e.g., Yang et al., 2014, fig. 3.Ba – 3.Cb), whereas *Pl. corniger* has an anterior carina that extends to the middle or posterior part of the unit. Remarkable differences between *Pl. regularis* and *Pa. xuanhanensis* can be observed in their multielement apparatuses. Their P_2, S and M elements show distinct difference (Kolar-Jurkovšek et al., submitted).

Remarks: *Platyvillosus regularis* and *Pl. corniger* sp. nov. share some similarities, but they can be differentiated based on morphological differences and different stratigraphic distribution. Both species have also been found at the Mokrice section in eastern Slovenia (Kolar-Jurkovšek et al., submitted) where two zones can be distinguished, as in the present study.

Stratigraphic distribution: Olenekian, *Platyvillosus corniger* Zone (UA 5).

Material: 12 well preserved specimens obtained from the Žiri-sortirnica 28 section, samples 28/6, 28/8, 28/9, 28/10, 28/15.

Platyvillosus regularis (Budurov & Pantić, 1973)

Figure 3.5.1–4; Figure 3.7.4

1973 *Pseudofurnishius regularis* n. sp. Budurov and Pantić, p. 65, pl. 1, fig. 16–18

Diagnosis: The P_1 element is a platform with a width: length ratio of about 1:2, 13–21 denticles on the upper surface. Denticles are evenly distributed but do not show any arranged pattern.

Description: In lateral view, denticles are discrete and occupy about half of the total depth of the element. Denticles are erect, but some specimens have posteriorly inclined denticles in the posterior part of the unit. The basal margin can be straight or curved, sometimes slightly upturned in the anterior part. In lower view, there is a concave basal cavity, which occupies about two-thirds of the total length of the unit, a small basal pit located in the center of the basal cavity, and a basal furrow extending from the basal pit toward the anterior end.

Comparisons: The present species resembles *Platyvillosus asperatus* by the lower surface as they both have a prominent basal cavity, but *Pl. regularis* has high denticles on the upper side compared with relatively low nodes in *Pl. asperatus*.

Remarks: Budurov & Pantić (1973) reported *Platyvillosus regularis* from the Early Triassic Campiller Beds. They assigned this species to the genus *Pseudofurnishius* and corrected the age of this species as Ladinian with a handwriting in their printed paper which is widespread (e.g., our copy; Ramovš, 1977; Bandel & Waksmundzki, 1985) probably because they thought that it was related to the Ladinian conodont *Pseudofurnishius huddlei* Boogard & Simon. However, Kozur and Mostler (1973) suggested assigning the species to the genus *Platyvillosus*, because they believed that *Pl. regularis* is Early Triassic in age, and it occurs much earlier than the genus *Pseudofurnishius*. Their suggestions were neglected in subsequent publications and *Pl. regularis* was treated as a Ladinian synonym of *Ps. murcianus* (e.g., Ramovš, 1977). We assign the present species to the genus *Platyvillosus* based on the suggestion of Kozur and Mostler (1973), and based on the similarity of the lower side of the P_1 element of *Platyvillosus* species (e.g., *Pl. asperatus* and *Pl. regularis*), which are characterized by a basal cavity and a basal furrow.

Kozur and Mostler (1973) proposed that *Platyvillosus regularis* is the forebear of *Foliella gardenae*, but our data do not support this scenario. According to data given above, 1) the oldest species of *Platyvillosus* probably developed from a blade-like (i.e. segminate) conodont; 2) *Foliella gardenae* does not co-occur with any *Platyvillosus* species in the Idrija–Žiri area and, moreover, there is a stratigraphic gap between them. The materials obtained from the present zone suggest rather that *Platyvillosus* is not related to *Foliella*. This strengthens the suggestion of Orchard (2007) that *Foliella* probably belongs to the conodont family Ellisoniidae and was derived from species of that family, although this has still to be verified with study of the conodont multielement apparatuses.

Stratigraphic distribution: Olenekian, *Platyvillosus regularis* Zone (UA 6).

Material: 5 well preserved specimens obtained from the Žiri-sortirnica 28 section, samples 28/17 and 28/18.

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Note:

Appendix 3.1 Data matrix for Unitary Association (UA) analysis

Appendix 3.2 Result of carbonate carbon isotope measurements

Appendix 3.1 Data matrix for Unitary Association (UA) analysis

Sections	code of sections	Rock samples	*Ns.r.pinus*	*Pl.regularis*	*Pl.corniger*	*Tr. symmetricus*	*Tr. hungaricus*	*P. inclinata*	*P. obliqua*	*F. gardenae*	*Ns. planus*	*Ns. robustus*	*N.tahoensis*	*H. aequabilis*
Žiri-sortirnica 28	1	29/19	0	0	0	1	0	0	0	0	0	0	0	0
	1	29/19c	1	0	0	0	0	0	0	0	0	0	0	0
	1	29/19b	1	0	0	0	0	0	0	0	0	0	0	0
	1	29/19a	1	0	0	0	0	0	0	0	0	0	0	0
	1	28c/1	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/2	0	0	0	1	0	0	0	0	0	0	0	0
	1	28c/3	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/4	0	0	0	1	0	0	0	0	0	0	0	0
	1	28c/5	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/6	0	0	0	0	1	0	0	0	0	0	0	0
	1	28c/7	0	0	0	0	1	0	0	0	0	0	0	0
	1	28c/8	0	0	0	0	1	0	0	0	0	0	0	0
	1	28c/9	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/10	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/11	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/12d	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/12c	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/12b	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/12a	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/13b	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/13a	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/14	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/15	0	0	0	0	1	0	0	0	0	0	0	0
	1	28c/16	0	0	0	0	0	0	0	0	0	0	0	0
	1	28c/17	0	0	0	0	1	0	0	0	0	0	0	0
	1	28/18c	0	0	0	0	1	0	0	0	0	0	0	0
	1	28/18b	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/18a	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/18	0	1	0	0	0	0	0	0	0	0	0	0
	1	28/17	0	1	0	0	0	0	0	0	0	0	0	0
	1	28/16	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/15	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/14	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/13	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/12	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/11	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/10	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/9	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/8	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/7	0	0	1	0	0	0	0	0	0	0	0	0
	1	28/6	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/5	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3.1 Data matrix for Unitary Association (UA) analysis

Sections	code of sections	Rock samples	*Ns.r.pinus*	*Pl.regularis*	*Pl.corniger*	*Tr. symmetricus*	*Tr. hungaricus*	*P. inclinata*	*P. obliqua*	*F. gardenae*	*Ns. planus*	*Ns. robustus*	*N.tahoensis*	*H. aequabilis*
Žiri-sortirnica 28	1	28/4	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/3	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/2	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/1	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/1x	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/2x	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/3x	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/4x	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/5x	0	0	0	0	0	0	0	0	0	0	0	0
	1	28/6x	0	0	0	0	0	0	0	0	1	1	0	0
	1	28/7x	0	0	0	0	0	0	0	0	0	1	0	0
Žiri-road cut 29	2	29z/5	0	0	0	0	0	1	1	0	0	0	0	0
	2	29z/4	0	0	0	0	0	1	1	0	0	0	0	0
	2	29z/3	0	0	0	0	0	1	1	0	0	0	0	0
	2	29z/2	0	0	0	0	0	1	1	0	0	0	0	0
	2	29z/1	0	0	0	0	0	1	1	1	0	0	0	0
	2	29z/0	0	0	0	0	0	1	1	0	0	0	0	0
Žiri-Vrsnik 61	3	61z/15	0	0	0	0	0	0	0	0	0	1	0	0
	3	61z/14	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/13	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/12	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/11	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/10	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/9	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/8	0	0	0	0	0	0	0	0	0	1	0	0
	3	61z/7	0	0	0	0	0	0	0	0	0	1	0	0
	3	61z/6	0	0	0	0	0	0	0	0	1	1	0	0
	3	61z/5	0	0	0	0	0	0	0	0	1	0	0	0
	3	61z/4	0	0	0	0	0	0	0	0	1	0	0	0
	3	61z/3	0	0	0	0	0	0	0	0	1	0	0	0
	3	61z/2	0	0	0	0	0	0	0	0	0	0	0	0
	3	61z/1	0	0	0	0	0	0	0	0	0	0	0	0
Krivi Potok	4	PK4/4	0	0	0	0	0	0	0	0	1	0	0	0
	4	PK4	0	0	0	0	0	0	0	0	1	0	0	0
	4	PK4/5	0	0	0	0	0	0	0	0	1	0	0	0
	4	PK5	0	0	0	0	0	0	0	0	1	0	0	0
	4	PK6	0	0	0	0	0	1	1	1	0	0	0	0
	4	PK7	0	0	0	0	0	0	1	1	0	0	0	0
Mokrice	5	R1/4	0	0	0	0	1	0	0	0	0	0	1	0
	5	R1/3	0	0	0	0	1	0	0	0	0	0	0	0
	5	R1/2	0	0	0	0	1	0	0	0	0	0	0	0
	5	R1/1g	0	1	0	0	0	0	0	0	0	0	0	0

Appendix 3.1 Data matrix for Unitary Association (UA) analysis

Sections	code of sections	Rock samples	*Ns.r.pinus*	*Pl.regularis*	*Pl.corniger*	*Tr. symmetricus*	*Tr. hungaricus*	*P. inclinata*	*P. obliqua*	*F. gardenae*	*Ns. planus*	*Ns. robustus*	*N.tahoensis*	*H. aequabilis*
Mokrice	5	R1/1f	0	1	0	0	0	0	0	0	0	0	0	0
	5	R1/1e	0	1	0	0	0	0	0	0	0	0	0	0
	5	R1/1d	0	0	1	0	0	0	0	0	0	0	0	0
	5	R1/1c	0	0	1	0	0	0	0	0	0	0	0	0
	5	R1/1b	0	0	1	0	0	0	0	0	0	0	0	0
	5	R1/1a	0	0	1	0	0	0	0	0	0	0	0	0
	5	R2/7	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/6	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/5	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/4	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/3	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/2	0	0	0	0	0	0	0	0	0	0	0	1
	5	R2/1	0	0	0	0	0	0	0	0	0	0	0	1
Krkoč 43	6	43k/8	0	0	0	0	0	0	0	0	0	0	0	0
	6	43k/7	0	0	0	0	0	0	0	0	0	0	0	0
	6	43k/6	0	0	0	0	0	0	0	0	0	0	0	0
	6	43k/5	1	0	0	0	0	0	0	0	0	0	0	0
	6	43k/4	1	0	0	0	0	0	0	0	0	0	0	0
	6	43k/3	0	0	0	0	0	0	0	0	0	0	0	0
	6	43k/2	0	0	0	0	0	0	0	0	0	0	0	0
	6	43k/1	0	0	0	0	0	0	0	0	0	0	0	0

Sections	code of sections	Rock samples	*E.costatus*	*E.hamadai*
Golob 44	7	44g/13	1	1
	7	44g/12	1	1
	7	44g/11	1	1
	7	44g/10	1	1
	7	44g/9	1	1
	7	44g/8	1	1
	7	44g/7	0	0
	7	44g/6	1	1
	7	44g/5	1	0
	7	44g/4	0	0
	7	44g/3	1	0
	7	44g/2	0	0
	7	44g/1	1	0

Appendix 3.2 Result of carbonate carbon isotope measurements

Sample	$\delta^{13}C$	$\delta^{18}O$
Ziri-Vrsnik61/1	6,9	-7,6
Ziri-Vrsnik61/4	5,6	-5,9
Ziri-Vrsnik61/7	5,0	-4,4
Ziri-Vrsnik61/8	5,3	-5,6
Ziri-Vrsnik61/9	5,4	-5,6
Ziri-Vrsnik61/13	3,7	-3,0
Ziri-Vrsnik61/14	3,9	-2,6
Ziri-road cut29/0	0,5	-4,3
Ziri-road cut29/1	2,0	-3,4
Ziri-road cut29/2	6,8	-2,6
Ziri-road cut29/3	5,9	-8,1
Ziri-road cut29/4	6,9	-8,2
Ziri28/005	3,3	-1,9
Ziri28/004	3,1	-1,9
Ziri28/1	2,7	-2,8
Ziri28/3	2,6	-2,0
Ziri28/5	2,6	-2,6
Ziri28/6(1)	2,5	-2,6
Ziri28/6(2)	2,7	-2,4
Ziri28/7	2,3	-2,1
Ziri28/8	2,4	-2,5
Ziri28/12	2,6	-2,1
Ziri28/13	2,5	-2,0
Ziri28/14	2,3	-2,0
Ziri28/15	2,4	-1,9
Ziri28/16	2,6	-1,4
Ziri28/17	2,4	-1,9
Ziri28/18	2,3	-4,3
Ziri28/18a	2,3	-2,7
Ziri28/18b	2,1	-3,1
Ziri28/18c	2,1	-2,2
Ziri28/19a	0,8	-2,1
Ziri28/19b	0,7	-2,1
Ziri28/19c	0,7	-2,5
Ziri28c/1	0,9	-2,3
Ziri28c/2	0,8	-2,3
Ziri28c/3	1,0	-2,2
Ziri28c/4	0,8	-2,7
Ziri28c/5	0,9	-2,7
Ziri28c/6	1,1	-2,1
Ziri28c/7	1,2	-2,6
Ziri28c/8	1,7	-3,0
Ziri28c/9	2,2	-2,2
Ziri28c/10	1,4	-2,4
Ziri28c/11	2,0	-2,3
Ziri28c/12a	1,7	-2,9

Appendix 3.2 Result of carbonate carbon isotope measurements

Sample	$\delta^{13}C$	$\delta^{18}O$
Ziri28c/12b	2,7	-2,7
Ziri28c/12c	1,3	-3,3
Ziri28c/12d	1,4	-2,5
Ziri28c/13a	2,1	-2,9
Ziri28c/13b	1,8	-2,5
Ziri28c/14	2,7	-2,0
Ziri28c/15	2,8	-2,4
Ziri28c/16	2,4	-3,1
Ziri28c/17	1,9	-3,3
Krkoč43/1	1,5	-4,9
Krkoč43/2	1,5	-4,5
Krkoč43/3	1,1	-4,5
Krkoč43/4	1,0	-5,8
Krkoč43/5	0,8	-6,6
Krkoč43/6	1,1	-6,1
Krkoč43/7	1,1	-5,8
Krkoč43/8	1,1	-6,1
Krkoč43/9	1,2	-6,0
Golob44/1	5,3	-5,8
Golob44/2	5,5	-8,1
Golob44/3	4,7	-8,3
Golob44/4	4,6	-8,4
Golob44/5	6,9	-8,4
Golob44/6	5,6	-8,2
Golob44/7	6,8	-8,2
Golob44/8	7,4	-8,3
Golob44/9	7,4	-8,3
Golob44/10	6,7	-7,6
Golob44/11	6,5	-8,1
Golob44/12	7,8	-7,7
Golob44/13	7,2	-4,3
Golob44/14	8,3	-8,0
Golob44/15	8,0	-7,5
Golob44/16	7,9	-8,0
Golob44/17	7,7	-8,2
Golob44/18	7,5	-7,6
Golob44/19	7,1	-8,4
Golob44/20	7,1	-8,5
Golob44/21	6,6	-8,7
Golob44/22	6,2	-8,5
Golob44/23	5,4	-8,4
Golob44/24	5,5	-8,7
Golob44/25	5,5	-8,8
Golob44/26	5,4	-8,7

CHAPTER 4

GEOMETRIC MORPHOMETRIC ANALYSIS REVEALS THE ALLOMETRY OF ANISIAN (MIDDLE TRIASSIC) SEGMINIPLANATE CONODONTS

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Abstract

Conodonts are a paramount clade of chordates in paleontology. Their tooth-like skeletal feeding apparatus are valuable indicator fossils for biostratigraphy. The segminiplanate conodonts represent an important morphological group ranging from the Upper Carboniferous to the Upper Triassic. However, the morphological similarity of segminiplanate P_1 elements generates problems for taxonomy, especially in Permian and Triassic clades. This paper represents the first study of morphological variation in Triassic segminiplanate conodonts using geometric morphometrics. Using linear regressions between relative warp scores from both upper and lateral views and conodont length, we demonstrate strongly allometric growth patterns for the species *Paragondolella bifurcata* Budurov & Stefanov, 1972. Based on our results, the species-group taxa *Pg. praeszaboi bystrickyi* (Kovacs, Papsova & Perri, 1996) is early growth stage of *Pg. bifurcata* and thus is synonymous. For the same reason, we treat *Pg. unilobata* as a synonym of *Pg. bulgarica*. We suggest that the allometry of conodonts should be considered seriously and using larger sized segminiplanate conodonts in the population of a rock sample for the definition of new species in future studies.

4.1. Introduction

Conodonts are a paramount clade of chordates (Sweet and Donoghue, 2001). Their tooth-like skeletal feeding apparatus is of central importance for the biostratigraphic correlation of Cambrian to Triassic marine deposits (e.g., Murdock et al., 2013; Krystyn et al., 2007). The high quality and quantity of their fossil record makes them an invaluable resource for studying their evolutionary patterns (e.g., Donoghue, 2001; Chen et al., submitted). Meanwhile, their occurrences and size variations can be used as indicators of the paleo-environmental conditions (e.g., Chen et al., 2013; Chen et al., 2015). Conodonts have become increasingly important for the estimation of paleo-temperatures of the seawater based on stable oxygen isotopes (e.g., Sun et al., 2012; Torter et al., 2015).

Since conodonts were first described in 1856 by Christian Heinrich Pander (Sweet & Donoghue, 2010), the description and comparison of their morphological features has been the method for taxonomy. However, this subjective judgment is not always reliable, which raised questions about the taxonomic validity of some conodont species.

Among conodonts, segminiplanate species is an important group which ranges from the Upper Carboniferous to the Upper Triassic. They are especially valuable for Permian and Triassic biostratigraphic division and correlation. However, the morphological similarity of segminiplanate P_1 elements is a problem for taxonomy (Klets & Kopylova, 2007; Wardlaw & Collinson 1979). Already Wardlaw and Collinson (1979) proposed to analyze a large numbers of individuals to better assess morphological variability and differences between species (Mei et al., 2004; Yuan et al., 2014).

Middle Triassic segminiplanate conodonts are much more common than Early Triassic one (c.f. Gallet et al., 1998; Wang et al., 2005; Chen et al., 2015), especially for the middle to late Anisian. In the late Anisian, many sections yield exclusively segminiplanate species (e.g., Wang et al., 2005; Gallet et al., 1998; this study). Kovacs (2003) suggested assigning his Pelsonian (middle Anisian) segminiplanate conodonts, which were obtained from Balaton Highland, Hungary, to three species, i.e., *Paragondolella bifurcata* Budurov & Stefanov, 1972, *Pg. bulgarica* Budurov & Stefenov, 1975 and *Pg. hanbulogi* Sudar & Budurov, 1979. He based this classification on the taxonomic principles of Budurov and Stefanov (1972) and Sudar & Budurov (1979). Although these three species has different stratigraphic distribution, Kovacs (2003) already noticed that there are numerous transitional morphologies, which make it difficult for the taxonomy, between these three species. The transitional morphologies are probably juvenile of *Pg. hanbulogi* and *Paragondolella bifurcata* which resemble their common ancestor – *Pg. bulgarica* – in their early growth stages.

Allometry is the statistical association between size and shape (Mosimann, 1970), and it is a ubiquitous property of organisms during their ontogenic process (Adams, 2013). Although allometric growth has been documented for conodonts in general and has been indicated as the major cause of shape variation for Devonian conodonts (e.g., Girard & Renaud, 2008), the shape-size relationship of Triassic conodonts has been rarely assessed.

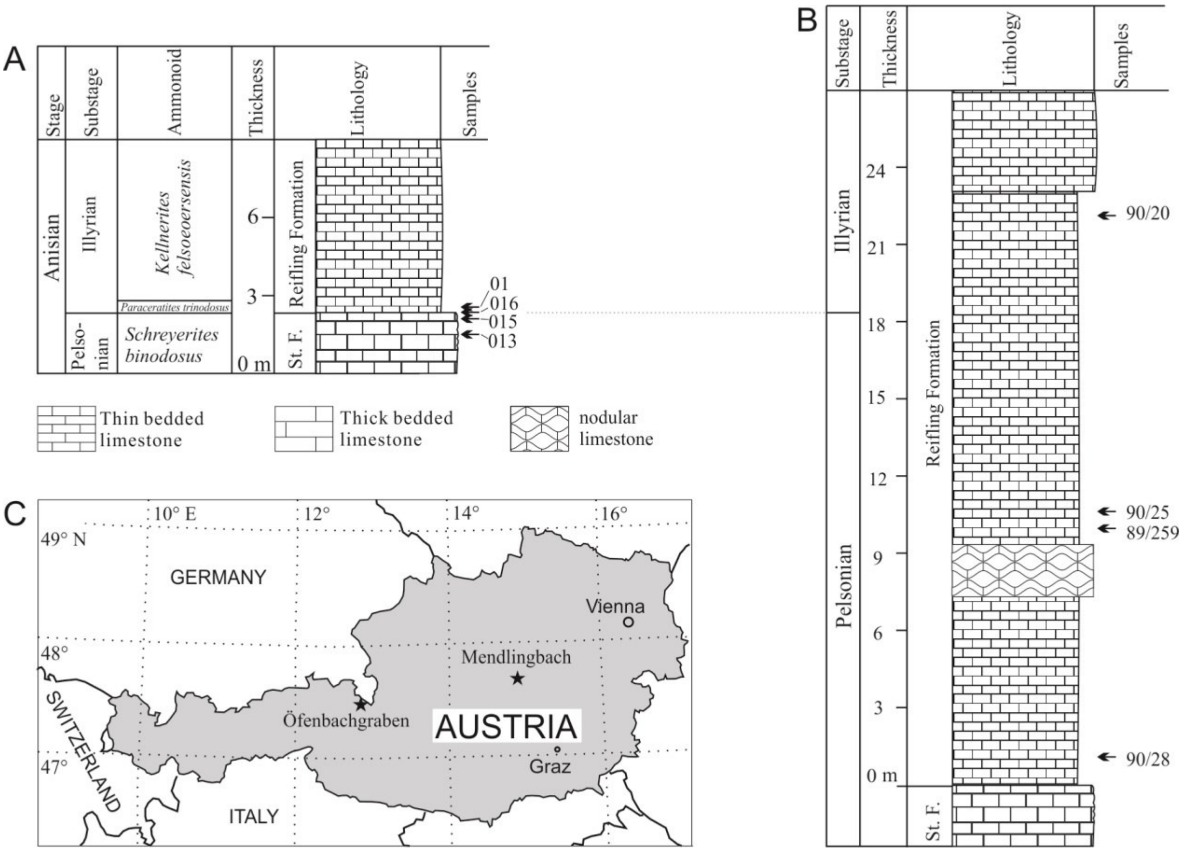

Figure 4.1. Lithology of the Öfenbachgraben Section (A) and Mendlingbach Section (B) and their geographic position (C) in Austria. St. F. = Steinalm Formation.

In the present investigation we apply for the first time geometric morphometrics to Triassic segminiplanate conodonts, incorporating as much quantitative shape information as possible. The development of geometric morphometrics was a ‘quantification revolution’ for the analysis of shape (Bookstein, 1998), bringing both biology and paleontology from a descriptive field to a quantitative science (Adams et al., 2004). The purpose of this study is to reveal the ontogenetic allometry of segminiplanate conodonts by means of a specific example from the Anisian of Austria. The results have significant implications for the taxonomy of Middle Triassic segminiplanate conodonts.

4.2. Material and geological background

Conodonts were obtained from rock samples from the two sections Öfenbachgraben (47°27'30.69"N; 12°52'11.06"E) and Mendlingbach (47°44'50.98"N; 14°52'42.14"E) in Austria (Figure 4.1), spanning the Pelsonian and Illyrian substages (Anisian, Middle Triassic). Both sections are located in the central part of the Northern Calcareous Alps (Mandl, 2000) and comprise the Steinalm Formation, followed by the Reifling Formation (Figure 4.1A–B).

The Steinalm Formation was deposited in carbonate platform facies and is composed of thick-bedded crinoidal bioclastic limestone. The Reifling Formation is interpreted as deposited in a deeper basin environment (e.g., Gallet et al., 1998), consisting of grey to yellowish and cherty hemipelagic limestones of various thicknesses interbedded with nodular limestones and shales. The drawing of the Steinalm Platform, with deposition of basinal sediments on platform sediments occur earlier in Mendlingbach than in Öffenbachgraben. Öffenbachgraben is also considered sedimentologically as more proximal than Mendlingbach.

Well preserved conodont specimens, irrespective of their size, were picked out for morphological analysis and length measurements. In total, 254 P_1 elements were analyzed in this study. Typical morphologies are shown in Figure 4.2. We suggest that all these specimens belong to a single species, i.e., *Paragondolella bifurcata* Budurov & Stefanov, 1972, and our taxonomical identification has been supported by the morphological analysis. The individual abundance of conodonts per rock sample is quite different, ranging from three well preserved specimens from sample 013 to 120 specimens from sample 90/28.

4.3. Methods

All analyses in this study are based on scanning electron microscope (SEM) photos. Two photos were taken for each conodont, one for lateral view, the other for upper view. In total, 508 SEM photos were taken at the Institute of Earth Sciences, University of Graz, using a Zeiss DSM 982 Gemini. Because the material comprises sinistral and dextral P1 elements in the conodont apparatus (c.f. Purnell et al., 2000), in the upper view the carina can bend to the right side or to the left side. Specimens were reproduced in mirror image if the carina does not bend to the left side in the upper view. The same strategy has been applied to the photos of lateral view.

To cover as many morphological details as possible, we used a combination of landmarks and semilandmarks for the geometric morphometric analysis. Landmarks define homologous anatomical loci that can be found unambiguously on every specimen (Zelditch, et al., 2004). Semilandmarks are used to characterize curves where no homologous point can be defined exactly (Bookstein, 1997a, b; Gunz & Mitteroecker, 2012). They are allowed to slide along the curve to optimize their spacing with respect to the average shape (Gunz et al., 2005; Mitteroecker & Gunz, 2009; Gunz & Mitteroecker, 2012).

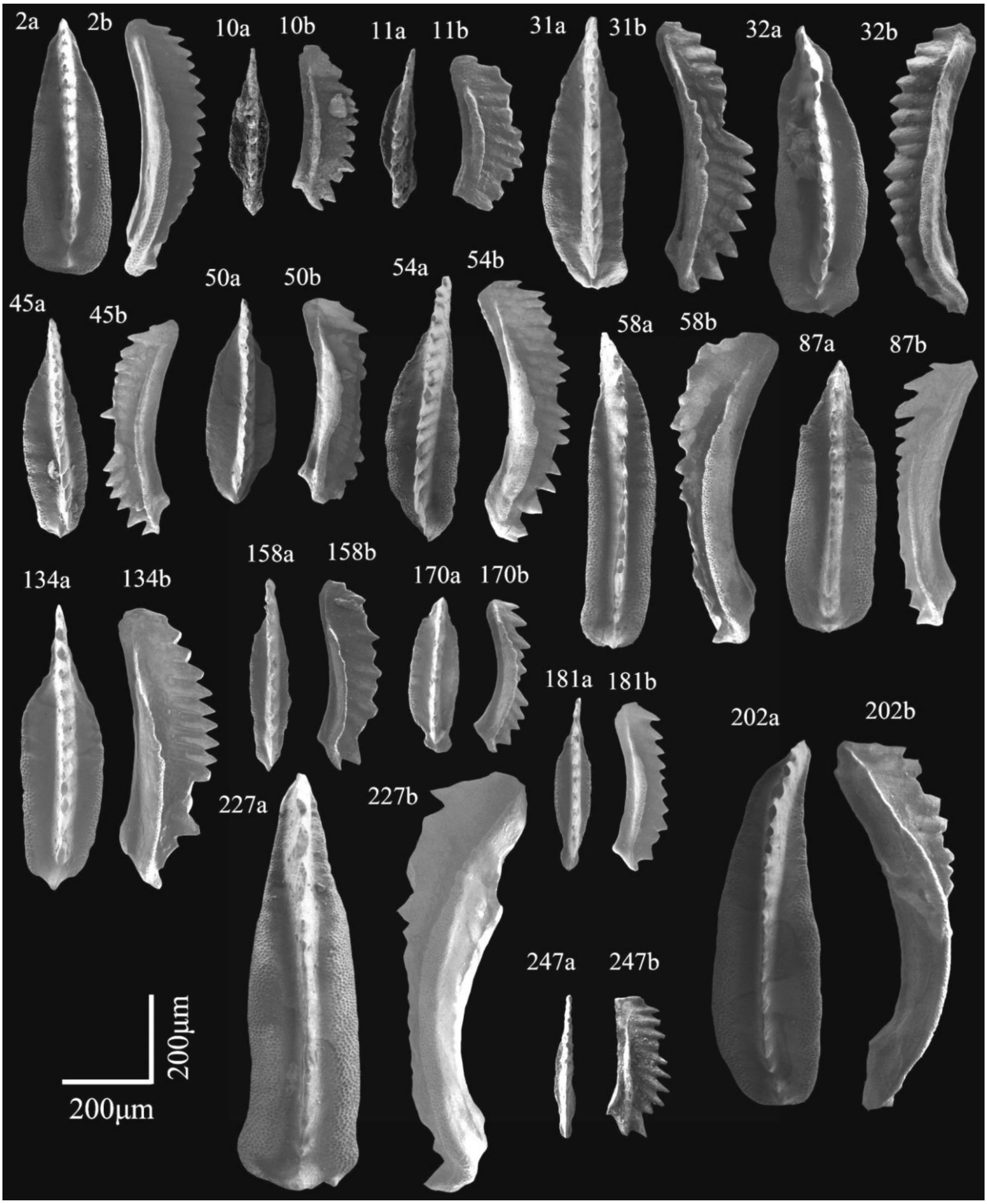

Figure 4.2. Pelsonian-Illyrian (Middle Triassic) conodonts of this study showing the size and morphological variations of *Paragondolella bifurcata*. Numbers in the figure correspond to the numbered specimens in this study. The letters indicate different views: a, upper view; b, lateral view.

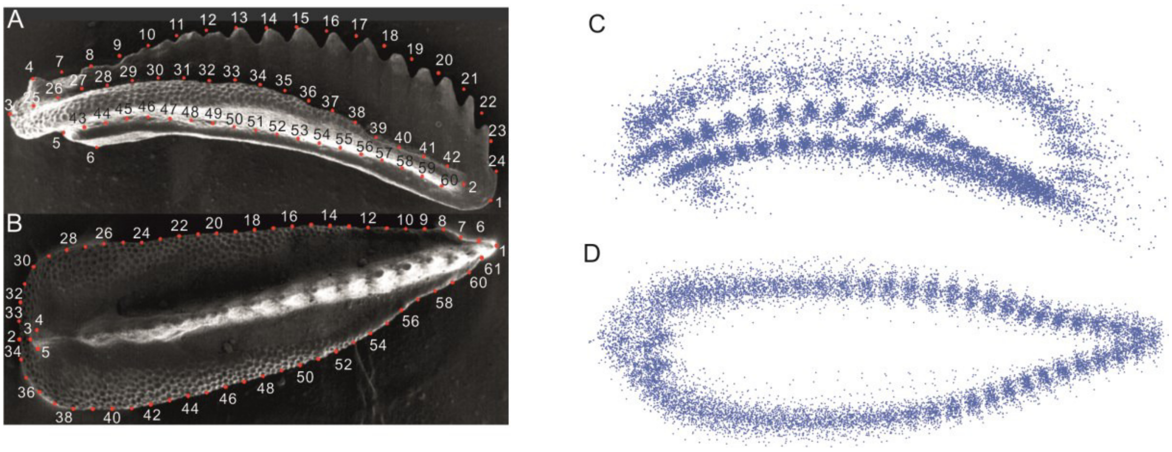

Figure 4.3. Definition (A and B) and superimposition (C and D) of landmarks.

In lateral view (Figure 4.3A), 6 Type II landmarks and 54 sliding semilandmarks were defined covering relevant homologues points and curves (Table 4.1). In upper view (Figure 4.3B), 5 Type II landmarks and 56 sliding semilandmarks were defined. Landmarks and semilandmarks were placed using the software TpsDig2 Version 2.16 (Rohlf, 2005) and were conducted for each specimen by the same person (Yanlong Chen). For defining the semilandmarks, we constructed curves along the platform margin (upper view) and carina (lateral view), respectively, which were then resampled to create an equal number of points.

Table 4.1. Definition of landmarks and semilandmarks.

Views	Landmark	Description
Lateral	1	Anterior extremity
	2	Anterior end of platform
	3	Posterior end of platform
	4	Acme of the denticle of the posterior end
	5	Posterior end of keel
	6	Posterior end of groove
	7–24	Sliders between landmark 1 and 6, along the acme of denticles
	25–42	Sliders between landmark 2 and 3, along the upper brim of the platform
	42–60	Sliders between landmark 2 and 8, along the lower brim of the platform
Upper	1	Anterior extremity
	2	Posterior end
	3	Posterior end of carina
	4	End of the carina on the left side of cusp
	5	End of the carina on the right side of cusp
	6–33	Sliders between landmark 1 and 2 along the left brim of the platform
	34–61	sliders between landmark 1 and 2 along the right brim of the platform

After digitizing all the landmarks and curves, the software TpsUtil Version 1.47 (Rohlf, 2005) was applied to transfer curves to landmarks and create the sliders file defining the semilandmarks.

The superimposition method applied here is the Generalized Procrustes Analysis (Figure 4.3C and 4.3D), computed by the software TpsRelw Version 1.49 (Rohlf, 2003). It computes the average configuration of landmarks, referred to as a 'consensus' configuration, which serves as the reference for the superimposition of all specimens. Semilandmarks are slid by minimizing Procrustes distances between individual specimens and the average configuration (Zelditch et al., 2004; Rohlf, 2005). Relative warps (RW) and thin-plate splines were used to evaluate the morphospace and the relation of shape variables with size.

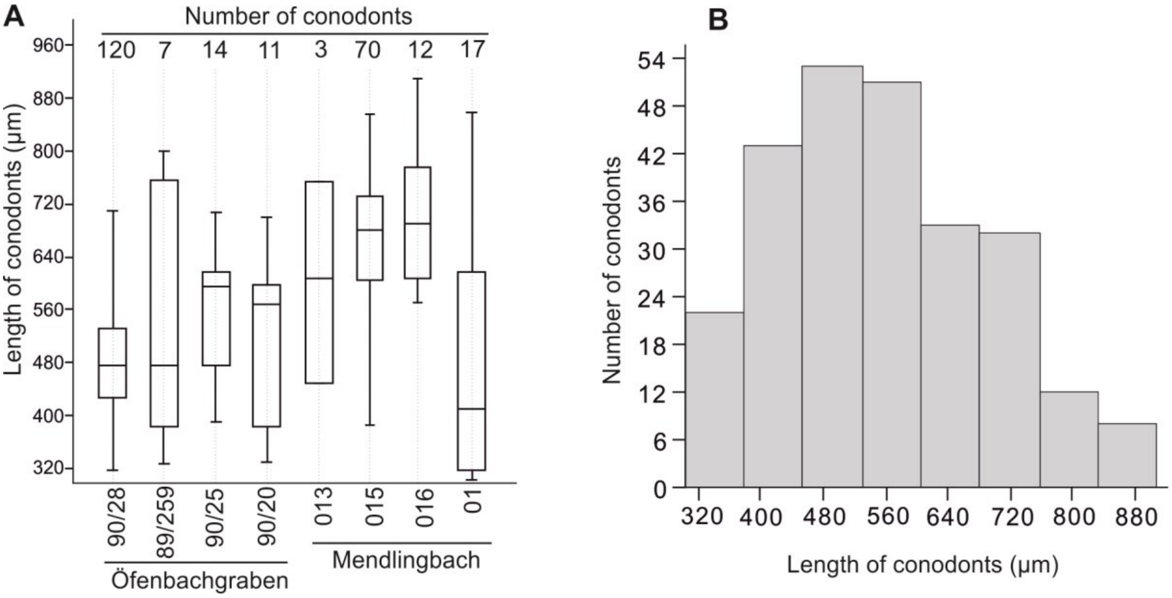

Figure 4.4. Length of conodonts used for geometric morphometric analysis. A. Box plot of conodont lengths per rock sample. For each sample, the 25%–75% quartiles of length (L) are shown by a box; the horizontal line inside each box shows the median value; and the maximum and minimum values are shown as short horizontal lines; B. Histogram of overall length distribution.

The length of conodont, which is considered to be a good proxy of their size (e.g., Luo et al., 2008; Chen et al., 2013), was measured from landmark 1 to 2 in upper view (Figure 4.4 B). To test the hypothesis that conodont shape varies with size (common logarithm of length), the program TpsRegr Version 1.38 (Rohlf, 2011) is applied to conduct a regression analysis. And the relationship between shape and size was also assessed using linear regressions between RW1 and common logarithm of length, performed in PAST Version 2.13 (Hammer et al., 2001).

4.4. Results

4.4.1. Length measurements

As it is shown in Figure 4.4A–B, the size of the conodont P1 elements varies considerably across samples, ranging from 320 µm to 900 µm. However, no general trend of conodont size increase or decrease over time can be observed from either section. In total, the size of the P1 elements shows a non-normal distribution (Shapiro-Wilks test: $W = 0.9772$, $p < 0.001$; Skewness $G_1 = 0.333$; Figure 4.5B). Such right-tailed distribution is typical across many different animal clades (e.g., Maurer et al., 1992; Knouft & Page, 2003; Clauset & Erwin, 2008).

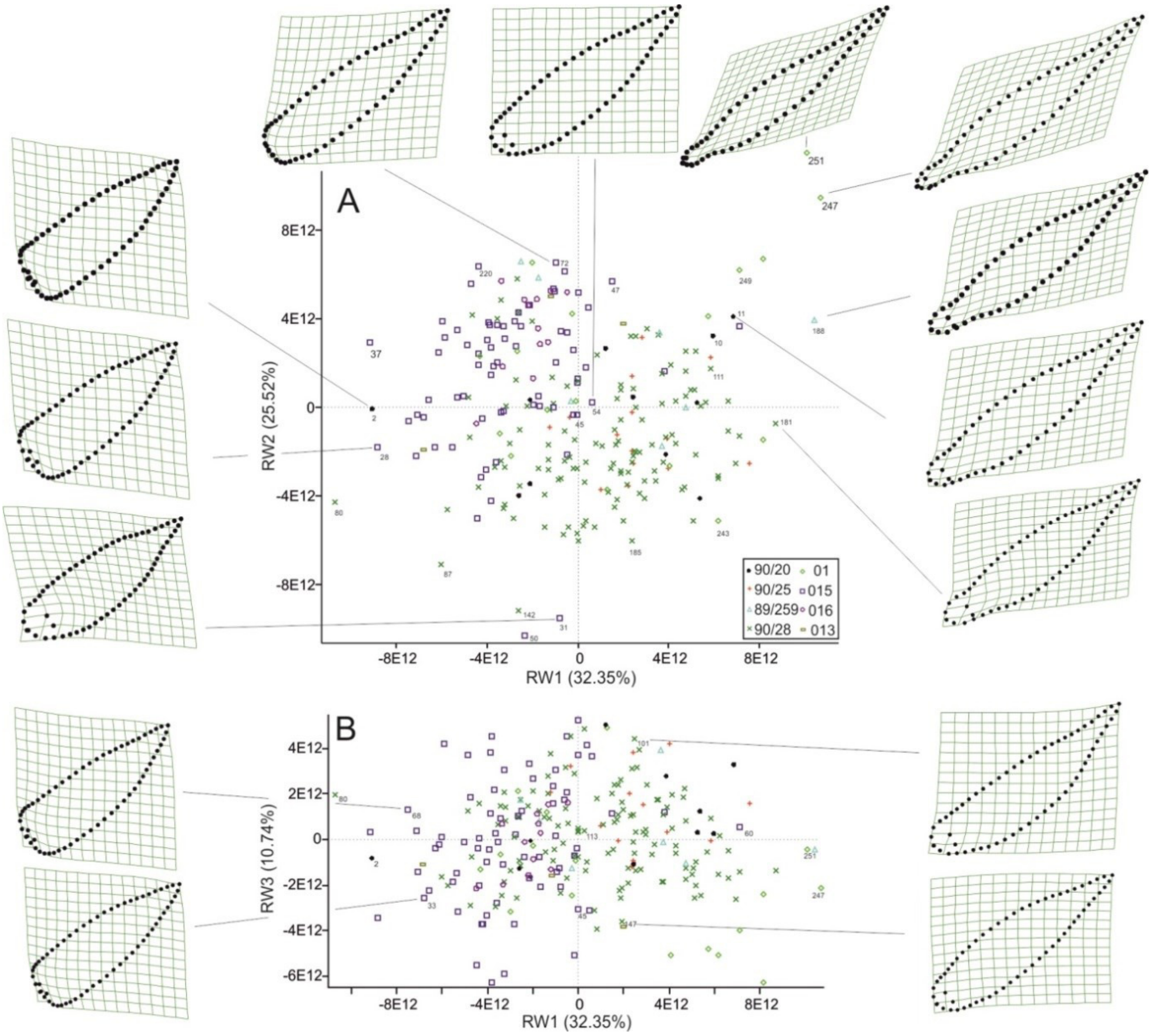

Figure 4.5. Plots for relative warps 1, 2 (A) and 3 (B) of the Relative Warp Analysis of the shape of the upper view with indication of characteristic thin-plate splines.

4.4.2. Morphometric analysis of the upper view

In total, 118 relative warp scores were obtained from the analysis. The first relative warp score (RW1) accounts for 32.35% of the total shape variation (Figure 4.5), followed by 25.52%, 10.74% and 8.47% for RW2, RW3 and RW4, respectively. The plot shows differences between the average morphologies of conodonts from different rock samples but without very clear distinction.

In the center part of Figure 4.5A, conodont morphology is close to the mean shape, as it is shown by the thin-plate splines. Specimens which have large positive scores of RW1 generally show a narrower platform, and there is constriction at the posterior end of the Specimen. Relatively to the mean shape, these conodonts are laterally compressed. Specimens which have large negative scores of RW1 show a wider posterior platform and a truncated posterior platform end. Relatively to the mean shape, these specimens are laterally elongated, but are compressed posteriorly and anteriorly. The strongest compression can be seen at the posterior end. Specimens which have positive scores of RW2 have a cusp located on the posterior end, while these specimens which have negative scores of RW2 generally have cusp locaed far from the posterior end. RW3 mainly explains the unsymmetrical of platforms (Figure 4.5B). Conodonts which have positive RW3 scores have well developed platform on the right side of the element. However, the negative values indicates well developed platform on the left side of the element.

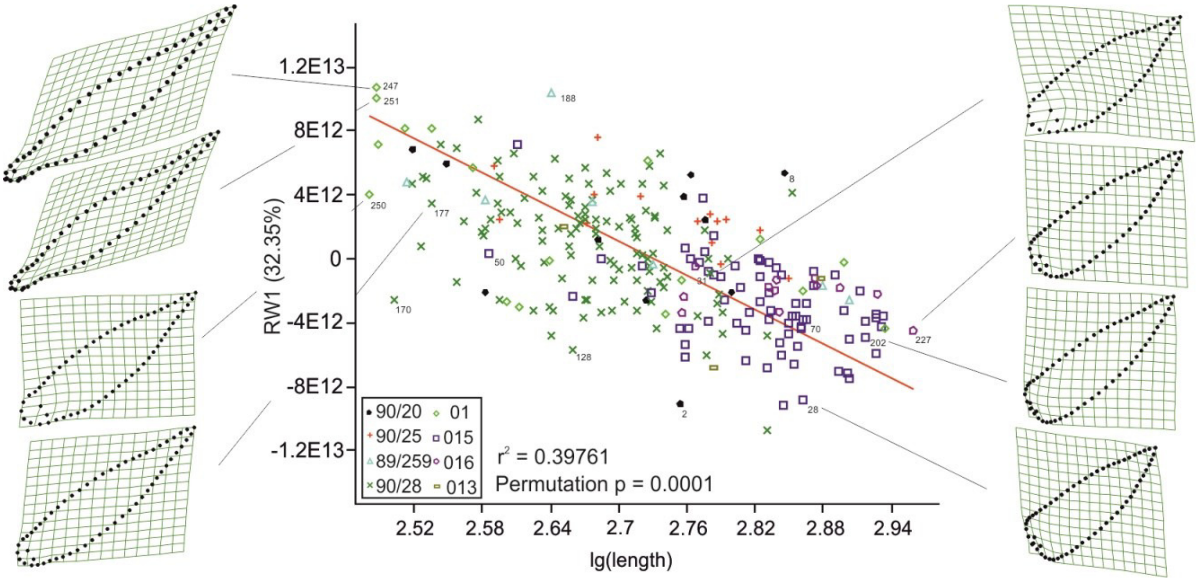

Figure 4.6. The linear regression of the shape of the upper view with conodont length, with indication of characteristic thin-plate splines.

Regression of overall upper shape on size (common logarithm of length) using multivariate regression gives a Wilks' Lambda test of significance of 0.157, meaning that the upper shape changes as a function of size significantly. The linear regression of RW1 and length indicates a strong relationship between shape and size ($r^2 = 0.398$, $p = 0.0001$; Figure 4.6). Small conodonts have narrow, elongated platforms widest in the middle part, tapering both anteriorly and posteriorly, while platforms of large conodonts are broad and widest close to a truncated posterior end and tapering towards the anterior end gradually (Figure 4.2; Figure 4.6). Specimens in between exhibit elongated leaf-shaped morphologies with the widest portion close to the posterior end. The position of the posterior end of the carina plays no role in the relationship with size.

4.4.3. Morphometric analysis of the lateral view

In total, 122 relative warp scores were obtained from the analysis of lateral view. The first relative warp score (RW1) accounts for 48.25% of the total shape variation (Figure 4.7). RW2, RW3 and RW4 express 17.17%, 11.77% and 4.75% of the total shape variation

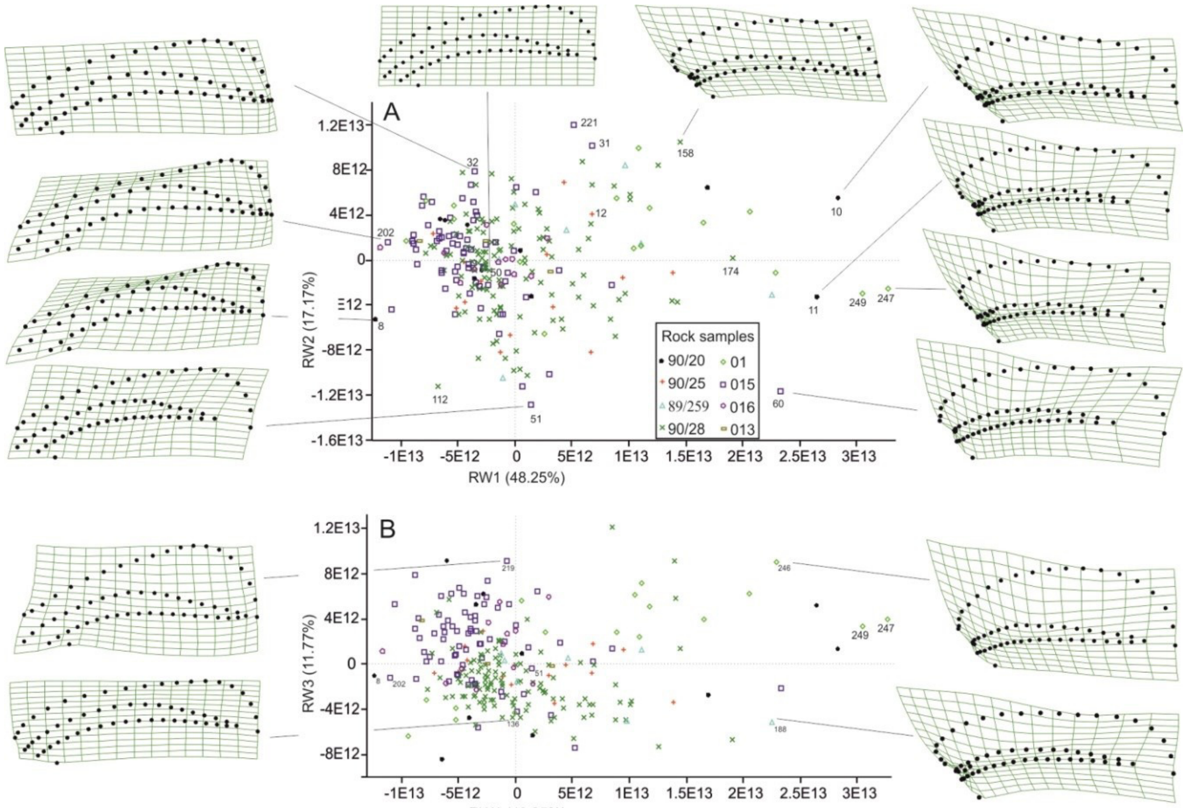

Figure 4.7. Plots for relative warps 1, 2 (A) and 3 (B) of the Relative Warp Analysis of the shape of the lateral view with indication of characteristic thin-plate splines.

respectively. The same as for the analysis of the upper view, there is no distinction of conodont morphologies between different biostratigraphic position of rock samples and between both sections.

Specimens with RW1 and RW2 scores close to zero, are similar to the mean shape of these 254 specimens. Specimens with positive RW1 scores (right part of Figure 4.7A) have uniformly higher carina, thin platform which resembles a lateral ridge and badly developed posterior platform as indicated by the strongly compressed grids on the posterior part. While specimens with positive RW1 scores (left part of Figure 4.7A) have low posterior carina. And relatively to the mean shape, the carina of the middle and posterior part are strongly compressed, as the grids are strongly compressed in the upper left part of the thin-plate spline. The anterior carina is higher than the posterior carina. RW2 mainly differentiates the distance between the anterior end of the specimen and the anterior end of the platform. Specimens which have positive RW2 scores have a small distance between the anterior end of the specimen and the anterior end of the platform, while negative RW2 scores indicate a large distance. RW3 mainly explains the relative highness of the anterior carina (Figure 4.7B). Specimens with positive RW3 scores have relatively high anterior carina, while negative scores indicate low anterior carina.

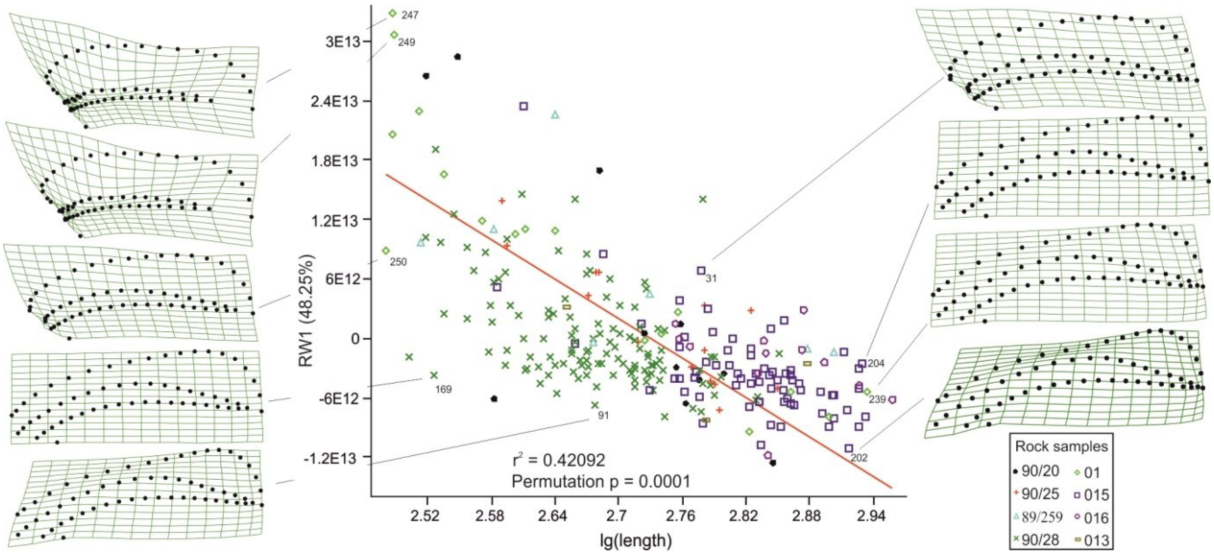

Figure 4.8. The linear regression of the shape of the lateral view with conodont length, with indication of characteristic thin-plate splines.

Regression of overall lateral shape on size (common logarithm of length) using multivariate regression gives a Wilks' Lambda test of significance of 0.083, meaning that lateral shape changes as a function of size significantly. Not surprisingly, also for lateral view the linear regression of RW1 and platform length indicates a strong relationship between shape and size ($r^2 = 0.421$, $p = 0.0001$; Figure 4.8). Here, the differentiation between large and small conodonts largely corresponds to the varied shape of carina. Small conodonts comprise a great variety of morphologies, including broad to narrow, regularly semicircular to sloping carinas. Larger conodonts in turn expose a more restricted morphological spectrum and exclusively show carinas that are posteriorly lowered and anteriorly elevated. Additionally, platforms are on average thinner in young individuals.

4.5 Discussions

4.5.1. Size of conodonts

The conodonts analyzed in this study cover a wide size spectrum, which differs across rock samples. Size was most probably controlled by paleoenvironmental factors such as temperature, food and oxygenation (e.g., Twitchett, 2007; Chen et al., 2013), as there is no consistent trend of size change at either section. The rock samples 015 and 016 which yield larger conodonts derive from crinoidal bioclastic limestones indicating the most ecologically favorable facies for Triassic conodonts. The rock sample 90/28 is a slightly bituminous, sponge spicules-bearing wackestone of a deeper basin facies showing weak oxygenation, going along with smaller conodonts.

4.5.2. Allometry and implications for conodont taxonomy

Mosher (1968a, b) established the genus *Paragondolella* on the basis of its allometry. Accroding to his observation, the earliest growth stage of P_1 elements of *Paragondolella* is bladelike with uniformly high carina but without a lateral ridge, whereas the second growth stage does have a ridge but the carina becomes less uniformly high, and following stages have a well-developed platform which is truncated on the posterior end, a high carina on the anterior part of the element and a low carina on the posterior part (cf. Mosher, 1968a, fig. 3). The allometry of *Paragondolella* conodonts has been adopted by Hirsch (1994), but was neglected by many conodont workers.

One of us (L.K.) has hold the opinion for a long time that some of these Pelsonian and Illyrian segminiplanate conodont species are not tenable, as some proposed species are probably different growth stages of a natural species. Species determination of conodonts is often hampered by the great number of similar morphospecies with transitional characters (e.g., Kovacs, 2003). To some extent the difficulty probably arises from allometry, which is commonly neglected by most authors. A central question in studies of ontogenetic allometry is how these transformations in size and shape are interrelated. To understand the morphology of segminiplanate conodonts we have to study the entire continuum of the conodont developmental process.

The relationship between conodont size and shape can be well predicted by the linear models as shown in Figures 4.6 and 4.8. In early growth stages, the studied segminiplanate conodonts have very poorly developed platforms, constricted near the posterior end, and mostly uniformly high carinas, and thin, short platforms. The cusp is usually not prominent and cannot be easily distinguished from the denticles. These characters are diagnostic of the morphospecies *Paragondolella praeszaboi bystrickyi* (Kovacs, Papsova & Perri, 1996), suggesting that this subspecies was probably based on early growth stage. Meanwhile, *Pg. praeszaboi bystrickyi* was reported co-occur with *Pg. bifurcata* thus is probably an early growth stage of *Pg. bifurcata*. For the same reason, *Pg. unilobata* (Gedik, 1975) shows characters of early growth stage and co-occur with *Pg. bulgarica*, we follow Nicora (1977) in treating *Pg. unilobata* as synonym of *Pg. bulgarica*.

In the middle growth stage, the widest part of the platform is located on the posterior part or the posterior end of the element (Figure 4.6), the platform may be slightly upturned, and attains about half of the total height of the carina (Figure 4.2; Figure 4.8). The cusp can be distinguished but is relatively small and low (e.g., Figure 4.2-2). Usually, the carina is the highest in the anterior part of the element. These features show high similarity with *Pg. bulgarica*. However, as *Pg.bulgarica* was already present in older strata before *Pg. bifurcata* was developed, thus they are not synonymized. The high similarity between the middle growth stage of *Pg. bifurcata* and the adult *Pg.bulgarica* indicates *Pg. bifurcata* was evolved from *Pg.bulgarica*.

In the latest growth stage, the widest part of the platform is located on the posterior end or close to the posterior end of the element (Figure 4.6). There, the platform is truncated or round, tapering gradually to the anterior end. The cusp can be easily recognized, and sometimes it can be very prominent (e.g., Figure 4.2-227). The carina is low on its middle and posterior part of the element but elevated on the anterior part of the element (Figure 4.8). These characters are typical for the species *Paragondolella bifurcata* (Budurov & Stefanov, 1972).

However, predicting morphology of lateral view from size is constrained. Small conodonts exhibit a broader morphological spectrum in lateral view (particularly regarding carina shape) than large individuals (Figure 4.8). Small sized conodonts which have high Relative Warp score 1, are here explain as dwarfed individuals. Thus, to claim an early stage of conodont based on the small size is not reliable. Larger sized conodonts are relatively conservative regarding their morphology (Figure 4.8) of both lateral and upper view. Therefore, we propose that taxonomy of segminiplanate conodont should be based on large individuals in a population yielded by a rock sample.

The continuous transition in shape, coupled with size change (Figure 4.6 and 4.8), supports that the analyzed 254 specimens are only one natural species. There is no clear distinction between conodonts from different samples or sections in our samples; they rather form a morphological continuum. The geometric morphometric analysis indicates that some former definitions of species around the late Pelsonian and Early Illyrian may be arbitrary, especially for these species which are taxonomically defined by juvenile specimens, e.g., *Gondolella praeszaboi bystrickyi* (Kovacs et al., 1996) and *Pg. unilobata* (Gedik, 1975). Ruling out these artificial species in this time interval, the observation that conodonts are in a phase of slow phylomorphogenetic changes in the ammonoid *Paraceratites trinodosus* Zone (Kozur, 2003) is true.

4.6. Conclusions

The present investigation demonstrates the strong relationship of conodont shape and size. In the juvenile stage, *Paragondolella bifurcata* has a mostly uniformly high carina, thinner and narrower platform, which tapers both posteriorly and anteriorly. In adult specimens the carina is posteriorly low and anteriorly elevated, and the platform is more or less truncated posteriorly and tapers anteriorly. The linear model of size and morphology particularly applies for large specimens, whereas smaller conodonts expose higher shape variability in lateral view.

The observed differences in size and shape likely reflect local morphological variation of a single polymorphic species. We consider the species-group taxa *Paragondolella praeszaboi bystrickyi* as a synonym of *Pg. bifurcata*. *Pg. bulgarica* is phylogenetically closely related to *Pg. bifurcata*, thus these species can have similar allometric pattern. And we follow Nicora (1977) in treating *Pg. unilobata* as synonym of *Pg. bulgarica*.

We suggest that the allometry of segminiplanate conodonts should be considered seriously in the process of conodont taxonomy and description. The small size conodonts may highly unstable with their morphology and thus the large sized individuals in the population of segminiplanate conodonts of a rock sample are more suitable for the taxonomical classification and for definition of new species.

4.7. References

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CHAPTER 5

A REVIEW OF THE EVOLUTION, BIOSTRATIGRAPHY, PROVINCIALISM AND DIVERSITY OF MIDDLE AND EARLY LATE TRIASSIC CONODONTS

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Abstract

The taxonomy, diversity, evolutionary lineages, and stratigraphic distributions of Middle and early Late Triassic conodonts is reviewed and re-evaluated. Twenty-five genera are recognized in the Middle and early Late Triassic, including a new genus cited in open nomenclature. Of these, 24 genera are assigned to two families and seven subfamilies. The family Gondolellidae consists of the subfamilies Cornudininae, Epigondolellinae, Neogondolellinae, Novispathodinae, Paragondolellinae, and Pseudofurnishiinae. The family Gladigondolellidae is monotypic, consisting of the subfamily Gladigondolellinae. The genus *Neostrachanognathus* is not assigned to any family or subfamily as its origin is unclear. Conodont provincialism was low in the early Anisian, but from the late Anisian faunistic differences started to increase and became stronger during the early Ladinian reaching a peak around the mid-Ladinian. Provincialism remained strong until the earliest Carnian and changed to an all-Triassic low in the early Tuvalian. The provincialism between North America and Tethys rebounded on the specific level during the late Tuvalian. Diversities on generic and specific levels have been established and two major conodont diversity cycles are recognized: the first ranges from the Bithynian (early Anisian) to the Julian (late early Carnian), and the second is restricted to the Tuvalian (late Carnian).

5.1. Introduction

Conodonts are an extinct group of eel-like chordates. Elements of their phosphatic feeding apparatus, which are usually 0.1 – 4 mm in size, can be found in marine sediments with an age range from Cambrian to Triassic. They are an excellent group for stratigraphic purposes (Mosher 1973), and their importance has been further enhanced in four ways: applications of colour alteration indices (e.g. Epstein *et al.* 1977; Rejebian 1987), provide palaeotemperatures of host rocks; oxygen stable isotopes in conodont apatite are an indicator of prevailing oceanic temperature (e.g. Joachimski and Buggish 2003; Trotter *et al.* 2008; Sun *et al.* 2012; Romano *et al.* 2013); size may be a parameter for environmental stress (e.g. Chen *et al.* 2013); and latitudinal differentiation is a guide to biogeographic/palaeoclimatic reconstructions (e.g. Charpentier 1984; Henderson and Mei 2007; Ishida and Hirsch 2011).

The first described conodont species of Middle and early Late Triassic were published in 1956 in papers by Diebel and by Tatge where several important Middle Triassic taxa, e.g. *Nicoraella kockeli* (Tatge, 1956), *Neogondolella mombergensis* (Tatge, 1956), and *Budurovignathus mungoensis* (Diebel, 1956) were introduced. In 1968, Mosher proposed the first evolutionary relationships of these Middle and Late Triassic conodonts and distinguished three lineages: 1) the *Neospathodus – Paragondolella* lineage; 2) the *Neogondolella* lineage; and 3) the gladigondolellid lineage (Mosher 1968*a*). These lineages became the fundamental basis for the Middle and Late Triassic conodont taxonomy. Budurov (1976), Orchard (1983, 1991a), Kozur and Mock (1991), Hirsch (1994*a*; 1994*b*), and Budurov and Petrunova (2000) prepared further contributions to Triassic conodont evolution and stratigraphic distribution, but their studies are restricted to a comparably small group of species. More recent contributions to the understanding of the Middle Triassic and Carnian conodont lineages are: (1) Orchard (2005) reconstructed the apparatuses of some Triassic conodont species; (2) a quantitative method (cladistics) was applied to evaluate Carnian conodont lineages (Mazza *et al.* 2012*a*); and (3) new criteria for Carnian conodont taxonomy and evolutionary lineages were proposed (Orchard 2013, 2014).

In this paper, we present a summary of all Middle and early Late Triassic (Carnian) conodonts, mainly focusing on their evolutionary lineages, stratigraphic distribution, provincialism, and diversity. The proposed phyletic relationships are present on figures following the style of Orchard (2007a). Our conclusions about the taxonomy are based on the conodont lineages with revisions presented for each taxonomic unit or group. Conodont provincialism is briefly summarized. Based on our stratigraphic framework, conodont diversity curves for short-ranged time intervals correlating largely to Tethyan standard ammonoid zones have been achieved.

5.2. Age constraints for conodonts

Biochronology of all studied conodonts is based on an inter-calibration between North American and Tethyan ammonoid zones (Fig. 5.1). Correlation of conodont and ammonoid zones follows Orchard and Tozer (1997), Gallet et al. (1994, 1998), Kozur (2003), Krystyn et al. (2005), Ogg (2012), and Orchard (2014); use of unpublished data is specifically identified by author initials (LK, MJO).

The base of the Anisian is dated to 247.2 Ma (Cohen *et al.* 2013) with the conodont *Chiosella timorensis* as proposed marker for its base (Kozur 2003). However, a Global Boundary Stratotype Section and Point (GSSP) has yet to be recognized by the International Commission on Stratigraphy (ICS) and the use of *Ch. timorensis* has been challenged (Goudemand *et al.* 2012).

The base of the Ladinian is defined in an ICS ratified GSSP in northern Italy by the first occurrence (FO) of the ammonoid *Eoprotrachyceras curionii* (Brack *et al.* 2005) with a radiometric age of *c*. 242 myr (Cohen *et al.* 2013). This ammonoid datum is close to the FO of *Budurovignathus praehungaricus* (Kovacs). The base of the Longobardian substage is approximately at the base of the *Protrachyceras longobardicum* ammonoid zone in the Alpine zonation (Ogg 2012).

The Carnian base is defined in an ICS ratified GSSP in northern Italy by the first occurrence (FO) of the ammonoid *Daxatina canadensis,* which is very close to the FO of *Quadralella polygnathiformis* (Budurov and Stefarov); in the Tethys the boundary is also close to the FO of *Budurovignathus diebeli* (Kozur and Mostler), and in Canada, it is close to the FO of *Quadralella intermedius* (Orchard, 2007*b*). The Carnian stage originally was subdivided into three substages following the Austrian geologist Mojsisovics (von Mojsisovics *et al*. 1895). These substages, based on specific ammonoid zones, were Cordevolian, Julian and Tuvalian. The Cordevolian corresponded to the *Trachyceras aon* zone, Julian to the *Trachyceras aonoides* zone, and Tuvalian to the *Tropites subbullatus* zone (Fig. 5.1; Ogg 2012). However, Krystyn (1978) evaluated the original definitions of the Cordevolian and Julian substages and determined that the stratotypes of the two substages referred to the same time interval and were synonymous. Thus the presently distinguished early Carnian *Austrotrachyceras austriacum*, *Trachyceras aonoides*, *T. aon* and *Daxatina*

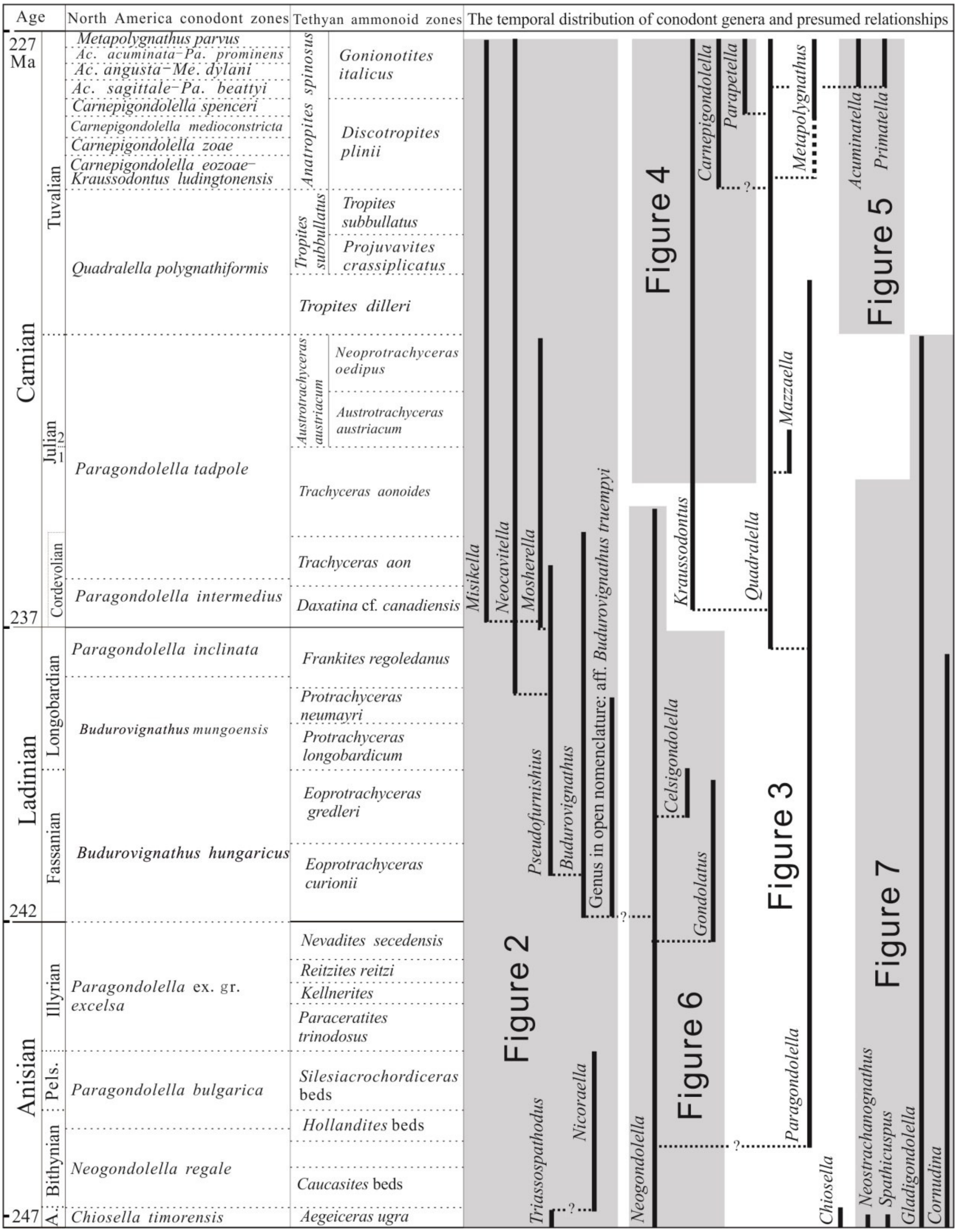

Figure 5.1. Correlations of conodont and ammonoid zones and the conodont generic distribution. Dashed lines indicate the absolute ages are not yet constrained or indicate the protential evolutionary relationships. North America conodont zones are defined after Orchard and Tozer (1997), and Orchard (2007, 2010, 2014). Tethyan ammonoid zones are defined after Gallet *et al*. (1994), Krystyn *et al*. (2004) and Ogg (2012). Absolute age

constraints after Cohen *et al*. (2013). Abbreviations: *Ac*. = *Acuminatella*; *Me*. = *Metapolygnathus*; *Pa*. = *Parapetella*; A. = Aegean; Pels. = Pelsonian.

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canadensis zone all belong to the Julian but are occasionally combined into a general *Trachyceras* zone (e.g. Mietto *et al*. 2012). The use of "middle Carnian" (e.g. Kozur 2003) to include the *T. aonoides* and *A. austriacum* zones is not adopted here.

The base of the Norian has been interpolated to 227 Ma (Fig. 5.1; Gallet *et al.* 1994; Cohen *et al.* 2013). There are two well-studied candidates for a GSSP: the Black Bear Ridge section, British Columbia, Canada (Orchard 2014; Zonneveld *et al*. 2010), where the base of *Primatella asymmetrica-Norigondolella* Subzone corresponds to the traditional base of Norian at the base of the *Stikinoceras kerri* Zone (Orchard 2014), and the Pizzo Mondello section, western Sicily, Italy (Mazza *et al.* 2011), where the first appearance datum of *Carnepigondolella gulloae* has been proposed as the base of the Norian (Mazza *et al.* 2012b). As a Norian base GSSP has yet to be confirmed by ICS, our analyses ends at the base of the *Metapolygnathus parvus* conodont zone of North America (Fig. 5.1; Orchard 2014), which is a more easily recognized datum that lies within the ultimate Carnian ammonoid zone of *Klamathites macrolobatus*.

5.3. Lineages and stratigraphic distributions

Twenty-five genera are here discussed with most of them assigned to the family Gondolellidae Lindström, 1970, except for two: *Gladigondolella* and *Neostrachanognathus*. *Gladigondolella* belongs to the family Gladigondolellidae Ishida and Hirsch, 2011, whereas family and subfamily assignments of the genus *Neostrachanognathus* are uncertain.

5.3.1. Method

The subfamilies and genera are listed below according to their appearances in Figures 5.2–5.7. In this paper, we follow the multielement nomenclature of Purnell *et al*. (2000) in which elements of the conodont apparatus are designated as P_1, P_2, S_0-S_4, and M. Natural clusters of conodonts elements indicate that there are at least two kind of apparatuses in the Middle and early Late Triassic, composed of 14 and 15 elements respectively. The apparatus of the genus *Neostrachanognathus* has been reconstructed as comprising14 elements, paired P_1, P_2, P_3, S_1, S_2, S_3, and S_4 elements (Agematsu *et al*. 2008). Orchard (2005) reconstructed 26 apparatuses of Triassic conodont species which were assigned to the superfamily

Gondolelloidea. All these apparatuses consist of 15 elements: paired P_1, P_2, S_1, S_2, S_3, S_4, M elements, and unpaired S_0 element. Goudemand *et al.* (2012) studied a natural cluster of conodonts, and switched the position of S_1 and S_2 elements within this apparatus. Hence, the S_1 and S_2 elements of former authors (e.g. Orchard and Rieber 1999; Orchard 2005; Sun *et al.* 2009) are here noted as S_2 and S_1 respectively. Among all these elements, S_2 bears characters for the superfamily diagnosis, and S_0 and S_3 elements are important for the subfamily assignment (Orchard 2005). It follows that the characters of S_0, S_2 and S_3 elements are most important for the presumed relationships of conodonts.

The reconstruction of Middle and early Late Triassic conodont apparatuses is still limited to a few species. Information on conodont species without known apparatus is inferred from the P_1 element. Stratigraphic ranges of conodonts are based on both the literature and on the authors' own data, and correlated with their first occurrence (FO) and last occurrence (LO) to the corresponding conodont or ammonoid zone (Fig. 5.1). Given absolute ages of FOs and LOs are estimated – except for a few species, e.g., *Chiosella timorensis* (Nogami, 1968) or *Paragondolella trammeri* (Kozur, 1972), which have been radiometrically constrained (e.g. Lehrmann *et al.* 2006; Brack *et al.* 2005).

Some species are very similar based on their apparatus reconstruction, e.g., the Bithynian/Pelsonian species *Nic. parabudaensis* Sun, Hao, Sun and Jiang (Sun *et al.* 2009) and the Julian *Mosherella newpassensis* (Mosher, 1968) despite a large record gap between these two taxa. There are two plausible explanations: the two species are in direct lineage but a poor record or specific palaeoecological/palaeobiogeographic restrictions has hampered the recovery of a transitional form; or this is a perfect example of convergent evolution with *Nic. parabudaensis* deriving from the genus *Triassospathodus* Kozur, 1998, and *Mo. newpassensis* evolving from the genus *Pseudofurnishius*; here we favour the second solution (see below for discussion).

The genus *Algherella* Bagnoli, Perri and Gandin, 1985, is not discussed in this paper because its elements probably represent the ramiform elements of other genera. The same is thought to be true for *Ellisonia dinodoides* (Tatge, 1956), the Early Triassic to Norian age range of which (Koike 1994) is much greater than that of *Ellisonia* Müller, 1956, which is probably confined to the late Early Triassic (e.g. Hirsch 1994b, fig. 5).

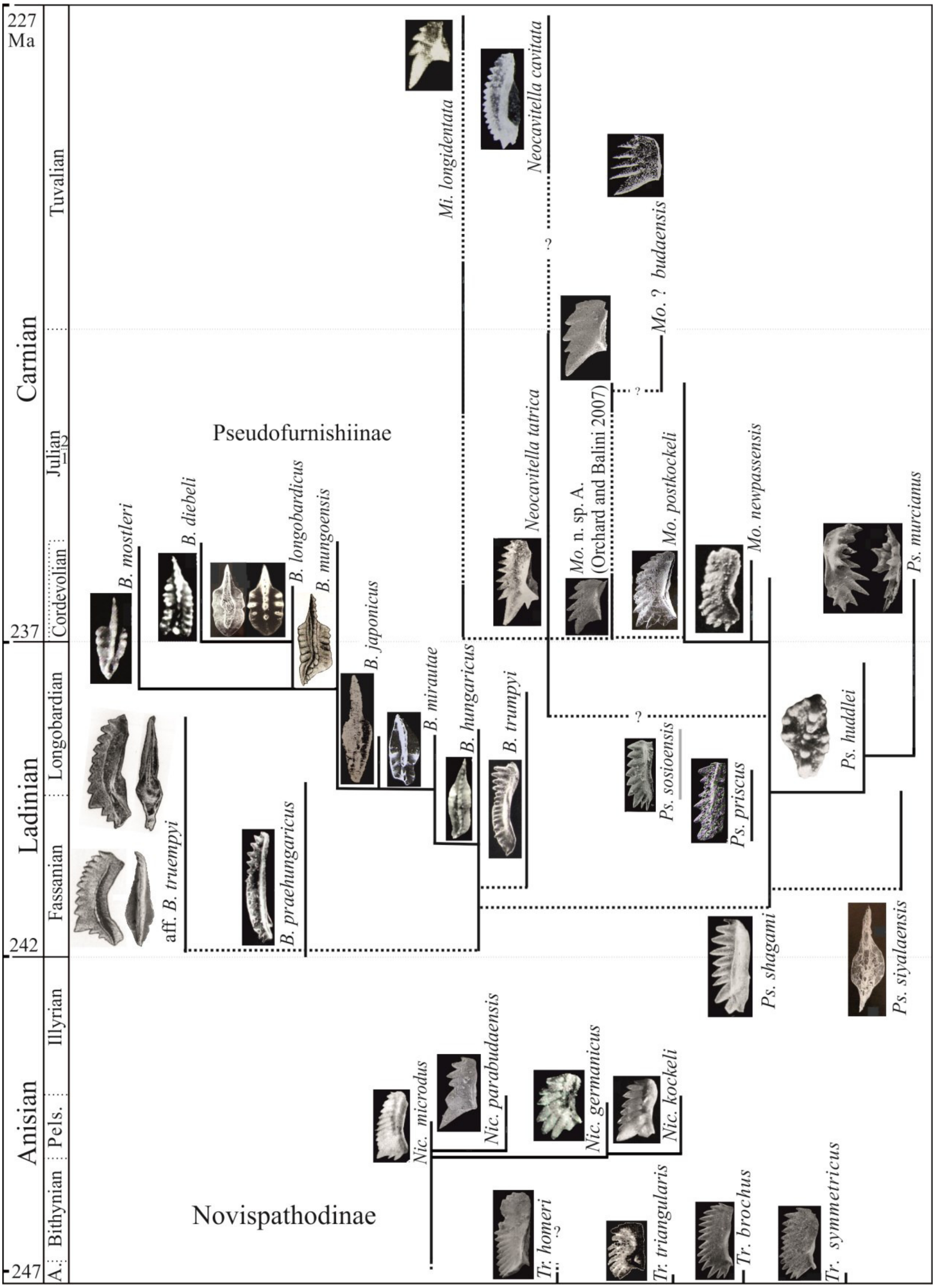


Figure 5.2. The stratigraphic distribution of Middle and early Late Triassic conodonts of the subfamilies Novispathodinae and Pseudofurnishiinae showing presumed relationships.

Vertical dashed lines indicate uncertainty of stratigraphic distribution, the horizontal dashed lines indicate uncertainty of the relationship, and the grey vertical line indicates synonymous species. Conodont figures are holotypes re-illustrated from publications (see Supplemental Appendix Chen *et al*. 2015). The conodonts noted as aff. *Budurovignathus truempyi* was obtained by Krystyn and Kovacs from Greece. Abbreviations: A. = Aegean; Pels. = Pelsonian; *Tr*. = *Triassospathodus*; *Nic*. = *Nicoraella*; *Ps*. = *Pseudofurnishius*; *B*. = *Budurovignathus*; *Mo*. = *Mosherella*.

5.3.2. Subfamily Novispathodinae Orchard, 2005

Species of this this subfamily have segminate P_1 elements (Fig. 5.2), alate S_0 elements, digyrate S_1 elements, and non-bifid S_3 elements (Orchard 2005). Goudemand *et al*. (2012) changed the position of S_3 and S_4 elements, which were recognized by Orchard (2005) as S_4 and S_3, respectively.

5.3.2.1. Genus *Triassospathodus* Kozur, 1998

The original diagnosis of this genus was based on the P_1 element of *Triassospathodus homeri* (Bender, 1970), which is characterized by an inconspicuous cusp, a slightly concave lower margin, and a downward curved posterior end of the lower margin of the basal cavity (Kozur *et al*. 1998). The origination of this species lies in *Novispathodus* Orchard during the Spathian (Orchard 2005). *Triassospathodus* ranges from the Spathian to the lower part of the Anisian (e.g. Orchard, 2007*a*; Goudemand *et al*. 2012). The genus has a wide distribution, important localities including northern Italy (Perri and Andraghetti 1987), Greece (Bender 1970), Romania (Orchard *et al*. 2007*a*), Oman (Orchard, 1995), Pakistan (Sweet 1970), Northern India (Goel 1977; Matsuda 1983), Tibet (Wu *et al*. 2007), South China (Orchard et al., 2007b; Zhao *et al*. 2007; Wang *et al.* 2005), eastern Russia (Buryi 1989), and North America (Orchard 1994).

Triassospathodus brochus (Orchard, 1995), *Tr. symmetricus* (Orchard, 1995) and *Tr.? triangularis* (Bender, 1970) have been reported to overlap with the first appearance of *Ch. timorensis* (e.g. Orchard 1995; Orchard *et al*. 2007*a*), and to range into the Aegean (e.g. Wang *et al*. 2005; Orchard *et al*. 2007*a*, *b*; Goudemand *et al*. 2012).

Buryi (1989, pl. 3, fig. 5) illustrated a broken P_1 element as the holotype of *Ns. gorbushini*, which may be the posterior part of *Tr. homeri*. The other two specimens of *Ns.*

gorbushini illustrated in this paper should be assigned to *Sp. spathi* (Sweet, 1970) (Buryi 1989, plate 3, fig. 6) and *Nic. kockeli* (Buryi 1989, plate 3, fig. 7).

5.3.2.2. Genus *Nicoraella* Kozur, 1980

The P_1 elements of this genus are blade-like with a relatively long anterior process and a shorter posterior process, and an only slightly widened basal cavity. *Nicoraella* ranges from Aegean to Pelsonian, and has been reported from important regions such as Germany (Tatge 1956; Kozur 1972), Poland (Trammer, 1975; Narkiewicz and Szulc 2004), northern Italy (Pisa *et al.* 1980), Austria (Mosher 1968b; Gallet *et al.* 1998), Hungary (Kovacs 2003), Bulgaria (Boyanov and Budurov 1979), Greece (Dürkoop *et al.* 1986), Turkey (Gedik 1975), Himalaya (Krystyn *et al.* 2004), south China (e.g. Sun *et al.* 2009, Wang *et al.* 2005), and western USA (Nicora 1976).

The genus is here assigned to the subfamily Novispathodinae under the assumption that *Nicoraella* evolved from certain '*Neospathodus*' species during the early Anisian (Kozur, 1989*a*), which Kozur *et al.* (1998) later assigned to the genus *Triassospathodus*. Hirsch (1994*b*) suggested an alternative derivation of *Nicoraella kockeli* from *Chiosella aegea* (Bender, 1970), a synonym of *Ch. timorensis*.

The apparatuses of both *Triassospathodus homeri* and *Chiosella* were reconstructed by Orchard (2005) and that of *Nicoraella* was described by Sun *et al.* (2009). Comparing these apparatuses, the S_3 of *Chiosella* has bifurcated anterior processes (e.g. Orchard 2005, fig.12D), while that of *Triassospathodus* (Orchard 2005, fig.19B) and *Nicoraella* (Sun *et al.* 2009, fig3G; Huang *et al.* 2009; 2010) has only one anterior process without bifurcation. The similarity of most other ramiform elements in the apparatuses of *Tr. homeri* and *Nic. kockeli* also point to a relationship between the two. The larger difference in the P_2 elements of *Nicoraella* and *Triassospathodus* may be explained by rapid evolution.

According to its earlier appearance, *Nicoraella germanicus* is interpreted as the forebear of *Nic. kockeli* (Narkiewicz and Szulc 2004), and in turn *Neospathodus microdus* Mosher, 1968 from Hallstatt, Austria may be the forebear of all *Nicoraella* species. However, our data (LK) indicate that the apparatus of *Nic. kockeli* from the Germanic Basin is different from the Tethyan species of *Nicoraella*. Unpublished data from Nevada (MJO) includes several *Nicoraella* species too but no apparatus data is currently available: more work is required to fully undertand this group.

5.3.3. Subfamily Pseudofurnishiinae Ramovs, 1977

Pseudofurnishius, which has a common root to *Budurovignathus* Kozur, 1989 (= *Sephardiella* March, Budurov, Hirsch and Márquez-Aliaga, 1990) (Plasencia *et al.* 2007), is interpreted to have given rise to the Carnian segminate genera *Mosherella*, *Neocavitella*, and *Misikella*. Here we follow Plasencia *et al.* (2007) in assigning all these genera to one subfamily but use instead of their newly introduced Sephardiellinae the valid older term Pseudofurnishiinae transcribed from Pseudofurnishiidae Ramovs, 1977.

5.3.3.1. Genus *Budurovignathus* Kozur, 1989a

The original diagnosis of this genus was based on P_1 elements of relatively young species (Kozur 1988) that are characterized by a free blade in the anterior part and bearing nodes on the anterior platform margins, e.g., *Budurovignathus mungoensis* (Fig. 5.2). However, stratigraphically older species do not show all characters of the younger species but rather they show smaller denticles behind the cusp, a sinuous carina, a platform without marginal denticulation, and lack a free blade, e.g. *B. truempyi* (Hirsch, 1971). The genus ranges from Fassanian to the lowest Julian (Fig. 5.1) and is to be found worldwide. It occurs in Spain (March *et al.* 1990), southern France (Hirsch 1972), Italy (Bagnoli *et al.* 1985; Mastandrea *et al.* 1998), Austria (Gallet *et al.* 1998), Slovenia (Kolar-Jurkovsek 1990), Bulgaria (Budurov 1976), Turkey (Gedik 1977), south China (Wang *et al.* 2005), Malaysia (Ishida and Hirsch 2011), Japan (Hayashi 1968), western Canada (e.g. Orchard, 2007*b*), and Nevada, USA (Mosher 1968*b*; Orchard and Balini 2007). Earlier reports from the Cretaceous of Cameroon, West Africa (Diebel 1956) were erroneous, arising from the mixing of collections in the Berlin museum (Förster 1979).

Gullo and Kozur (1991) assign *Polygnathus mungoensis*(Diebel, 1956), *Polygnathus japonicus* Hayashi, 1968, *Tardogondolella diebeli* Kozur and Mostler, 1971, *Epigondolella hungaricus* Kozur and Vegh, 1972, *Epigondolella mostleri* Kozur, 1972, *Metapolygnathus mirautae* Kovacs and Kozur, 1980*a*, and *Metapolygnathus longobardicus* Kovacs, 1983 to the genus *Budurovignathus*. One of us (MJO) also includes *Gondolella praehungaricus* in the genus.

Kovacs (1994) proposed an origin of the genus *Budurovignathus* by derivation from *Paragondolella trammeri*. However, the conodont apparatus does not support Kovacs' (1994) position. The apparatus of *Budurovignathus mungoensis* has been reconstructed by Orchard (2005) and Plasencia *et al.* (2007), and that of *Pg. trammeri* by Orchard (2005). The S_3

element of *Budurovignathus mungoensis* does not have an accessory anterior process, while S_3 elements of *Pg. trammeri* have an accessory anterior process branching from the anterior end. Because the S_3 elements do not support the former suggestion, the origin of *Budurovignathus* is still to be clarified. On the basis of the P_1 element, one of us (MJO) regards the origin of the genus lies in *Neogondolella aequidentata* Kozur, Krainer and Lutz via *Budurovignathus praehungaricus*.

Kozur (1972, 1980) suggested a derivation of *Budurovignathus hungaricus* from *B. truempyi*. The morphological differences are minor between these two *Budurovignathus* species and their stratigraphic ranges may be identical too, contrary to Kozur (1972) who regarded *B. truempyi* as older than *B. hungaricus*. Ammonoid-controlled section data from Epidaurus, Greece (Krystyn 1983) and northern Italy (Brack et al. 2005) consistently prove the onset of *B. hungaricus* in the lower Ladinian whereas all published occurrences of *B. truempyi* lack exact stratigraphic control. The author's (LK) collections from Tarasci (Turkey) document the latter species co-occurrence with *B. mungoensis,* the bivalve *Daonella lommeli*, and the ammonoids *Israelites* and *Protrachyceras*, all of them indicating a late Ladinian age. Of importance maybe the fact that *B. truempyi* seems to prefer the Sephardic realm whereas *B. hungaricus* is an open sea species inhabiting all world oceans.

Transitional forms between *Budurovignathus hungaricus* and *B. mungoensis*, which are illustrated by Gullo and Kozur (1991, pl. 2, figs. 3-5), indicate that *B. mungoensis* should have evolved from *B. hungaricus*, probably via *B. mirautae* and/or *B. japonicus* (Fig. 5.2). The posteriorly rounded *B. longobardicus* resembles *B. mungoensis* by its elongation and curved keel behind the basal pit and is seen as an offshoot that may have given rise to *B. diebeli* and eventually to *B. mostleri*. *Budurovignathus lipoldi* Ramovs, 1995 from the upper Fassanian of Slovenia (Ramovs 1995) is probably a synonym of *Paragondolella trammeri*.

5.3.3.2. Genus nov. sp. nov.

The P_1 element of this genus has a prominent cusp in the posterior part of the unit (Fig. 5.2), a posterior process that is not well developed bearing two or three denticles, and an anterior process that is well developed and usually bears 8-10 denticles. The platform is of variable size – it can be well developed and widest on the posterior one third of the unit, tapering both anteriorly and posteriorly, or poorly developed as a lateral ridge on each side of the element. A basal cavity is located on the posterior part of the unit, and occupies about one third of the total length of the unit; it has a small basal pit located at its centre, and a keel that extends behind the basal cavity a short distance.

The new genus is differentiated from *Budurovignathus* (e.g., *Budurovignathus hungaricus* and *B. truempyi*) by its prominent basal cavity, a rather narrow adult platform, and by lack of a sinuous keel. Juveniles may look similar to similar sizeed specimens of *B. hungaricus* but they show a later and narrower platform onset.

5.3.3.3. Genus *Pseudofurnishius* van den Boogaard, 1966

The original diagnosis of this genus was based on the holotype of *Pseudofurnishius murcianus* van den Boogaard, 1966, which is a stratigraphically relatively young and advanced form within the genus (van den Boogaard 1966). Together with *Ps. huddlei* van den Boogaard and Simon, 1973, these species are characterized by a blade with denticulate ornament on one or both sides. Early species have no well-developed platform and lack lateral denticulation, e.g., *Ps. shagami* (Benjamini and Chepstow-Lusty, 1986) and *Ps. siyalaensis* Sadeddin and Kozur, 1992. Species of the genus *Pseudofurnishius* have been reported mainly around the Mediterranean Sea – Sinai, Egypt (Eicher and Mosher, 1974), Jordan (Sededdin and Kozur 1992), Israel (Benjamini and Chepstow-Lusty 1986), Turkey (Nicora 1981 and own coll.), and Spain (van den Boogaard 1966; Plasencia *et al.* 2010) – where they are common and characterize the Sephardic conodont province of Hirsch (1994*a*). Other reports come from Northern Italy (Mastandrea *et al.* 1998), Slovenia (Ramovs 1977), Hungary (Kozur 1993*a*), and Malaysia (Ishida and Hirsch 2011).

This genus ranges from the Ladinian to the lowest Julian (Fig. 5.1). Though *Ps. murcianus* is cited from the early Ladinian *Eoprotrachyceras curionii* zone of Spain (Fig. 5.1; Plasencia and Márquez-Aliaga 2011), we follow here the view of Nicora (1981), Gullo and Kozur (1991), and Ramovs (1977) who treat the species as late Ladinian. One of us (LK) questions the presence of *Eoprotrachyceras curionii* in Spain because similar Sephardic protrachyceratid ammonoids with ceratitic suture with which it may be confused range well into the late Ladinian; they co-occur in Israel with the ammonoids *Israelites* and *Gevanites*, genera that are chronostratigraphically well constrained to the upper Ladinian in the Himalayas (Wang and He 1976; unpubl. coll. from Spiti) and Turkey (Nicora 1981).

Pseudofurnishius shagami is cited from the ammonoid *Paraceratitoides brotzeni* zone (Benjamini and Chepstow-Lusty 1986), which is thought by Pérez-Valera (2005) to correspond to the Anisian, uppermost Illyrian *Nevadites secedensis* zone – a very doubtful attribution as the *brotzeni* zone is only 15 m thick and underlies directly the *Israelites* beds (Zak 1986, fig. 5), which we interpret to be of early late Ladinian age. *Ps. siyalaensis* and *Ps. priscus* Sadeddin, 1990 were recently stratigraphically re-adjusted to the Anisian, Pelsonian (Plasencia *et al*. 2015) on the basis of a mere lithostratigraphic correlation between the Middle Triassic sequences of Jordan and Israel. We view the Ladinian age assignment of Sadeddin (1990) as better corroborated.

Sadeddin and Kozur (1992) suggested a derivation of *Pseudofurnishius* from a *Neogondolella* species, which consequently indicates a derivation of the Subfamily Pseudofurnishiinae from *Neogondolella*. Since *Neogondolella* has a S_3 element with bifurcated anterior processes (Orchard and Rieber 1999) which is missing in *Pseudofurnishius* (Plasencia and Márquez-Aliaga 2007), the loss of bifurcated anterior processes on S_3 elements in this lineage still needs verification.

Pseudofurnishius murcianus was originally documented as an unnamed species (Diebel 1956, plate 4, figs 6–7), and only later named by van den Boogaard (1966). Derivation of *Ps. murcianus* has been discussed by Gullo and Kozur (1991) and Sadeddin and Kozur (1992), and has been revised by Plasencia *et al*. (2015). Here we summarize these proposed relationships as the morphocline *Ps. shagami –>Ps. huddlei–> Ps. murcianus* and treat *Ps. sosioensis* Gullo and Kozur as younger synonym of *Ps. shagami*, because of their very similar morphology. Plasenica et al. (2015) treat *Ps. huddlei* and *Ps. murcianus* as synonyms but we consider this unlikely due to their different stratigraphic range (Fig. 5.2).

‘*Pseudofurnishius*’ *regularis* Budurov and Pantic, 1973 was reported from the ‘Campill Beds’ of Western Serbia (Budurov and Pantic 1973), an outdated term for Olenekian shallow water strata in the Balkans. The species has nevertheless been treated as Ladinian by some conodont workers (e.g. Budurov and Pantic 1973; Plasencia *et al*. 2015). New findings from the Žiri area of Slovenia confirm its age as Early Triassic and its taxonomic assignment to the genus *Platyvillosus* (see Chapter 3).

5.3.3.4. Genus *Mosherella* Kozur, 1972

Mosherella newpassensis, the type species, has a segminate P_1 element bearing a small and narrow basal cavity and occurs during the Middle-Late Triassic transition. A conspicuous similarity of *Mosherella* species with the Anisian genus *Nicoraella* induced several authors (e.g. Mosher 1968*a*; Kozur 1993*b*) to describe them under the latter genus name despite a more than 5 Ma long stratigraphic gap between the two genera. The earliest report of this genus dates to the Lower Carnian of Nevada and British Columbia and the youngest to the late Julian of Hungary (Orchard and Balini 2007; Orchard 2007; Kozur 1993*b*).

Mosherella is here interpreted to have evolved from *Pseudofurnishius* with *Ps. shagami as* the transitional form between *Pseudofurnishius* and *Mosherella*, because of similar morphology. There are two different groups within the genus, one represented by *Mo. newpassensis* and *Mo. postkockeli* characterized by a prolongation of posterior process behind the relatively small main denticle; and a second group consisting of *Mo.*? *budaensis* with the latter originally introduced as *Nicoraella* by Kozur and Mock (1989) and characterized by lack of a posterior process behind the main denticle (cusp).

5.3.3.5. Genus *Neocavitella* Sudar and Budurov, 1979

The genus is based on *Neocavitella cavitata* Sudar and Budurov, 1979 characterized by a large, deep and elliptic basal cavity, and by a well-developed cusp (Sudar and Budurov 1979). The genus was first reported from Tuvalian sediments in Trebevic Mountain close to Sarajevo, Bosnia, and later from upper Tuvalian deposits in Slovakia (Channell *et al*. 2003) and Sicily (Mazza *et al*. 2012a); we can add unpublished occurrences (LK) from the late Tuvalian of Austria (Feuerkogel) and Turkey (Antalya nappes), and (MJO) from western Canadian terranes and Alaska.

Neospathodus tatrica (Zawidzka, 1972) was first reported from the western Tatra Mountains, Poland, and originally dated as Anisian (Zawidzka 1972). This age assignment remains doubtful, because it is only based on megaspores and calcareous algae (Zawidzka 1972). Kozur (1980) and Kovacs and Kozur (1980*b*) revised '*Neospathodus*' *tatrica* as a late Ladinian species which ranges up to the Julian, and assigned it to the genus *Neocavitella*. A reason for this assignment was Zawidzka's figure (1972, fig. 2) which resembles strikingly *Neocavitella cavitata* for the expended elliptic basal cavity and the strongly inclined posterior denticles.

5.3.3.6. Genus *Misikella* Kozur and Mock, 1974

The Carnian P_1 element of the present genus is characterized by short length, small size, a strongly expanded basal cavity, and a cusp on the posterior end of the unit (Kozur and Mock 1974). *Misikella* ranges from the lowermost part of the Carnian (e.g. Orchard and Balini 2007) to the Rhaetian (e.g. Gazdzicki 1978). The type species of the genus *Misikella* is the early Norian species *Misikella longidentata* Kozur and Mock, 1974. The species was also reported from late Carnian of Canada (Orchard. 1991*a*, pl. 4, fig. 2), the lowest Carnian in Nevada (Orchard and Balini 2007), and from Southern Italy (Mastandrea *et al*. 1999) and Cyprus (Fahraeus and Ryley 1989).

The apparatus of *Misikella* has not yet been reconstructed completely (Fahraeus and Ryley 1989) despite natural clusters having been found in Southern Italy (Mastandrea *et al*. 1999, plates 3 and 4). Within these, S_3 and S_4 elements can be distinguished. Since the S_3 element does not have a bifurcated anterior process, we tentatively assign *Misikella* to the subfamily Pseudofurnishiinae.

The P_1 element of *Mo*. n. sp. A (see Orchard and Balini 2007) has a posteriorly located cusp and a weakly expanded basal cavity, characters that indicate that *Mo*. n. sp. A could be the forerunner of the genus *Misikella* (Fig. 5.2). Another plausible hypothesis, based on the similar very prominent cusp, is a derivation of *Mi. longidentata* from *Neocavitella tatrica*. These scenarios have to be tested by a complete apparatus reconstruction.

5.3.4. Subfamily Paragondolellinae Orchard, 2005

This subfamily was introduced on the basis of the reconstructed apparatus of Ladinian species of *Paragondolella*. Species of this genus allegedly have P_1 elements that pass from a segminate to a segminiplanate character during early growth. According to the reconstruction of Orchard (2005), S_0 elements have two anterior-lateral processes branching far anterior of the cusp, and S_3 elements which have an accessory anterior process branching from near its anterior end. Seven genera are assigned to the present subfamily based on their presumed common origination, although neither growth stage characteristics nor diagnostic apparatus composition have been demonstrated.

5.3.4.1. Genus *Paragondolella* Mosher, 1968

The P_1 elements of the type species of genus *Paragondolella* (*Pg. excelsa* Mosher, 1968) are characterized by a high carina and a flat, oval platform; stratigraphic range extends from Anisian to Carnian (Fig. 5.3). The genus has a world-wide distribution, occurring in northern Italy (Brack *et al*. 2005), Austria (Mosher 1968), Slovenia (Kolar-Jurkovsek 1983), Croatia (Jelaska *et al*. 2003), Hungary (Kovacs 2003), Poland (Narkiewicz and Szulc 2004), Bulgaria (Budurov 1976), Greece (Krystyn 1983), Turkey (Gedik 1975), India (Krystyn *et al*. 2007), south China (Wang *et al*. 2005), Japan (Igo 1989), and North America (Orchard 2007*b*).

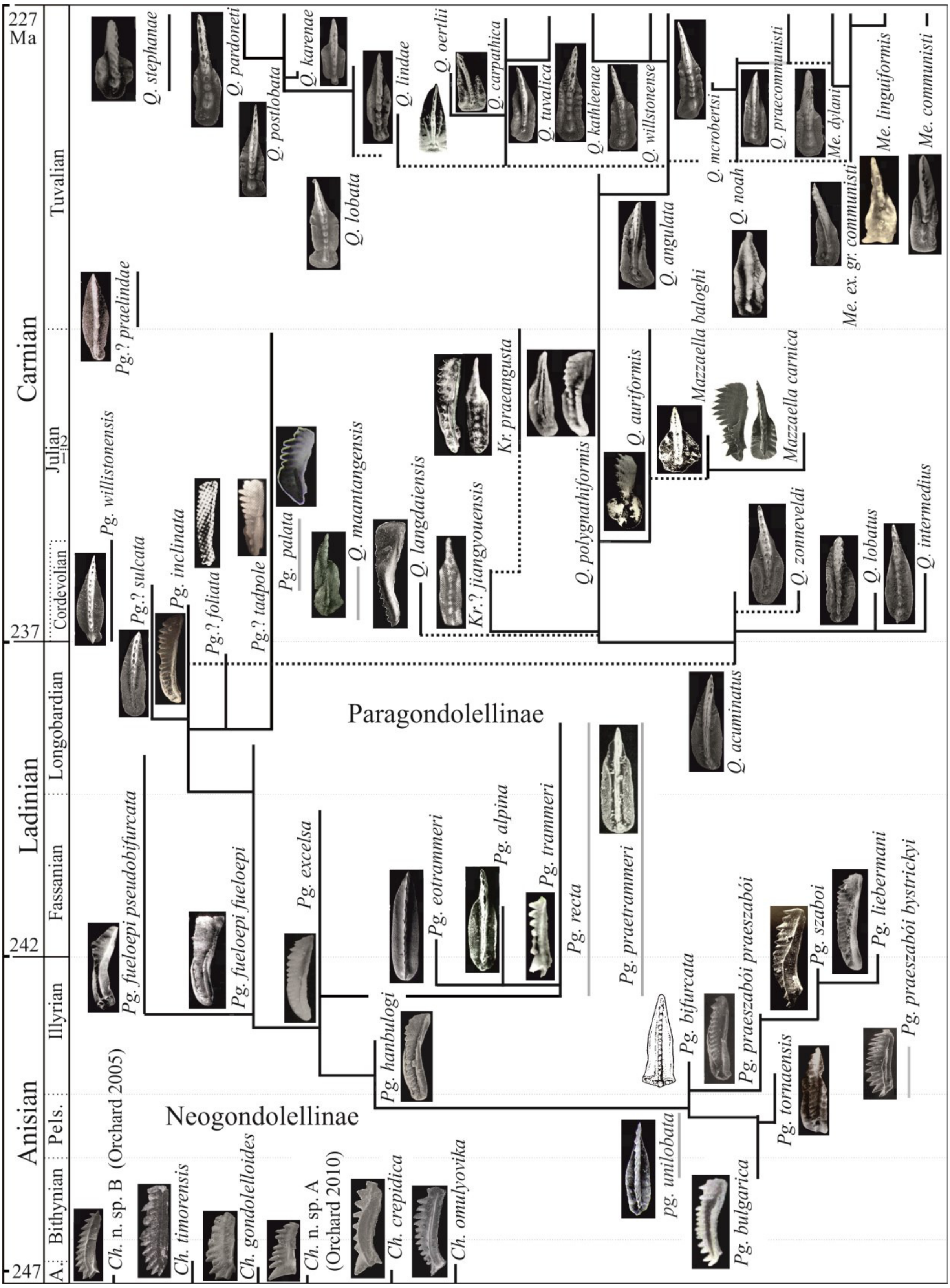


Figure 5.3. The stratigraphic distribution of Middle and early Late Triassic conodonts of the subfamilies Paragondolellinae and Neogondolellinae showing presumed relationships. Dashed and grey vertical lines refer to Figure 5.2. Conodont figures are holotypes re-illustrated from

publications (see Supplemental Appendix Chen *et al*. 2015). Abbreviations: A. = Aegean; *Ch*. = *Chiosella*; Pels. = Pelsonian; *Me*. = *Metapolygnathus*; *Pg*. = *Paragondolella*; *Q*. = *Quadralella*.

The origin of *Paragondolella* is still ambiguous. Mosher (1968*a*, *b*), established the genus *Paragondolella* and distinguished it from *Neogondolella* on the basis of their differing growth series. The earliest growth stage of P_1 elements of *Paragondolella* is bladelike without a lateral ridge, whereas the second growth stage does have a ridge, and following stages have a well-developed platform. In contrast *Neogondolella* shows a platform from its earliest growth stage. This generic differentiation has been adopted by Hirsch (1994*b*), but a full growth series has been documented for very few constituent species. On the other hand, Orchard (2005) differentiated the genera on the basis of their reconstructed multielement apparatuses.

Mosher (1968*b*) thought that *Paragondolella* derived from segminate forms (i.e., genus *Triassospathodus*). However, Mosher's (1968*b*) conclusion has been challenged by an apparatus comparison of *Paragondolella* and *Triassospathodus*. The S_3 of *Paragondolella* has an accessory anterior process branching from its anterior end which is missing in *Triassospathodus* (Orchard 2005). Kozur (1989*a*) suggested a derivation of *Paragondolella* from the Early Triassic genus *Pseudogondolella* which is now viewed as a synonym of the genus *Borinella* (Orchard 2007*a*). As *Borinella* went extinct during the late Smithian (Orchard 2007*a*) it cannot be the direct forebear of *Paragondolella*. Nicora (1977) linked *Neogondolella* ex gr. *regale* with *Paragondolella* via *Pg. bulgarica* Budurov and Stefenov, 1975 (Fig. 5.1), which is favoured as both species are morphologically close and overlap during the early Bithynian.

Two different *Paragondolella* lines appear rooted in *Pg. bulgarica*: a long-lived one which leads through *Pg. hanbulogi* to *Pg. excelsa*, *Pg. fueloepi*, *Pg. inclinata*, *Pg. praelindae*, and a short-lived one including *Pg. bifurcata, Pg. szaboi* and *Pg. liebermanni*.

Pg. hanbulogi Sudar and Budurov, 1979 and *Pg. bifurcata* Budurov and Stefanov, 1972 show still some similarity and transitional forms have also been mentioned between *Pg. hanbulogi* and *Pg. excelsa* (Sudar and Budurov 1979). Kovacs (1994) suggested that *Pg. inclinata* (Kovacs) evolved from *Pg. excelsa*, with *Pg. fueloepi* Kovacs, 1994 as transitional species, a view also supported by Hirsch (1994*a*, 1994*b*). *Paragondolella praelindae* Kozur, 2003*b* is described from the lower Tuvalian. It may be an offspring from *Pg. inclinata*.

Paragondolella? *foliata* Budurov and *Pg.*? *tadpole* (Hayashi, 1968) from the late Ladinian already show intermediate characters to typical *Quadralella* species such as *Q. polygnathiformis*. These two species may provide the transitional forms between the genera *Paragondolella* and *Quadralella*, and we thus assign them to *Paragondolella* tentatively.

We follow Nicora (1977) and Kovacs (2003) in treating *Neogondolella unilobata* Gedik, 1975 as synonym of *Pg. bulgarica*. The holotype of *Paragondolella praeszabói bystrickyi* (Kovac, Papsova and Perri) is regarded as an early growth stage of *Pg. bifurcata* (Fig. 5.3), therefore a junior synonym. Kozur and Mostler (1992) suggested *Pg. palata* (Bender, 1970) to be a synonym of *Q. auriformis* (Kovacs, 1977) but we regard the high anterior carina with long individualized denticles of this species as indicating a close relationship or synonymy with *Pg. tadpole* (Hayashi, 1968).

The conodont genus *Trammerella* Orchard, 2005, based on *Paragondolella trammeri*, is abandoned here because the genus name is preoccupied by an ostracode group (cf. Kozur 1973). Here we provisionally return the genus to *Paragondolella*. According to Kovacs (1994), *Pg. alpina* (Kozur and Mostler, 1982) is closely related to *Pg. trammeri*. Krystyn (1983) introduced *Pg. eotrammeri* (Krystyn, 1983) as forerunner of *Pg. trammeri*. In North America, typical mature specimens of the latter species have not been identified although *Pg. alpina* does occur. Furthermore, one of us (MJO) believes that derivatives of the latter also occur in Nevada, as illustrated by Orchard (2010, fig. 19. 16, 17) as *Neogondolella* ex gr. *pridaensis* (Nicora, Kozur & Mietto), and *Ng*. n. sp. B.

The *trammeri* group has been rooted by Kovacs (1994) in *Pg. szaboi* but is here linked to *Pg. excelsa* with which it shares a similarly large basal pit and the wide oval adult platform outline. *Paragondolella recta* Durdanovic, 1973 was established on juvenile specimens which are here assigned to *Pg. trammeri*. *Pg. praetrammeri* Kozur and Mostler, 1982 and *Ng. slugovensis* Ramovs, 1995, both based on adult specimens, are also treated as synonyms of *Pg. trammeri* (see also Krystyn 1983).

5.3.4.2. Genus *Quadralella* Orchard, 2013

The P_1 elements of *Quadralella* species generally have an elongate platform, an anterior free blade, and poorly differentiated nodes on the anterior platform margin (Orchard 2013). The genus is mainly restricted to the Carnian (Fig. 5.1; Orchard 2013) and occurs worldwide, including Austria (Mosher 1968b), Hungary (Kovacs 1977), Slovakia (Channell *et al*. 2003), Bulgaria (Budurov 1976), Turkey (Gedik 1977, Krystyn *et al*. 1994), south China (Wang *et al*. 2005), and North America (Mosher 1968*b*; Orchard 2013, 2014).

Here we assign *Quadralella* to the subfamily Paragondolellinae based on its derivation from *Paragondolella* (Hirsch 1994*b*; Mazza *et al*. 2012*a*). The genus is rather important as it gives rise to various late Carnian genera (Fig. 5.1; Orchard 2013, 2014) and to the Epigondolellinae, the faunistically and biostratigraphically most important Norian conodont group.

Many authors have linked *Quadralella polygnathiformis* phylogenetically to *Paragondolella inclinata* or to *Pg. foliata* (Budurov and Petrunova 2000). Hirsch (1994*b*, fig. 5) sees a close relationship between *Pg. inclinata* and *Pg. foliata.* Orchard (2007*b*) described several new species of both *Paragondolella* and '*Metapolygnathus*' from the latest Longobardian and Julian of British Columbia but later restricted the taxonomic scope and hence the stratigraphic age of genus *Metapolygnathus* to the upper Tuvalian and earliest Norian (Orchard 2013, 2014). Here we follow Orchard (2013, 2014) in assigning '*M.*' *polygnathiformis*, as well as its offshoots, to the genus *Quadralella*.

Neogondolella maantangensis Dai and Tian, 1983, originally discovered in Sichuan province, south China (Tian *et al*. 1983), is here seen as a junior synonym of *Q. polygnathiformis*. Another species reported from south China is *Q. langdaiensis* (Yang, 2002) characterized by a prolongation of the keel behind the basal pit which thereby moves to the posterior one fourth of the keel (Yang *et al*. 2002).

True paragondolellids from the late Julian are relatively rare. *Quadralella auriformis* and *Mazzaella baloghi* (Kovacs, 1977) were believed to originate in the late Ladinian (Kovacs 1977), but later they were found to be of exclusively Julian age (Krystyn *et al*. 1994; Mastandrea 1995).

The potential evolutionary lineages of Tuvalian 'polygnathiform' conodonts have been discussed by Orchard (1991*a*, 2007*c*, 2014) and Mazza *et al*. (2012*a*). Here we try to summarize these in part contradicting relationships proposed by Orchard (1991*a*, 2007*c*, 2014) and Mazza *et al*. (2012*a*). Orchard (2013, 2014) roots *Quadralella* in "*Paragondolella*" *polygnathiformis*, which extends the range of the genus to the basal Carnian (Fig. 5.3). The cladistic analyses of Mazza et al. (2012*a*) indicates a close relationship between *Quadralella oertlii* (Kozur, 1980) and *Q. carpathica* (Mock, 1979), and Orchard (2007*c*) outlined the evolutionary lineage between the species *carpathica* and a generalized *nodosa* (based around the original *Gladigondolella nodosa* Hayashi, 1968), which is now differentiated into several species, including *Q. lobata* Orchard, 2013 and *Q. postlobata* Orchard, 2014. These and other taxa were combined in "*Metapolygnathus nodosus*" by Orchard prior to 2013, but his suggestions that *Q. lindae* evolved from this plexus (Orchard 1991*a*, *b*) remains valid. *Quadralella praecommunisti* (Mazza, Rigo and Nicora, 2011) was assigned to the genus *Metapolygnathus* (Mazza *et al*. 2012a), but according to Orchard's criteria of these genera, it should be placed in the genus *Quadralella* (Orchard 2013, 2014). Considering the morphological features and the stratigraphic distribution, this species probably derived from *Q. noah* (Mazza *et al*. 2012*a*; Orchard, 2014).

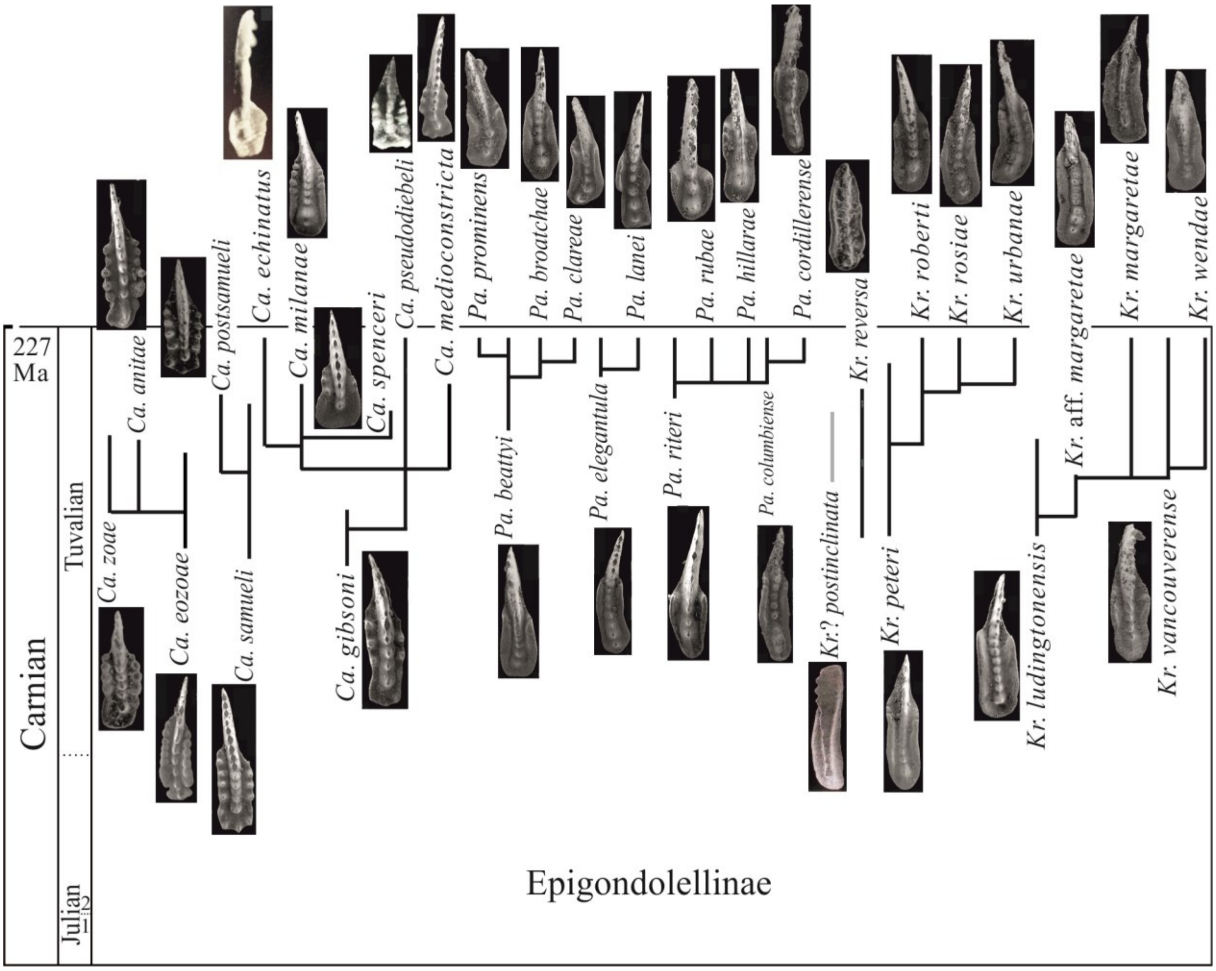


Figure 5.4. The stratigraphic distribution of Carnian conodonts of the subfamily Epigondolellinae showing presumed relationships (after Orchard 2014; Mazza *et al*. 2012). Dashed and grey vertical lines refer to Figure 5.2. Conodont figures are holotypes re-illustrated from publications (see Supplemental Appendix Chen *et al*. 2015). Abbreviations: *Ca*. = *Carnepigondolella*; *Kr*. = *Kraussodontus*; *Pa*. = *Parapetella*.

5.3.4.3. Genus *Kraussodontus* Orchard, 2013

The P_1 element of this genus is characterized by subparallel lateral platform margins, a narrow and tapered posterior platform, and inornate or weakly ornate anterior platform margins (Orchard 2013). It has been introduced for a series of late Carnian species in Canada (Fig. 5.3 and 5.4; Orchard 2014). Based on the original diagnosis of this genus, we assign here *Gondolella praeangusta* Kozur, Mirauta and Mock, 1980 (Kozur 1980), and *Neogondolella jiangyouensis* (Wang and Dai, 1981) to the present genus, thus expanding the range of the genus downward into the early Carnian (Figs 5.1 and 5.3).

Neogondolella jiangyouensis from the early Carnian Tianjingshan Formation (Wang and Dai 1981) co-occurs with *Q. polygnathiformis* and *Pg. tadpole* (Yang et al. 2002). Seen from its platform outline, it fits better with the recently introduced genus *Kraussodontus.* Morphological similarities with *Q. polygnathiformis*, suggest it developed from the latter.

5.3.4.4. Genus *Mazzaella* Kilic, Plasencia, Ishida and Hirsch, 2015

The P_1 element of *Mazzaella* is characterized by nodes on the platform margin, a well-developed free blade, and a high anterior carina (Kilic *et al*. 2015). The genus has only two species and a rather short range whereby both *M. baloghi* and *M. carnica* (Krystyn, 1975) have been shown to be restricted to a very short time interval around the Julian 1 to 2 boundary (Fig. 5.1; Krystyn 1983; Gallet *et al*. 1994).

Kozur et al. (2009) synonymized *Mazzaella carnica* with "*Gladigondolella*" *nodosa* Hayashi from the undated Triassic Adoyama chert of Japan. We reject this assignment because of the uncertain age of the latter species compared to the well described and dated *M. carnica* which by its short stratigraphic range is an excellent index species for the mid-Julian (Fig. 5.3).

5.3.4.5. Genus *Metapolygnathus* Hayashi, 1968

The P_1 element of *Metapolygnathus* is characterized by a subrectangular platform commonly reduced to about half length of the unit, by lacking strong marginal anterior platform nodes, and by a forward shifted basal cavity (Orchard 2013, 2014). Following these criteria, 4 species can be recognized presently during the Tuvalian: *Me. communisti, Me. linguiformis* Hayashi, 1968*, Me. dylani* Orchard, 2014, and *Me. parvus* Kozur, 1972. Several morphotypes of *Me.* ex gr. *communisti* sensu Orchard (2014) include the oldest species of this genus.

Following Orchard's (2013, 2014) recent taxonomic revision of Carnian Paragondolellins – which includes a restriction of *Metapolygnathus* to the latest Tuvalian – all earlier described North American species of '*Metapolygnathus*' from the Julian of British Columbia (Orchard 2007*b*) and Nevada (Orchard and Balini 2007) with a free anterior blade and a sudden down-step anterior platform margin have now to be attributed to the genus *Quadralella.* Mazza *et al*. (2012a) and Rigo *et al*. (2007) assigned these early Julian '*Metapolygnathus*' species to the genus *Paragondolella*.

5.3.4.6. Genus *Parapetella* Orchard, 2013

Based on the original diagnosis of Orchard (2013), the P_1 element of this genus is characterized by raised anterior platform margins that resemble parapets; the platform anterior edges descend gradually or abruptly to meet the anterior free blade (Fig. 5.4). Species of *Parapetella* are suggested to have evolved from *Quadralella* (Orchard 2013). The evolutionary relationships within this genus have been proposed by Orchard (2007*c*, 2014) and we have summarized these relationships in Figure 5.4.

5.3.4.7. Genus *Carnepigondolella* Kozur, 2003

The P_1 element of this genus is characterized by a squared-off posterior platform, and a relatively flat platform that bears rounded nodes or sharp denticles on the anterior, or both the anterior and posterior lateral platform margins (Fig. 5.4). In lateral view, the denticles or nodes on the platform margin commonly equal between 10% and 30% of the total depth of the platform (Orchard 2013). Some species are characterized by platform constrictions in the posterior to medial part of the platform (Orchard 2013). The genus is known from Austria (Krystyn 1980), Slovakia (Channell *et al*. 2003), Sicily (Mazza *et al*. 2012*a*), Greece (Krystyn 1983), Turkey (Kristan-Tollmann and Krystyn 1975), India (Krystyn *et al*. 2004), Nevada (Balini *et al*. 2015), and British Columbia (Orchard 2013, 2014).

Carnepigondolella samueli Orchard, 1991*b* and *Ca. gibsoni* Orchard, 2014 are the oldest species of *Carniepigondolella* in Canada during the Tuvalian (Orchard 2007*c*, 2014), thus they are probably the forerunners of all the other *Carniepigondolella* species. The cladistic analyses of Mazza *et al*. (2012a, fig.8) indicated that *Ca*. *pseudodiebeli* Kozur, 1972 developed from *Quadralella carpathica* or from a species closely related to *Q. carpathica.* However, Orchard (2014) suggested that *Ca*. *pseudodiebeli* rooted in the older *Ca. gibsoni*

(Orchard 2014), which is the oldest species known from the British Columbia sections and without an obvious precursor. Thus the origin of *Carnepigondolella* remains unclear.

5.3.5. Subfamily Epigondolellinae Orchard, 2005

Species of this subfamily have segminiplanate P_1 elements, S_0 element with anterior processes branching from a denticle immediately anterior of the cusp, and S_3 elements without an accessory anterior process (Orchard 2005).

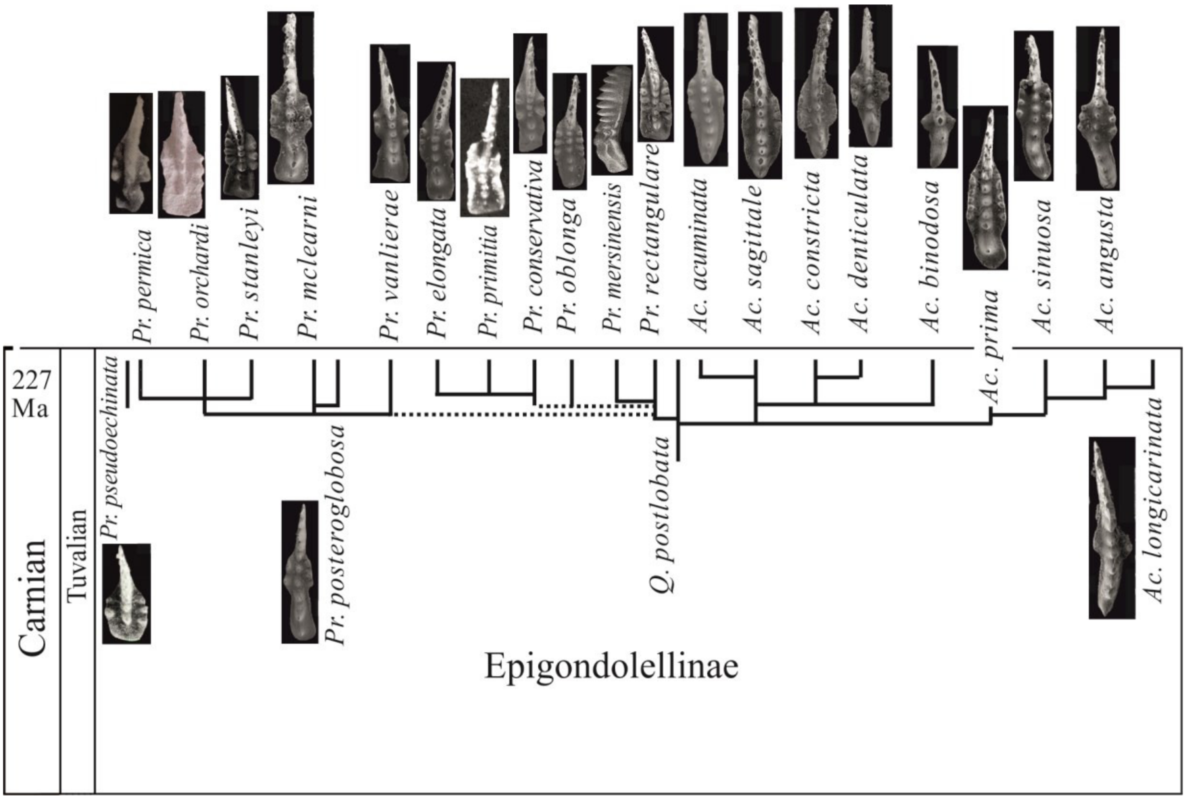


Figure 5.5. The stratigraphic distribution of Carnian conodonts of the subfamily Epigondolellinae showing presumed relationships (after Orchard 2014; Mazza *et al*. 2012). Dashed and grey vertical lines refer to Figure 5.2. Conodont figures are holotypes re-illustrated from publications (see Supplemental Appendix Chen *et al*. 2015). Abbreviations: *Ac.* = *Acuminatella*; *Pr.* = *Primatella*.

5.3.5.1. Genus *Acuminatella* Orchard, 2013

The P_1 element of this genus is characterized by a reduced platform that tapers or narrows posteriorly, by ornate anterior platform margins, and a sub-medially located basal pit (Fig. 5.5; Orchard 2013). Orchard (2013) demonstrated that *Acuminatella* probably evolved from *Quadralella*, specifically from *Q. postlobata* (see Orchard 2014). Orchard (2013) described two species from the latest Tuvalian of Canada, i.e. *Ac. acuminata* and *Ac. angusta*. Subsequently, further nine new species were introduced by Orchard (2014) and we reproduce his phylogenetic concept of the genus.

5.3.5.2. Genus *Primatella* Orchard, 2013

The genus *Primatella* was established as a transitional genus between *Quadralella* and *Epigondolella* (Fig. 5.5; Orchard 2013). The P_1 element of the present genus is characterized by an anterior ornate platform and a usually inornate posterior platform; relatively high blunt to sharp anterior platform margin denticles; a carina that terminates in front of the posterior platform margin; and a platform brim behind the carina (Orchard 2013).

The genus *Primatella* is believed to have developed from *Quadralella* (Orchard 2013, 2014). Following this scenario and based on the morphological features of holotypes, *Primatella* probably derived from *Q. postlobata* (Fig. 5.5; Orchard 2014). The presumed relationships have been summarized and shown in Figure 5.5 based on Orchard (2013, 2014) and Mazza *et al*. (2012*a*).

5.3.6. Subfamily Neogondolellinae Hirsch, 1994

Species of this subfamily have segminiplanate P_1 elements, S_0 elements with anterior processes branching from the cusp or from a denticle immediately anterior of it, S_1 elements with a single denticulated anterolateral process, and S_3 elements with an accessory anterior process (Orchard 2005).

5.3.6.1. Genus *Chiosella* Kozur 1989

The most important character of *Chiosella* is its mid-lateral rib or reduced narrow platform of the P_1 element. It ranges from uppermost Spathian to Aegean. Reported important localities of this genus include Romania (e.g., Orchard *et al*. 2007*a*), Oman (Orchard 1995), Himalaya (Krystyn *et al*. 2004), south China (Wang *et al*. 2005), Timor (Nogami 1968), Nevada (Orchard and Bucher 1992), southeastern Alaska and western Canada (Orchard and Bucher 1992; Golding et al. in press), and Svalbard (Nakrem et al. 2008).

Bender (1970) and Kozur (1989*a*) assumed the root of *Chiosella gondolelloides* (Bender, 1970) in *Triassospathodus homeri*, as we discussed under the genus *Paragondolella*. This has been challenged by Goudemand *et al*. (2012) who suggested a derivation of

Chiosella from *Neogondolella* by platform loss. It seems that the multi-element dataset does not support a derivation of *Chiosella* from *Tr. homeri*. The S_3 element of *Chiosella* as reconstructed by (Orchard 2005, fig.12D) is bifurcated in the anterior part and two anterior processes can be observed, unlike in the S_3 element of *Tr. homeri*, which has only one anterior process (Orchard 2005, fig.19I). As reconstructed, the apparatuses of *Chiosella* and *Neogondolella* are very similar and this led Orchard (2005) to assign both to the subfamily Neogondolellinae. If *Chiosella* derived from *Neogondolella* (Goudemand *et al*. 2012), then the illustrated specimens of *Chiosella omulyovika* by Klets and Kopylova (2008) may be the transitional forms.

Neogondolella aega Bender, 1970 is considered a synonym of *Chiosella timorensis*. The first appearance datum of *Ch. timorensis* was suggested as a marker of the base of the Anisian (Kozur 2003*a*), although the species is now known to occur with ammonoids traditionally regarded as late Spathian (Goudemand *et al.* 2012).

5.3.6.2. Genus *Neogondolella* Bender and Stoppel, 1965

As discussed under the genus *Paragondolella*, *Neogondolella* is characterized by a well-developed platform from the earliest growth stage onwards (Mosher 1968*a*, *b*; Hirsch 1994*b*), and by a bifurcated anterior process of the S_3 element (Orchard 2005). Type species is the late Anisian *Gondolella mombergensis* from the Germanic Muschelkalk (Fig. 5.6). The genus is recognized worldwide including Germany (Kozur 1968), Poland (Narkiewicz and Szulc 2004), Austria (Krystyn 1980), northern Italy (Brack *et al.* 2005), Slovenia (Kolar-Jurkovsek 1983), Romania (Orchard *et al*. 2007*a*), Greece (Dürkoop 1986), Spiti, north India (Garzanti *et al.* 1995), south China (Wang *et al.* 2005), Japan (Nakazawa 1967), Nevada (Hopkin and McRoberts 2005), western and northern Canada (Orchard 2007*b*, 2008; Golding et al. 2014*a*; 2014*b*; in press), and Svalbard (Nakrem et al. 2008).

Kozur (1989*a*) suggested *Chiosella* as the forbear of *Neogondolella* but this seems unlikely because the latter already existed in the Early Triassic (Orchard and Rieber 1999; Orchard 2007*a*). The oldest Middle Triassic *Neogondolella* species include a broad group united by high carinas that have previously been referred to *Ng.* ex gr. *regale* in the Spathian (Orchard 2007*a*). Various morphotypes occur, including those from the Aegean of Romania (Orchard et al. 2007*a*, figs 5, 35–37), and of south China (Orchard et al. 2007b, figs. 6, 4–6). The latter specimen, illustrated as *Ng.* sp., has a prominent posterior cusp and highly fused denticles in the middle part of the carina, as does the younger *Ng. cornuta*, which differs in its generally lower carina. *Ng.* ex gr. *regale* Mosher was often suggested to be the forebear of Tethyan late Anisian *Neogondolella* species (e.g. Hirsch 1994*a*, *b*; Budurov and Petrunova 2000), but elongate neogondolellans with relatively low carinas are known from both the late Spathian and lower Anisian of Nevada (Orchard 2007a, fig. 1, *Ng.* n. sp. H) and provide alternate forerunners of younger Anisian species. . The middle Anisian knowledge gap of *cornuta*-like neogondolellids in the Tethys contrasts with the North American record where a rich, largely unpublished record exists (e.g. Golding et al. 2014; in prep.).

Three different *Neogondolella* lines (Fig. 5.6) root in *Ng. cornuta* of which the *pseudolonga* line has the widest, pan-Tethys, distribution; the second one (*excentric*a line) characterizes the Balkanid subprovince but its members occur also in the Tethys province whereas the third (*mombergensis* line) is restricted to the Germanic basin. They all apparently end in the early Longobardian or even before. The main features of both the *pseudolonga* and *excentric*a lines are a P_1 element with a tendency towards increased asymmetry of the posterior end coupled with a slight forward shifting of the basal pit. Morphotrends are very different within the *mombergensis* line leading to lateral platform reduction and miniaturization of the P_1 element, perhaps as a result of ecological deterioration by increasing temperature and/or salinity within the progressively isolated Germanic basin.

Within the *pseudolonga* line, *Ng. cornuta* is thought to give rise to *Ng. pseudolonga* in the late Illyrian which in turn is followed by the Fassanian *Ng. transita,* and possible derivatives leading to *Budurovignathus praehungaricus*.

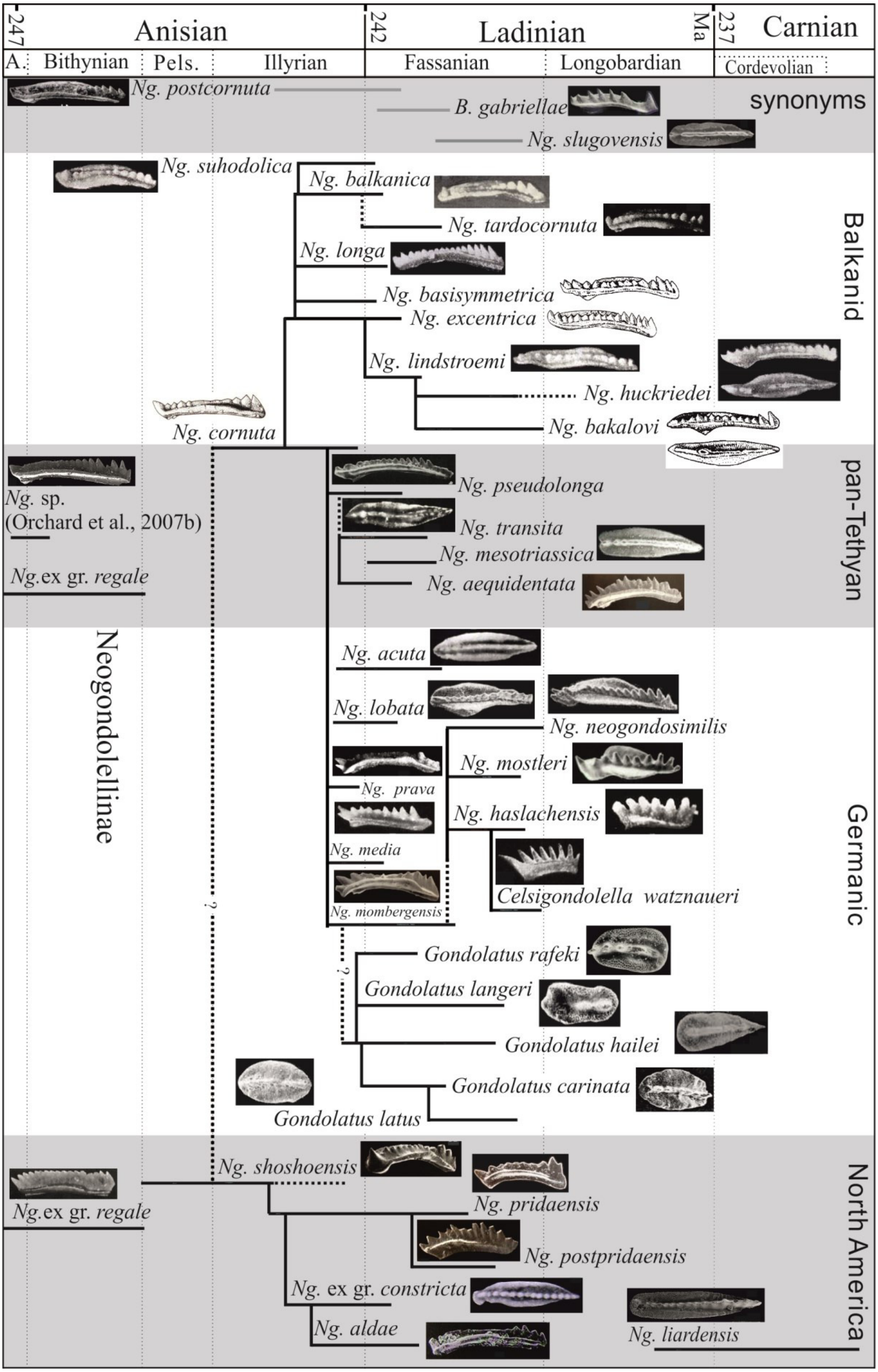
The evolution of the *excentrica* line within the Balkanid conodont subprovince has been well established by Budurov and Stefanov (1973) and variously discussed by Budurov and Stefanov (1984) and Budurov and Petrunova (2000). *Ng. cornuta* there gives rise to many species during late Anisian and early Ladinian time including *Ng. tardocornuta*, *Ng. balkanica*, *Neogondolella suhodolica*, *Ng. excentrica*, *Ng. bakalovi*, *Ng. huckriedei*, *Neogondolella longa*, *Ng. basisymmetrica*, *Ng. lindstroemi* (Fig. 5.6). Several of those species look rather similar and may be synonymous but a revision without topotypic material is impossible and beyond the scope of this paper.

Nicora (1976) reported an unusual early occurrence of *Ng. excentrica* in the Bithynian *Lenotropites caurus* ammonoid zone of Nevada but does not mention those forms in her following monograph on Anisian conodonts from that area (Nicora 1977). The two figured specimens are not really distinctive and are here specifically questioned.

Denticles of *Neogondolella mombergensis* are lowest in the middle part of the carina and are fused to a ridge. The posterior two or three denticles of the carina are always larger (Kozur *et al*. 1994b; see Orchard and Rieber, 1999, fig. 1). The endemic *mombergensis* line has been established by Kozur (1968) and accepted by Hirsch (1994*a*) and Narkiewicz and Szulc (2004); it successively includes *Ng. prava, Ng. media*, *Ng. mombergensis*, *Ng. haslachensis* and ends in the nearly platform-less *Celsigondolella watznaueri* (Kozur, 1968) (Fig. 6). The holotype of *Ng. prava* resembles *Pg. bifurcata* by the denticle on the lateral side of the cusp which is a critical character of *Pg. bifurcata*. This resemblance led Kovacs (2003) to synonymize the two species but his view was not accepted by later workers. Since *Ng. prava* shares region, age and also morphologic characters with *Ng. mombergensis*, i.e. the highly fused denticle ridge in the middle part of the unit, we accept it as a *Neogondolella*.

The Panthalassan *Neogondolella* line incorporates elements of Eurasian faunas other than the *mombergensis* line. Documentation of the North American faunas is underway, building on earlier work by Nicora et al. (1981) in Nevada and Orchard and Tozer (1997) in Canada. Collections spanning most of the Anisian are known (e.g. Orchard and Bucher 1992; Bucher and Orchard 1995), and a less well known Ladinian-early Carnian record exists (e.g. Orchard and Balini 2007; Orchard 2007*b*). Broad groups of Anisian *Neogondolella* species are assigned to morphotypes of *Ng*. ex gr. *regale* and *Ng*. ex gr. *constricta*, from which *Ng. shoshonensis* (Nicora *et al*. 1981), *Ng. pridaensis*, and several new species developed. The *Ng. constricta* group, including *Ng. aldae* Kozur and others related to *Ng. cornuta,* are the most common elements in both Nevada (Bucher and Orchard 1995) and Canada (Orchard and Tozer 2007). Fewer examples of *Ng. aequidentata* appear close to the Anisian-Ladinian boundary in Nevada (Orchard 2010) as a precursor to *Budurovignathus*. The youngest species assigned to *Neogondolella*, *Ng. liardensis,* occurs in the late Ladinian to earliest Carnian of British Columbia (Orchard 2007*b*).

Rafek (1977) based the genus *Budurovella* on a neogondolellid from the Germanic Ladinian characterized by a short free blade on the posterior end of the P_1 element. This character can, however, also be observed in *Ng. huckriedei* Budurov and Stefanov, 1973 and *Ng. mostleri* (Kozur, 1980) and we propose to suppress this genus by incorporating its type species *B. neogondosimilis* in the genus *Neogondolella*. *Ng. postcornuta* Kovacs, 1994 and *Ng. cornuta ladinica* Kozur, Krainer and Mostler, 1994 are here interpreted as younger synonyms of *Ng. pseudolonga*. *Budurovignathus gabriellae* Kozur, Krainer and Mostler, 1994


247
Anisian
242
Ladinian
Ma
237
Carnian
A.
Bithynian
Pels.
Illyrian
Fassanian
Longobardian
Cordevolian
synonyms
Ng. postcornuta
B. gabriellae
Ng. slugovensis
Balkanid
Ng. suhodolica
Ng. balkanica
Ng. tardocornuta
Ng. longa
Ng. basisymmetrica
Ng. excentrica
Ng. lindstroemi
Ng. huckriedei
Ng. bakalovi
Ng. cornuta
pan-Tethyan
Ng. sp.
(Orchard et al., 2007b)
Ng.ex gr. regale
Ng. pseudolonga
Ng. transita
Ng. mesotriassica
Ng. aequidentata
Neogondolellinae
Germanic
Ng. acuta
Ng. lobata
Ng. neogondosimilis
Ng. mostleri
Ng. prava
Ng. haslachensis
Ng. media
Celsigondolella watznaueri
Ng. mombergensis
?
Gondolatus rafeki
Gondolatus langeri
Gondolatus hailei
Gondolatus carinata
Gondolatus latus
North America
Ng.ex gr. regale
Ng. shoshoensis
Ng. pridaensis
Ng. postpridaensis
Ng. ex gr. constricta
Ng. aldae
Ng. liardensis

← **Figure 5.6.** The stratigraphic distribution of Middle and early Late Triassic conodonts of the subfamily Neogondolellinae showing presumed relationships. Dashed and grey vertical lines refer to Figure 5.2. Conodont figures are holotypes re-illustrated from publications (see Supplemental Appendix Chen *et al*. 2015). Abbreviations: A. = Aegean; Pels. = Pelsonian; *Ng*. = *Neogondolella*.

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is seen as a possible synonym of *Budurovignathus praehungaricus*. *Ng. celeiana* Kolar-Jurkovsek, 1989 is regarded as a small specimen of *Gladigondolella malayensis*.

5.3.6.3. Genus *Celsigondolella* Kozur, 1968

Celsigondolella is characterized by small size and near platform-loss. It was reported from the late Ladinian of the Germanic Basin (e.g. Narkiewicz and Szulc 2004). Narkiewicz and Szulc (2004) and Kozur (1989b) suggested that there is lineage from *Ng. mombergensis* to *Ce. watznaueri*. If this is true, probably *Ng. haslachensis* is the transitional species between them (Budurov and Petrunova 2000). *Ce. baiyunensis* Chen and Wang, 2002 from south China is with respect to the ascribed Germanic basin endemism of the genus rather unusual, and with regard to morphologic features is more probably a juvenile of a specifically undeterminable *Paragondolella*.

5.3.6.4. Genus *Gondolatus* Rafek, 1977

Gondolatus is characterized by small size, a rounded to elongate-oval platform, and a platform surrounding the carina completely without a free blade (Fig. 5.6). Kozur (1989*b*) related the Germanic Basin endemic genera *Gondolatus* and *Celsigondolella* to *Neogondolella*. However, an uncertainty of relationship between *Gondolatus* and *Neogondolella* exists since no transitional forms between these two genera have been observed. *Gondolatus* was reported by Rafek (1977) from the Germanic *Ceratites spinosus* ammonoid zone which corresponds to the *Nevadites secedensis* zone (Fig. 5.1; Kozur 1998). Thus, this genus is Illyrian to Fassanian in age, although rare elements corresponding to *Gondolatus* are also known from the early Anisian of British Columbia (MJO, unpublished).

Based on the stratigraphic distribution and the morphological features, *Gondolatus rafeki* Kozur, 1980 probably developed from *Go. hailei* Rafek, 1977. The former species has a broader anterior and a narrower posterior platform. Rounded species, such as *Go. carinata*

Rafek, 1977 and *Go. latus* Rafek, 1977 probably also directly derived from *Go. hailei*. Whether differentiation of all five described species (see Fig. 5.6) is justified is questionable.

5. 3.7. Subfamily Cornudininae Orchard, 2005

Two genera, *Cornudina* Hirschmann, 1959 and *Spathicuspus* Orchard, 2005, were assigned to the present subfamily by Orchard (2005). *Spathicuspus spathi* ranges from Spathian to Aegean (Orchard 2005; Orchard *et al*. 2007b).

5.3.7.1 Genus *Cornudina* Hirschmann, 1959

The P_1 elements are characterized by a prominent cusp, normally located at the posterior end, a short anterior process, and a notable basal cavity (Orchard 2005). It ranges from late Smithian to late Longobardian (Fig. 5.7). It develops especially in the Germanic Basin (Kozur 1968). Apart from Germany, species of this genus were also reported from south China (Orchard *et al*. 2007*b*) and Japan (Koike 1998).

Cornudina breviramulis Tatge, 1956 was described from the Pelsonian of the Germanic Basin and its apparatus has been reconstructed by Koike (1998) to show very similar P_1 and P_2 elements. Kozur (1968) illustrated a subspecies *Cor. breviramulis breviramulis* from the upper Illyrian and Ladinian of the Germanic Basin, whose morphological features are quite different from the holotype of *Cor. breviramulis*. The different age and morphology indicate that *Cor. breviramulis breviramulis* illustrated by Kozur is probably an independent species. Further studies on the apparatus of *Cornudina* species in the Pelsonian and Illyrian are needed. *Cor. breviramulis breviramulis* looks also similar to the P_1 elements of *Cor. igoi*, but the age difference makes it unlikely that the two are a single species.

Based on the apparatus reconstruction of the Anisian *Cornudina*? *igoi* (e.g. Orchard 2005), the form elements *Cor. tortilis* Kozur and Mostler, 1970, *Cor. multidentata* Kozur and Mostler, 1970, and *Cor. pandodentata* are regarded as P_2 elements of *Cornudina*? *igoi*, and thus synonyms. The species *Cor. latidentata* Kozur and Mostler, 1970 was believed to range from the Anisian to the Tuvalian (Kozur and Mostler 1970). In the apparatus of *Nicoraella parabudaensis* and *Mosherella newpassensis* as reconstructed by Sun *et al*. (2009) and Orchard (2005) respectively, the P_2 elements show high similarity with the holotype of *Cor. latidentata*. Therefore, we regard specimens of this species as P_2 elements of either the genus *Nicoraella* or *Mosherella*.

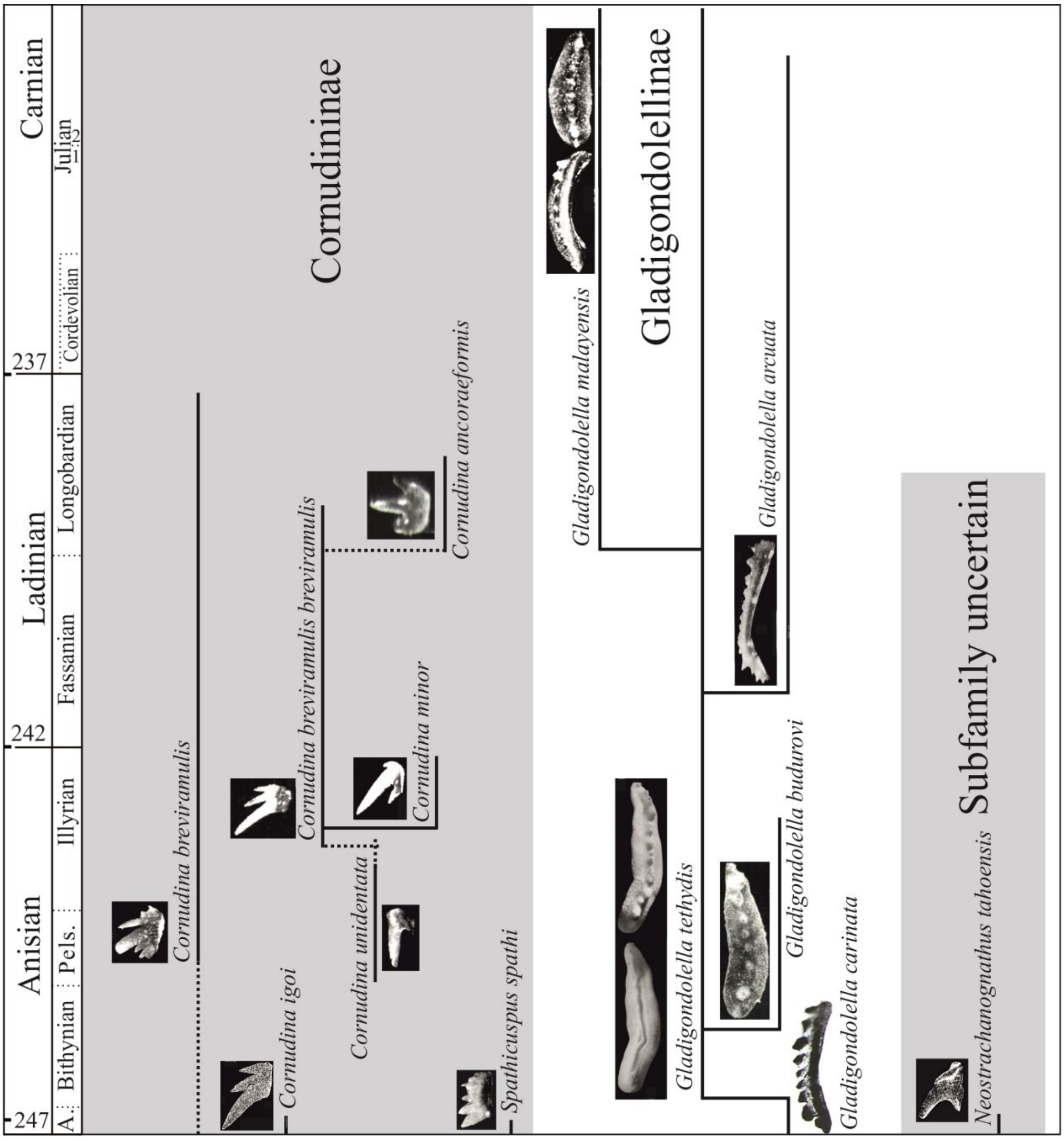

Figure 5.7. The stratigraphic distribution of Middle and early Late Triassic conodonts of the subfamilies Cornudininae, Gladigondolellinae and the genus *Neostrachanognathus* showing presumed relationships. Dashed and grey vertical lines refer to Figure 5.2. Conodont figures are holotypes re-illustrated from publications (see Supplemental Appendix Chen *et al*. 2015). Abbreviations: A. = Aegean; Pels. = Pelsonian.

5.3.8. Subfamily Gladigondolellinae Hirsch, 1994

The genus *Cratognathodus* Mosher, 1968, is synonymous with the genus *Gladigondolella* Müller, 1962, because the P_1 elements of *Cratognathodus* have been considered as P_2 elements of the genus *Gladigondolella* (Ishida and Hirsch 2011). However, not withstanding the preoccupation of the name by a beetle *Cratognathus* Dejean,1829, the elements reconstructed as part of a Spathian *Cratognathus* by Orchard (2005) do not belong to *Gladigondolella*, a well preserved multielement apparatus of which is shown by Orchard (2005, fig. 6).

5.3.8.1. Genus *Gladigondolella* Müller, 1962

The P_1 element of this genus is characterized by discrete, low, and rounded carina nodes; a narrow to moderately wide, elongated platform; and a keel posterior to the pit. *Gladigondolella carinata* Bender, 1970 and *Gl. arcuata* Budurov, 1973 have a relatively narrower platform, while those of *Gl. tethydis* (Huckriede, 1958), *Gl. budurovi* and *Gl. malayensis* Nogami, 1968 are wider (Fig. 5.7). The genus ranges from the Spathian to the early Carnian and is widely reported from the Tethys region, such as Austria (Huckriede 1958), Romania (Orchard *et al*. 2007a), Bulgaria (Budurov 1973), Greece (Bender 1970), Turkey (Gedik 1975), Oman (Hauser *et al*. 2001), the Himalayas (Krystyn *et al*. 2004), south China (Orchard *et al*. 2007*b*), and Malaysia (Nogami 1968). Panthalassan reports are from terrane locations in Japan (Nogami 1968), USA (Nestell and Orchard 1991) and Canada (Orchard *et al*. 1999).

Gladigondolella tethydis followed immediately *Gl. carinata* during the lowest Anisian (Orchard *et al*. 2007*a*, *b*) supporting the conclusion that *Gl. tethydis* evolved from the latter form (Fig. 5.7). *Gladigondolella budurovi* appears during the Bithynian and disappears before the Ladinian. It is distinguished by a shorter, comparably thick platform and a subterminal basal cavity, and is a short-lived species within the genus. The apparatuses of *Gl. arcuata* and *Gl. malayensis* have not yet been reconstructed, but based on the morphological features of their P_1 elements, we conclude that both evolved from *Gl. tethydis*. *Gl. malayensis* developed by widening of the platform, and *Gl. arcuata* by narrowing. *Gl. arcuata* was reported from the Ladinian (Budurov 1973) in Bulgaria to upper Julian in Italy and South Germany (Mastandrea 1995; Hornung *et al*. 2007*a*). *Gl. malayensis* ranges from the late Ladinian (Chhabra and Kumar 1984) to the early Carnian. The unillustrated Bithynian report of *Gl. malayensis* (Berra *et al*. 2012) refers probably to *Gl. budurovi*.

5.3.9. Subfamily uncertain

5.3.9.1. Genus *Neostrachanognathus* Koike, 1998

The apparatus of this genus consists of 14 elements (Agematsu *et al*. 2008) and differs from that of the Gladigondolellidae and Gondolellidae, which consist of 15 elements. The P_1 and P_2 elements of *Neostrachanognathus* are coniform elements. The coniform P_1 elements have either anterior and posterior processes or only an anterior process with one to two denticles. The one named species, *Neostrachanognathus tahoensis* Koike, 1998, is known from Japan, and a second identified as *N*. sp. A is known from Oman (Agematsu *et al*. 2008). Since Koike (1998) included the Anisian form species *Cornudina oezdemirae* Gedik, 1975 from Turkey to his Sa (now referred as P_1) element of *Neostrachanognathus tahoensis*, the genus ranges from the Early Triassic into the basal Middle Triassic (Fig. 5.7).

5.4. Conodont provincialism

Two large conodont domains can be distinguished during the studied time interval: a Tethyan and a Panthalassan or North American one. Both regions show a high degree of generic correspondence but differ in the frequency and ranges of various genera. The Anisian to Carnian western Panthalassan conodont record is meagre, restricted to Japanese terranes whose origin is in dispute but having a largely Tethyan aspect. Compared with the Tethys, eastern Panthalassa is characterized during the Middle Triassic by lower generic and species diversity but an expanded and more common presence of the genus *Neogondolella* , and by an extraordinary late Carnian species richness. Opposite trends can be seen in the Tethys where generic and species diversity is rather high during the late Middle Triassic. The common Tethyan genus *Gladigondolella* occurs in eastern Panthalassa terranes with Tethyan fauna (i.e. Cache Creeke, Baker terrane) (Orchard *et al*. 1999). Distinctly missing in North America may be *Pg. trammeri,* several *Budurovignathus* species, and the genus *Pseudofurnishius. Neogondolella mombergensis, Ng. prava, Ng. media*, *Ng. haslachensis* and *Celsigondolella watznaueri* are believed to be endemic for the Germanic Basin (Hirsch 1994*a*; Budurov and Petrunova 2000; Narkiewicz and Szulc 2004). Earlier use of the species name *Neogondolella mombergensis* in North American records (Mosher 1973; Nicora and Kovacs 1984; Ritter 1989) is erroneous.

A higher Ladinian diversity in the Tethys may have resulted from the creation of new marginal marine – Perimediterranean – basins in the western Tethys: Germanic and Balkanid subprovinces in the north, and Sephardic subprovince in the south (Figs 5.2 and 5.6), the latter ranging from southern France through Spain, North Africa, the Middle East to eastern Turkey (Central Taurids). All three subprovinces miss the open-marine pan-Tethyan taxa

Gladigondolella, *Paragondolella trammeri,* and advanced *Budurovignathus* species. Germanic and Balkanid subprovinces further show discrete neogondolellid lines whereas the Sephardic subprovince is characterized by dominance of the genus *Pseudofurnishius*. The pan-Tethyan subprovince, earlier also called as Alpine-Mediterranean province (Kozur 1973), shows a rather uniform character from the Alps through the Himalaya and Southeast Asia to China and in part to Japan. It shares various *Neogondolella* species with the Balkanid and certain *Pseudofurnishius* species with the Sephardic subprovince, though all of them occurring subordinately.

In general, Panthalassa vs. Tethys provincialism is low in the Anisian with rather uniform faunas till the middle Anisian. From the late Anisian faunistic differences start to increase and get stronger during the early Ladinian to reach a peak around the mid-Ladinian. Provincialism remains strong till the lowermost Carnian to change to an all-Triassic low in the early Tuvalian. With the late Tuvalian faunistic recovery the provincialism between N. America and Tethys rebounds on the specific level.

5.5. Conodont diversity

Based on the results of the stratigraphic distributions shown in Figure 5.2-5.7, the numbers of genera and species for each time interval (equivalent to one or two ammonoid zones) can be calculated. The Bithynian, Fassanian, Longobardian, and Tuvalian substages are split into intervals equalling ammonoid zones. The Illyrian substage is divided into two intervals of which each corresponds to two ammonoid zones (Figs. 5.1 and 5.8). The Julian substage is divided into three intervals, the first interval corresponds to two ammonoid (sub-)zones, and the second and third interval equal one ammonoid zone each.

Twenty-five genera and *c*. 195 species are recognized during the Middle and early Late Triassic which lasted for *c*. 20 myr (Cohen *et al*. 2013; Fig. 5.1) which results on average in 6 genera and about 49 species for each 5 myr. This contrasts sharply with the 34 genera and *c*. 140 species of the Early Triassic (Orchard 2007*a*, figs 1–3) which lasted for less than 5 myr (Cohen *et al*. 2013). One possible explanation is episodic harsh environmental conditions during the Early Triassic (e.g. Payne *et al*. 2004; Richoz 2006; Sun *et al*. 2012; Romano *et al*. 2013) with multiple small-scaled extinctions and following elevated origination rates (Stanley 2009; Wei *et al*. 2014) that may have caused a high turnover rate, resulting in a relatively high diversity when the species number is summed up for the complete Early Triassic. However there could be also an artificial bias as there are around 203 conodont publications for the

Early Triassic (*c*. 4.8 myr) and only 73 per 5 myr for the Anisian to Carnian (for a more detailed data set, see Supplemental Appendix: Chen *et al*. 2015). To date, the North American record is relatively poorly known and many new species will be added to the present numbers.

As shown in Figure 5.8, the number of genera varies little whereas that of species displays strong variations related to either extinctions or radiations. Generally, the specific richness is especially large during the Anisian-Ladinian transition and during the latest Carnian. During the first interval of the Fassanian, corresponding to the *Eoprotrachyceras curionii* zone (Fig. 5.1), 39 species are present (Fig. 5.8). In the third interval of the Tuvalian which corresponds to the *Anatropites spinosus* zone, more than 80 species have been described. However, many intervals show much lower abundances (6 to 18 species) than these two intervals.

Two major diversity cycles can be recognized in the Middle and early Late Triassic, each starting with an increase in diversity as a first step and a diversification phase in the second step. These steps coincide with contemporaneous diversity trends of ammonoids which show also low specific richness during the early Anisian and Carnian but high specific richness during the Anisian-Ladinian transition and during the latest Carnian (Brayard *et al*. 2006). The low conodont diversity at the Julian-Tuvalian boundary corresponds strikingly with a time-equivalent ammonoid extinction event, the strongest within the Triassic (Krystyn 1991).These seemingly comparable diversity trends in conodonts and ammonoids have to be explained. A reason could be seen in a similar life style, since it is assumed that most ammonoids had a juvenile planktic phase and a later benthic phase (Brayard *et al*. 2006; Jacobs and Chamberlain 1996). The ecology of Middle Triassic conodonts is still uncertain, but their forebears, species of *Neogondolella* around the Permian-Triassic boundary are thought to have a nektobenthic life in well-oxygenated waters (Tian 1993; Lai *et al*. 2001).

5.5.1. The first cycle

This cycle ranges from the Bithynian to the end of the Julian (Fig. 5.8). Early Aegean conodonts show still a striking Lower Triassic character and may represent the end of a fore-going cycle. From the Aegean to the first interval of the Bithynian, the number of conodont genera strongly decreases, from 7 genera during the early Aegean to 4 genera in the early Bithynian. The extinct genera include *Chiosella*, *Neostrachanognathus*, *Triassospathodus* and

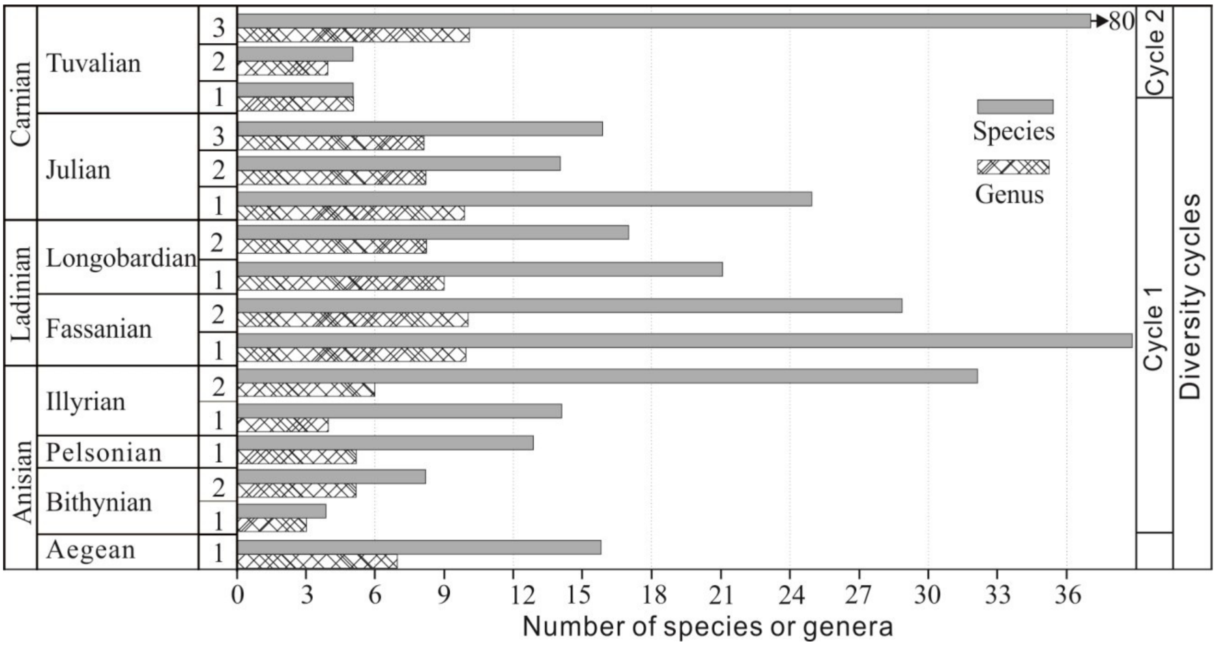

Figure 5.8. The generic and specific richness of conodonts in the Anisian, Ladinian and Carnian.

Spathicuspus with a single innovation represented by *Nicoraella*. It seems that the loss of conodont diversity during the early Anisian coincides also with a contemporaneous ammonoid diversity decline (Brayard *et al.* 2009, fig. 1). However, no comparable diversity loss is known from benthic organisms such as foraminifera (Payne *et al.* 2011, fig. 3) or bivalves (Ros *et al.* 2011). A mechanism for the low ammonoid and conodont diversity in the early Anisian is presently not clear.

The time interval from the late Bithynian to the first interval of the Fassanian was favourable for conodont diversification with increasing specific richness, a trend seen also in foraminifera (e.g., Payne *et al.* 2011). Despite our significant stratigraphical and taxonomic revisions compared with earlier papers (Martinez-Perez *et al.* 2013), we reached at a comparable conclusion with a peak in species numbers during the early Fassanian. This peak results not only from a high abundance of species of *Paragondolella* and *Neogondolella*, but is also due to the initiation of new genera such as *Pseudofurnishius* and *Gondolatus*, which developed during the Illyrian-Fassanian transition and start flourishing during the Fassanian. The peak interval also corresponds to an increased provincialism during the late Anisian and early Ladinian. During the whole Ladinian, generic richness kept relatively high for about 5 myr but shows a decreasing trend in species richness. The high generic and specific richness of the late Anisian and Ladinian coincides with a contemporaneous high ammonoid diversity reported by Brayard *et al*. (2009).

Within the earliest Julian another species peak is reached connected to a diversification of the newly arising genera *Quadralella*, *Neocavitella* and *Misikella*. From the first to the second interval of the Julian (Fig. 5.8) generic richness is considerably reduced, from 10 to 8 genera by the disappearance of three genera (*Neogondolella, Budurovignathus*, and *Pseudofurnishius*), but generation of one new genus (*Mazzaella*). Specific richness also suffers a loss, from 25 to 14 species. This dramatic reduction may in part be explained by habitat losses due to a major regression in the Sephardic subprovince as well as another one along the northern Tethys margin following the Cimmerian (Indosinian) collision. No change in diversity is seen during the Carnian Pluvial Event, which is dated by Krystyn (1991) to the base of interval 3 corresponding to the *Austrotrachyceras austriacum* zone (Fig. 5.1).

5.5.2. The second cycle

This cycle is rather short spanning just the Tuvalian. It starts with a nearly 50% loss in genera and 70% loss of species at the Julian-Tuvalian boundary which is mirrored in a dramatic extinction and turnover event in ammonoids (Krystyn 1991). From the low conodont species number in the early Tuvalian with merely 5 genera and 8 species, diversity rebounds explosively to an all-time Triassic high of 10 genera with more than 80 species by the end-Tuvalian time interval. This peak has also been recognized by Martinez-Perez *et al*. (2013), and corresponds to a high ammonoid diversity rate during the late Carnian (Brayard *et al*. 2009).

5.6. Conclusions

About 195 species assigned to 25 genera are recorded during the Middle and early Late Triassic. The presumed relationships between genera and species have been summarized from literature or are newly proposed. Compared to the high amount of conodont genera and species in the Early Triassic, the lower diversity of the Middle and early Late Triassic can be explained by more stable environmental conditions and a resulting low turnover rate and relatively low diversity. There may also be a bias introduced through incomplete documentation of North Amercian faunas.

Provincialism is low in the Anisian with rather uniform faunas untill the late Anisian. It starts to increase from the late Anisian and reaches its peak around the mid-Ladinian.

Provincialism remains strong till the earliest Carnian. By the late Tuvalian faunistic recovery provincialism between N. America and Tethys becomes re-established on the species level.

Two major diversity cycles can be recognized in the Middle and early Late Triassic, each starting with low in diversity in a first step, and a diversification phase in the second step. The first cycle starts with an all-time Triassic low in generic and specific richness at the base of the Bithynian, followed by a long-lasting diversification from the late Bithynian to the late Julian; the much shorter second cycle mirrors the first one by an increase in generic and specific richness in the late Tuvalian. During the Middle and early Late Triassic, conodonts and ammonoids show parallel diversity trends. This may result from a comparatively similar life style of these two stratigraphically important groups.

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5.8. References

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Note:

Appendix 5.1 List conodont holotypes illustrated in this paper

Appendix 5.2 Statistic analyses of early, middle and early late Triassic (Carnian) publications

Appendix 5.1 List conodont holotypes illustrated in this paper

A review of the evolution, biostratigraphy, provincialism and diversity of the Middle and early Late Triassic conodonts

– Supplementary File Archives, **5.1** –

LIST OF CONODONT HOLOTYPES RE-ILLUSTRATED

Following is the list of figures of conodont holotypes re-illustrated in this paper, exceptions are mentioned. Note that some of these figures of holotypes are not re-illustrated from the original paper, but from re-illustration of later publications. References refer to Supplementary File Archives, part II.

Acuminatella acuminata Orchard, (Orchard, 2013)
Acuminatella angusta Orchard, (Orchard, 2013)
Acuminatella binodosa Orchard, (Orchard, 2014)
Acuminatella constricta Orchard, (Orchard, 2014)
Acuminatella denticulate Orchard, (Orchard, 2014)
Acuminatella longicarinata Orchard, (Orchard, 2014)
Acuminatella prima Orchard, (Orchard, 2014)
Acuminatella sinuosa Orchard, (Orchard, 2014)
Acuminatella sagittale Orchard, (Orchard, 2014)

Budurovignathus diebeli (Kozur & Mostler), (Kozur and Mostler 1971)
Budurovignathus? *gabriellae* (Kozur, Krainer & Mostler), (Kozur et al., 1994)
Budurovignathus japonicus (Hayashi), (Hayashi, 1968)
Budurovignathus hungarica (Kozur & Vegh), (Kozur and Mock, 1972)
Budurovignathus longobardicus (Kovacs), (Kovacs, 1983)
Budurovignathus mirautae (Kovacs), (Kovacs, 1978)
Budurovignathus mostleri (Kozur), (Kozur, 1972)
Budurovignathus mungoensis (Diebel), (Diebel, 1956)
Budurovignathus trumpyi (Hirsch), (Hirsch, 1971)

Carnepigondolella anitae Orchard, (Orchard, 2014)
Carnepigondolella eozoae Orchard, (Orchard, 2013)
Carnepigondolella echinatus (Hayashi), (Hayashi, 1968)
Carnepigondolella gibsoni Orchard, (Orchard, 2014)
Carnepigondolella medioconstricta Orchard, (Orchard, 2013)
Carnepigondolella milanae Orchard, (Orchard, 2014)
Carnepigondolella postsamueli Orchard, (Orchard, 2014)
Carnepigondolella pseudodiebeli (Kozur), (Kozur, 1972)
Carnepigondolella samueli (Orchard), (Orchard, 1991)
Carnepigondolella spenceri Orchard, (Orchard, 2014)
Carnepigondolella zoae (Orchard), (Orchard, 1991)

Celsigondolella watznaueri (Kozur), (Kozur, 1968)

Cornudina ancoraeformis Kozur & Mostler, (Kozur and Mostler, 1970)
Cornudina breviramulis Kozur, (Kozur, 1968)
Cornudina breviramulis breviramulis (Tatge), (Tatge, 1956)
Cornudina igoi Koike, (Koike, 1996)

Cornudina minor Kozur, (Kozur, 1968)
Cornudina unidentata Kozur & Mostler, (Kozur and Mostler, 1970)

Chiosella crepidica (Klets & Kopylova), (Klets and Kopylova, 2008)
Chiosella gondolelloides (Bender), (Orchard, 1995)
Chiosella omulyovika (Kopylova & Klets), (Klets and Kopylova, 2008)
Chiosella timorensis (Nogami), (Nogami, 1968)

Epigondolella heinzi Mazza, Cau & Rigo, (Mazza et al., 2012)
Epigondolella miettoi Mazza, Cau & Rigo, (Mazza et al., 2012)
Epigondolella spatulata (Hayashi), (Hayashi, 1968)
Epigondolella vialovi (Buryi), (Buryi, 1997)

Gladigondolella arcuata Budurov, (Budurov, 1973)
Gladigondolella budurovi Kovacs & Kozur, (Kovacs & Kozur, 1980)
Gladigondolella carinata Bender, (Bender, 1970)
Gladigondolella malayensis Nogami, (Nogami, 1968)
Gladigondolella tethydis (Huckriede), (Huckriede, 1958)

Gondolatus carinata Rafek, (Rafek, 1977)
Gondolatus hailei Rafek, (Rafek, 1977)
Gondolatus langeri Rafek, (Rafek, 1977)
Gondolatus latus Rafek, (Rafek, 1977)
Gondolatus rafeki Kozur, (Kozur, 1980)

Kraussodontus aff. *margaretae* Orchard, (Orchard, 2014)
Kraussodontus? *jiangyouensis* (Wang & Dai), (Wang and Dai, 1981)
Kraussodontus ludingtonensis Orchard, (Orchard, 2014)
Kraussodontus margaretae Orchard, (Orchard, 2014)
Kraussodontus? *postinclinata* (Kozur), (Kozur, 2003)
Kraussodontus peteri Orchard, (Orchard, 2013)
Kraussodontus praeangusta (Kozur, Miräuta & Mock), (Kozur et al., 1980)
Kraussodontus reversa (Mosher), (Orchard, 1991)
Kraussodontus roberti Orchard, (Orchard, 2014)
Kraussodontus rosiae Orchard, (Orchard, 2014)
Kraussodontus urbanae Orchard, (Orchard, 2014)
Kraussodontus vancouverense Orchard, (Orchard, 2014)
Kraussodontus wendae Orchard, (Orchard, 2014)

Mazzaella baloghi (Kovacs), (Kovacs, 1977)
Mazzaella carnica (Krystyn), (Kristan-Tollmann and Krystyn 1975)

Metapolygnathus communisti Hayashi, (Hayashi, 1968)
Metapolygnathus dylani Orchard, (Orchard, 2014)
Metapolygnathus ex. gr. communisti, (Orchard, 2014)
Metapolygnathus linguiformis Hayashi, (Hayashi, 1968)

Misikella longidentata Kozur & Mock, (Kozur and Mock, 1974)

Mosherella? *budaensis* (Kozur), (Kozur, 1991)
Mosherella newpassensis (Mosher), (Mosher, 1968)

Mosherella postkockeli (Kozur), (Kozur, 1993)

Nicoraella germanicus (Kozur), (Kozur, 1972)
Nicoraella kockeli (Tatge), (Tatge, 1956)
Nicoraella microdus (Mosher), (Mosher, 1968)
Nicoraella parabudaensis Sun, Hao, Sun & Jiang (Sun et al., 2009)

Neocavitella cavitata Sudar & Budurov, (Sudar and Budurov, 1979)
Neocavitella n. sp. A. (Orchard & Balini, 2007)
Neocavitella tatricus Zawidzka, (Zawidzka, 1974)

Neogondolella aequidentata Kozur, Krainer & Lutz, (Kozur et al., 1994)
Neogondolella acuta (Kozur), (Kozur, 1972)
Neogondolella aldae Kozur, (Nicora and Kovacs, 1984)
Neogondolella balkanica Budurov & stefanov, (Budurov and stefanov, 1975)
Neogondolella basisymmetrica Budurov & stefanov, (Budurov and stefanov, 1972)
Neogondolella bacalovi Budurov & stefanov, (Budurov and stefanov, 1972)
Neogondolella cornuta Budurov & stefanov, (Budurov and stefanov, 1972)
Neogondolella constricta (Mosher & Clark), (Mosher and Clark, 1965)
Neogondolella excentrica Budurov & stefanov, (Budurov and stefanov, 1972)
Neogondolella haslachensis Tatge, (Tatge, 1956)
Neogondolella huckriedei Budurov & stefanov, (Budurov and stefanov, 1973)
Neogondolella lobata Rafek, (Rafek, 1977)
Neogondolella longa Budurov & stefanov, (Budurov and stefanov, 1972)
Neogondolella liardensis Orchard, (Orchard, 2007)
Neogondolella lindstroemi Budurov & Stefanov, (Budurov and Stefanov, 1973)
Neogondolella mesotriassica Kozur & Mostler, (Kozur and Mostler, 1982)
Neogondolella media Kozur, (Kozur, 1968)
Neogondolella mombergensis (Tatge), (Tatge, 1956)
Neogondolella mostleri Kozur, (Kovacs and Kozur, 1980)
Neogondolella neogondosimilis Rafek, (Rafek, 1977)
Neogondolella postcornuta Kovacs, (Kovacs, 1994)
Neogondolella postpridaensis Kozur, Krainer & Mostler, (Nicora et al., 1981)
Neogondolella praehungaricus Kovacs, (Kovacs, 1994)
Neogondolella prava Kozur, (Kozur, 1968)
Neogondolella pridaensis Nicora, Kozur & Mietto, (Nicora et al., 1981)
Neogondolella pseudolonga Kovacs, Kozur & Mietto, (Kovacs et al., 1980)
Neogondolella regale Mosher, (Mosher, 1970)
Neogondolella shoshoensis Nicora, (Nicora, 1976)
Neogondolella slugovensis Ramovs, (Ramovs, 1995)
Neogondolella suhodolica Budurov & Stefanov, (Budurov and Stefanov, 1973)
Neogondolella transita Kozur, (Kozur, 1971)
Neogondolella tardocornuta Budurov & Stefanov, (Budurov and Stefanov, 1984)

Neostrachanognathus tahoensis Koike, (Koike, 1998)

Parapetella beattyi Orchard, (Orchard, 2014)
Parapetella broatchae Orchard, (Orchard, 2014)
Parapetella columbiense Orchard, (Orchard, 2014)
Parapetella cordillerense Orchard, (Orchard, 2014)
Parapetella clareae Orchard, (Orchard, 2014)

Parapetella elegantula Orchard, (Orchard, 2014)
Parapetella hillarae Orchard, (Orchard, 2014)
Parapetella lanei Orchard, (Orchard, 2014)
Parapetella prominens Orchard, (Orchard, 2013)
Parapetella riteri Orchard, (Orchard, 2014)
Parapetella rubae Orchard, (Orchard, 2014)

Pseudofurnishius huddlei Boogaard & Simon, (Boogaard and Simon, 1973)
Pseudofurnishius murcianus Boogaard, (Figures are not holotype; cited from Ramovs, 1977)
Pseudofurnishius priscus Sadeddin, (Sadeddin, 1990)
Pseudofurnishius shagami (Benjamini & Chepstow-Lusty), (Benjamini and Chepstow-Lusty, 1986))
Pseudofurnishius siyalaensis Sadeddin & Kozur, (Sadeddin and Kozur, 1992)
Pseudofurnishius sosioensis Gullo & Kozur, (Gullo and Kozur, 1989)

Paragondolella bulgarica Budurov & Stefanov, (Budurov and Stefenov, 1975)
Paragondolella bifurcata Budurov & Stefanov, (Budurov and Stefanov, 1972)
Paragondolella excelsa Mosher, (Mosher 1968)
Paragondolella fueloepi fueloepi (Kovacs), (Kovacs, 1994)
Paragondolella fueloepi pseudobifurcata (Kovacs), (Kovacs, 1994)
Paragondolella? *foliata* Budurov, (Budurov, 1975)
Paragondolella hanbulogi Sudar & Budurov, (Sudar and Budurov, 1979)
Paragondolella inclinata (Kovacs), (Kovacs, 1983)
Paragondolella liebermani (Kovacs & Krystyn), (Kovacs, 1994)
Paragondolella praeszabói praeszabói (Kovacs, Papsova & Perri), (Kovacs et al., 1996)
Paragondolella praeszabói bystrickyi (Kovacs, Papsova & Perri), (Kovacs et al., 1996)
Paragondolella palata (Bender), (Bender, 1970)
Paragondolella? *praelindae* Kozur, (Kozur, 2003)
Paragondolella szaboi (Kovacs), (Kovacs, 1983)
Paragondolella? *sulcata* Orchard, (Orchard, 2007)
Paragondolella tornaensis (Kovacs), (Kovacs, 1983)
Paragondolella? *tadpole* (Hayashi), (Hayashi, 1968)
Paragondolella unilobata (Gedik), (Gedik, 1975)
Paragondolella willistonensis Orchard, (Orchard, 2007)

Primatella conservativa Orchard, (Orchard, 2013)
Primatella elongata Orchard, (Orchard, 2014)
Primatella mersinensis (Kozur & Moix), (Moix et al., 2007)
Primatella mclearni Orchard, (Orchard, 2014)
Primatella orchardi (Kozur), (Kozur, 2003)
Primatella oblonga Orchard, (Orchard, 2014)
Primatella permica (Hayashi), (Hayashi, 1968)
Primatella primitia (Mosher), (Mosher, 1970)
Primatella posteroglobosa Orchard, (Orchard, 2014)
Primatella rectangulare Orchard, (Orchard, 2014)
Primatella stanleyi Orchard, (Orchard, 2014)
Primatella vanlierae Orchard, (Orchard, 2014)

Quadralella acuminatus (Orchard), (Orchard, 2007)
Quadralella auriformis (Kovacs), (Kovacs, 1977)
Quadralella angulata (Mazza Cau & Rigo), (Mazza et al., 2012)

Quadralella carpathica (Mock), (Mock, 1979)
Quadralella intermedius (Orchard), (Orchard, 2007)
Quadralella kathleenae Orchard, (Orchard, 2014)
Quadralella karenae Orchard, (Orchard, 2014)
Quadralella langdaiensis (Yang), (Yang et al., 2002)
Quadralella lobatus (Orchard), (Orchard, 2007)
Quadralella lobata (Orchard), (Orchard, 2013)
Quadralella lindae (Orchard), (Orchard, 1991)
Quadralella mcrobertsi Orchard, (Orchard, 2014)
Quadralella maantangensis (Dai & Tian), (Tian et al., 1983)
Quadralella nodosa (Hayashi), (Hayashi, 1968)
Quadralella noah (Hayashi), (Hayashi, 1968)
Quadralella oertlii (Kozur), (Kozur, 1980)
Quadralella polygnathiformis (Budurov & Stafanov), (Mosher, 1968; figures are not holotype)
Quadralella pardoneti Orchard, (Orchard, 2014)
Quadralella postlobata Orchard, (Orchard, 2014)
Quadralella? *pseudoechinata* (Kozur), (Kovacs and Kozur, 1980)
Quadralella praecommunisti (Mazza, Rigo & Nicora), (Mazza et al., 2011)
Quadralella stephanae (Orchard), (Orchard, 1991)
Quadralella tuvalica (Mazza & Rigo), (Mazza et al., 2012)
Quadralella willstonense Orchard, (Orchard, 2014)
Quadralella zonneveldi Orchard, (Orchard, 2007)

Spathicuspus spathi (Sweet), (Sweet, 1970)

Trammerella? *alpina* (Kozur & Mostler), (Kozur and Mostler, 1972)
Trammerella eotrammeri (Krystyn), (Krystyn, 1983)
Trammerella praetrammeri (Kozur & Mostler), (Kozur and Mostler, 1982)
Trammerella trammeri (Kozur), (Kozur and Mock, 1972)

Triassospathodus brochus (Orchard), (Orchard, 1995)
Triassospathodus homeri (Bender), (Bender, 1970)
Triassospathodus symmetricus(Orchard), (Orchard, 1995)
Triassospathodus triangularis (Bender), (Bender, 1970)

Appendix 5.2 Statistic analyses of early, middle and early late Triassic (Carnian) publications

A review of the evolution, biostratigraphy, provincialism and diversity of the Middle and early Late Triassic conodonts
– Supplementary File Archives, **5.2** –

STATISTICAL ANALYSES OF EARLY, MIDDLE AND EARLY LATE TRIASSIC (CARNIAN) PUBLICATIONS

PURPOSE AND METHODS

To know if the hight diversity of Early Triassic and the comparatively low diversity of Middle and early Late Triassic (Carnian) contain an artificial component or not, we made a statistic anylize of publications concering Early, Middle and early Late Triassic (Carnian) conodonts. We try to retrieve most of the publications which illustrate conodont with plates or figures. They are listed below. Publications which only mention conodonts species but without illustrating conodont in plates or figures are not included here. These publications will whatever not contribute to the diversity of conodont, since a new species needs a holotype and it has to be illustrated as figures.

The Permian-Triassic boundary is quite a special stratigraphic interval and it has been intensively studied for the end-Permian mass extinction. The publications concerning latest Permian and earliest Triassic conodonts are listed separately in '3.1 Permian-Triassic boundary', and these publications are not listed again in '3.2 Early Triassic'. Publications concering both Early and Middle Triassic conodonts are listed both in '3.2 Early Triassic' and in '3.3 Middle Triassic'.

RESULTS

Table 1, Anount of publications about Early, Middle and early Late Triassic (Carnian) conodonts

	Early Triassic		Middle Triassic and Carnian	
	P-T boundary	Early Triassic	Middle Triassic	Carnian
Anount of publications	47	156	209	84
Total publication	203		293	
Amount of species	*c.* 140		195	
Duration (Ma)	*c.* 4.8		*c.* 20	
Average of publication (5 Ma)	211		73	
Average of species (5 Ma)	146		49	

As it is shown in Table 1, the Early Triassic last ~4.8 million years (Ma), we found 203 publications and ~140 species. The Middle and early Late Triassic last ~20 Ma, we found 293 publications, and 195 species can be recognized. For the Middle and early Late Triassic, there are only 73 publications and 49 species for each 5 Ma. It seems that the amount of species increases in proportion to the amount of publications. Thus the high diversity of conodonts during early Triassic and the relatively low diversity of Middle and early Late Triassic have probably an artificial component, which is difficult to exactly evaluate.

LIST OF PUBLICATIONS

PERMIAN-TRIASSIC BOUNDARY

Chen J., Beatty T.W., Henderson C.M., Rowe H.,

2009. Conodont biostratigraphy across the Permian-Triassic boundary at the Dawen section, Great Bank of Guizhou, Guizhou Province, South China: Implications for the Late Permian extinction and correlation with Meishan. Journal of Asian Earth Sciences, v. 36, p. 442–458. (Six plate with conodont from Permian-earlist Triassic)

Farabegoli E., Perri M.C.,

1998. Stop 4.3 – Permian/Triassic boundary and Early Triassic of the Bulla section (Southern Alps, Italy) : Lithostratigraphy, facies and conodont biostratigraphy. Giornale di Geologia, ser. 3a, v. 60, p. 292–311. (One plate with conodonts from Early and Middle Triassic)

Henderson C.M., Mei S.L.,

2007. Geographical clines in Permian and lower Triassic gondolellids and its role in taxonomy. Palaeoworld, v. 16, p. 190–201. (Five plates with Permian-Triassic conodonts)

Haas J., Demény A., Hips K., Zajzon N., Weiszburg T.G., Sudar M., Pálfy J.,

2007. Biotic and environmental changes in the Permian-Triassic boundary interval recorded on a western Tethyan ramp in the Bükk Mountains, Hungary. Global and Planetary Change, v. 55, p. 136–154. (One figure with conodonts from Late Permain-earliest Triassic)

Kozur H.,

2004. Pelagic uppermost Permian and the Permian-Triassic boundary conodonts of Iran. Part 1: Taxonomy. Hallesches Jahrbuch für Geowissenschaften, v. 18, p. 39–68. (Six plates with conodonts from Late Permian-earliest Triassic)

Ji Z.S., Yao J.X., Isozaki Y., Matsuda T., Wu G.C.,

2007. Conodont biostratigraphy across the Permian-Triassic boundary at Chaotian, in Northern Sichuan, China. Palaeogeography Palaeoclimatology Palaeoecology, v. 252, p. 39–55. (Two plates with conodonts from Permian-early Triassic)

Jiang H.S., Lai X.L., Luo G.M., Aldridge R., Zhang K.X., Wignall P.,

2007. Restudy of conodont zonation and evolution across the P/T boundary at Meishan section, Changxing, Zhejiang, China. Global and Planetary Change, v. 55, p. 39–55. (Five plates with conodont)

Jiang H.S., Aldridge R., Lai X.L., Yan C.B., Sun Y.D.,

2010. Phylogeny of the conodont genera *Hindeodus* and *Isarcicella* across the Permian-Triassic boundary. Lethaia, v. 44, p. 374–382. DOI: 10.1111/j.1502-3931.2010.00248.x. (One plate, they describe a new species, *Isarcicella* sp. nov., from Early Triassic)

Jiang H.S., Lai X.L., Yan C.B., Aldridge R., Wignall P., Sun Y.D.,

2011. Revised conodont zonation and conodont evolution across the Permian-Triassic boundary at the Shangsi section, Guangyuan, Sichuan, South China. Global and Planetary Change, v. 77, p. 103–115. (Five plates with conodont)

Jin Y.G., Shen S.Z., Zhu Z.L., Mei S.L., Wang W.,

1996. The Selong section, candidate of the Global stratotype section and point of the Permian-Triassic boundary. In: Yin H.F., (eds.), NSFC project: the Palaeozoic-Mesozoic boundary candidates of Global stratotype section and point of the Permian-Triassic boundary. China Unicersity of Geosciences press, p. 127–137. (One plate with conodonts from Permian-Early Triassic)

Koike T.,

1996. The first occurrence of Griesbachian conodonts in Japan. Trans. proc. palaeont. Soc. Japan, N.S., v. 181, p., 337–346. (One plate with conodonts from *H. parvus* Zone)

Kozur H., Mostler H., Rahimi-Yazd A.,

1975. Beiträge zur Mikrofauna permotriadischer Schichtfolgen Teil II: Neue Conodonten aus dem Oberperm und der basalen Trias von Nord- und Zentraliran. Geol. Paläont. Mitt.

Innsbruck, v. 5, p. 1–23. (Seven plates with conodonts from Permian-Triassic boundary)

Kozur H.,

1977. Revision der Conodontengattung *Anchignathodus* und ihrer Typusart. Z. geol. Wiss. v. 5, p. 1113–1127. (One plate with conodonts from Permian-Triassic boundary)

1995. Some remarks to the conodonts Hindeodus and Isarcicella in the latest Permian and earliest Triassic. Palaeoworld, v. 6, p. 64–77. (Three plate with conodont from Late Permian-earliest Triassic)

1995. The importance of *Hindeodus parvus* (Conodonta) for the definition of the Permian-Triassic boundary and evaluation of the proposed sections for a global stratotype section and point (GSSP) for the base of the Triassic. Geologija, v. 37, 173–213. (One plate with earliest Triassic conodonts)

1996. The conodonts *Hindeodus*, *Isarcicella* and *Sweetohindeodus* in the uppermost Permian and lowermost Triassic. Geol. Croatica, v. 49(1), p. 81–115. (Five plates with conodonts from lowermost Triassic)

1998. Problems for Evaluation of the scenario of the Permian-Triassic Boundary biotic crisis and its causes. Geol. Croat., v. 51(2), p. 135–162. (One plate with conodonts from strata close to the Permian-Triassic Boundary)

2007. Biostratigraphy and event stratigraphy in Iran around the Permian-Triassic Boundary (PTB): Implications for the causes of the PTB biotic crisis. In: Yin Hongfu, Warrington, G. & Xie, Shucheng (eds.): Environmental and biotic changes during the Palaeozoic-Mesozoic transition.– Global and Planetary Change, Special Issue, 55(1–3), p. 155–176. (Two plates with conodonts from Permian-Triassic Boundary)

Kozur H., Pjatakova M.,

1976. Die Conodontenart Anchignathodus parvus n. sp. eine wichtige leitform der basalen Trias. Proc. Kon. Nederl. Akad. Wetensch., Ser. B, v. 79(2), p. 123–128. (One plate with conodonts from basal part of Triassic)

Kolar-Jurkovsek T., Jurkovsek B.,

2007. First record of Hindeodus–Isarcicella population in Lower Triassic of Slovenia. Palaeogeography Palaeoclimatology Palaeoecology, v. 252, p. 72–81. (One plate with conodonts from the lowermost Triassic)

Kolar-Jurkovsek T., Jurkovsek B., Aljinovic D.,

2011. Conodont biostratigraphy and lithostratigraphy across the Permian-Triassic boundary at the Lukac section in western Slovenia. Rivista Italiana di Paleontologia e Stratigrafia, v. 117(1), p. 115–133. (Seven plates with conodonts from Permian-Triassic)

Krystyn L., Richoz S., Baud A., Twitchett R.J.,

2003. A unique Permian-Triassic boundary section from the Neotethyan Hawasina Basin, Central Oman Mountains. Palaeogeography Palaeoclimatology Palaeoecology v. 191 p. 329–344. (One plate with conodonts from Permian-Triassic boundary)

Lehrmann D.J., Payne J.L., Felix S.V., Dillett P.M., Wang H.M., Yu Y.Y., Wei J.Y.,

2003. Permian-Triassic Boundary Sections from Shallow-Marine Carbonate Platforms of the Nanpanjiang Basin, South China: Implications for Oceanic Conditions Associated with the End-Permian Extinction and Its Aftermath. Palaios v. 18, p. 138–152. (One figure with conodonts from lowermost Triassic)

Li Z.S., Zhan L.P., Dai J.Y., Jin R.G., Zhu X.F., Zhang J.H., Huang H.Q., Xu D.Y., Yan Z., Li H.M.,

1989. Study on the Permian-Triassic biostratigraphy and event stratigraphy of northern Sichuan and southern Shaanxi. Geological Memoirs, Series, vol. 29. Geological Publishing House, Beijing. 435 pp. (Fifteen plates with conodonts from Permian-Early Triassic).

Mei S.L., Zhang K.X., Wardlaw B.R.,

1998. A refined succession of Changhsingian and Griesbachian neogondolellid conodonts from the Meishan secion, candidate of the global stratotype section and point of the Permian-Triassic boundary. Palaeogeography Palaeoclimatology Palaeoecology, v. 143 p. 213–226. (Five plates with conodonts from strata around the Permian-Triassic boundary)

Metcalfe I., Nicoll R.S., Wardlaw B.R.,

2007. Conodont index fossil *Hindeodus changxingensis* Wang fingers greatest mass extinction event. Palaeoworld, v. 16, p. 202–207. (One figure with conodonts from Latest Permian and earliest Triassic)

Metcalfe I., Nicoll R.S.,

2007. Conodont biostratigraphic control on transitional marine to non-marine Permian-Triassic boundary sequences in Yunnan-Guizhou, China. Palaeogeography Palaeoclimatology Palaeoecology, v. 252, p. 56–65. (One plate with conodonts from Permian.Early Triassic)

Mou C.L., Ma Y.S., Guo X.S., Tan Q.Y., Li G..,

2005. Discovery of conodonts from the Permian-Triassic boundary beds in Muoshuihe Section of Tongjiang, Sichuan. Journal of Stratigraphy, v. 29(4), p. 372–375. (One plate with conodonts from Permian-Early Triassic)

Nicoll R.S., Metcalfe I., Wang C.Y.,

2002. New psecies of conodont genus *Hindeodus* and the conodont biostratigraphy of the Permian-Triassic boundary interval. Journal of Asian Earth Sciences, v. 20, p. 609–631. (13 plates with conodonts from Permian-Triassic boundary interval)

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1994. Conodonts from the lower Griesbachian Otoceras latilobatum bed of Selong, Tibet and the position of the Permian-Triassic boundary. Canadian Society of Petroleum Geologists, Memoir 17, p. 823–843. (Three plate with conodonts form Permian-Triassic)

Orchard M.J., Krystyn L.,

1998. Conodonts of the Lowermost Triassic of Spiti, and new zonation based on *Neogondolella* successions.Revista Italiana di Paleontologia e Stratigraphia, v. 104, p. 341–368. (Six plates with condodonts from Permian-earliest Triassic)

Perri M.C., Farabegoli E.,

2003. Conodonts across the Permian-Triassic boundary in the Southern Alps. Cour. Forsch. - Inst. Senckenberg, v. 254, p. 281–313. (Four plates)

Perri M.C., Molloy P.D., Talent J.A.,

2004. Earliest Triassic conodonts from Chitral, Northernmost Pakistan, Italy. Rivista Italiana di Paleontologia e Stratigrafia, v. 100(2), p. 467–478. (Two plates with conodonts from Permian-Early Triassic)

Schönlaub H.P.,

1991. The Permian-Triassic of the Gartnerkofel-1 Core (Carnic Alps, Austria): conodont biostratigraphy. Abh. Geol. B.-A., v. 45, p. 79–98. (One plate with conodonts from Permian-Early Triassic)

Teichert C., Kummel B., Sweet A.W.,

1973. Permian-Triassic strata, Kuh-e-Ali Bashi, Northwestern Iran. Bulletin of the Museum of Comparative Zoology, v. 145, p. 359–472. (Three plates with conodonts from Permian-Triassic)

Tian S.G.,

1993. The Permo-Triassic boundary and conodont zones in northwestern Hunan province. Bulletin of the Chinese academy of Geological sciences, n. 26, p. 137–147. (Two plates with conodonts from Permian-earliest Triassic)

1993. Late Permian-earliest Triassic conodont palaeoecology in Northwestern Hunan. Acta Palaeontologica Sinica, v. 32(3), p. 332–345. (One plate with conodonts from Permian-earliest Triassic)
1993: Evolution of conodont genera Neogondolella, *Hindeodus* and *Isarcicella*. Professional Papers of Stratigraphy and Palaeontology, v. 24 p. 128–144. (Three plates with conodonts from Permian and earliest Triassic)
Wang Z.H., Wang Y.G.,
1995. Permian-Lower Triassic conodonts from Selong Xishan of Nyalam, S. Tibet, China. Acta Micropalaeontologica Sinica, v. 12(4), p. 333–348. (Two plates with conodonts from Permian and Early Triassic)
Wang C.Y.,
1994. A conodont based high-resolution eventostratigraphy and biostratigraphy for the Permian-Triassic boundaries in South China. Palaeoworld 4, 234–248. (One plate with conodonts from Permian-Early Triassic)
1995a. Conodonts of Permian-Triassic boundary beds and stratigraphic boundary. Acta Palaeontologica Sinica, v. 34, p. 129–151 (Three plates with conodonts from Permian-earliest Triassic).
1995b. Conodonts of Permian-Triassic boundary beds and biostratigraphic boundary in Zhongxin Dadui section, Changxing, Zhejiang. Chinese Science Bulletin 40 (8), 719–722. (One figure with conodonts from Permian-Early Triassic)
Wang C.Y., Wang S.Q.,
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Xia F.S., Zhang B.G.,
1992. Age of the Selong Group in Xishan, Selong of Xizang and the Permian-Triassic boundary. Journal of Stratigraphy, v. 16(4), p. 256–263. (Three plates with conodonts from Permian-Early Triassic)
Yao J.X., Li Z.S.,
1987. Permian-Triassic conodont faunas and the Permian-Triassic boundary at the Selong section in Nyalam country, Xizang, China. Chinese Science Bulletin, v. 32, p. 22. (One plate with conodont from Permian-Early Triassic)
Yin H.F., Zhang K.X.,
1996. Eventostratigraphy of the Permian-Triassic boundary at Meishan Section, South China. In: Yin H.F., (eds.), NSFC project: the Palaeozoic-Mesozoic boundary candidates of Global stratotype section and point of the Permian-Triassic boundary. China Unicersity of Geosciences press, p. 84–96. (Four plates with conodonts from Permian-Early Triassic)
Zhang K.X.,
1987. The Permo-Triassic conodont fauna in Changing area, Zhejiang province and its stratigraphic significance. Earth Science - Journal of Wuhan College of Geology, v. 12(2), p. 163-200. (One plate with conodonts from Late Permian and Early Triassic)

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2008. Reconstruction of an apparatus of Neostrachanognathus tahoensis from Oritate, Japan and Species of Neostrachanognathus from Oman. Palaeontology, v. 51, p. 1201–1211 (Five figures with conodonts from Early Triassic)
Aljinovic D., Kolar-Jurkovsek T., Jurkovsek B.,

2006. Lithofacies and conodont zonation of Lower Triassic in northwestern external Dinarides (Gorski Kotar, Croatia). RMZ – Materials and Geoenvironment, v. 52(3), p. 581–596. (One figure with conodont species *Hindeodus parvus*)

2006. The lower Triassic shallow marine succession in Gorski Kotar region (External Dinarides, Croatia): Lithofacies and conodont dating. Rivista Italiana di Paleontologia e Stratigrafia, v. 112(1), p. 35–53. (One plate with conodont from Early Triassic)

Aljinovic D., Kolar-Jurkovsek T., Jurkovsek B., Hrvatovic H.,

2011. Conodont dating of the Lower Triassic sedimentary rocks in the external Dinarides (Croatia and Bosnia and Herzegovina). Rivista Italiana di Paleontologia e Stratigrafia, v. 117(1), p. 135–148. (One plate with conodonts from Early Triassic)

Beccaletto L., Bartolini A.C., Martini R., Hochuli P.A., Kozur H.,

2005. Biostratigraphic data from the C¸etmi Melange, northwest Turkey: Palaeogeographic and tectonic implications. Palaeogeography Palaeoclimatology Palaeoecology, v. 221, p. 215–244. (One plate with conodonts from Early and Middle Triassic)

Beranek L.P., Mortensen J.K., Orchard M.J., Ullrich T.,

2010. Provenance of North American Triassic strata from west-central and southeastern Yukon: correlations with coeval strata in the Western Canada Sedimentary Basin and Canadian Arctic Islands: Canadian Journal of Earth Sciences, v. 47, p. 53–73.

Beyers J.M., Orchard M.J.,

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SUPPLEMENTARY INFORMATION

1. First author publication
   - 1.1. 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. Journal of Asian Earth Sciences 105, 104–121.
2. Co-author publications
   - 2.1. Song, H.J., Wignall, P.B, Tong J.N., Bond, D.P.G., Song, H.Y., Lai, X.L., Zhang, K.X., Wang, H.M., Chen Y.L., 2012. Geochemical evidence from bio-apatite for multiple oceanic anoxic events during Permian–Triassic transition and the link with end-Permian extinction and recovery, Earth and Planetary Science Letters 353–354, 12–21.
   - 2.2. Sun, Y.D., Joachimski, M.M., Wignall, P.B., Yan, C.B., Chen, Y.L., Jiang, H.S., Wang, L.N., Lai, X.L., 2012. Lethally Hot Temperatures during the Early Triassic Greenhouse. Science 338, 366–370
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   - 2.4. 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 conodont at Bianyang Section, Guizhou province, South China. Palaios 28, 509–522.
   - 2.5. Sudar, M.N., Chen, Y.L., Kolar-Jurkovšek, T., Jurkovšek, B., Jovanović, D., Forel, M.B., 2014. Lower Triassic (Olenekian) microfauna from Jadar Block (Gučevo Mt., NW Serbia). Annales Geologiques de Peninsule Balkanique 75, 1–15.
   - 2.6. Song, H.J., Wignall, P.B, Tong, J.N., Song, H., Chen, J., Chu, D., Tian, L., Luo, M., Zong, K., Chen, Y.L., Lai, X., Zhang, K., Wang, H., 2015. Integrated Sr isotope variations and global environmental changes through the Late Permian to early Late Triassic. Earth and Planetary Science Letters 424, 140–147.
   - 2.7. Sun, Y.D., Wignall, P.B., Joachimski, M.M., Bond, D.P.G., Grasby, S.E., Sun, S., Yan, C.B., Wang, L.N., Chen, Y.L., Lai, X.L., 2015. High amplitude redox changes in the late Early Triassic of South China and the Smithian–Spathian extinction. Palaeogeography Palaeoclimatology Palaeoecology 427, 62–78.
   - 2.8 Kolar-Jurkovšek, T., Chen, Y.L., Jurkovšek, B., Poljak, M., Aljinović, D., Richoz, S. Conodont biostratigraphy of Olenekian (Early Triassic) in Mokrice, western Slovenia, and the reconstruction of some conodont apparatuses. (Submitted to *Palaeontology*)