

RECONSTRUCTION OF THE MULTIELEMENT APPARATUS OF THE CONODONT *GLADIGONDOLELLA TETHYDIS* (HUCKRIEDE) USING MULTIVARIATE STATISTICAL ANALYSIS; IMPLICATIONS FOR TAXONOMY, STRATIGRAPHY, AND EVOLUTION

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Abstract. The multielement apparatus of the Spathian (late Early Triassic) to Carnian (early Late Triassic) conodont *Gladigondolella tethydis* (Huckriede, 1958) is reconstructed here using multivariate statistical analysis to determine the co-occurrence of elements previously assigned to the *Gl. tethydis* apparatus by other authors. Disagreements on the apparatus composition of *Gl. tethydis* have focussed around whether or not the species contained two pairs of P2 elements, or only one pair. Some reconstructions consider elements referred to *Cratognathodus* as belonging to the multielement apparatus of *Gladigondolella*, whereas other workers consider these elements to belong to their own multielement apparatus. In the absence of fused clusters or bedding plane assemblages, multivariate statistical analysis of isolated elements provides the best method for constraining apparatus composition. Examination of collections from the Anisian (early Middle Triassic) of China and Romania, together with published occurrences from the Anisian and Carnian from around the world, has allowed the development of a database for both abundance and presence/absence of elements assigned to the *Gladigondolella tethydis* apparatus. Bray-Curtis indices for abundance data and Jaccard indices for presence/absence data both demonstrate that *Cratognathodus* elements occur as frequently with other elements belonging to the *Gladigondolella tethydis* apparatus as those elements do with each other. This lends support to the hypothesis that *Cratognathodus* elements also belong to the *Gladigondolella tethydis* apparatus. Therefore, the *Gladigondolella tethydis* apparatus proposed herein consists of the following elements: *Gladigondolella tethydis* (P1); *Cratognathodus* sp. (P2a); *Ozarkodina saginata* (Huckriede, 1958) (P2b); *Roundya lautissima* (Huckriede, 1958) (S0); *Lonchodina spengleri* (Huckriede, 1958) (S1); an enantiognathid element (S2); *Hindeodella petrae-viridis* (Huckriede, 1958) (S3); *Hindeodella multihamata* (Huckriede, 1958) (S4); and *Lonchodina venusta* (Huckriede, 1958) (M). Several of the elements assigned to the apparatus exhibit morphological variability, including the P1 element of *Gladigondolella tethydis*.

INTRODUCTION

The conodont genus *Gladigondolella* is a long-lived component of Triassic conodont faunas, ranging in age from late Olenekian (Spathian; Chen et

al. 2021) to early Carnian (Julian; Chen et al. 2016). Originally named by Müller (1962) with the Julian species *Gl. tethydis* as type species, the genus has subsequently been recognized as a dominant part of lower Anisian faunas (Orchard 2010). With current interest in defining the Global Stratotype Section and Point (GSSP) for the base of the Anisian, it is necessary to better understand the conodont

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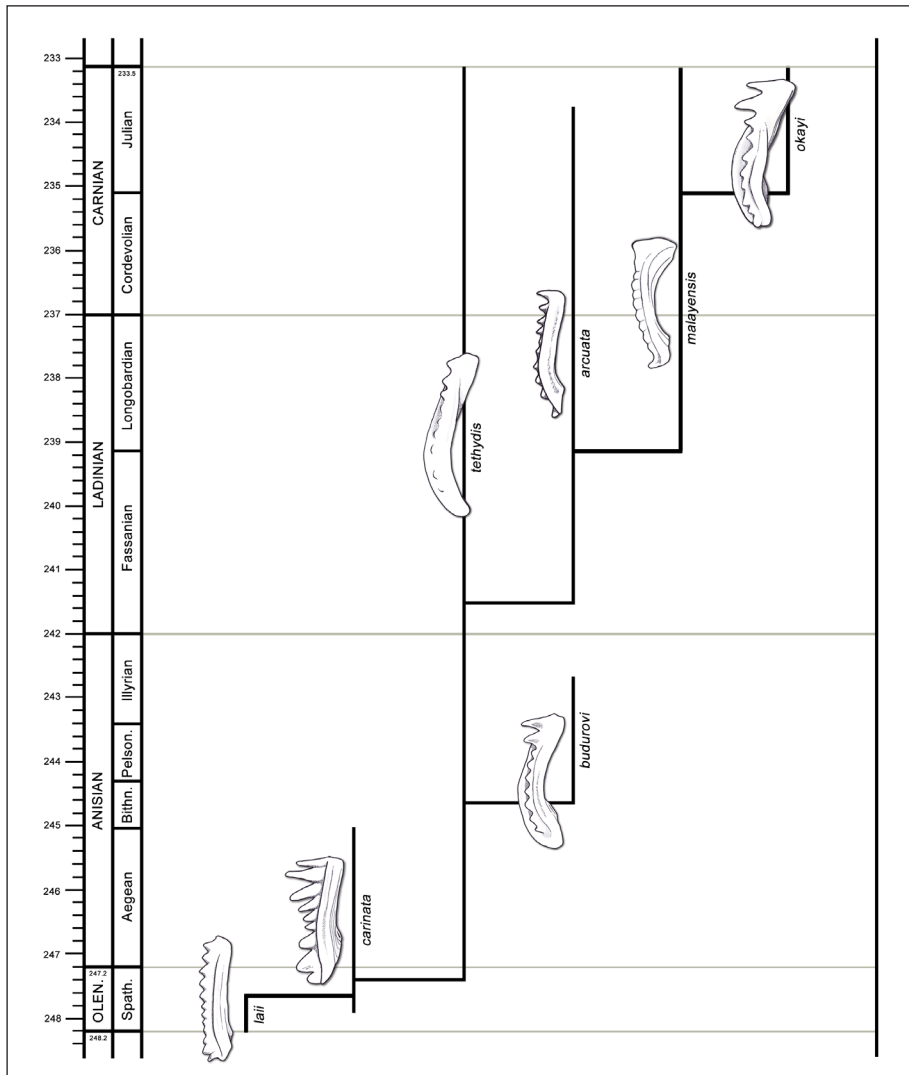


Fig. 1 - Range chart showing the stratigraphic range of the seven species belonging to the genus *Gladigondolella*. Abbreviations: OLEN. = Olenekian; Bithn. = Bithynian; Pelson. = Pelsonian.

faunas of the lowermost substage of the Anisian, termed the Aegean. Although the favoured biotic proxies for recognition of the boundary are currently either an ammonoid (e.g., Grădinaru 2021) or the conodont *Chiosella timorensis* (Nogami, 1968) (e.g., Chen et al. 2020), the first occurrence of *Gl. tethydis* has also been discussed as an alternative indicator of proximity to the boundary (Orchard 2010). Thus far, six different species have been assigned to *Gladigondolella*: *Gl. tethydis*, *Gl. arcuata* Budurov, 1973, *Gl. malayensis* Nogami, 1968, *Gl. budurovi* Kovács & Kozur, 1980, *Gl. okayi* Kılıç, 2016 and *Gl. carinata* Bender, 1970 (Fig. 1)

Despite the importance of the genus for Middle Triassic biostratigraphy, the composition of its multielement apparatus is not clear. No natural assemblages containing specimens of *Gladigondolella* have yet been recovered; therefore, existing reconstructions have been made based on the recognition of repeated associations of elements, particularly in

monogeneric samples. Although several of the elements belonging to the apparatus have been agreed upon in previous studies (see reconstructions in Orchard 2005; Ishida & Hirsch 2011; Kılıç et al. 2013), there remains uncertainty about whether *Gladigondolella* possessed one or two sets of P2 elements. Ishida and Hirsch (2011) first suggested that the *Gladigondolella* apparatus may have had two sets of P2 elements, and therefore consist of 17 elements; although it is commonly accepted that Triassic conodonts possessed 15 elements in an octomembrate apparatus (2xP1, 2xP2, 2xM, 2xS1, 2xS2, 2xS3, 2xS4, 1xS0; Orchard 2005), some older conodonts have been shown to possess a greater number of elements in an apparatus (e.g. Aldridge et al. 2013). In contrast, Kılıç et al. (2013) considered the P2 elements to be sexually dimorphic, wherein an individual organism would have possessed only one pair of P2 elements, but different organisms within the genus would have had different P2 element

	Kılıç et al. (2013)	Koike (1999)	Orchard (2005)	
	<i>Gladigondolella</i>	<i>Cratognathodus</i>	<i>Gladigondolella</i>	<i>Cratognathodus</i>
P1	<i>Gladigondolella tethydis</i>	<i>Cratognathodus kochi</i>	<i>Gladigondolella tethydis</i>	<i>Cratognathodus</i> sp.
P2a	<i>Ozarkodina saginata</i>	<i>Cratognathodus saginatus</i>	Ozarkodinid	Ozarkodinid
P2b	<i>Cratognathodus kochi</i>	-	-	-
S0	<i>Roundya laustissima</i>	<i>Diplodella lautissima</i>	Roundyid	Roundyid
S1	Enantiognathid	Enantiognathid	Enantiognathid	Enantiognathid
S2	<i>Lonchodina spengleri</i>	<i>Cypridodella spengleri</i>	Lonchodinid	Lonchodinid
S3	<i>Hindeodella petrae-vidris</i>	<i>Hindeodella petrae-vidris</i>	Hindeodellid	Hindeodellid
S4	<i>Hindeodella multihamata</i>	<i>Hindeodella multihamata</i>	Hindeodellid	Hindeodellid
M	<i>Lonchodina venusta</i>	<i>Cypridodella venusta</i>	Lonchodinid	Lonchodinid

Tab. 1 - Table showing the various elements assigned to the *Gladigondolella* and *Cratognathodus* apparatuses in reconstructions by previous authors.

pairs. Such dimorphism is commonly attributed to sexual dimorphism, and has been implied for other conodonts (e.g. *Mesogondolella* and *Jinogondolella* in the Permian (Lambert et al. 2007); *Kladognathus* and *Idioprioniodus* in the Carboniferous (Merrill & Merrill 1974; Purnell 1993)).

The reconstruction of the *Gladigondolella* apparatus by Kılıç et al. (2013) is in contrast to the previous effort of Orchard (2005), who recognised an octomembrate apparatus with one set of P2 elements, based on collections from the Middle Triassic of Romania and Hungary. The two interpretations share much in common (see list of elements in Table 1), with the main difference being the inclusion of elements of the genus *Cratognathodus* as P2 elements in the reconstruction of Kılıç et al. (2013). This genus was first named by Mosher (1968a), with a type species, *Cr. kochi* (Huckriede), from the Julian. Other species subsequently assigned to the genus include *Cr. angulata* Budurov, *Cr. sp. A* sensu Orchard and *Cr. sp. B* sensu Orchard (Fig. 1). Orchard (2005) considered *Cratognathodus* to be a separate genus from *Gladigondolella* and reconstructed a multielement apparatus for *Cratognathodus* based on monogeneric collections from the Early Triassic of Oman. This reconstruction differs somewhat from a previous attempt made by Koike (1999), based on monogeneric collections of *Cratognathodus* from the Middle Triassic Taho Formation of Japan (Table 1). Orchard (2005) suggested that the differences may be due to the different ages of the specimens in the two reconstructions. Additionally, the denticulation of *Gladigondolella* and *Cratognathodus* resembles that of elements of *Guangxidella*, as reconstructed

by Zhang and Yang (1991); however, the morphology of the elements of *Guangxidella*, in particular those assigned to the M and S3 positions, differs from those previously assigned to the apparatus of *Gladigondolella* or *Cratognathodus*. Similarly, some of the ramiform elements assigned to the multielement apparatus of the Spathian *Neospathodus chinensis* (Bender, 1970) by Koike (2004) also resemble those assigned to *Gladigondolella* and *Cratognathodus*, although the S2 element is grodeliform (breviform digyrate) rather than extensiform digyrate and the M element is cypridodelliform rather than lonchodiniform.

Despite the differences in these previous reconstructions, it is also clear that there are many similarities (Table 1). The following elements are widely accepted to belong either to the *Gladigondolella* or *Cratognathodus* apparatus (or both): *Ozarkodina saginata* Huckriede, P2 element; *Roundya lautissima* Huckriede, S0 element; *Lonchodina spengleri* Huckriede, S1 element; an enantiognathid S2 element; *Hindeodella petrae-vidris* Huckriede, S3 element; *Hindeodella multihamata* Huckriede, S4 element; and *Lonchodina venusta* Huckriede, M element. These elements were all present in the collections of Huckriede (1958), and reproductions of the illustrations of these elements from this paper are shown in Figure 2.

In an attempt to provide new constraints on the apparatus composition of *Gladigondolella* and *Cratognathodus*, we investigated several archival conodont samples housed at the Geological Survey of Canada, as well the published literature, and recorded the existence of the ramiform elements (as

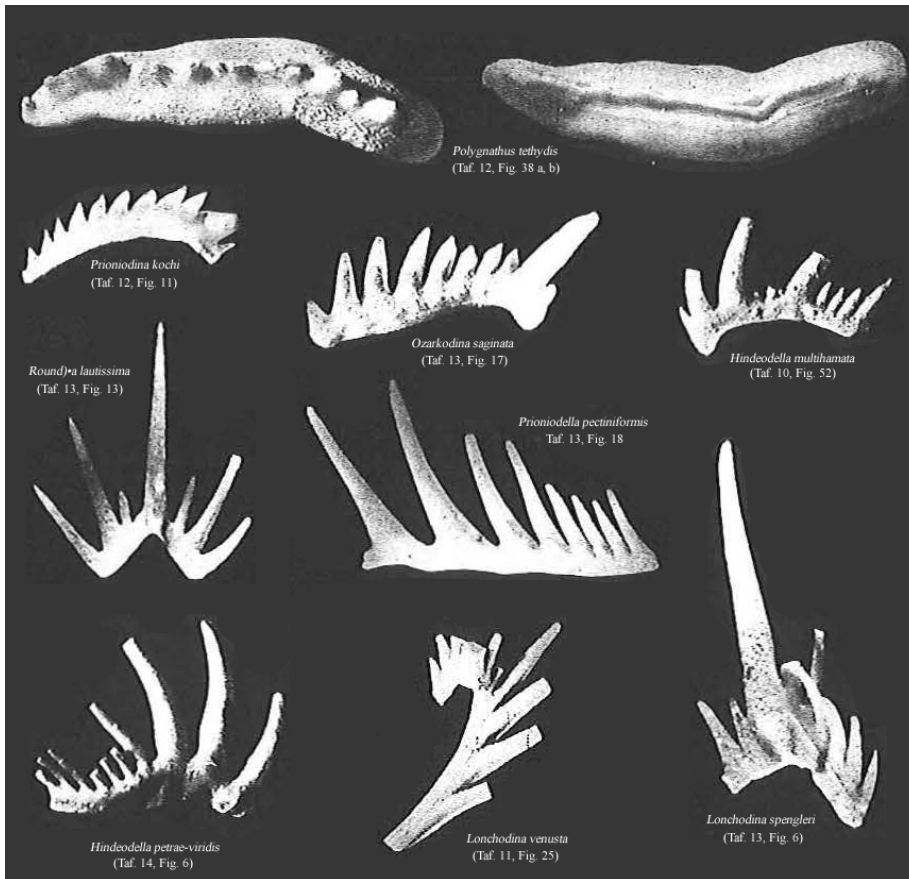


Fig. 2 - Elements commonly assigned to either the *Gladigondolella* or *Cratognathodus* multielement apparatus (see list of elements in Table 1). Reproduced from Huckriede (1958).

defined in Table 1) that occurred together with P1 elements of *Gladigondolella tethydis* and/or *Cratognathodus*. We then conducted a multivariate statistical analysis of all these elements to determine their relative frequency of co-occurrence. If elements of *Cratognathodus* occur together with those of *Gladigondolella tethydis* as frequently, or more frequently, than the ramiform elements previously assigned to the *Gladigondolella* apparatus, this would lend support to the hypothesis of Ishida and Hirsch (2011) and Kılıç et al. (2013) that *Cratognathodus* also belongs to the *Gladigondolella* multielement apparatus, or at least to that of *Gl. tethydis*.

MATERIALS AND METHODS

Material

This study utilises both new and published records of *Gladigondolella tethydis* and *Cratognathodus* specimens from several localities across the world (Fig. 3). When compiling data from the published literature, the only papers included were those with records of elements of either *Gladigondolella tethydis* or *Cratognathodus* occurring together with ramiform

elements previously referred to the multielement apparatus of these species. Table 1 contains a list of most of these elements, as recorded in the reconstructions of *Gladigondolella* by Kılıç et al. (2013) and Orchard (2005), and of *Cratognathodus* by Koike (1999) and Orchard (2005); in addition, specimens of *Lonchodina* sp. included in the *Cratognathodus* apparatus by Orchard (2005) as S2 (now S1) and M elements were also counted, as were specimens of *Anastrophognathus*, included in the *Gladigondolella* apparatus as S0 elements by Ishida and Hirsch (2011) and Kılıç (2021). Using these restrictions, samples used in this study come from the Anisian Hallstätterkalk, Partnachschichten and Schryeralmkalk in Austria (Mosher 1968a); from the Anisian Tahoe Formation in Japan (Nogami 1968; Koike 1982); from the Anisian Marmarotrapeza Formation in Greece (Bender 1970; Vrielynck 1987); from the Anisian Tepeköy Formation and other Anisian limestones in Turkey (Gedik 1975; Önder 1984); from Anisian olistoliths in Bulgaria (Spasov & Ganey 1960; Budurov 1976b); from the Anisian limestone of Timor (Nogami 1968); from the Anisian limestone of Slovakia (Kozur & Mock 1973a); from the Anisian Kalapani Formation of the Himalaya (Sahni



Fig. 3 - Paleogeographic map showing the location of samples used for this study during the Triassic (base map modified from Scotese and Schettino 2017). Locations marked with a yellow star represent records taken from the literature, whereas those marked with a red star represent collections examined by the authors. Codes for localities: 1) Japan; 2) South China (this study); 3) Timor; 4) Malaysia; 5) Himalaya; 6) Turkey; 7) Greece; 8) Romania (this study); 9) Bulgaria; 10) Slovakia; 11) Austria; 12) Italy. Modified from Scotese and Schettino (2017).

& Chhabra 1974); from conglomeratic limestone of Malaysia, thought to be late Anisian in age (Nogami 1968; Koike 1982); from the Carnian San Cassiano Formation of Italy (Mastandrea 1995; Vrielynck 1987); and from several Anisian, Ladinian and Carnian limestone formations in Austria (Huckriede 1958).

These published records were supplemented by new counts made by the authors of elements preserved in collections from China and Romania (Fig. 3). The Chinese samples come from the Luolou and Xingyuan formations at the Guandao section, deposited off the margin of the Great Bank of Guizhou and preserved in Guizhou Province, south China (Lehrmann et al. 2006). Conodonts from this section were previously reported by Orchard et al. (2007b), but no ramiform elements were recorded. The Romanian samples come from the GSSP candidate section for the base of the Anisian, at Deșli Caira in North Dobrogea (Grădinaru et al. 2007). The conodonts from this section come from the Hallstatt-type limestones preserved there and were reported on by Grădinaru et al. (2006), Orchard et al. (2007a) and Golding (2021); none of these publications discussed the ramiform elements in the samples, although some were illustrated by

Orchard (2005) as part of his multielement reconstruction of *Gladigondolella*.

A total of 358 samples (308 samples from the literature, 50 new samples examined by the authors) have been utilized for this study (see Supplementary Material Table 1). Some samples in the literature, and all the new samples, allowed the abundance of each element-type to be determined; for others, only presence-absence data was available.

Methods

After the presence-absence data was tabulated, the resulting data matrix (Supplementary Material Table 2) was interrogated using multivariate statistical analysis. This data matrix consisted of the whole dataset; those samples with abundance data were converted to presence-absence data prior to the analysis. Each pair of elements was analysed using the Jaccard similarity index, which is defined as follows (Jaccard 1912):

$$\text{Jaccard}(A,B) = \frac{|A \cap B|}{|A| + |B| - |A \cap B|} \quad (1)$$

where $|A|$ and $|B|$ are the number of specimens in each sample set. In this study, each

sample set consisted of the occurrences of one element type (Table 2).

For the abundance data, the multivariate Bray-Curtis dissimilarity index (non-normalized) was used. This index is defined as follows (Bray & Curtis 1957; Clifford & Stevenson 1975):

$$\text{Bray-Curtis (A,B)} = 1 - 2 \frac{|C|}{|A| + |B|} \quad (2)$$

where $|A|$ and $|B|$ are the total number of specimens counted in each sample set, and $|C|$ is the sum of the lesser counts of only those species found in each sample set. As for the presence-absence data, each sample set in this study consisted of the occurrences of one element type (Table 2).

Numerous indices of similarity exist (Shi 1993), and the Jaccard index has been chosen for this study because it has been shown to provide some of the most reliable results when compared with simulated data (Shi 1993). The Bray-Curtis index for abundance data was chosen as it is the complement of the Jaccard index for presence-absence data (Hammer & Harper 2006). Although both of these indices have been shown to be suitable for this kind of analysis, they also have weaknesses, particularly as they are both sensitive to sample size (Shi 1993; Hammer & Harper 2006).

Potential sources of bias exist in our analysis, although we have done our best to minimize the effects of these biases. Conodont taxonomy has been standardized between samples, to ensure that the record of a particular species is accurately captured. The uneven distribution of fossils within samples presents a possible source of bias, which cannot easily be controlled, as it is not clear that all the elements have the same preservation potential (von Bitter & Purnell 2005). Additionally, varying depositional, ecological and tectonic conditions between samples means that many of the samples do not contain complete sets of multielement apparatuses.

Results

The occurrence of elements in each sample are shown in the Supplementary Material Table 1. The results of the pairwise comparison of elements using both the Jaccard similarity index and the Bray-Curtis dissimilarity index are shown in

Table 2. The numbers in these tables represent the frequency with which each pair of elements co-occur; the larger the number, the more commonly the elements occur together.

The co-occurrence of *Gladigondolella tethydis* elements with *Cratognathodus* elements is 0.32 (Jaccard) and 0.13 (Bray-Curtis). The *Gladigondolella tethydis* elements show similar values for their co-occurrence with *Ozarkodina saginata* (J: 0.38; B: 0.15); *Roundya lautissima* (J: 0.25; B: 0.26); enantiognathid elements (J: 0.13; B: 0.13); *Lonchodina spengleri* (J: 0.41; B: 0.29); *Hindeodella petrae-viridis* (J: 0.45; B: 0.40); *Hindeodella multibamata* (J: 0.28; B: 0.24); and *Lonchodina venusta* (J: 0.40; B: 0.19). Equally, the indices for co-occurrence between *Cratognathodus* elements and ramiform elements are similar to (or higher than) those seen for *Gladigondolella tethydis*: *Ozarkodina saginata* (J: 0.47; B: 0.56); *Roundya lautissima* (J: 0.38; B: 0.24); enantiognathid elements (J: 0.34; B: 0.43); *Lonchodina spengleri* (J: 0.47; B: 0.47); *Hindeodella petrae-viridis* (J: 0.53; B: 0.39); *Hindeodella multibamata* (J: 0.44; B: 0.51); and *Lonchodina venusta* (J: 0.34; B: 0.53). The ramiform elements named above mostly show high levels of similarity between each pair, ranging from lows of 0.40 in Bray-Curtis (for the pair *Lonchodina venusta* and *Hindeodella petrae-viridis*) and 0.27 in Jaccard (for the pair *Hindeodella petrae-viridis* and an enantiognathid), to highs of 0.81 in Bray-Curtis (for *Ozarkodina saginata* and *Lonchodina venusta*) and 0.55 in Jaccard (for *Ozarkodina saginata* and *Lonchodina spengleri*). The elements of *Lonchodina* thought to represent the S2 and M elements of the *Cratognathodus* reconstruction in Orchard (2005) both have very low levels of similarity with all other elements; for *Lonchodina* sp. (S1), this ranges from 0.00 in Jaccard for the pairing with enantiognathid elements up to a maximum of 0.19 with *Lonchodina venusta* (no abundance data was available for the *Lonchodina* sp. (S1) element, so it records only zeros for the Bray-Curtis index); for *Lonchodina* sp. (M), it has the lowest pairing with *Lonchodina venusta* (J: 0.09; B: 0.10) and the highest with the enantiognathid element (J: 0.41; B: 0.34). Notably, both show very low levels of similarity with both *Gladigondolella tethydis* (J: 0.09 and 0.03; B: 0.00 and 0.14) and *Cratognathodus* (J: 0.16 and 0.09; B: 0.00 and 0.13), lower than any other element in Table 1. *Anastrophognathus sagittalis*, suggested as an alternative S0 element by Kılıç (2021) has similarity indices below 0.10 (Jaccard) and 0.06 (Bray-Curtis) with every other element in the study.

		Bray-Curtis										Jaccard															
		<i>Ozarkodina saginata</i>	<i>Ronduya lanatissima</i>	Enantiognathid	<i>Lonchodina spengleri</i>	<i>Hindeodella petrae-viridis</i>	<i>Hindeodella multibamata</i>	<i>Lonchodina venusta</i>	<i>Lonchodina sp. (Crato. S2)</i>	<i>Lonchodina sp. (Crato. M)</i>	<i>Anastrophognathus sagittalis</i>	<i>Gladigondolella</i>	<i>Cratognathodus</i>			<i>Ozarkodina saginata</i>	<i>Ronduya lanatissima</i>	Enantiognathid	<i>Lonchodina spengleri</i>	<i>Hindeodella petrae-viridis</i>	<i>Hindeodella multibamata</i>	<i>Lonchodina venusta</i>	<i>Lonchodina sp. (Crato. S2)</i>	<i>Lonchodina sp. (Crato. M)</i>	<i>Anastrophognathus sagittalis</i>	<i>Gladigondolella</i>	<i>Cratognathodus</i>
<i>Ozarkodina saginata</i>	1.00	0.44	0.69	0.70	0.42	0.70	0.81	0.00	0.20	0.00	0.15	0.56			1.00	0.51	0.43	0.47	0.39	0.42	0.41	0.39	0.10	0.21	0.00	0.38	0.47
<i>Ronduya lanatissima</i>	0.44	1.00	0.54	0.47	0.49	0.42	0.41	0.00	0.38	0.00	0.26	0.24			0.51	1.00	0.53	0.44	0.44	0.32	0.46	0.36	0.04	0.23	0.00	0.25	0.38
Enantiognathid	0.69	0.54	1.00	0.60	0.54	0.58	0.62	0.00	0.34	0.00	0.13	0.43			0.43	0.53	1.00	0.32	0.27	0.39	0.27	0.00	0.41	0.00	0.13	0.34	
<i>Lonchodina spengleri</i>	0.70	0.47	0.60	1.00	0.49	0.68	0.71	0.00	0.12	0.00	0.29	0.47			0.60	0.44	0.32	1.00	0.46	0.46	0.42	0.09	0.13	0.12	0.01	0.41	
<i>Hindeodella petrae-viridis</i>	0.42	0.49	0.54	0.49	1.00	0.46	0.40	0.00	0.00	0.00	0.40	0.39			0.46	0.32	0.27	0.46	1.00	0.41	0.51	0.13	0.14	0.12	0.06	0.45	
<i>Hindeodella multibamata</i>	0.70	0.42	0.58	0.68	0.46	1.00	0.71	0.00	0.12	0.00	0.24	0.51			0.41	0.46	0.41	0.42	0.41	1.00	0.35	0.04	0.14	0.14	0.10	0.44	
<i>Lonchodina venusta</i>	0.81	0.41	0.62	0.71	0.40	0.71	1.00	0.00	0.00	0.00	0.06	0.44			0.46	0.36	0.27	0.42	0.51	0.35	1.00	0.19	0.09	0.03	0.40	0.44	
<i>Lonchodina sp. (Crato. S2)</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00			0.39	0.36	0.27	0.42	0.42	0.04	0.19	1.00	0.00	0.00	0.13	0.06	
<i>Lonchodina sp. (Crato. M)</i>	0.20	0.38	0.34	0.12	0.29	0.12	0.10	0.00	0.00	0.13	0.14	0.03			0.41	0.04	0.41	0.09	0.13	0.14	0.09	0.00	1.00	0.00	0.09	0.16	
<i>Anastrophognathus sagittalis</i>	0.00	0.00	0.00	0.01	0.06	0.05	0.01	0.00	0.00	0.00	0.06	0.03			0.41	0.23	0.41	0.13	0.12	0.14	0.03	0.00	0.00	0.00	0.00	0.09	
<i>Gladigondolella</i>	0.15	0.26	0.13	0.29	0.40	0.24	0.19	0.00	0.14	0.00	0.06	0.03			0.38	0.25	0.13	0.41	0.45	0.28	0.40	0.13	0.09	0.03	1.00	0.32	
<i>Cratognathodus</i>	0.56	0.24	0.43	0.47	0.39	0.51	0.53	0.00	0.13	0.03	0.13	1.00			0.47	0.38	0.34	0.47	0.53	0.44	0.34	0.06	0.16	0.09	0.32	1.00	

Tab. 2 - Results of the similarity analyses, using the Bray-Curtis Dissimilarity Index (for abundance data) and the Jaccard Similarity Index (for presence/absence data). Results are for pairwise comparison of elements.

DISCUSSION

Co-occurrence of elements

The frequency of co-occurrence of elements analysed in this study is similar, regardless of which pair of elements are being compared. In particular, the similarity indices between *Gladigondolella tethydis* and *Cratognathodus* (J: 0.32; B: 0.13) are in line with those between *Gladigondolella tethydis* and ramiform elements widely accepted as belonging to the *Gladigondolella* multielement apparatus, for example between *Gladigondolella tethydis* and *Roundya lautissima* (J: 0.25; B: 0.26), and *Gladigondolella tethydis* and *Hindeodella multibamata* (J: 0.28; B: 0.24). The similarity indices between pairs of ramiform elements in Table 1 are also similar, supporting the suggestion of previous authors that these belonged to one apparatus. If these other ramiform elements do indeed belong to the multielement apparatus of *Gladigondolella tethydis*, the results of our analysis suggest that *Cratognathodus* is likely to have also been a part of the same apparatus, in support of the hypothesis of Ishida and Hirsch (2011) and Kılıç et al. (2013).

This study suggests that the apparatus of *Gladigondolella tethydis* consisted of the following elements (Fig. 4): *Gladigondolella tethydis* (P1); *Cratognathodus* sp. (P2a); *Ozarkodina saginata* (P2b); *Roundya lautissima* (S0); *Lonchodina spengleri* (S1); an enantiognathid element (S2); *Hindeodella petrae-viridis* (S3); *Hindeodella multibamata* (S4); and *Lonchodina venusta* (M). The taxonomy of these elements is discussed in further detail in the Systematic Paleontology section. As shown in Figure 5, these elements consistently co-occur in collections re-examined for this study, from China, Romania, and Turkey. It is not certain whether all elements were present in a single, 17-element apparatus, as Ishida and Hirsch (2011) suggested, or whether the P2b elements were dimorphic elements in a 15-element apparatus, as suggested by Kılıç et al. (2013).

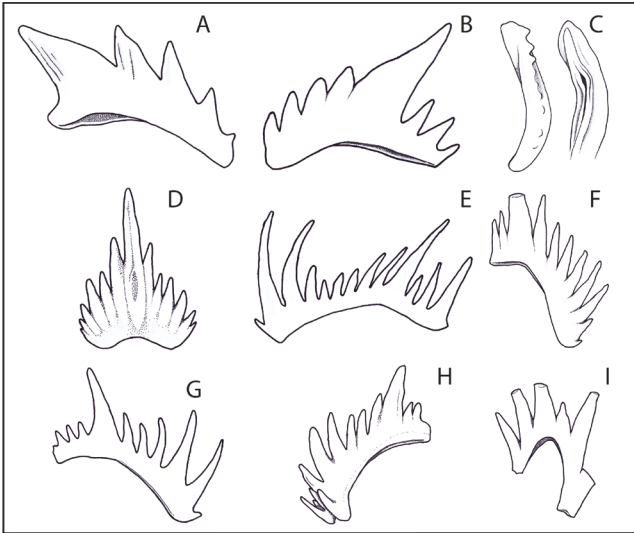


Fig. 4 - Representative sketches of the elements of the *Gladigondolella tethydis* apparatus. A) P2a element; B) P2b element; C) P1 element; D) S0 element; E) S1 element; F) S2 element; G) S4 element; H) S3 element; I) M element. Sketches based on material from Anisian Tepeköy Formation of the Kocaeli Peninsula, Turkey.

This reconstruction is similar to previous reconstructions that have utilized a combination of repeated co-occurrence of elements and mono-specific collections. The reconstruction is most like those proposed by Ishida and Hirsch (2011) and Kılıç et al. (2013), sharing the presence of a *Cratognathodus* P2 element, although lacking the dimorphic S0 element of Ishida and Hirsch (2011). The reconstruction is also close to that of Koike (1999) for *Cratognathodus*, with the only difference being the addition of *Gladigondolella* as the P1 element. Similarly, the reconstruction of *Gladigondolella* by Orchard (2005) shares all of the elements of this reconstruction other than the *Cratognathus* P2. The collections that Orchard (2005) used to reconstruct the multielement apparatus of *Gladigondolella* have been re-examined as part of this study, and do not contain any P elements of *Cratognathodus*; however, the samples that were used to reconstruct the multielement apparatus of *Cratognathodus* have also been re-examined, and these do contain P elements of *Gladigondolella*. Only two of the elements (lonchodininid S1 and lonchodininid M) assigned to the *Cratognathodus* multielement apparatus by Orchard (2005) likely do not belong to the *Gladigondolella tethydis* apparatus, as they do not consistently occur in the samples utilized in this study. The proposed S1 element does not occur in any of the samples utilized in this study (Supple-

mentary Material Table 2), whereas the proposed M element does occur but still has very low similarity indices with other elements of the apparatus (Supplementary Material Table 2). Similarly, the anastrophognathid element considered by Ishida and Hirsch (2011) and Kılıç (2021) to represent an alternative S0 element in the *Gladigondolella* apparatus does not appear to occur in any of the samples utilised in this study, outside of Turkey, and so it also has near-zero similarity indices. It is not clear at this point what multielement apparatus these three elements belonged to.

Age range of elements

P elements of *Gladigondolella tethydis* have been recovered from the Spathian (Muttoni et al. 2019) to the Julian (Chen et al. 2016). Similarly, the P elements of *Cratognathodus* also appear for the first time in the Spathian (Orchard 2007), and range in age to the Carnian (Huckriede 1958). The age range of the ramiform elements is harder to determine, as without the P elements it may not be clear that these elements belong to *Gladigondolella tethydis* or *Cratognathodus*, and ramiform elements are often not described in publications. Bearing these limitations in mind, it does appear as though the majority of ramiform elements belonging to these genera are present starting in the Anisian (Spasov & Ganev 1960; Mosher 1968a; Nogami 1968; Bender 1970; Sahni & Chhabra 1974; Gedik 1975; Budurov 1976b; Čatalov & Budurov 1978; Koike 1982; Önder 1984), and at least *Roundya lautissima*, *Ozarkodina saginata*, *Lonchodina spengleri*, *Hindeodella petrae-viridis*, *Hi. multibamata* and *Lo. venusta* continue until the Carnian (Huckriede 1958; Vrielynck 1987; Mastandrea 1995). The similar age range of these elements lends further support to their inclusion in one apparatus. However, these ramiform elements may belong to the apparatuses of different species or genera at different times; for example, elements resembling the S3 and S4 elements have been reported in association with *Neospathodus chionensis* (Koike 2004) and *Guangxidella* (Zhang & Yang 1991), and the S0 and S3 elements have also been found in North American strata lacking P elements of either *Gladigondolella* or *Cratognathodus* (Mosher & Clark 1965).

The new multielement reconstruction has relevance for biostratigraphy around the Olenekian-Anisian boundary, as the first occurrence of

Gladigondolella tethydis has been suggested as an indicator of this time interval (Orchard 2010). Elements of *Cratognathodus* appear earlier than specimens of *Gl. tethydis* or *Gl. carinata* at both Deşli Caira and Guandao (Orchard et al. 2007a, 2007b), suggesting that the range of *Gladigondolella* may be longer than has previously been recognized at these sections, with either *Gl. carinata* or *Gl. tethydis* extended deeper into the Spathian.

Morphological variation of elements

The present study is based primarily on Anisian and Carnian material; however, there does not appear to be variation in the composition of the apparatus between the samples from the Anisian and those from the Carnian (see Supplementary Material Table 1). There does however appear to be variation in the morphology of some of the constituent elements of the apparatus. The degree of variation in the P1 and P2a elements is quite large, and has led to several species being named; however, there also appears to be more minor differences in the morphology of the ramiform elements. These differences include: variability in the number of posterior denticles in *Ozarkodina saginata*, ranging from one (e.g. Vrielynck 1987, pl. 14, fig. 11) to five (e.g. Gedik 1975, pl. 5, fig. 22); the angle between the two processes of *Lonchodina spengleri*, from relatively narrow (e.g. Orchard 2005, fig. 5, part C) to relatively wide (e.g. Koike 1999, fig. 5, part 3); and the distance along the anterior process of *Hindeodella petrae-viridis* at which the secondary process splits off, ranging from one denticle (e.g. Bender 1970, pl. 5, fig. 3) to four (e.g. Orchard 2005, fig. 5, part F).

Additionally, there appears to be some degree of variation in the morphology of the P1 elements of the long-ranging species *Gladigondolella tethydis*. The Carnian holotype of this species (Huckriede 1958) is relatively broad, with a long posterior elongation to the platform and keel (Huckriede 1958, pl. 12, fig. 38). In contrast, the Anisian specimens assigned to this species show a thinner platform, and a shorter keel (Fig. 6). However, there is quite a lot of morphological variation in this species, with specimens from the same sample showing a range of platform widths depending on growth stage (e.g. Dürkoop et al. 1986, plate 18; Kılıç 2016, fig. 5). This is well illustrated by the Julian specimens from Turkey shown in Fig.

6 (parts 4 – 9, 9), which are all from one sample. Within the Anisian forms re-studied for the current paper, there is little morphological difference between the P1 elements from China and Romania although there is a widening of the platform in the youngest specimens from Guandao (Fig. 6, part 8); these wider forms from Guandao are similar to those that have been illustrated from the GSSP candidate section at Wantou in South China (Chen et al. 2020).

It has been proposed that *Gladigondolella tethydis* evolved from *Gl. carinata* in the Aegean (Orchard et al. 2007a; Chen et al. 2016); however, the occurrence of specimens of *G. tethydis* in the Spathian requires an older date for this evolution. In the wider genus, there is also likely an evolutionary lineage between the Ladinian – Carnian species *Gl. arcuata* – *Gl. malayensis* – *Gl. okayi*, distinguished by broadening and straightening of the platform, and the development of a free blade. The much older Anisian species *Gl. budurovi* may also be directly related to this lineage, and was originally included as a subspecies of *Gl. malayensis* (Kovács & Kozur 1980a); however, there appears to be a significant stratigraphic gap between *Gl. budurovi* and the rest of this lineage, and so this relationship is uncertain. The oldest named species of *Gladigondolella* is *Gl. laii* from the early Spathian of China (Chen et al. 2021; Leu et al. 2022), although older specimens of *Gl. sp.* are known from the earliest Spathian of Oman (Leu 2021). The similarity in carinal dentition between these oldest specimens and species of the Smithian – Spathian genus *Borinella* (compare fig. 9, parts A-H (*Bo. sweeti* (Kozur & Mostler 1976)) with fig. 9, parts Z-AA (*Gl. laii*) in Orchard 2021) may suggest an origin of *Gladigondolella* within *Borinella*, although this hypothesis requires more study; an alternative origin for the genus may be found in the Smithian genus *Guangxidella*, whose P1 elements resemble the cratognathodiform P2 elements of *Gladigondolella* (see pl. 1, figs. 1, 2 in Zhang & Yang 1991).

SYSTEMATIC PALEONTOLOGY

- Class **CONODONTA** Pander, 1856
 Order **Ozarkodinida** Dzik, 1976
 Family Uncertain
 Genus *Gladigondolella* Müller, 1962

Gladigondolella tethydis (Huckriede, 1958)**P1 element (Fig. 5, parts 1, 9, 17; Fig. 6)**

Polygnathus tethydis, Huckriede, 1958, p. 157 – 158, pl. 11, figs. 39, 40, pl. 12, fig. 38, non fig. 1, pl. 13, figs. 2, 4, 5, non fig. 13; Budurov, 1960, p. 117, pl. 2, figs. 29, 33, non figs. 28, 30; Spasov & Ganey, 1960, p. 85, pl. 1, fig. 27, pl. 2, fig. 16, non pl. 1, fig. 26; non Mosher & Clark, 1965, p. 563, pl. 66, fig. 13; Budurov & Pévny, 1970, pl. 17, figs. 15?, 16;

Gladigondolella tethydis (Huckriede), Ishii & Nogami, 1966, pl. 1, fig. 1, non fig. 2; Nakazawa & Nogami, 1967, pl. 1, fig. 14; Hayashi, 1968, p. 69, pl. 3, fig. 8; Mosher, 1968a, p. 937, pl. 116, figs. 1, 5, 8?, non fig. 2; Mosher, 1968b, pl. 119, figs. 9, 10, 7?, non fig. 8; Nogami, 1968, p. 123 – 124, pl. 9, figs. 1 – 3, 5, 7, 9, 10, non figs. 4, 6, 8, pl. 11, figs. 5, 6; Hirsch, 1969, pl. 1, figs. 1, 2?, 3; non Bender, 1970, p. 505 – 506, pl. 2, figs. 2 – 5; Hayashi, 1971, pl. 2, fig. 11; Kozur & Mostler, 1971, pl. 1, figs. 1, 2; Mock, 1971, pl. 3, fig. 26; Sweet et al., 1971, pl. 1, fig. 28; Zawadzka, 1972, pl. 1, fig. 8?, 11; Budurov, 1973, p. 802, pl. 1, figs. 4 – 7; non Kozur & Mock, 1973a, pl. 1, fig. 5; non Kozur & Mock, 1973b, pl. 1, fig. 3; Sweet in Ziegler, 1973, p. 91 – 94, pl. “*Anchignathodus I*”, fig. 4; Gedik, 1975, p. 120 – 121, pl. 3, figs. 15, 17?, non fig. 16; Sladić-Trifunović & Ljubović, 1975, p. 170, pl. 2, figs. 1 – 3?, figs. 9 – 11?, non figs. 4 – 8; Budurov, 1976a, pl. 5, fig. 5; Budurov, 1976b, p. 102, pl. 2, fig. 19; non Kemper et al., 1976, p. 105, pl. 6, fig. 1; Sudar, 1977, pl. 6, figs. 28?, 29?, non figs. 17, 26, 27; non Boyanov and Budurov, 1979, pl. 2, fig. 6; Mietto & Petroni, 1981, p. 8, pl. 1, fig. 4, pl. 2, fig. 4; Isozaki & Matsuda, 1980, pl. 1, fig. 8; Kovács & Kozur, 1980a, pl. 3, figs. 5, 6; Krystyn, 1980, pl. 11, fig. 11?; Matsuda, 1980, pl. 1, fig. 5; Pisa et al., 1980, p. 816 – 817, pl. 60, fig. 3; Kovács & Kozur, 1980b, pl. 3, figs. 5, 6; Gupta & Budurov, 1981, pl. 2, figs. 1 – 2; non Koike, 1981, pl. 1, fig. 39; Kolar-Jurkovsek, 1983, pl. 3, figs. 1a, b, 2a – c; Farabegoli et al., 1984, fig. 4, part e; Dürkoop et al., 1986, pl. 18, figs. 6 – 14, non figs. 5, 15; Vrielynck, 1987, p. 130 – 131, pl. 1, figs. 19 – 21, pl. 2, figs. 1 – 3; Igo, 1989, fig. 6, part 3; non Birkenmajer et al., 1990, pl. 2, fig. 2; Gaetani et al., 1992, pl. 17, fig. 7; Kozur & Mostler, 1992, pl. 2, figs. 19, 20; Neri et al., 1995, pl. 2, fig. 1; Mastandrea, 1995, pl. 2, figs. 1, 2; Samankassou, 1996, p. 524, pl. 1, figs. 11, 12; Hornung & Brandner, 2005, fig. 10, part n; Hornung, 2006, p. 26, pl. 1, figs. 3 – 6; Hornung et al., 2007, p. 279, fig. 7, parts c, d; Orchard et al., 2001, pl. 1, figs. 20, 21; Orchard, 2005, fig. 5, part A; Orchard et al., 2007b, fig. 6, part 35; Orchard et al., 2007a, fig. 5, parts 29, 30; Ishida & Hirsch, 2011, fig. 7, parts 1, 2; Yao et al., 2011, pl. 2, figs. 10, 13, 17; Di Stefano et al., 2014, pl. 1, fig. 9; Lehrmann et al., 2015, fig. 6, parts 26, 27; Ishida et al., 2015, pl. 1, figs. 2, 3; Liang et al., 2016, fig. 6, parts 23, 24; Kılıç, 2016, p. 461, figs. 5.1 – 5.9, 6.8, 6.9; Maron et al., 2019, fig. 4, part 7; Chen et al., 2020, fig. 5, part 5; Golding & Orchard, 2021, p. 16, pl. 13, figs. 36 – 42.

P2a element (Fig. 5, parts 2, 10, 18)

Lonchodina angulata, Budurov, 1971, p. 28, pl. 1, figs. 1, 2;
Lonchodina? posterognathus (Mosher), Kozur & Mostler, 1971, pl. 1, fig. 10; Kozur & Mostler, 1972, p. 19, pl. 10, figs. 6, 7, 11;
Cratognathodus posterognathus angulatus (Budurov), Gedik, 1975, p. 113, pl. 8, figs. 25, 26.
Prioniodina kochi Huckriede, 1958, p. 159, pl. 11, fig. 37?, pl. 12, figs. 11, 12, pl. 14, fig. 4; Spasov & Ganey, 1960, p. 89, pl. 1, fig. 23, pl. 2, fig. 12; *Catalov* & Stefanov, 1966, pl. 1, fig. 3; Hirsch, 1969, pl. 1, fig. 7; Bender, 1970, p. 527, non pl. 5, fig. 12; Hirsch, 1969, pl. 1, fig. 7?;
Neoprioniodus cf. kochi (Huckriede), Ishii & Nogami, 1966, non pl. 1, fig. 12;
Cratognathodus kochi (Huckriede), Mosher, 1968a, p. 919, pl. 113, figs. 3, 4?, non fig. 7; Jenkins & Jenkins, 1971, non fig. 5, no. 29; Sahni & Chhabra, 1971, p. 263, pl. 3, figs. D, E?, F, non I;

Gedik, 1975, p. 111 – 112, pl. 5, fig. 23; Budurov, 1976b, pl. 4, fig. 29; Sudar, 1977, pl. 5, fig. 4; Catalov & Budurov, 1978, pl. 1, fig. 8; Koike, 1981, pl. 1, fig. 21; Koike, 1982, p. 20, pl. 9, fig. 15, non fig. 16; Önder, 1984, p. 76, pl. 22, figs. 7?, 8?; Dürkoop et al., 1986, pl. 18, figs. 1 – 4; Ishida & Hirsch, 2011, fig. 7, parts 9 – 12; Ji et al., 2011, fig. 4, part 4; Muto et al., 2018, fig. 10, part K?; Sashida et al., 2022, p. 433, figs. 7.45, 7.46;

Cratognathodus cuspidatus Koike, 1982, p. 20 – 21, pl. 9, figs. 17?, 18; non *Prioniodina kochi germanica* Kozur, 1968a, p. 139 – 140, pl. 1, figs. 24, 25; Kozur 1968b, pl. 3, figs. 15, 19, 21; Kozur, 1968c, p. 1081;

Gladigondolella tethydis (Huckriede), Birkenmajer et al., 1990, pl. 2, fig. 2;

Gladigondolella ozarkodinid element, Kılıç, 2021, figs. 6.1, 6.12.

Cratognathodus sp. A, Orchard, 2005, fig. 6, part A;

Cratognathodus sp. A Orchard et al., 2007b, fig. 6, part 13; Orchard et al., 2007a, fig. 5, parts 11, 12, 22; Tekin et al., 2021, p. 9, pl. 2, fig. 16.

Cratognathodus sp. B Orchard et al., 2007b, fig. 6, parts 14, 15; Orchard et al., 2007a, fig. 5, parts 18 – 21.

P2b element (Fig. 5, parts 3, 11)

Ozarkodina saginata Huckriede, 1958, p. 153 – 154, pl. 13, figs. 16, 17, 20; Mosher, 1968a, p. 932, pl. 115, fig. 14, non fig. 15;

Pseudozarkodina saginata (Huckriede), Vrielynck, 1987, p. 229 – 230, pl. 14, figs. 9 – 11;

Cratognathodus posterognathus Mosher, 1968a, p. 919, pl. 113, figs. 10, 14; Gedik, 1975, p. 112, pl. 5, figs. 19, 20, 22, non pl. 8, figs. 25, 26; Koike, 1981, pl. 1, fig. 30; Koike, 1982, p. 20, pl. 9, figs. 20, 21?; Önder, 1984, p. 77, pl. 22, figs. 9 – 11; Dürkoop et al., 1986, pl. 23, fig. 1 non fig. 2;

Lonchodina? posterognathus (Mosher), non Kozur & Mostler, 1971, pl. 1, fig. 10; Mock, 1971, pl. 1, fig. 9; non Kozur & Mostler, 1972, p. 19, pl. 10, figs. 6, 7, 11; Birkenmajer et al., 1990, pl. 2, fig. 5;

Lonchodina angulata Budurov, Čatalov & Budurov, 1975, p. 1248, pl. 1, fig. 8;

Xaniognathus saginatus (Huckriede), Koike, 1982, pl. IX, figs. 8 – 12;

Cratognathodus multihamatus Pb element, Koike, 1999, fig. 4, parts 1 – 5 only;

Gladigondolella tethydis (Huckriede) P2 element, Orchard, 2005, fig. 5, part B;

Cratognathodus sp. P2 element, Orchard, 2005, fig. 6, part B.

S0 element (Fig. 5, parts 4, 12, 19)

Roundya lautissima Huckriede 1958, p. 160, pl. 11, fig. 41, pl. 13, figs. 13 – 15; Spasov & Ganey, 1960, p. 90, pl. 2, fig. 15, non fig. 22; Ishida & Hirsch, 2011, fig. 8, parts 6, 8, 9, non part 7;

Diplodella lautissima (Huckriede), Ishii & Nogami, 1966, pl. 1, fig. 15; Mosher, 1968a, p. 924, pl. 114, fig. 20; Sahni & Chhabra, 1974, p. 270, pl. 3, fig. S?; Budurov, 1976b, pl. 4, fig. 36; Sudar, 1977, pl. 5, fig. 2; Koike, 1982, plate VII, figs. 21, 22;

Hibbardella lautissima (Huckriede), Kozur & Mostler, 1971, pl. 1, fig. 13; Mock, 1971, pl. 3, figs. 7, 13; Vrielynck, 1987, p. 195 – 196, pl. 11, figs. 3 – 7;

Hibbardella magnidentata (Tatge), Gedik, 1975, p. 122 – 123, pl. 4, figs. 8 – 10 only;

Cratognathodus multihamatus Sa element, Koike, 1999, fig. 4, parts 20 – 24;

Gladigondolella tethydis (Huckriede) S0 element, Orchard, 2005, fig. 5, part E;

Cratognathodus sp. S0 element, Orchard, 2005, part H;

Gladigondolella roundyid element, Kılıç, 2021, figs. 6.3, 6.4.

S1 element (Fig. 5, parts 7, 23)

Lonchodina spengleri Huckriede, 1958, p. 152, pl. 10, figs. 54, 55?, 56?, pl. 11, fig. 6, pl. 12, fig. 9, pl. 13, figs. 1, 6, 10, pl. 14, fig. 11; Bender, 1970, p. 513 – 514, pl. 3, figs. 12, 13? – 15, non fig. 17;

Prioniodina spengleri (Huckriede), Budurov, 1976b, pl. 3, figs. 8, 9?, 11? – 15, 16 – 18, non figs. 20 – 25, non pl. 4, figs. 37 – 39; Sudar, 1977, pl. 5, fig. 11; Čatalov & Budurov, 1978, pl. 1, fig. 5, non figs. 4, 6, pl. 2, fig. 20, non figs. 19, 21;

Prioniodina (Flabellignathus) spengleri spengleri (Huckriede) Gedik, 1975, p. 146, pl. 7, figs. 23, 31, 33;

Prioniodina (Flabellignathus) spengleri sapanlii Gedik, 1975, p. 146 – 147, pl. 7, figs. 22, 26, 27, 30;

Cypridodella spengleri (Huckriede), Mosher, 1968a, p. 922, pl. 113, figs. 19, 20, 25, non fig. 18; Sahni & Chhabra, 1974, p. 269, fig. 3, part O?; Önder, 1984, p. 78, non pl. 22, figs. 3, 4;

Hindeodella (Metaprioniodus) spengleri (Huckriede), Kozur & Mostler, 1971, pl. 1, fig. 12; Mock, 1971, pl. 2, fig. 13?, non fig. 14; Mastandrea, 1995, pl. 3, fig. 3;

Cratognathodus multibamatus (Huckriede) Sb2 element, Koike, 1999, fig. 5, parts 1 – 8;

Gladigondolella tethydis (Huckriede) S2 element, Orchard, 2005, fig. 5, part C;

Gladigondolella prioniodinid element, Kılıç, 2021, fig. 6.2 only.

S2 element (Fig. 5, parts 5, 16, 22)

Prioniodina petrae-viridis (Huckriede), Mosher, 1968a, pl. 116, figs. 30, 31 only;

Hindeodella stoppeli, Bender, 1970, p. 510, pl. 2, figs. 6, 15 – 17;

Enantiognathus petraeviridis (Huckriede), Ishida & Hirsch, 2011, fig. 9, parts 1 – 3;

Enantiognathus jungi (Mosher), Vrielynck, 1987, pl. 9, figs. 7 – 9;

Cratognathodus multibamatus (Huckriede), Sb1 element, Koike, 1999, fig. 4, parts 25 – 32;

Gladigondolella tethydis (Huckriede) S1 element, Orchard, 2005, fig. 5, part H;

Cratognathodus sp. S1 element, Orchard, 2005, fig. 6, part F;

Gladigondolella prioniodinid element, Kılıç, 2021, fig. 6.9 only.

S3 element (Fig. 5, part 15)

Hindeodella petrae-viridis Huckriede, 1958, p. 149 – 150, pl. 11, fig. 46?, pl. 13, figs. 7?, 8?, 9, 11, 12, 14, pl. 14, fig. 6, non fig. 7; Spasov & Ganey, 1960, p. 81, pl. 1, figs. 3, 4, pl. 2, fig. 3; Ishii & Nogami, 1966, pl. 1, fig. 14?; Čatalov & Stefanov, 1966, pl. 1, figs. 4, 7, 16?; Hirsch, 1969, pl. 1, fig. 4; Ishida & Hirsch, 2011, fig. 9, parts 6, 7;

Prioniodina petrae-viridis (Huckriede), Mosher, 1968a, p. 934 – 935, pl. 116, figs. 28, 29, non 30, 31; Sahni & Chhabra, 1974, p. 284 – 285, fig. 5 A?, non C, D?, E?; Sudar, 1977, pl. 5, figs. 7?, 12?; Önder, 1984, p. 86 – 87, pl. 23, figs. 16 – 21;

Prioniodina (Flabellignathus) petraeviridis (Huckriede), Gedik, 1975, p. 145 – 146, pl. 8, figs. 11, 27;

Prioniodina spengleri (Huckriede), Budurov, 1976b, pl. 4, figs. 38, 39, non fig. 37;

Parachirognathus petrae-viridis (Huckriede), Bender, 1970, p. 524, pl. 5, figs. 1?, 2, 3, 4?, 5?, 6, non figs. 8, 9;

Enantiognathus petraeviridis (Huckriede), Mock, 1971, pl. 1, fig. 3, non figs. 4, 10, pl. 2, fig. 17; Vrielynck 1987, p. 188, pl. 9, fig. 10?, non figs. 11, 12; Mastandrea, 1995, pl. 3, figs. 1?, 2?;

Diplodella petraeviridis (Huckriede), Koike, 1981, pl. 1, fig. 26; Koike, 1982, p. 26 – 27, pl. 7, fig. 25;

Prioniodina (Flabellignathus) latidentata (Tatge), Gedik, 1975, p. 143 – 144, pl. 8, figs. 13 – 15, 16? – 18, 20, 21, 23, 24;

Cratognathodus multibamatus (Huckriede) Sc1 element, Koike, 1999, fig. 5, parts 9 – 17;

Gladigondolella tethydis (Huckriede) S4 element, Orchard, 2005, fig. 5, part G;

Cratognathodus sp. S4 element, Orchard, 2005, fig. 6, part G.

S4 element (Fig. 5, parts 8, 14, 20)

Hindeodella multibamata Huckriede, 1958, p. 148 – 149, pl. 10, figs. 52, 53, pl. 12, fig. 23; Spasov & Ganey, 1960, pl. 1, figs. 6?, 7?, 8?; Čatalov & Stefanov, 1966, pl. 1, fig. 15?; Mosher, 1968a, p. 925, pl. 114, fig. 19; Bender, 1970, p. 508 – 509, pl. 2, figs. 18?, 20; Kozur & Mostler, 1971, pl. 1, fig. 9; Sahni & Chhab-

ra, 1974, p. 274 – 275, fig. 4 A, D; Budurov, 1976b, pl. 4, fig. 40; Koike, 1982, p. 30, pl. 9, figs. 23, 25, non fig. 24; Vrielynck, 1987, p. 201 – 202, pl. 14, fig. 6?, non figs. 4, 5; Ishida & Hirsch, 2011, fig. 10, parts 3, 6 only;

Neobindeodella multibamata (Huckriede), Koike, 1981, pl. 1, fig. 17;

Hindeodella (Metaprioniodus) pectiniformis (Huckriede), Vrielynck, 1987, pl. 14, fig. 1 only;

Prioniodina (Flabellignathus) pectiniformis (Huckriede), Gedik, 1975, p. 144 – 145, pl. 8, fig. 22;

Prioniodina (Flabellignathus) multibamata (Huckriede), Gedik, 1975, p. 144, pl. 8, fig. 21;

Prioniodina libita Mosher, 1968a, p. 934, pl. 115, figs. 17, 26, 29; Önder, 1984, p. 86, pl. 23, figs. 13, 14;

Cratognathodus multibamatus (Huckriede) Sc2 element, Koike, 1999, fig. 5, parts 18 – 21;

Gladigondolella tethydis (Huckriede) S3 element, Orchard, 2005, fig. 5, part F;

Cratognathodus sp. S3 element, Orchard, 2005, fig. 6, part E;

Gladigondolella prioniodinid element, Kılıç, 2021, figs. 6.10, 6.11 only.

M element (Fig. 5, parts 6, 13, 21)

Lonchodina venusta Huckriede, 1958, p. 152 – 153, pl. 11, fig. 25; Spasov & Ganey, 1960, p. 82, pl. 1, figs. 15 – 17; Hirsch, 1969, pl. 1, fig. 5; Bender, 1970, p. 514 – 516, pl. 3, figs. 18 – 20; Ishida & Hirsch, 2011, fig. 8, parts 1 – 5;

Cypridodella venusta (Huckriede), Mosher, 1968a, p. 922 – 923, pl. 114, figs. 1, 7, 13?; Gedik, 1975, p. 115 – 116, pl. 7, figs. 16 – 18; Koike, 1982, p. 23, pl. 7, fig. 47; Önder, 1984, p. 78 – 79, pl. 22, figs. 5, 6;

Prioniodina (Cypridodella) venusta (Huckriede), Kozur & Mostler, 1971, pl. 1, figs. 3, 4; Mock, 1971, pl. 2, figs. 5, 10, 11; Mastandrea, 1995, pl. 4, figs. 11, 12;

Prioniodina venusta (Huckriede), Čatalov & Budurov, 1975, p. 1284, pl. 1, fig. 12; Budurov, 1976b, pl. 4, figs. 23 – 26; Sudar, 1977, pl. 5, fig. 9; Čatalov & Budurov, 1978, pl. 1, fig. 1; Dürkoop et al., 1986, pl. 23, fig. 8; Vrielynck, 1987, p. 226 – 228, pl. 10, fig. 15, pl. 11, figs. 1, 2; Birkenmajer et al., 1990, pl. 2, fig. 6;

Cypridodella? pronoides (Budurov), Koike, 1982, p. 22, pl. 7, figs. 48, 49;

Cratognathodus multibamatus (Huckriede) M element, Koike, 1999, fig. 4, parts 15 – 19;

Gladigondolella tethydis (Huckriede) M element, Orchard, 2005, fig. 5, part D;

Gladigondolella lonchodinid element, Kılıç, 2021, fig. 6.8 only; breviform digyrate element, Sashida et al., 2022, fig. 7.39.

Revised Diagnosis: Apparatus is nonomembrate, with a segminiplanate P1 element and two potentially dimorphic P2 elements, one ozarkodiniform and the other cratognathodiform. The alate S0 element possesses lateral processes that diverge from the cusp, and the bipennate S3 element bears an additional process that splits from inner side of the main anterior process. Remaining ramiform elements conform to the morphologies determined by Orchard (2005) for the Gondolellidae.

Remarks. The nonomembrate apparatus of *Gladigondolella tethydis* differs from those of the Gondolellidae, which possess many of the same element morphologies as *Gladigondolella*, yet seem to consist of only eight types of elements, and in which dimorphism has not been observed. Therefore, the familial placement of the genus *Gladigondolella* is uncertain. The similarity of element morphology between *Gladigondolella tethydis* and genera of the Gondolellidae allows the elements of the former to

be assigned to anatomical positions following the notation system of Purnell et al. (2000).

In the synonymy list above, only occurrences of ramiform elements which occur together with specimens of *Gladigondolella tethydis* P1 elements or cratognathodid P2a elements have been considered; other examples of these ramiforms in the literature may belong to other genera. For instance, the form genus *Enantiognathus* contains many species, several of which have been assigned to various multielement genera within the Gondolellidae by Orchard (2005). The forms recovered from samples with *Gladigondolella tethydis* show a variety of morphologies, and have been referred to by several species names, and so only those which occur together with specimens of *Gladigondolella tethydis* P1 elements or cratognathodid P2a elements have been included in the synonymy list for the S2 element.

As noted by Orchard (2005), Huckriede's (1958) original definition of *Hindeodella petrae-viridis* is based on a broken element. Some of the occurrences recorded in the synonymy list are also fragments of a larger element, but have been included here as they clearly represent the anterior process of the full element. The name *Hindeodella petrae-viridis* has also been applied to the full element by several authors, and the same approach is followed here.

Occurrence. *Gladigondolella tethydis* ranges in age from Spathian (late Olenekian) to Julian (early Carnian). The geographic range of the genus is global, and includes occurrences in Austria, Italy, Slovenia, Serbia, Albania, Greece, Romania, Bulgaria, Turkey, Poland, Oman, Iran, India, China, Japan, Malaysia, Indonesia and the allochthonous terranes of western Canada.

Description. The morphology of each element of the apparatus is described separately below.

P1 element – The P1 element of the apparatus is segminiplate, with a platform that ranges in width from very narrow to very wide, and normally extends to encompass both the anterior and posterior ends of the element. The cusp is positioned at, or just posterior to the midpoint of the element, and is normally only slightly larger than the surrounding denticles, although it is commonly robust. The posterior carina ranges in length from only one or two denticles to several, and the posterior part of the element as a whole may be diverted to the side or downwards. To the anterior, the denticles of the carina become higher and more widely spaced. In lower view,

the basal pit is small and shifted to the anterior, with a keel of variable length developed to the posterior.

P2a element – The P2a element of the apparatus is segminate (cratognathodiform), with a large, posteriorly inclined cusp situated at (e.g. *Cr.* sp. B), or just in front of (e.g. *Cr. kochi*), the posterior end of the element. The anterior denticles are usually significantly smaller than the cusp, and maintain a consistent height to the anterior end of the element. The posterior end of the element is commonly downturned, and the denticles on the posterior process are small. The posterior process is commonly quite short; however, in *Cr. angulata* it possesses more than five denticles and its strongly downturned. In lower view, the keel is very slender and terminates in a narrow basal pit.

P2b element – The P2b element of the apparatus is angulate (ozarkodiniform), with a long anterior process bearing large, widely spaced denticles, and a much smaller posterior process bearing shorter, more densely spaced denticles. The angle between the two processes is very wide, and the cusp is large and posteriorly inclined.

Fig. 5 - SEM photos of conodonts belonging to the apparatus of *Gladigondolella tethydis*.

- 1-8) from sample 9050 from the Anisian (Aegean) of Deşli Caira, Romania. 1 - GSC cur. no. 139668, gladigondolelliform P1 element; 2 - GSC cur. no. 139669, cratognathodiform P2a element; 3 - GSC cur. no. 139670, ozarkodiniform P2b element; 4 - GSC cur. no. 139671, roundyiform S0 element; 5 - GSC cur. no. 139672, enantiognathiform S2 element; 6 - GSC cur. no. 139673, lonchodiniform M element; 7 - GSC cur. no. 139674, lonchodiniform S1 element; 8 - hibbardelliform S4 element.
- 9-16) from samples OU-5 (11, 12) and OU-10 (9, 10, 13-16) from the Anisian (Aegean) of Guandao, South China. 9 - GSC cur. no. 139675, gladigondolelliform P1 element; 10 - GSC cur. no. 139676, cratognathodiform P2a element; 11 - GSC cur. no. 139677, ozarkodiniform P2b element; 12 - GSC cur. no. 139678, roundyiform S0 element; 13 - GSC cur. no. 139679, lonchodiniform M element; 14 - GSC cur. no., 139680, hibbardelliform S4 element; 15 - GSC cur. no. 139681, hibbardelliform S3 element; 16 - GSC cur. no. 139682, enantiognathiform S2 element.
- 17-23) from samples KTM4-0150 (18), KTM4-0172 (19), KTM4-0158 (20, 22), KTM4-0191 (23) and KTM4/2-0206 (21) from the Anisian (Pelsonian) of the Kocaeli Peninsula, and from sample 1889 (17) from the Carnian (Julian) of the Central Pontides, both in Turkey; elements were previously illustrated in Kılıç (2016; 17) and Kılıç (2021; 18-23); 17 - gladigondolelliform P1 element; 18 - cratognathodiform P2a element; 19 - roundyiform S0 element; 20 - hibbardelliform S4 element; 21 - lonchodiniform M element; 22 - enantiognathiform S2 element; 23 - lonchodiniform S1 element.



Figure 5

S0 element – The S0 element of the apparatus is alate (roundyiform), with two short lateral processes diverging from the tall, upright cusp. The processes are of equal length and form a relatively narrow angle around the cusp. The denticles on the

processes are high and discrete, and incline further away from the cusp at the distal end of the process.

S1 element – The S1 element of the apparatus is extensiform digyrate, with two lateral processes, one shorter than the other, both forming

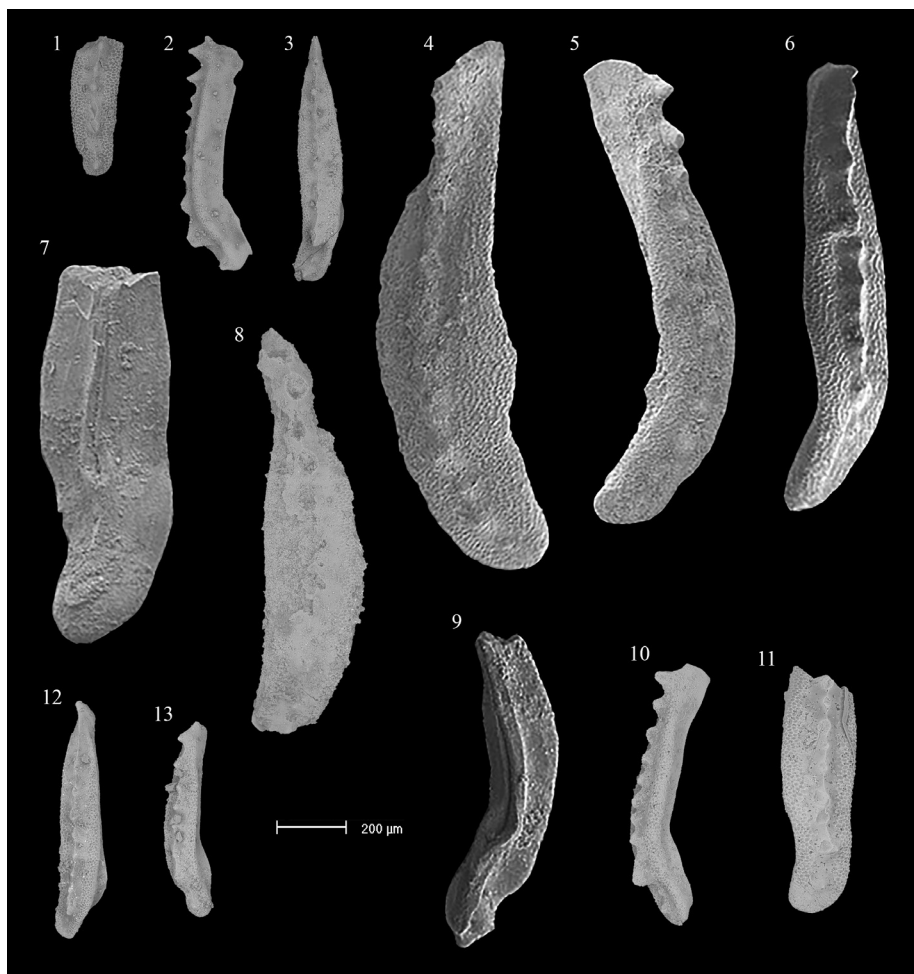


Fig. 6 - SEM photos of P1 elements of *Gladigondolella tethydis* (Huckriede 1958), illustrating morphological variation with growth and stratigraphic age.

1-3) from the Anisian (Aegean) of Deşli Caira, Romania; 1 - GSC cur. no. 139683, sample 9049; 2 - GSC cur. no. 139684, sample 9050; 3 - GSC cur. no. 139685, sample 9048.

4-7, 9) from the Carnian (Julian) of the Central Pontides, Turkey (specimens previously illustrated in Kılıç, 2016); 4 - sample 1889; 5 - sample 1892; 6 - sample 1889; 7 - sample 1889; 9 - sample 1889.

8, 10-12, 13) from the Anisian (Aegean) of Guandao, South China; 8 - GSC cur. no. 139686, sample OU-30; 10 - GSC cur. no. 139687, sample OU-25; 11 - GSC cur. no. 139688, sample OU-10; 12 - GSC cur. no. 139689, sample OU-32; 13 - GSC cur. no. 139690, sample OU-23.

a wide angle around the cusp. Both processes are denticulate, and the denticles are high and widely spaced. The cusp is upright and positioned above a flaring basal cavity.

S2 element – The S2 element of the apparatus is breviform digyrate (enantiognathiform), with a shorter lateral process bearing relatively low denticles, and a longer anterior process bearing high denticles, both oriented at acute angles relative to the cusp, which is large and upright.

S3 element – The S3 element of the apparatus is bipennate (hindeodelliform), with a long, straight posterior process bearing high, discrete denticles which increase in size to the posterior of the element. The anterior process is shorter, incurved, and possesses an additional short process, which splits off from the main process near its anterior end. Both anterior processes are denticulate. The cusp is large and inclined to the posterior.

S4 element – The S4 element of the apparatus is bipennate (hindeodelliform), with a long, straight posterior process bearing high, discrete denticles which increase in size to the posterior of

the element, and a shorter, incurved posterior process that also bears high discrete denticles. The cusp is large and posteriorly inclined, as are the posterior denticles; in contrast, the anterior denticles are more upright.

M element – The M element of the apparatus is makellate (lonchodiniform), and possesses two long antero-lateral processes, both of which bear long, widely-spaced denticles which fan out from the central cusp, which is itself commonly inclined to one side or twisted towards the inner part of the element. The denticles on the longer of the two processes are commonly higher than both the cusp and the denticles on the other process; however, both processes are commonly broken.

CONCLUSIONS

Multivariate statistical analysis of elements previously ascribed to the multielement apparatuses of *Gladigondolella* and *Cratognathodus* demonstrates that the P elements of *Gl. tethydis* and *Cratognathodus*

co-occur with a similar level of frequency as they do with other elements of their putative apparatuses. Therefore, it is highly likely that both belong to the same multielement apparatus during the Anisian and Carnian, as previously suggested by Ishida and Hirsch (2011) and Kılıç et al. (2013). In the present reconstruction, the multielement apparatus of this species in the Anisian and Carnian consists of *Gladigondolella tethydis* (P1); *Cratognathodus* sp. (P2a); *Ozarkodina saginata* (P2b); *Roundya lautissima* (S0); *Lonchodina spengleri* (S1); an enantiognathid element (S2); *Hindeodella petrae-viridis* (S3); *Hindeodella multibamata* (S4); and *Lonchodina venusta* (M). Other genera have been postulated to have multiple P2 elements, including the Permian *Mesogondolella* and *Jimogondolella* (Lambert et al. 2007) and the Carboniferous *Kladognathus* and *Idioproniodus* (Merrill & Merrill 1974; Purnell 1993); the apparatus of *Gladigondolella* may be dimorphic, as has been suggested for these other genera. Several of the elements assigned to the apparatus of *Gladigondolella tethydis* exhibit morphological variability, including the P1 element, which appears to have a thinner platform in the Anisian than in the Carnian. The recognition that *Cratognathodus* belongs to the *Gladigondolella tethydis* apparatus has implications for biostratigraphy around the Olenekian-Anisian boundary, as earlier occurrences of *Cratognathodus* at many boundary sections suggest that the age range for *Gl. tethydis* and/or *Gl. carinata* at these sections may be longer than previously thought.

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