Phylogenetic classification and evolution of Early Triassic conodonts

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ABSTRACT

Conodonts are some of the most important biostratigraphic index fossils in the Paleozoic and Triassic because of their rapid evolution and extensive distribution. Here we present a cladistic analysis of Early Triassic conodonts to reexamine the systematic classification and evolutionary relationships of the three related families Anchinognathodontidae, Ellisonidae, and Gondolellidae. The tree consists of 38 Early Triassic conodont species with multielement apparatus documented, based on parsimony analysis of 73 discrete morphological characters including 40 P1 element characters, 4 P2 element characters, 27 S element characters and 2 M element characters. Based on the phylogenetic time tree, a series of evolutionary lineages are supported: Parafurnishius xuanhanensis—Furnishius trissatus—Platyvillius regularis; Scythogondolella mosheri—Scythogondolella milleri; Discrateria—Conservatella—Pauella meki; Triassospathodus homeri—Chiosella; and Triassospathodus symmetricus—Triassospathodus chiensis. Reassignment of Ellisonia agordina to be Hadrodontina agordina is supported while Neospathodus planus should be reigned to the genus Triassospathodus. Meanwhile, Parafurnishius and Furnishius may belong to Gondolellidae rather than Ellisonidae or Ellisonidae may be a polyphyletic group rather than a monophyletic group. The cladogram suggests that Hindeodus, Hadrodontina and Pachycladina are monophyletic, whilst Novispathodus and Triassospathodus are paraphyletic and polyphyletic, respectively. In addition, a P1 element with a round basal cavity is an important trait to distinguish Novispathodus from Triassospathodus. The cladogram and revised classification provide a robust phylogenetic foundation for further investigations on systematic classification and evolutionary rates of conodonts during the Early Triassic.

1. Introduction

The Permian-Triassic mass extinction (PTME) was the largest biotic crisis in the Phanerzoic and it altered marine ecosystems from Paleozoic to Modern type (Sepkoski Jr., 1984; Erwin, 1994). This catastrophic event eliminated over 90% of marine species (Jin et al., 2000; Song et al., 2010), resulting in a low point of biodiversity in the Early Triassic followed by a delayed recovery of life (Payne et al., 2004; Chen and Benton, 2012; Song et al., 2018), and reshaped biogeographic patterns in the Early Triassic (Button et al., 2017; Dai and Song, 2020; Song et al., 2020). Five families of conodontophorids occurred at the beginning of the Changhsingian, but only three (perhaps four genera) survived up to the Permian–Triassic (P–Tr) boundary when three new genera appeared (Orchard, 2007). However, no major changes are noted among ellipsoids due to their poor records whereas up to 70% of species of Neogondolella, Clarkina and Hindeodus crossed the P–Tr boundary (Orchard, 2007).

Conodonts show multiple extinction-recovery processes in the Early Triassic rather than a delayed recovery following the PTME (Orchard, 2007; Stanley, 2009), suggesting that conodonts might be perfect fossils for deciphering the nature of the extinction and the eventual recovery. Early Triassic conodonts have been intensively studied for decades and used widely as reliable indicators of biostratigraphic divisions and correlations (e.g. Yin et al., 2001; Tong et al., 2003; Gradinariau et al., 2006; Orchard, 2010; Ogg et al., 2016; Wang and Wang, 2016; Lyu et al., 2020; Chen et al., 2020). For example, the P–Tr boundary is defined by the first occurrence of Hindeodus parvus and its Global Stratotype Section and Point has been ratified at Meishan, South China using the conodont datum (Yin et al., 2001). In addition, conodonts are good proxies for palaeoenvironmental and palaeoclimatic changes (Duan, 1989; Zhang and Guo, 1991; Tian, 1993; Lai and Zhang, 1999; Lai et al., 2001; Yang et al., 2001; Song et al., 2012, 2015; Joachimski et al., 2012, 2019; Schobben et al., 2014; Chen et al., 2016; Shen et al., 2018). However, there are many controversies in their systematics and processes of evolution. Taxa such as Triassospathodus, Novispathodus and Neospathodus have been debated for decades, and no agreement has been reached (e.

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ideal because incompleteness of the fossil record means that there are morphological attributes (Henderson and Mei, 2007). This is far from make testable predictions of these ranges and examine the current evolutionary relationships and systematical classifications (Donoghue, 2001). The methods have been applied to certain aspects of conodont systematics (Donoghue, 2001; Donoghue et al., 2008; Jiang et al., 2011; Mazza et al., 2012; Karadi et al., 2020), but cladistic analyses of Early Triassic conodonts have been limited to the hindeodid taxa (Jiang et al., 2011) and did not use the full range of characters seen in a complete conodont apparatus. The entire apparatus can deliver a high taxonomic signal in classification (Orchard, 2005) and many multi-element associations of Early Triassic conodonts have been reported during the last decades (e.g. Koike et al., 2004; Koike et al., 2004, Koike, 2016; Orchard, 2005; Goudemand et al., 2012; Agematsu et al., 2015, 2017; Sun et al., 2020a, 2020b), enabling a cladistic analysis including other P, S and M elements. In this study, we present a cladistic analysis of Early Triassic conodonts, based both on P elements alone and on the whole apparatus, testing the current hypothesis of evolutionary relationships and systematic classification and present several new hypotheses. Most taxa have been diagnosed using P1 elements alone, so a comparative analysis of the P1 element tree and the apparatus tree can show whether this is a reliable approach.

2. Materials and methods

We use a database of published conodont apparatuses (38 species) from the Early Triassic (see Appendix A for detail). The morphology of conodont elements is subject to appreciable variation during ontogeny because of particular growth patterns that reflect heterochronous shifts in the timing of developmental stages (Donoghue, 1998). Therefore, we consider only adult specimens, excluding juveniles and super-adults, which often differ substantially morphologically. For example, most adult taxa with platforms favour a robust platform, well-developed carina and fused denticles in the lower part rather than a slender platform, undeveloped carina and isolated denticles (Luo et al., 2006); most juvenile hindeodids have a thin and translucent basal cavity while in adults this is thick and non-translucent (Luo et al., 2008).

The coding of characters was based mainly on direct observation of holotypes and diagnoses and figures from reliable authorities (e.g. Kozur, 1996; Orchard, 2005). Contingent coding (Hawkins et al., 1997) can avoid the pitfalls of strict presence/absence coding (Donoghue et al., 2008), and therefore we follow this strategy in our study. Detailed steps are: 1) confirm the presence of a character. 2) If the character exists, we describe the nature of the character, otherwise, a question mark is used to indicate its inapplicability here. We formalize the statement by dividing it into several independent and non-overlapping character states. It is worth noting that a polymorphic coding strategy (represented as A, B, C and D in our data matrix) is used to represent polymorphic characters. Character statements are mainly modified after the descriptions in Donoghue et al. (2008), Jiang et al. (2011) and Mazza et al. (2012), and some new characters (e.g. 7, 8, 9, 10, 24, 25 in Fig. 2) are gleaned from existing characters, figures, and descriptions in the published literature and personal observations. For instance, we devised some quantitative boundaries (e.g. 18, 39 in Fig. 2) to redefine the qualitative or ambiguous descriptions of size in previous studies. Statements of characters have been modified in order to improve reproducibility and operability. For example, standard terms were used to describe the morphology of conodont elements, such as carminate and digyrate, which can mask similarities between different shapes (Donoghue et al., 2008). For this reason, we divided these complex morphological features into a series of relatively simpler component parts, such as ‘anterior processes’, ‘posterior processes’, and ‘lateral processes’ (Fig. 1). All studied taxa have been scored for 73 characters, including 40 P1 element characters, 4 P2 element characters, 27 S element characters and 2 M element characters. Most of these concern morphology, length, or ornament of elements, while 54 (74%) are presence-absence characters. Phylogenetic analysis of the complete data matrix (Table 1) was performed with TNT version 1.5 (Goloboff et al., 2008) (See Appendix C and D for original TNT file). All characters were equally weighted and unordered while Paracordylodus gracilis was set as the outgroup. The parsimony analysis was performed using ten traditional (heuristic) search replicates, with Tree Bisection Reconnection (TBR) branch-swapping and ten trees held at each step. Then, the second round of TBR swapping was run to find all the most parsimonious trees (MPTs) if the replications overflowed. We constructed two strict consensus trees for the P1 element and apparatus trees. Consistency and Retention indices (CI; RI) and Bremer Support of each node were noted.

3. Results

The P1 element strict consensus tree (Fig. 3A) is based on 532 MPTs of 117 steps, with a CI of 0.353, and a RI of 0.6.47 while the apparatus tree (Fig. 3B) recovered 4 MPTs, 259 steps long each, with a CI of 0.310 and RI of 0.628.

The apparatus tree (Fig. 3B) can be divided into three monophyletic subclades. Subclade A is composed of Hindeodus and Subclade B mainly consists of Ellisionidae, although Parafurarnishius xuanhanensis and Furarnishius triserratus are excluded. Gordolellidae, regarded as a paraphyletic group, constitutes Subclade C together with Para. xuanhanensis and Fur. triserratus. The whole ingroup monophyly is resolved in a relatively basal position as Subclade A + B and Subclade C. In Subclade B, Hadrodontina and Pachycladina are resolved as monophyletic and Hadrodontina is resolved as sister clade to the Ellisonia + Pachycladina clade. Subclade C is divided into two major clades in a relatively basal position. The first clade comprises most of subfamily Neogondolellinae and the genera Wapitiodus and Paddellia, all with a platform. The other clade is composed of the blade-like subfamily Novispathodinae and Cornudininae and genus Neospathodus.

Although the P1 element tree (Fig. 3A) is poorly resolved at family level, it is comparable to the apparatus tree (Fig. 3B) in some certain clades. Hindeodus (Subclade A), planate and blade-like taxa of Subclade C are also resolved as monophyletic respectively, and the difference is that Subclade A is resolved as sister clade of blade-like Subclade C rather than Subclade B.

4. Discussion

By combining data from Early Triassic conodonts, we present two phylogenetic resolutions and estimates of the interrelationships among three families, including Ellisionidae, Anchignathodontidae, and Gon- dolellidae (Fig. 3). Ellisionidae (Subclade B) and blade-like Subclade C are not resolved in the P1 element tree, but the clades of Hindeodus and planate Subclade C (=Wapitiodus + Sythogondolella + Neogondolella + Columbitella clade) have a similar topological structure to the apparatus tree (Fig. 3). Therefore, it is feasible to analyze the evolutionary relationships in the Hindeodus clade and Wapitiodus + Sythogondolella + Neogondolella + Columbitella clade by relying on the characteristics of P1 elements when an apparatus is absent.

In the following text, these three families are discussed in detail and systematically refined based on our phylogenetic trees (Fig. 3) and time tree (Fig. 4).
4.1. Ellisonidae Clark, 1972

Many hypotheses have been proposed to reconstruct the multielement apparatuses of Ellisonidae, but they are controversial because the included conodonts have mainly been discovered as isolated materials. Based on a natural assemblage composed of 11 elements from the uppermost Permian of Japan, Koike et al. (2004) described the multielement structure of Ellisonia, which is comparable to the standard 15-element plan of ozarkodinids. Koike (2016) summarized a septimembrate apparatus structure of the ellisonid apparatus containing 15 elements on the basis of natural assemblages previously reported and provided a description of its morphological features.

4.1.1. Systematic classification in Ellisonidae

According to morphologies, especially of its P1 elements, the family can be divided into two types. Generally speaking, type A has platforms, like Furnishius and Parafurnishius, while type B lacks platforms, such as Ellisonia, Pachycladina, and Hadrodontina (Fig. 3).

From the apparatus tree (Fig. 3B), we can see that taxa of type B including Hadrodontina, Ellisonia and Pachyclidina are clustered to constitute Subclade B. All these taxa have a pair of angulate P1 and P2 elements, extensive digyrate S1-2 elements, bipennate S3-4 elements, makellate M elements and a single alate S0 element. Denticles of all elements are thick and have rounded cross-section. Our apparatus tree (Fig. 3B) supports the reallocation proposed by Powell et al. (2019) that Ellisonia agordina with a seximembrate apparatus should be species of Hadrodontina, although Ellisonia agordina had been widely accepted (Perri and Andraghetti, 1987). Initially, the most significant diagnoses of Ellisonia and Hadrodontina was that Ellisonia has a S0 element with a posterior process but S0 element of Hadrodontina has no posterior process. However, many Hadrodontina have an alate S0 element that has a posterior process, such as Hadrodontina aequabilis and Hadrodontina aniceps. Based on the cladistic analysis of conodont multi-elements, Donoghue et al. (2008) indicated that a posterior process on the S0 element is not a diagnostic character between these two genera and our apparatus tree (Fig. 3B) gave a consistent conclusion. Powell et al. (2019) and Koike (2016) interpreted that Ellisonia can be distinguished from other ellisonids by its S1 element which has a slightly arched outer lateral processes without bending. Both Character 51 and 55 are clear that Ellisonia has a S1 element with arched and unbent outer-lateral process while the outer-lateral process of the Ellisonia agordina S1 element is horizontal and bent. Hadrodontina can differs from other ellisonids by its S elements. The lateral process of the S0 element (Character 47) and anterior process of the S3/4 element (Characters 64 and 68) are downward. The lateral processes of S1/2 are unequal in length (Character 54) and bent (Character 55). Thus, Ellisonia agordina should be reassigned as Hadrodontina agordina.

The hypothesis that Hadrodontina aniceps and Pachycladina peculiaris comprise a natural group (Orchard, 2007) is not supported by our apparatus tree (Fig. 3B) as these two species are situated in two clades.

As for type A, the P1 elements of Parafurnishius xuanhanensis established by Yang et al. (2014) from the Panlongdong section of Sichuan show a transitional character between blade-like and platform conodonts. Yang et al. (2014) noted that the S element of Parafurnishius has a strong cusp and divorced denticles with U-shaped gap, which is similar to Ellisonia. However, this classification is not supported in our apparatus tree (Fig. 3B). Indeed, Parafurnishius has S elements with peg-like denticles as in Ellisonidae, yet the P1 elements of Parafurnishius are like...
those of *Platyvilloisus regularis* and quite different form Ellisoniidae, in being transitional forms from blade to planate and they have stouter denticles, a platform and basal cavity. It is worth noting that *Merrillina/ Ellisionia?* n. sp. A and *Merrillina/Ellisionia?* n. sp. B in Orchard (2007) are very similar to the *P* elements of *Parafurnishius* and they all occurred from Griesbachian to Dienerian. Unfortunately, the absence of a published apparatus of these two species prevents us from including relevant data for analysis. Thus, Ellisoniidae may be a polyphyletic group rather than a monophyletic group, or alternatively, *Parafurnishius* and *Furnishius* perhaps should be reassigned to *Gondolellidae*.

### 4.1.2. Evolution of Ellisoniidae

Although many apparatuses have been reconstructed in Ellisoniidae, relationships are still obscure (Orchard, 2007; Koike, 2016). Orchard (2007) indicated that three species of *Hadrodontina* evolved from *Ellisionia triassica* while *Pachycladina enomerra* and *Pachycladina enomerra* are descendants of *Hadrodontina agordina*. This view is not supported in our time tree (Fig. 4) because *Ellisionia triassica* and *Pachycladina* share a different clade with *Hadrodontina*.

Our time tree (Fig. 4) proposed two new evolutionary lineages: *Hadrodontina agordina*—*Had. equispinus*—*Had. anceps*; and *Ellisionia triassica*—*Pachycladina enomerra*—*Pachy. obliqua*—*Pachy. peculiaris*.

In the first lineage, the evolutionary trend is that the basal margin of the *P* element gradually changes from straight to arched (Character 16), driving the cusp to gradually become upright (Character 9) and the posterior process of the *P* element shifts gradually downward (Character 44) (Fig. 4). In the second lineage, the progressive development occurred mainly in the *P* elements. The cusp tends to be smaller (Characters 2 and 4), the basal margin arched gradually (Character 16), and the longitudinal ridge is on the blade and developed along the whole length (Characters 22 and 23) (Fig. 4).

The lineage of *Parafurnishius xuanhanensis*—*Furnishius triserratus*—*Platyvilloisus regularis* proposed here (Fig. 4) supports the hypotheses that *Parafurnishius xuanhanensis* is ancestors of *Furnishius triserratus* (Yang et al., 2014) and *Platyvilloisus evolutus* from *Furnishius* (Orchard, 2007). Yang et al. (2014) proposed that *Parafurnishius evolutus* evolved from *Isarcicella* by developing random denticles on the platform on the premise that *Isarcicella* has similar ramiform elements to *Platyvilloisus*. At present, the multietlement associations of *Isarcicella* remains unknown and it is widely accepted that *Isarcicella* shares similar *P* elements slightly homeomorphic with *Parafurnishius* and *Merrillina* and *Merrillina* elements slightly homeomorphic with *Isarcicella* and *Hadrodontina*.
makes it impossible to test this hypothesis. At least from the available data, *Parafurnishius* shares different clade with *Ellisonidae* and *Hindeodus* (Fig. 4).

Our time tree (Fig. 4) show that *Parafurnishius* might have evolved from segminate elements, but absent of apparatus data of earlier Griesbachian and Dienerian segminate or segminiplanate elements such as *Neospathodus svalbardensis* and *Neoclarkina discreta* restrict the integrity and reliability of this evolutionary hypothesis.

4.2. Evolution of Anchignathodontidae Clark, 1972

Anchignathodontidae was established by Clark (1972). It has a seximembrate skeletal apparatus including carminiscaphate P₁ elements, angulate P₂ elements, and alate S₀ elements (Sweet, 1988). Early Triassic Anchignathodontidae mainly comprise *Hindeodus*, *Isarcicella* and *Sweetohindeodus* (Orchard, 2007). Because there is no apparatus fossil record for *Isarcicella* or *Sweetohindeodus*, only *Hindeodus* is included in this analysis. Agematsu et al. (2015) reported natural assemblages of *Hindeodus parvus* and *Hindeodus typicalis* in the Mino Terrane of Japan comprising a pair of carminiscaphate P₁ elements, angulate P₂ element, Makellate M element, digyrate S₂ element, bipennate S₃–₄ element and a single alate S₀ element. Later, another two digyrate S₂ element were found through synchrotron radiation X-ray micro-tomography (Agematsu et al., 2017).

*Hindeodus* is ruled out as a monophyletic group in both P₁ element and apparatus trees (Fig. 3), and they have very similar topological structure, indicating that morphological analysis for the P₁ element is feasible in the *Hindeodus* clade. Cladistic analysis of 22 hindeodid species demonstrates that *Hindeodus parvus* did not directly evolve from *Hindeodus praeparvus* (Jiang et al., 2011) and this view is supported in our time tree (Fig. 4). The evolutionary lineage of *Hindeodus typicalis–H. latidentatus* (Kozur, 1989) is supported although *Hindeodus latidentatus* is
not the direct descent of *Hindeodus typicalis* (Fig. 4).

### 4.3. Gondolellidae Lindström, 1970

Gondolellidae is a dominant conodont group from the Permian to Triassic, which was established by Lindström (1970). Huckriede (1958) attempted to reconstruct their multi-element apparatus. Initial research suggested that it comprises only pectiniform elements. However, the discovery of clusters and natural assemblages (Rieber, 1979; Orchard, 2005; Goudemand et al., 2012; Takahashi et al., 2019) shows that the multi-element apparatus comprises pectiniform and ramiform elements. Orchard (2005) drew on abundant well-dated conodont material from North America, Europe, and Asia, and reconstructed the apparatus blueprint for Gondolellidae consisting of 15 elements. According to the cluster of *Novispathodus pingdingshanensis*, Goudemand et al. (2012) revised the position of S1 and S2 in Gondolellidae as well as S3 and S4 in Novispathodinae.

#### 4.3.1. Systematic classification in Gondolellidae

Orchard (2005) argued that ramiform elements, especially S0, S1, and S2 carry a high taxonomic signal in classification within the Gondolellidae. Although the P1 element tree in Gondolellidae is poorly resolved, the *Waptiodus + Scythogondolella + Neogondolella + Columbitella* clade has a similar topological structure with apparatus tree (Fig. 3). It may be attributed to their similar S1 elements, and 80% (13 of 16) characters have the same character state. Therefore, it is feasible to analyze relationships among these four genera using only P1 elements.

Mosher (1968) established *Neospathodus*, and nearly all segminate elements in the Early Triassic were assigned to it. Later, Kozur et al. (1998) established the new genus *Triassopathodus* and assigned 13 species to it based on their P1 elements. Orchard (2005) described their multi-element apparatus and established a new genus *Novispathodus*. Goudemand et al. (2012) revised the template of the *Novispathodus* apparatus proposed by Orchard on the basis of a cluster from South China. According to the apparatus tree (Fig. 3B), *Neospathodus planus* clusters with most *Triassopathodus*. *Neospathodus planus* has similar P1 elements as *Triassopathodus hungaricus* both showing a square basal cavity (Character 21), thick denticles with round cross-section (Character 7), and the ratio of length and height in profile close to 1:1 (Character 18). The most significant difference between these two species is that *Neospathodus planus* has a wider and inflated basal cavity and longer unit. Besides the P1 elements, *Neospathodus planus* also shares very similar angulate P2 elements and breviniform digyrate S1-S2.
elements with *Triassospathodus chioensis* and *Triassospathodus symmetricus*. *Neospathodus planus* should be reassigned to *Triassospathodus planus*, but it still needs a more complete apparatus to test according to its absence of $S_0$ and $S_{3,4}$ elements.

The apparatus tree (Fig. 3B) shows that *Novispathodus* is paraphyletic whereas *Triassospathodus* is polyphyletic. Taxonomic classification between *Novispathodus* and *Triassospathodus* is still controversial. The shape of basal cavity in the $P_1$ element may be a stable diagnosis to
5. Conclusion

The evolutionary relationship between Scythogondolella mosheri and Scythogondolella milleri (Orchard, 2007) is supported by our time tree (Fig. 4).

Columbitella elongata and Neogondolella ex. gr. regalis were said to have evolved from Borinella (Orchard, 2007), but our time tree (Fig. 4) shows a close relationship between this clade and Scythogondolella. Orchard (2007) suggested that Borinella and Scythogondolella are parallel clades. Because there is no apparatus for Borinella, this genus is not included in our analysis. Evolution of Columbitella elongata and Neogondolella ex. gr. regalis still needs more apparatus data, especially for Borinella.

The Discretella–Conservatella–Pa.meeki lineage (Orchard, 2007) is supported by our time tree (Fig. 4). The overall evolutionary trend for P1 elements, is that the denticles became gradually inclined, and the whole apparatus turns downward from the horizontal and spacing between the denticles gradually reduces (Characters 41 and 43) (Fig. 4).

Besides, our time tree (Fig. 4) also supports the lineages of Triassospathodus homer–Chiosella and Triassospathodus symmetricus–Triassospathodus chioensis proposed by Orchard (2007) (Fig. 4).

5. Conclusion

The application of cladistic analysis to Early Triassic conodont results in two phylogenetic trees, one based on P1 elements and the other on whole apparatuses, reflecting patterns of evolution in the aftermath of the Permian-Triassic mass extinction. We report the following findings: 1) The lineages of Parafurnishius xuanhanensis–Furnishius tri серии–Platevillosus regularis, Scythogondolella mosheri–Scythogondolella milleri, Discretella–Conservatella–Paulella meeki, Triassospathodus homer–Chiosella, Triassospathodus symmetricus–Triassospathodus chioensis are supported. 2) Ellisonia agordina should be redefined as Hadrodonata agordina and Neogondolella planus should be reassigned as a Triassospathodus species. 3) The original assignment of Parafurnishius and Furnishius to Ellisonidae is doubtful and they might be reassigned to Gondolellidae. 4) Hindeodus, Hadrodonata and Pachycladina are monophyletic, Novispathodus is paraphyletic but Triassospathodus is polyphyletic. 5) Parafurnishius xuanhanensis might be derived from segminate elements. 6) Hadrodonata can be distinguished from other Ellisonidae genera by its 5 elements, and the P1 elements of Novispathodus have a round basal cavity while Triassospathodus has a squared or oval one.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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