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A database of Triassic conodonts from a comprehensive revision of literature

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ABSTRACT

The revision of a comprehensive amount of bibliography has made possible the development of a database containing the stratigraphic ranges of the conodont species from the uppermost Permian and the Triassic, with a total of 336 species in 52 genera. This database is aimed at biostratigraphy and studies related to biological, evolutional and palaeodiversity dynamics.

Keywords: Conodonts, stratigraphic ranges, database, Triassic.

RESUMEN

La revisión de una amplia cantidad de bibliografía ha hecho posible el desarrollo de una base de datos en la que figuran los rangos estratigráficos de las especies de conodontos presentes desde el Pérmico superior y el Triásico, con un total de 336 especies y 52 géneros. Esta base de datos está dirigida a la bioestratigrafía y a estudios relacionados con las dinámicas biológicas, evolutivas y de paleodiversidad.

Palabras clave: Conodontos, rangos estratigráficos, base de datos, Triásico.

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1. INTRODUCTION

Conodonts are an extinct animal group, which originated in the Middle Cambrian and lasted until the base of the Jurassic (e.g., Kozur, 1993; Pàlfy *et al*., 2007). Over more than 300 million years, conodonts showed a continuous evolution and rapid diversification that, combined with a high abundance and widespread geographical distribution, make them a very valuable tool in the study of many palaeontological aspects, such as biostratigraphy and palaeobiogeography. After experiencing diversity peaks during the Ordovician and Devonian periods, conodonts began a progressive long-term decline during the Carboniferous, reaching a biodiversity minimum during the Upper Permian.

The Triassic, as the first period of the Mesozoic, is a significant stage in the evolution of life, starting and ending with a great biotic crisis, both of which belonged to the so-called "Big Five" extinction events, marking the decadence of the Palaeozoic evolutionary fauna and the expansion of the modern evolutionary faunas (Sepkoski, 1981).

The first event was the Permian-Triassic (PTB) boundary, regarded as the most severe crisis in the history of life (e.g., Hallam & Wignall, 1997; Benton & Twitchett, 2003), which represented a global turnover in the biosphere, especially in marine ecosystems (Erwin, 2006). The ecological recovery from this extinction is regarded to have been slower than after other extinction events, in many cases lasting until the Middle Triassic (Benton & Twitchett, 2003; Lehrmann *et al*., 2006). However, this is not the case for conodonts, which experienced a quick recovery during the earliest part of the Triassic (Plasencia & Márquez-Aliaga, 2005; Stanley, 2009; Fröbisch *et al*., 2012), followed by several crises and recoveries in the course of the Middle and Upper Triassic.

Most of the genera of three families (Anchignathodontidae, Ellisonidae and Gondolellidae) survived, crossing the Permian-Triassic boundary into the Triassic. However, there were significant changes at the specific level, the main one being the diversification of the Anchignathodontidae family during the latest Permian, compensating for the reduction of representatives of the Gondolellidae.

The second event was the Triassic-Jurassic boundary (TJB), which sealed the disappearance of conodonts that had gradually been starting during the latest part of the Triassic. While the TJB extinction is regarded as less important than that at the end of the Permian, at least in the context of ecosystem changes, it nevertheless represents a large taxonomic turnover (more than 50 % of species lost; Sepkoski, 1996).

As a result of research over several generations, a comprehensive amount of information has been accumulated on many different aspects of conodonts.

We have compiled the stratigraphic ranges and worldwide geographic distribution of Triassic conodont species, as comprehensively as possible and adapted to the modern taxonomy, in which the species present in the uppermost Wuchiapingian and the Changhsingian of the Lopingian (Late Permian) are included, in order to evaluate the effects that the mass extinction of the PTB could have had on the group.

In the present paper we present part of this database, which consists of a list of accepted species with their stratigraphic ranges. This data will be the base for future works in order to study the evolutionary dynamics of conodonts across the PTB and the Triassic. It can be used as a reference for other studies, beyond the study of conodonts, for a much wider audience interested in the study of biological, evolutional and palaeodiversity dynamics.

Biodynamical analysis papers related to Triassic conodonts are scarce, apart from the above-cited works by Clark (1987) and De Renzi *et al*. (1996), diverse aspects of the groups have also been studied by Clark (1983) and Plasencia & Márquez-Aliaga (2005). Recently, Stanley (2009) developed an analysis of the Early Triassic conodonts using data from Orchard (2007a), but this paper was not originally developed for this purpose and lacks some important data, mainly the ranges of the members of the Anchignathodontidae family, which is the most important in the earliest part of the Triassic. There has also been a significant number of new species described since Orchard's paper was published in 2007.

2. MATERIALS AND METHODS

In comparison with other groups, research into Triassic conodonts is relatively recent; Eicher (1946) reported for the first time the presence of conodonts in strata of unequivocally Triassic age in Sinai (Egypt). This was received with some scepticism [see the discussion by Branson & Mehl (1946) at the end of the same paper], and it was not until the 1950s that the existence of Triassic conodonts was finally fully recognized and accepted, with pioneer works such as those by Youngquist (1952), Müller (1956) and Tatge (1956) marking the beginning of a continuous research work that has lasted until the present day.

2.1. Development of the database

For the purposes of the present study, a revision of the available bibliography from the early 1950s until 2012 was undertaken, in order to identify as many different candidate taxa as possible. The resulting list of species was studied to include or exclude species as "valid". We tried to reduce subjective aspects as much as possible by setting several criteria that a species should meet in order to be considered valid but, ultimately, any selection will have some subjectivity and is open to discussion. So, all the accepted species needed to meet the following requirements:

1) An adequate taxonomic diagnosis and description. When needed, a translation from the original language was undertaken. An adequate illustration of at least the holotype was considered desirable but not essential when better pictures of other specimens, clearly identifiable as being of the same species, are available. This requirement obliged us to exclude species in open nomenclature. A few exceptions were made (*Vjalovognathus* n. sp. B, *Merrillina* sp.) in order to make explicit the presence of both genera in the Wuchiapingian and lower Changhsingian.

2) Support from a list of different papers with a coherent characterization of the species, following the original description. As a general rule, at least three different references were required. However, exceptions were made, especially for species recently described but not yet considered in other works, or having morphologies that present clear diagnostic characteristics but with a limited distribution.

3) A well-defined stratigraphic range.

4) We did not take into consideration subspecies or morphotypes as independent taxa; the stratigraphic range of these taxonomic levels was grouped together in order to summarize the complete stratigraphic range of the species.

Two lists were established: one for the species that adequately met all the established criteria (Accepted Species) and a second for those species that were rejected.

2.2. Selected bibliography

Several hundreds of papers were compiled during the development of the database. Not all of these contained useful information about the stratigraphic ranges of the species, and most were basically redundant. Since a complete list of this bibliography would be impractical, we selected one to three papers for each species that justified the stratigraphic range that we have accepted.

The papers selected for the Upper Permian species were: Algeo *et al.* (2012), Beyers & Orchard (1991), Gullo & Kozur (1992), Henderson (1997), Jiang *et al.* (2011a,b), Korte & Kozur (2010), Kozur (1990, 1995a, b, 2004, 2005, 2007), Kozur & Weems (2011), Mei *et al.* (1994, 1998), Nafi *et al.* (2006), Orchard (2007a, 2010), Orchard & Krystyn (1998), Orchard *et al.* (2001a), Perri (1991), Perri & Angraghetti (1987), Perri & Farabegoli (2003), Shen (2007), Shen & Mei (2010), Sweet & Mei (1999) and Wang *et al. (*1987).

For the Lower Triassic species: Balini *et al.* (2000), Baud *et al.* (2011), Goudemand *et al.* (2012), Hirsch (1994), Ji *et al.* (2010), Jiang *et al.* (2007, 2011b), Koike (1998), Koike *et al.* (1985), Kozur (1996), Kozur *et al.* (1997), Krystyn *et al.* (2007), Liang *et al.* (2011), Meço (1999), Metcalfe *et al.* (2008), Orchard (1995, 2007b, 2008, 2010), Orchard & Zonneveld (2009), Orchard *et al.* (2007a), Perri & Farabegoli (2003), Posenato (2008), Trammer (1975), Zhao (2004), Zhao *et al.* (2007, 2008).

For the Middle Triassic species: Balini *et al.* (2000), Benjamini *et al.* (2005), Brack & Nicora (1998), Brack *et al.* (2005), Budurov & Stefanov (1973), Budurov & Sudar (1988), Buser *et al.* (2007), Chen & Wang (2002), Gullo & Kozur (1989), Hirsch (1994), Hornung *et al.* (2007), Ishida *et al.* (2006), Koike (1999), Kovács (1994), Kovács & Kozur (1980), Kozur (2003), Kozur *et al.* (1994), Márquez-Aliaga *et al.* (2000), Mastandrea *et al.* (1997), Mietto & Petroni (1980), Mietto *et al.* (2007), Muttoni *et al.* (2000, 2004), Nakazawa *et al.* (1994), Nakrem *et al.* (2008), Narkiewicz (1999), Narkiewicz & Szulc (2004), Orchard (2010), Orchard & Tozer (1997), Plasencia & Márquez-Aliaga (2011), Plasencia *et al.* (2007), Rigo *et al.* (2007), Sun *et al.* (2006) and Vrielynck (1984).

For the Upper Triassic species: Belvedere *et al.* (2008), Budurov & Sudar (1990), Buryi (1996), Buser *et al.* (2007), Carter & Orchard (2007), Channell *et al.* (2003), Hirsch (1994), Ishida & Hirsch (2001), Ishida *et al.* (2006), Kolar-Jurkovsek (1982, 2011), Kozur (2003), Kozur & Mock (1991), Krystyn (1983, 2008), Krystyn *et al.* (2007, 2009), Mazza *et al.* (2010, 2011, 2012), Moix *et al.* (2007), Mosher (1973), Muttoni *et al.* (2000, 2010), Nicora *et al.* (2007), Noyan & Kozur (2007), Orchard (1991, 2010), Orchard *et al.* (2001b, 2007b), Rigo *et al.* (2007), Rozic *et al.* (2009), Swift (1989) and Yang (1995).

3. RESULTS

A total of 336 species and 52 genera were considered. This number was significantly higher than other similar databases used in previous works: about 100 species in 19 genera in Clark (1987), and 107 species and 26 genera in De Renzi *et al.* (1996). Part of this difference was due to the number of species that have been described since these two papers were published (25 and 16 years, with 131 and 73 new species described, respectively); our database also comprises a number of species only present in the Permian (33) that were probably not taken in count by the authors.

The complete data has been summarized in the supplementary information as an Excel spreadsheet.

In this file the stratigraphic ranges of the accepted species are given, including the observed first and last appearances of each one. In order to facilitate the review of the data and justify the assigned age, one or two papers (in some rare cases, up to three) were selected for each species from which the range information can be checked. Where possible, the most modern and complete papers were selected; the list can be found pointing section 2.2. This information is set out in the Excel sheet named "Species". The sheet "RAW" contains a binary representation of the data: 1 for presence and 0 for absence of a species within a unit of time.

Chronostratigraphic scale: we used the ICS (International Commission on Stratigraphy) scale in which the Lopingian (Upper Permian) is subdivided into two stages, while the Triassic comprises three series and seven stages (Fig. 1). While not formally accepted by the ICS, the 15 substage divisions of the Triassic (Tab. 1) have been widely used by specialists for many years and represent a standard for the period.

Time units: a further subdivision of each substage in the Early, Middle and Late units is in use, with the exception of the Sevatian, which has only two subdivisions (Early and Late); for each of the Changhsingian and Rhaetian the three units were made equivalent to substages, and only the upper part of the Wuchiapingian was considered in our study. In total, there were 51 divisions, named "time units" (Tab. 1).

Each of these units was made equivalent to an ammonoid or conodont biozone, as shown in the Table 1, in order to simplify the data selection: if a conodont species was recognized in one of these biozones (or equivalent), it was marked as "1" in the corresponding time unit in the spreadsheet, and if not, a "0" was marked. The biozones were taken from Orchard (2007a) for the Lower Triassic and Balini *et al.* (2010) for the Middle and Upper Triassic [with Channell *et al.* (2003) for the Sevatian]. When other biozones were used, they were correlated using the files "8_Lower_Triassic.pdf" (Ogg & Ogg, 2006a) and "7_Upper_Trias.pdf" (Ogg & Ogg, 2006b), available at https://engineering.purdue.edu/Stratigraphy/charts/Timeslices/ and the synthetic tables found in Balini *et al.* (2010).

In summary, five families, 10 genera and 52 species were present in the Upper Permian, the most significant being *Hindeodus* Rexroad & Furnish 1964 and *Clarkina* Kozur 1989 (Figs 1a-1d). Three of these families and 17 species crossed into the Lower Triassic. The entire Lower Triassic comprised a total of 132 species, with 33 genera. The most significant genera were: for the Family Anchignathodontidae, *Hindeodus* and *Isarcicella* Kozur 1975 (Figs 1a-1b), for the Family Ellisonidae *Ellisonia* Múller 1956 (Fig. 1c) and for the Family Gondolellidae *Neogondolella* Bender & Stoppel 1965 and *Neospathodus* Mosher 1968 (Figs 1e-1f). At the end of the Early Triassic, only the Family Gondolellidae remained, with seven species crossing into the Middle Triassic, and with a total of 85 species for the whole series, comprising 11 genera. Apart from *Neogondolella,* the most significant genera are *Paragondolella* Mosher 1968, *Gladigondolella* Müller 1962 and *Sephardiella* March, Budurov, Hirsch & Márquez-Aliaga (Fig 1g-1i). Of these, 18 species crossed into the Upper Triassic, with a total of 102 species in 15 genera, with the most significant being *Metapolygnathus* Hayashi 1968, *Epigondolella* Mosher 1968 and *Misikella* Kozur & Mock 1974 (Figs 1j-l).

Species rejected: a total of 103 species were included in a category "not considered", found on the Excel sheet of the same name in the supplementary information. This list includes species that did not comply with the requirements explained above; the main motive they were discarded is synthesized as follows:

Incomplete diagnosis or description

Stratigraphic range not well defined

In synonymy

Subspecies

Multielement (the species have been regarded as a multielement of another species)

Outside the considered time interval (species that, despite being present in the Late Wuchiapingian, are not present in the later part of this period).

4. CONCLUSIONS

The database outlined in this paper is the result of a comprehensive revision of Triassic conodont literature. As a result, a database of species, including their stratigraphic ranges for the uppermost Permian and the Triassic, was compiled, incorporating a total of 329 species belonging to 52 genera.

Suplementary information

The supplementary information can be downloaded from: http://www.sepaleontologia.es/revista/volumenesanteriores.html.

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Table 1. Chronostratigraphic scale of the ICS for the Upper Permian (Lopingian) and Triassic, with the time units considered in the database. The codename for each time unit consist of one or two letters followed by the corresponding letter E (Early), M (Middle) or L (Late).

Period	Epoch	Stage	Substage	Time unit codename	Equivalent Ammonites biozone	Equivalent Conodont biozone
PERMIAN	LOPINGIAN	Wuchiapingian	(No Subdivisions)	W		
		Changhsingian	(No Subdivisions)	CE	*Iranites* Chart ICS 2006	
				CM	*Paratirolites* Chart ICS 2006	
				CL	*Pseudotirolites* Chart ICS 2006	
TRIASSIC	LOWER TRIASSIC	INDUAN	GRIESBACHIAN	GE	*Otoceras boreale* Orchard 2007a	
				GM	*Ophiceras commune* Orchard 2007a	
				GL	*Bukkenites strigatus* Orchard 2007a	
			DIENERIAN	DE		*Sweetospathodus kummeli* Chart ICS 2006
				DM		*Neospathodus dieneri+Ns. cristagalli* Chart ICS 2006
				DL		*Neospathodus pakistanensis* Chart ICS 2006
		OLENEKIAN	SMITHIAN	SE	*Hedenstroemia hedenstroemi* Orchard 2007a	
				SM	*Euflemingites romunduri* Orchard 2007a	
				SL	*Anawasatchites tardus* Orchard 2007a	
			SPATHIAN	SPE	*Tirolites* and *Columbites* Orchard 2007a	
				SPM	*Subcolumbites/Prohungarites* Orchard 2007a	
				SPL	*C.s stevensi+P. (Neopopanoceras) haugi* Orchard 2007a	
	MIDDLE TRIASSIC	ANISIAN	AEGEAN	AE	un-named Ogg & Ogg 2006a	
				AM	*Silberlingites mulleri* Ogg & Ogg 2006a	
				AL	*Lenotropelites caurus* Ogg & Ogg 2006a	
			BYTHINIAN	BE	*Arctohungarites ventroplanus* Ogg & Ogg 2006a	
				BM	*Arctohungarites triformis* Ogg & Ogg 2006a	
				BL	*Arctohungarites laevigatus* Ogg & Ogg 2006a	
			PELSONIAN	PE	*Cuccoceras cuccense* Ogg & Ogg 2006a	
				PM	*Baladorylaimus balatonicus* Ogg & Ogg 2006a	
				PL	*Schreyerites binodosus* Ogg & Ogg 2006a	
			ILLYRIAN	IE	*S. abichii+P.trinodosus+R. reitzi* Ogg & Ogg 2006a	
				IM	*Aplococeras avisianun + Ticinites crassus* Ogg & Ogg 2006a	
				IL	*S. serpianenis+Ch. chiesense* Ogg & Ogg 2006a	
		LADINIAN	FASSANIAN	FE	*Eoprotrachyceras curionii* Balini *et al* 2010	
				FM	*Protrachyceras margaritosum* Balini *et al* 2010	
				FL	*Eoprotrachyceras gredleri* Balini *et al* 2010	
			LONGOBARDIAN	LE	*Protrachyceras longobardicum* Balini *et al* 2010	
				LM	*Protrachyceras neumayri* Balini *et al* 2010	
				LL	*Frankites regoledanus* Balini *et al* 2010	
	UPPER TRIASSIC	CARNIAN	JULIAN	JE	*Daxatina canadiensis* Balini *et al* 2010	
				JM	*Trachyceras aon+Trachyceras aonoides* Balini *et al* 2010	
				JL	*Austrotrachyceras austriacum* Balini *et al* 2010	
			TUVALIAN	TE	*Tropites dilleri* Balini *et al* 2010	
				TM	*Tropites subbullatus* Balini *et al* 2010	
				TL	*Anatropites spinosus* Balini *et al* 2010	
		NORIAN	LACIAN	LAE	*Guembelites jandianus* Balini *et al* 2010	
				LAM	*Malayites paulckei* Balini *et al* 2010	
				LAL	*Juvavites magnus* Balini *et al* 2010	
			ALAUNIAN	ALE	*Cyrtopleurites bicrenatus* Balini *et al* 2010	
				ALM	*Himavatites ogarti* Balini *et al* 2010	
				ALL	*Halorites macer* Balini *et al* 2010	
			SEVATIAN	SEE		Mockina bidentata Channell *et al*. 2003
				SEL		Misikella hernsteini Channell *et al*. 2003
		RHAETIAN	(No Subdivisions)	RE	*Sagenites reticulatus* Balini *et al* 2010	
				RM	*Vandaites stuerzenbauni* Balini *et al* 2010	
				RL	*Choristaceras marshi* Balini *et al* 2010	

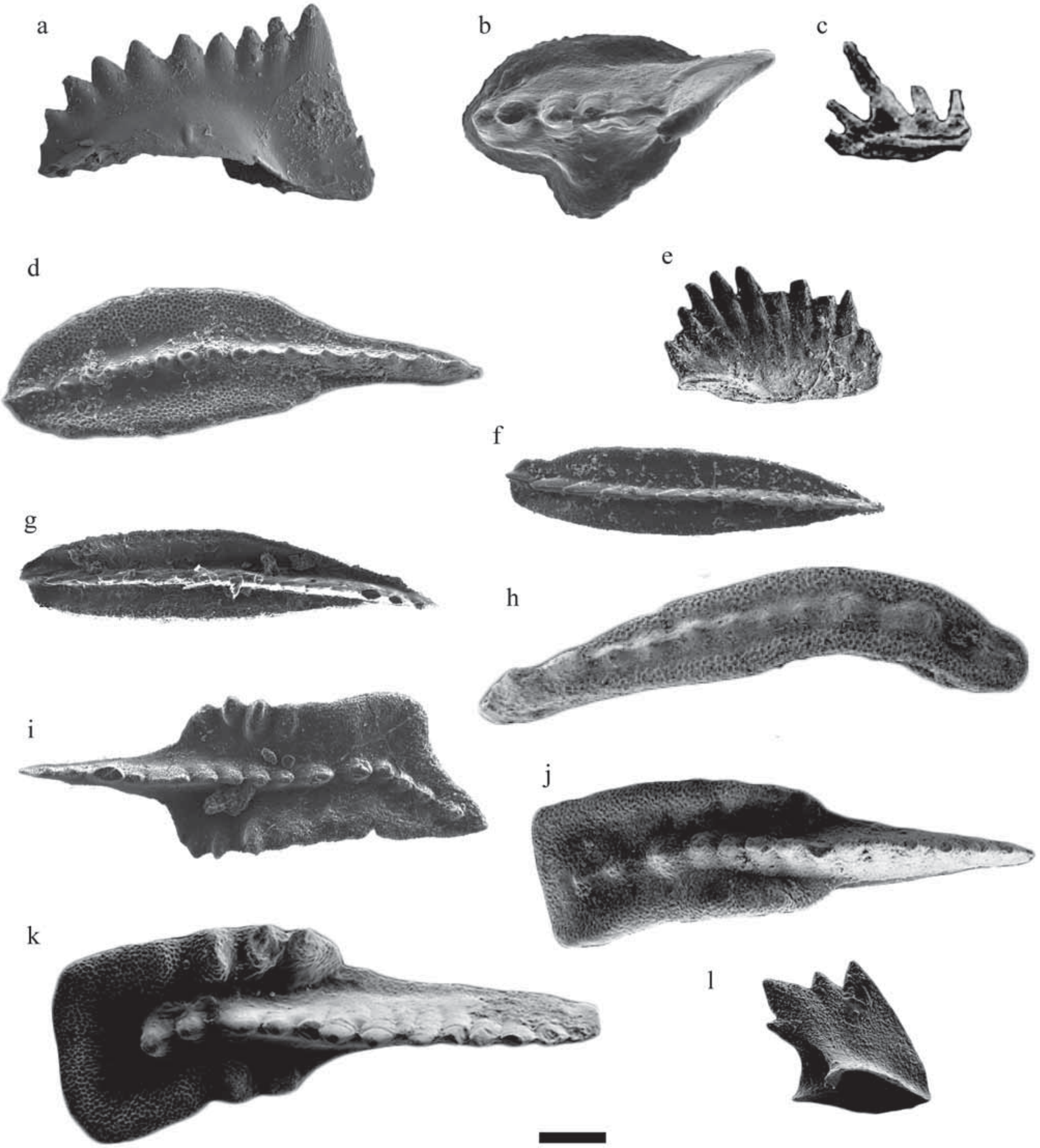

Figure 1. P_1 elements of the most significant conodont genera of the Triassic: **a)** *Hindeodus* Rexroad & Furnish 1964 (Upper Permian-Lowermost Triassic); **b)** *Isarcicella* Kozur 1975 (Lowermost Triassic); **c)** *Ellisonia* Múller 1956 (Permian-Early Triassic); **d)** *Clarkina* Kozur 1989 (Upper Permian-Lowermost Triassic); e**)** *Neospathodus* Mosher 1968 (Lower Triassic); **f)** *Neogondolella* Bender & Stoppel 1965 (Lower Triassic-Upper Triassic); **g)** *Paragondolella* Mosher 1968 (Middle-Upper Triassic); **h)** *Gladigondolella* Müller 1962 (Lower-Upper Triassic); **i)** *Sephardiella* March, Budurov, Hirsch & Márquez-Aliaga 1990 (Middle-Upper Triassic); **j)** *Epigondolella* Mosher 1968 (Upper Triassic); **k)** *Metapolygnathus* Hayashi 1968 (Upper Triassic); **l)** *Misikella* Kozur & Mock 1974 (Upper Triassic). Figure c comes from Koike *et al.* (2004), e from Liang *et al.* (2011), f, g, i from Plasencia (2009) and j-l from Mazza *et al.* (2012). Bar is 100 µm.

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