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Abstract: This paper summarizes 30 years of research on the biostratigraphy of Triassic radiolarians and presents a correlation of currently-used radiolarian zonations established in North America, Europe, Japan and Far East Russia. An up-to-date stratigraphic distribution of all hitherto described and still valid Triassic genera is provided. This new range chart consists of 282 genera and allows an accurate dating to substage level. It also clearly manifests general trends in radiolarian evolution through the Triassic. The end-Permian extinction, the most severe extinction in the history of radiolarians, was followed by a long recovery until the early Anisian. The middle and late Anisian were then characterized by a rapid explosion of new morphologies. Maximum generic diversity was attained during the early Carnian, but the first severe extinctions also occurred in the Carnian. A progressive decline of diversity took place through the Norian and Rhaetian, and ended in a mass extinction around the Triassic–Jurassic boundary.

Since the revolution that signified the use of the hydrofluoric acid method in extracting radiolarians from hard siliceous rocks, radiolarians have proven to be of great importance in reconstructing the stratigraphy of the Mesozoic, particularly the Triassic System. This methodology, discovered independently by Dumitrica (1970) and Pessagno & Newport (1972), together with the building of a new taxonomic system for Mesozoic radiolarians, opened the way to stratigraphic progress and zonal correlation. This contribution reviews the different biostratigraphic scales proposed in the past 30 years and discusses the validity of correlation. The first radiolarian range charts were proposed almost simultaneously in North America, Japan and Europe (Pessagno *et al.* 1979; Nakaseko & Nishimura 1979; Yao *et al.* 1980*a*; De Wever 1982). One of the most important aspects to be mentioned is the apparently low provincialism displayed by these zonations through the Triassic when compared to the classical schemes proposed for the Jurassic and Cretaceous. Another characteristic feature of these zonations is the accurate calibration to the standard chronostratigraphic stages and substages, which are established basically by means of ammonites and conodonts. But the most striking aspect is the time resolution of these biostratigraphic scales, which are better than those proposed for the Jurassic–Cretaceous. However, the potential use of Triassic radiolarians for stratigraphic purposes remains largely untapped. The reason for this is the great generic diversity shown by this group during the Triassic, probably the largest known in the history of the group, as has been illustrated in a recent stratigraphic and taxonomic review of genera (O'Dogherty *et al.* 2009*a*). The aim of this paper is also to show that the stratigraphic distribution of genera is a powerful tool that allows dating at the substage level and opens new insights for future research.

State of the art

Historical review of Triassic radiolarian biostratigraphy

In the late 19th and early 20th centuries, the Triassic System was the least studied Mesozoic system in terms of radiolarians. Compared to relatively numerous works on Jurassic and Cretaceous radiolarians (e.g. Rüst 1885; Squinabol 1903, and others), virtually nothing was known about Triassic radiolarians until 1970. A rare exception was Rüst (1892), who described 21 Triassic species (most from Felsöörs in Hungary, a well-known radiolarian locality today). The beginning of Triassic radiolarian research thus practically coincides with the discovery of etching techniques for siliceous rocks (Dumitrica 1970; Pessagno & Newport 1972) and with the development of scanning electron microscopy.

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Early studies of Triassic radiolarians focused on description of new species and intended to present either all representatives of certain families (Kozur & Mostler 1972, 1978; Dumitrica 1978*a*, *b*, 1982*a*, *b*, *c*) or radiolarian assemblages of certain stratigraphic levels (De Wever *et al.* 1979; Pessagno *et al.* 1979; Nakaseko & Nishimura 1979; Kozur & Mostler 1979, 1981; Dumitrica *et al.* 1980). The first radiolarian range charts were proposed in the late 1970s and early 1980s almost simultaneously in North America, Japan and Europe. The hitherto published radiolarian zonations are discussed below and summarized in Figure 1.

Development of zonal schemes and correlation

In North America, the study of Triassic radiolarians was initiated by Pessagno *et al.* (1979), who established two zones, *Capnodoce* Zone and *Pantanellium silberlingi* Zone, for the latest Carnian and Norian in Baja California. These zones were further emended and refined by Blome (1984) based on material from different sites in western North America (Oregon, Baja California and Queen Charlotte Islands). Blome (1984) divided the *Capnodoce* Zone into three subzones, that is, *Justium novum, Xipha striata* and *Latium paucum* subzones. He erected a new zone for the middle and late Norian, the *Betraccium* Zone, which was subdivided into two subzones, *Pantanellium silberlingi* Subzone (equivalent to former zone of Pessagno *et al.* 1979) and *Betraccium deweveri* Subzone.

The latest Norian and Rhaetian was studied by Carter (1990, 1993) in the Queen Charlotte Islands. On the basis of unitary associations (Guex 1977, 1991), Carter (1993) recognized Blome's *Betraccium deweveri* Zone at the base and divided the Rhaetian stage in two formal zones. These are the *Proparvicingula moniliformis* Zone, which represents the lower Rhaetian, and the *Globolaxtorum tozeri* Zone, representing the upper Rhaetian. The *Propavicingula moniliformis* Zone is subdivided into two distinct assemblages, that is, assemblages 1 and 2, with the second assemblage consisting of four subassemblages, that is, 2a to 2d. The *Globolaxtorum tozeri* Zone consists of a single assemblage (assemblage 3). Radiolarians older than late Carnian were reported only as single occurrences from tectonically complex areas (e.g. Blome *et al.* 1988; Blome & Reed 1992; Cordey 1998), so no radiolarian zonation has been established for the Early and Middle Triassic in North America. Blome *et al.* (1988) also created a zone below their *Capnodoce* Zone, namely the *Pseudostylosphaera* Zone, but this zone is rather vague and has not been employed. In the Middle and Upper Triassic of Oregon, Yeh (1989) recognized four assemblages separated by long empty intervals. At present, the zonations of Blome (1984) and Carter (1993) are the most widely used radiolarian zonations for the Norian and Rhaetian (Fig. 2, see also De Wever *et al.* 2001). In addition to their high resolution, which enables dating to substage level, these zonations provide ranges of a great number of taxa, which are regularly encountered elsewhere in the Tethys.

In Japan, Nakaseko & Nishimura (1979) established three assemblage zones, that is, *Tripocyclia* cf. *acythus, Emiluvia*? *cochleata*, and *Capnuchosphaera theloides* assemblages, and assumed that all three were Late Triassic in age. Further research revealed that only the *Capnuchosphaera theloides* assemblage is Late Triassic (Norian) in age, whereas the *Tripocyclia* cf. *acythus* and *Emiluvia*? *cochleata* assemblages are late Anisian–early Ladinian and late Ladinian, respectively (Kozur & Mostler 1994, Ramovš & Goričan 1995, Kozur *et al.* 1996). In the 1980s, many Japanese researchers independently proposed radiolarian biostratigraphic schemes for the Middle to Upper Triassic (Yao *et al.* 1980*a*, *b*, 1982; Yao 1982, 1990; Kishida & Sugano 1982; Nishizono & Murata 1983; Igo & Nishimura 1984; Kishida & Hisada 1986; Sato *et al.* 1986; Yoshida 1986; Sashida *et al.* 1993; Nishizono 1996; for correlations see Sugiyama 1997). The most commonly used scheme in the 1980s and early 1990s was that established by Yao (1982), who divided the Ladinian to Rhaetian interval into three rather long-ranging assemblages.

Pre-Ladinian radiolarian stratigraphy was first established by Sugiyama (1992), who presented three new assemblages for the Spathian to middle Anisian. Later, Sugiyama (1997) established 18 zones for the Spathian to the top of the Triassic. The lower two zones are assemblage zones, and the others are defined by the first or last occurrences of index taxa. Sugiyama's zonation is the only one that spans practically the whole Triassic Period with relatively high resolution. It is based on occurrences of 233 taxa in 21 continuous sections of siliceous rocks from central Japan, and the proposed zones are recognized globally in low latitudes. In comparison with other low-latitude radiolarian zonations, Sugiyama's zonation bears the longest and most continuous record of radiolarian events. On the other hand, because the investigated successions consist of siliceous claystone and bedded chert, radiolarian preservation is moderate, diversity is relatively low and other age-diagnostic fossils are rare. The zones TR 1 (Spathian), TR 2B (mid Anisian) and TR 4B (upper Ladinian–lower Carnian) are directly calibrated with co-occurring

AUTHOR(S)/YEAR	TIME INTERVAL	REGION	ZONES AND TYPE OF ZONES
Nakaseko & Nishimura 1979	late Anisian to Norian	SW and central Japan	3 assemblages: *Tripocyclia* cf. *acythus*, *Emiluvia*? *cochleata*, *Capnuchosphaera theloides*
Pessagno *et al*. 1979	latest Carnian to early late Norian	Baja California	2 Oppel zones: *Capnodoce* Zone, *Pantanellium silberlingi* Zone
Yao *et al*. 1980*a*, *b*, 1982; Yao 1982, 1990	Ladinian to Rhaetian	central Japan	3 assemblage zones: *Triassocampe deweveri*, *Triassocampe nova*, *Canoptum triassicum*
De Wever 1982	Ladinian to Norian	Greece, Sicily, Turkey	stratigraphic distribution of 44 taxa
Kishida & Sugano 1982; Kishida & Hisada 1986	late Anisian to Rhaetian	SW and central Japan	4 assemblage zones: *Eptingium manfredi*, *Emiluvia*? *clochleata*, *Capnodoce anapetes*, *Spongosaturnalis multidentatus*
Nishizono & Murata 1983	Ladinian to Norian	Kyushu, Japan	3 assemblages: *Archaeospongoprunum compactum*, *Emiluvia*? *cochleata*, *Capnodoce anapetes*
Igo & Nishimura 1984	Norian to Rhaetian	central Japan	2 assemblage zones: *Capnodoce anapetes - Capnodoce sarisa*, *Canoptum triassicum*
Blome 1984	latest Carnian to Late Norian	Oregon, Baja California, Queen Charlotte Islands	2 zones: *Capnodoce* Zone (Oppel Zone divided in 3 interval subzones), *Betraccium* Zone (Oppel zone divided in one Oppel and one interval subzone) (Fig. 2)
Kishida & Hisada 1985	Norian-Rhaetian?	central Japan	*Palaeosaturnalis multidentatus* Assemblage divided in *Canoptum* aff. *triassicum* and *Canoptum lubricum* subassemblages
Sato *et al*. 1986	late Anisian to Norian	Kyushu, Japan	5 range and concurrent range zones: *Archaeospongoprunum compactum*, *Emiluvia*? *cochleata*, *Capnuchosphaera triassica*, *Capnodoce*, *Betraccium deweveri*
Yoshida 1986	Carnian to Rhaetian	central Japan	6 interval zones: *Capnuchosphaera*, *Capnodoce*, *Acanthocircus*-*Pseudoheliodiscus*, *Betraccium deweveri*, *Livarella*-*Canoptum*, *Justium* cf. *novum*
Yeh 1989	Ladinian to ?Rhaetian	Oregon	4 assemblages: *Pseudostylosphaera magnispinosa*, *Poulpus carnicus*, *Corum parvum*, *Orbiculiforma* sp. A
Cheng 1989	Anisian, late Carnian? to Norian	Philippines	3 assemblages: *Pseudostylosphaera japonica*, *Pseudoheliodiscus* sp. F, *Betraccium deweveri*
Yeh 1990	Anisian to Rhaetian	Philippines	3 assemblages: *Busuanga chengi*, *Trialatus megacornutus*, *Livarella* sp. A
Carter 1990, 1993	Rhaetian	Queen Charlotte Islands	6 successive assemblages (defined by Unitary Associations) grouped in 2 zones: *Proparvicingula moniliformis* Zone, *Globolaxtorum tozeri* Zone (Fig. 2)
Bragin 1991	Spathian to Rhaetian	Far East Russia	7 interval zones, upper 3 zones divided in subzones (Fig. 2)
Tumanda 1991	Spathian to Rhaetian	Philippines	8 interval zones: *Pactarentinia koikei*, *Hozmadia altipedaria*, *Pseudostylosphaera japonica*, *Triassocampe deweveri*, *Muelleritortis cochleata*, *Capnuchosphaera*, *Capnodoce*, *Livarella*
Yang & Mizutani 1991	late Norian - Rhaetian	NE China	*Livarella* - *Canoptum rhaeticum* Assemblage

Fig. 1. (*Continued*)

AUTHOR(S)/YEAR	TIME INTERVAL	REGION	ZONES AND TYPE OF ZONES
Sugiyama 1992	Spathian to middle Anisian	central Japan	3 assemblage zones: *Parentactinia nakatsugawaensis*, *Hozmadia gifuensis*, *Triassocampe coronata*
Yeh 1992	Norian to Rhaetian	Philippines	2 assemblages: *Betraccium deweveri*, *Livarella longus*
Sashida *et al*. 1993	late Anisian to Norian	central Japan	5 assemblages: *Pseudostylosphaera japonica*, *Pseudostylosphaera helicata*, *Cryptostephanidium* sp., *Capnuchosphaera* sp., *Betraccium* sp.
Kozur & Mostler 1994	Anisian to Rhaetian	Italy, Hungary, Austria	9 zones based on FADs or LADs of index and several other species (Fig. 2)
Kozur 1995; Kozur & Mostler 1996; Kozur *et al*. 1996	late Anisian to Ladinian	Austria, Bosnia	subdivision of zones established by Kozur & Mostler 1994 (Fig. 2; full names of subzones: *Tiborella florida*, *Yeharaia annulata*, *Oertlispongus primitivus*, *Oertlispongus inaequispinosus*, *Ladinocampe annuloperforata*, *Ladinocampe vicentinensis*, *Pterospongus priscus*, *Spongoserrula rarauana*, *Spongoserrula fluegeli*)
Yeh & Cheng 1996	Rhaetian	Philippines	*Parabipedis pessagnoi* Assemblage
Nishizono 1996	early Anisian to late Norian	Kyushu, Japan	one unnamed zone and 5 interval zones based on FADs of index taxa: *Pseudostylosphaera compacta*, *Plafkerium cochleatum*, *Capnuchosphaera triassica*, *Capnodoce*, *Betraccium deweveri*
Sugiyama 1997	Spathian to Rhaetian	central Japan	18 zones: 2 assemblage zones (TR 0 and TR 1) and 16 zones defined by FADs or LADs of index species (Fig. 2)
Tekin 1999	Ladinian to Rhaetian	Turkey	stratigraphic distribution of 332 taxa
Feng *et al*. 2000, 2001	Anisian to Ladinian	south and southwest China	4 new interval zones in the Anisian: *Triassocampe dumitricai*, *T. coronata inflata*, *T. coronata coronata*, *T. deweveri*
Bragin 2000	late Olenekian to late Rhaetian	Far East Russia	*Pseudostylosphaera fragilis* Beds (upper Olenekian) and 14 zones: *Hozmadia gifuensis* (lower Anisian), *Triassocampe diordinis* (middle Anisian), *Triassocampe deweveri* (upper Anisian), *Triassocampe scalaris* (uppermost Anisian-lowermost Ladinian), *Oertlispongus inaequispinosus* (lower part of lower Ladinian), *Falcispongus falciformis* (upper part of lower Ladinian-lower part of upper Ladinian), *Muelleritortis cochleata* (middle-upper part of upper Ladinian), *Tritortis kretaensis kretaensis* (lower Carnian), *Capnuchosphaera theloides* (upper Carnian), *Capnodoce crystallina* (lower-middle Norian), *Lysemelas olbia* (lower part of upper Norian), *Betraccium deweveri* (upper part of upper Norian), *Livarella densiporata* (lower Rhaetian), and *Globolaxtorum tozeri* (upper Rhaetian)
Bragin 2007	Norian	Cyprus	stratigraphic distribution of 101 species
Moix *et al*. 2007	early Tuvalian	Turkey	*Spongotortilispinus moixi* Zone, taxon range zone

Fig. 1. (*Continued*) Development of Triassic radiolarian biochronology from the first publications in 1979 to the present. Note that in this table the Anisian and Ladinian are separated at the 'historical' boundary, that is, at the base of *Reitziites reitzi* Ammonoid Zone.

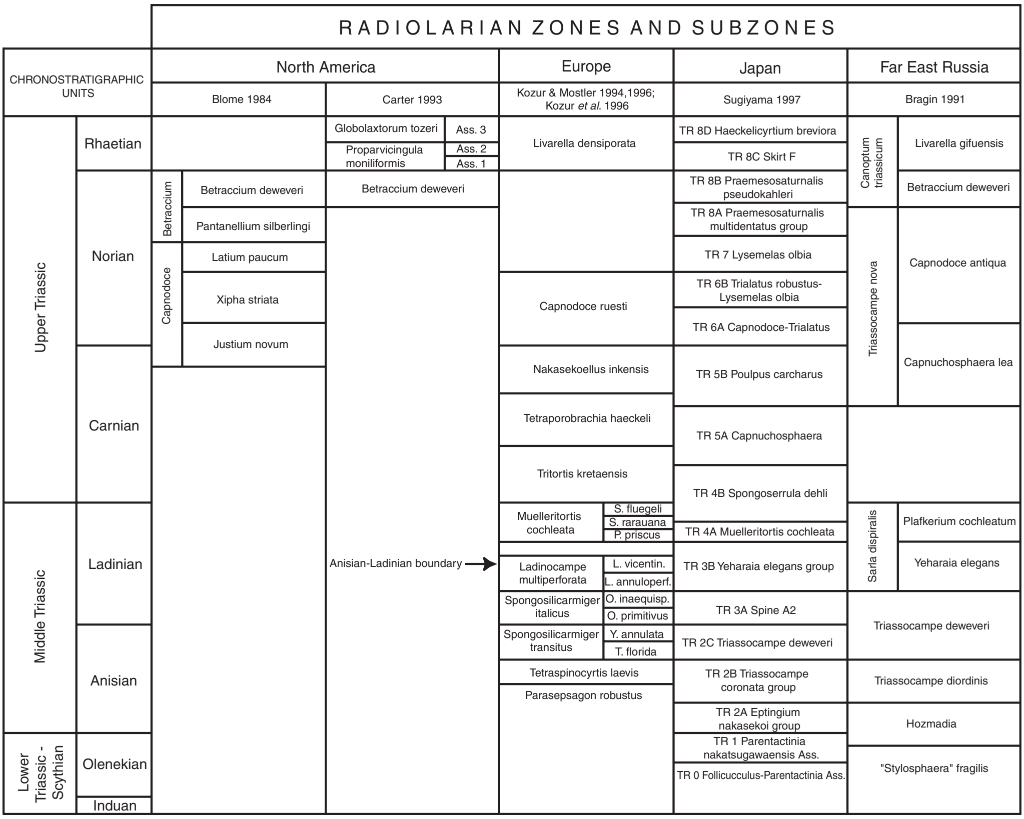


Fig. 2. Correlation of Triassic radiolarian zones and subzones (for full names of European subzones see Fig. 1).

conodonts, but all the other zones are calibrated through correlation with zonal schemes established in other regions (Sugiyama 1997).

In Europe (including Turkey), the first range chart for Triassic radiolarians was produced by De Wever (1982), who compiled the ranges of 44 Ladinian to Norian species based on previous works and his data from Greece, Sicily and Turkey (De Wever *et al.* 1979; De Wever 1982), but he did not define new zones. Although extensive systematic studies were carried out in Europe (Dumitrica 1978*a*, *b*, 1982*a*, *b*, *c*; Dumitrica *et al.* 1980; Kozur & Mostler 1972, 1978, 1979, 1981, 1983; Lahm 1984; Goričan & Buser 1990), no formal radiolarian zones were proposed. The reason for this delay was the lack of continuous radiolarian-bearing successions suitable for biochronological studies. Radiolarian occurrences in the western Mediterranean are limited in time and restricted to short pelagic intervals within relatively shallow-water deposits. However, these radiolarian assemblages come mostly from siliceous limestones and are thus generally well preserved and diverse with ammonoids and conodonts providing age control.

The first radiolarian zones were formally introduced by Kozur & Mostler (1994), who constructed a zonation on the basis of several sections from Hungary, Italy and Austria. They established nine zones for the Anisian to Rhaetian (Fig. 2). At that time, the lower Ladinian assemblages were by far the best studied and were divided into two zones (*Spongosilicarmiger italicus* and *Ladinocampe multiperforata*), which were subdivided into three and two subzones, respectively. Kozur (1995) and Kozur *et al.* (1996) elevated the rank of the *Spongosilicarmiger transitus* Subzone (i.e. lower subzone of the *Spongosilicarmiger italicus* Zone) to zonal level, defined two subzones within this zone and lowered the age to late Anisian. Kozur & Mostler (1996) further divided the upper Ladinian *Muelleritortis cochleata* Zone into three subzones.

In the late 1990s important biostratigraphic work was carried out in Turkey by Tekin (1999), who did not introduce new zones but presented a range chart with 332 Ladinian to Rhaetian species. Kozur

(2003*a*, *b*) presented an up-to-date correlation of radiolarian zones with ammonoid and conodont zones. He selected his own radiolarian zones for the Anisian, Ladinian and Carnian but used Japanese and North American zones for the Lower Triassic, Norian and Rhaetian. However, some radiolarian zones indicated in this publication have never been defined or described (e.g. *Stigmosphaerostylus turkensis* Zone in the upper Induan, *Muelleritortis firma* Zone in the Ladinian, *Tritortis kretaensis dispiralis* Subzone in the uppermost Ladinian, *Squinabolella*? *trispinosa* and *Laxtorum perfectum* zones in the Rhaetian). Therefore, in the present paper we reproduce only the zones proposed by Kozur in his previous publications. Overall, the Middle Triassic and Carnian radiolarian zonation of Kozur and co-workers is very precise (Fig. 2), but new findings of well preserved radiolarian faunas still allow for further refinement. For example, based on excellently preserved material from SE Turkey a new *Spongotortilispinus moixi* Zone has recently been inserted in the lower Tuvalian (Moix *et al.* 2007) and a zonal gap in the upper Ladinian–lowest Norian is expected to be filled based on the study of the radiolarian fauna from the chert member of the Zula Formation in Oman (Blechschmidt *et al.* 2004; Dumitrica & Hungerbühler 2007), which encompasses the upper Anisian to lowest Norian interval.

Some other radiolarian zonations have been proposed outside the aforementioned regions. For Far East Russia (Sikhote–Alyn, Koryak Upland, Sakhalin), Bragin (1991) proposed a zonation that covers almost the entire Triassic. The Spathian to Rhaetian interval is divided into seven zones, with the upper three zones subdivided into six subzones (Fig. 2). These zones are well dated with co-occurring conodonts, but in comparison with other zonations, include only a small number of radiolarian taxa, that is, the stratigraphic distribution of only 25 species is included in the range chart. For this reason, the zonation has rarely been used outside Russia. The zonation was later emended (Bragin 2000) to include 15 zones, with 9 zones newly defined (Fig. 1). Recently, Bragin (2007) presented the stratigraphic distribution of 110 Norian species from southern Cyprus and correlated the assemblages to his zones established in Far East Russia.

In the Philippines, Yeh & Cheng (Cheng 1989; Yeh 1990, 1992; Yeh & Cheng 1996) described several Middle and Upper Triassic assemblages that contain typical Tethyan faunas. These assemblages were extracted from bedded cherts, and, lacking independent age control, their ages could be determined based solely on radiolarians whose range had previously been established in other regions (for correlation see Sugiyama 1997). Another zonation for the Philippines was proposed by Tumanda (1991), who divided the Spathian to Rhaetian into eight interval zones.

Since the early 1990s, extensive research on Triassic radiolarians has been carried out in Thailand (e.g. Sashida & Igo 1992; Sashida *et al.* 1997, 2000*a*, *b*; Kamata *et al.* 2002; Feng *et al.* 2005), China (e.g. Yang & Mizutani 1991; Feng 1992; Feng *et al.* 2000, 2001; Xia & Zhang 2000; Yao & Kuwahara 2000; Wang *et al.* 2002, 2005; Feng & Liang 2003) and Indonesia (Sashida *et al.* 1999). Because the existing radiolarian range charts apply well in these areas, new local zonations have only exceptionally been proposed (e.g. Yang & Mizutani 1991; Feng *et al.* 2000, 2001).

Very few radiolarian localities have been studied in high latitudes, and most are concentrated in New Zealand where Early, Middle and Late Triassic radiolarians have been documented (Grapes *et al.* 1990; Aita & Bragin 1999; Takemura *et al.* 2002, 2003; Hori *et al.* 2003; Kamata *et al.* 2003; Takemura & Aono 2007; Takemura *et al.* 2007*b*; Kamata 2007; Kamata *et al.* 2007). This country is especially well known for Permian–Triassic boundary faunas at Arrow Rocks (Takemura & Aono 2007; Takemura *et al.* 2007*a*, *b*; Kamata 2007; Kamata *et al.* 2007). Middle Triassic high-latitude radiolarians have also been reported from the Omolon Massif in NE Siberia (Aita & Bragin 1999), and higher paleolatitudes were assumed for Late Triassic radiolarians from the Brooks Range in northern Alaska (Blome 1987). High-latitude faunas clearly differ from their low-latitude counterparts but, because data are very scarce, a separate high-latitude zonation has not been developed yet.

De Wever *et al.* (2001) combined zonations from different regions in order to obtain a complete succession of low-latitude radiolarian zones for the entire Triassic Period. They selected the zones of Kozur & Mostler (1994, 1996) and completed these zones with those of Sugiyama (1997) for the Olenekian to middle Anisian, and Blome (1984) and Carter (1993) for the Late Triassic. Herein, we correlate the currently used zonations for their entire extent (Fig. 2).

The genera revision project

The Mesozoic Working-Group of the International Association of Radiolarian Paleontologists (InterRad) has just completed a detailed taxonomic revision of Mesozoic radiolarians at the generic level (O'Dogherty *et al.* 2009*a, b*). The aim of this project, which began in 2006, was to compile and review the taxonomy of all existing genera as a basis for a refined Mesozoic radiolarian stratigraphy. The 'Mesozoic Generic revision project' was comprised of 11 scientists from 8 countries. This working group met twice in May 2006 and

May 2007 in two-week duration meetings that provided a forum for taxonomic discussions necessary to the making of a refined catalogue of genera. The basic purpose was to provide the scientific community with a catalogue of type-species in hopes of clarifying the correct generic assignment of Mesozoic species (more than 6000 species have been described for the Mesozoic alone). Nonetheless, taxonomy without stratigraphy has little significance and for this reason the generic catalogue also contains precise information on stratigraphic ranges. Generic ages are referred not to radiolarian zones or subzones, but to ICS stage subdivisions that can be correlated easily to faunal stages, a subdivision classically used by most of the researchers working on Triassic radiolarians (Figs 2 & 3).

The Working-Group review has shown that more than 900 genera have been published since the early work of Ehrenberg (1838), in which the genus *Cornutella* (a common Jurassic to Recent genus) was described. Many of these nominal genera are regarded as valid names according to the rules of the International Code of Zoological Nomenclature (ICZN), but a considerable number have to be treated as *nomina dubia*, synonyms or homonyms. The project consists of two distinct parts: the Triassic, and the Jurassic–Cretaceous. This division is justified by the low number of genera common to each part (only 30 genera cross the Rhaetian–Hettangian boundary: Fig. 4).

The Triassic part contains 381 described genera of which only 26% must be treated as invalid taxa according to ICZN rules. The compilation of species and genera has shown a very low number of *nomina dubia* (4%), which underscores the existence of the few publications dealing with Triassic radiolarians before the 1970s. This means that nearly all taxonomic publications since that time have held to a precise systematic concept (especially at the generic and specific level) and, in general, have good illustrations of the type-species. The Working-Group has revised and updated the stratigraphic distribution of 282 valid Triassic genera providing an accurate biostratigraphic chart for the Triassic that is reproduced in Figure 3. This range chart allows for dating samples at substage level by using the identification of characteristic taxa at the generic level. The reason this is so powerful is that the biostratigraphic ranges of many taxa are relatively short, that is, nearly 75% of the genera show a duration of less than four Triassic substages. This is, in part, the imprint of a homogeneous systematics, inherited by the low number of workers involved in both taxonomy and stratigraphy of the Triassic Period. A rapid analysis of authorship indicates that 75% of the generic systematics has been produced by only four authors: P. Dumitrica, H. Kozur, E. Pessagno and U. Tekin. In summary, we can say that the accurate taxonomy used in the systematics of Triassic genera, together with the rapid evolution of radiolarians during the Middle Triassic (De Wever *et al.* 2003, 2006), are the main reasons for the good biostratigraphic resolution, even at the generic level.

Triassic range chart of genera

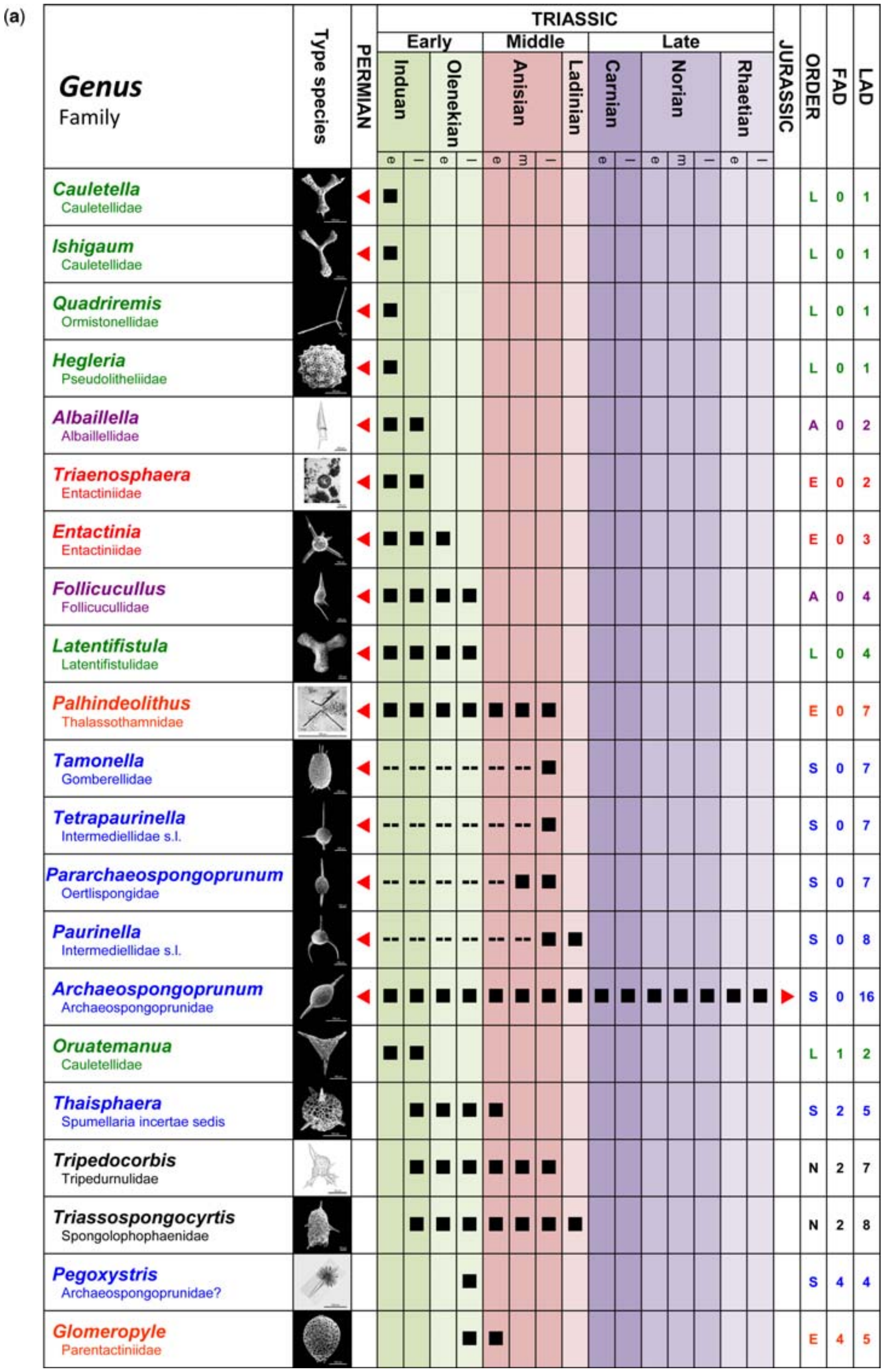
The discussion that follows is sufficient to outline our present understanding of generic occurrences of radiolarians through Triassic time, highlighting major evolutionary events in the history of the group. The genera discussed below were selected because they are sufficiently distinctive to be recognizable, and have been employed at a number of localities and in zonations, by more than one author. This information is based on the range chart (reproduced in Fig. 3) resulting from the new taxonomic revision of Triassic genera made by the InterRad Mesozoic working group discussed above (O'Dogherty *et al.* 2009*a, b*). For more comprehensive information on radiolarian systematics and terminology the reader is referred to the latest monograph on this group of microfossils (De Wever *et al.* 2001). Basic information for a less demanding audience is also available online (http://www.radiolaria.org).

Induan

The beginning of the Triassic is marked by the relatively common presence of Permian survivors (see below) and the occurrence of the first and primitive forms of monocyrtids (*Tripedocorbis*) and dicyrtids (*Triassospongocyrtis*).

Olenekian

Radiolarian diversity starts to increase measurably during the Late Olenekian with Entactinaria diversifying more rapidly than other groups. This interval records the first occurrence of primitive Eptingiidae such as *Spongostephanidium* (?*Pentabelus*) simultaneous with the initial occurrence of most simple Multiarcusellidae (*Tiborella*). The first Triassic spicular Entactinaria (*Archaeosemantis* and *Parentactinia*) occur through this interval. Among nassellarians, this period is characterized by the occurrence of the first primitive multicyrtids, characterized by bearing a low number of segments (*Anisicyrtis*), and the earliest representatives of the monocyrtid Poulpidae (*Hozmadia*). Also, it records the initial development of new spicular forms (*Verticiplagia*). The Olenekian–Anisian boundary is marked by the final disappearance of typical Paleozoic families (Follicucullidae, Latentifistulidae).



Genus Family	Type species	PERMIAN	TRIASSIC																JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late											
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian						
			e	l	e	l	e	m	l		e	l	e	m	l	e	l					
Cauletella Cauletellidae		◄	■																	L	0	1
Ishigaum Cauletellidae		◄	■																	L	0	1
Quadriremis Ormistonellidae		◄	■																	L	0	1
Hegleria Pseudolitheliidae		◄	■																	L	0	1
Albaillella Albaillellidae		◄	■	■																A	0	2
Triaenosphaera Entactiniidae		◄	■	■																E	0	2
Entactinia Entactiniidae		◄	■	■	■															E	0	3
Follicucullus Follicucullidae		◄	■	■	■	■														A	0	4
Latentifistula Latentifistulidae		◄	■	■	■	■														L	0	4
Palhindeolithus Thalassothamnidae		◄	■	■	■	■	■	■	■											E	0	7
Tamonella Gomberellidae		◄	--	--	--	--	--	--	■											S	0	7
Tetrapaurinella Intermediellidae s.l.		◄	--	--	--	--	--	--	■											S	0	7
Pararchaeospongoprunum Oertlispongidae		◄	--	--	--	--	--	■	■											S	0	7
Paurinella Intermediellidae s.l.		◄	--	--	--	--	--	--	■	■										S	0	8
Archaeospongoprunum Archaeospongoprunidae		◄	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		►	S	0	16
Oruatemanua Cauletellidae			■	■																L	1	2
Thaisphaera Spumellaria incertae sedis				■	■	■	■													S	2	5
Tripedocorbis Tripedurnulidae				■	■	■	■	■	■											N	2	7
Triassospongocyrtis Spongolophaenidae				■	■	■	■	■	■	■										N	2	8
Pegoxystris Archaeospongoprunidae?						■														S	4	4
Glomeropyle Parentactiniidae						■	■													E	4	5

Fig. 3. Range chart of Triassic radiolarian genera including family position and re-illustration of the type-species presented in chronological order. This table represents the main goal of the generic revision project undertaken by the Mesozoic Working Group of InterRad (O'Dogherty *et al.* 2009*a*). The FAD and LAD numbers refer to stage and

(b)

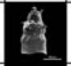
Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Anisicyrtis Anisicyrtiidae						■	■	■	■										N	4	7
Tiborella Austrisaturnalinae						■	■	■	■	■									E	4	8
Pentabelus Kungalariidae?						■	■	■	■	■	■								E	4	9
Pseudostylosphaera Hindeosphaerinae						■	■	■	■	■	■								E	4	9
Spongostephanidium Eptingiidae						■	■	■	■	■	■	■							E	4	10
Hozmadia Poulpidae						■	■	■	■	■	■	■							N	4	10
Archaeosemantis Archaeosemantidae						■	■	■	■	■	■	■	■	■					N	4	12
Parentactinia Parentactiniidae						■	■	■	■	■	■	■	■	■	■	■	■	▶	E	4	16
Verticiplagia Ximolzasinae						■	■	■	■	■	■	■	■	■	■	■	■	▶	N	4	16
Celluronta Acropyramididae							■	■											N	5	6
Planispinocyrtis Planispinocyrtiidae							■	■	■	■	■								N	5	9
Cryptostephanidium Eptingiidae							■	■	■	■	■	■							E	5	10
Triassocampe Ruesticyrtiidae							■	■	■	■	■	■	■						N	5	11
Eptingium Eptingiidae							■	■	■	■	■	■	■	■	■	■	■		E	5	15
Pseudosepsagon Heptacladidae								■											E	6	6
Arcicubulus Quinquecapsulariidae?								■											E	6	6
Fueloepicyrtis Nabolellidae								■											N	6	6
Ximolzas Ximolzasinae								■											N	6	6
Pessagnollum Spumellaria incertae sedis								■											S	6	6
Tandarnia Archaeosemantidae								■	■										N	6	7
Hexatortilisphaera Entactinaria incertae sedis								■	■										E	6	7

Fig. 3. (*Continued*) substage numbering used in O'Dogherty *et al.* (2009*a*). Radiolarian orders are indicated by letters; Albaillellaria (A); Latentifistularia (L); Entactinaria (E); Spumellaria (S); Nassellaria (N). The triangles indicate that the genus either ranges down to the Permian, or upward to the Jurassic.

(c)

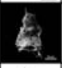
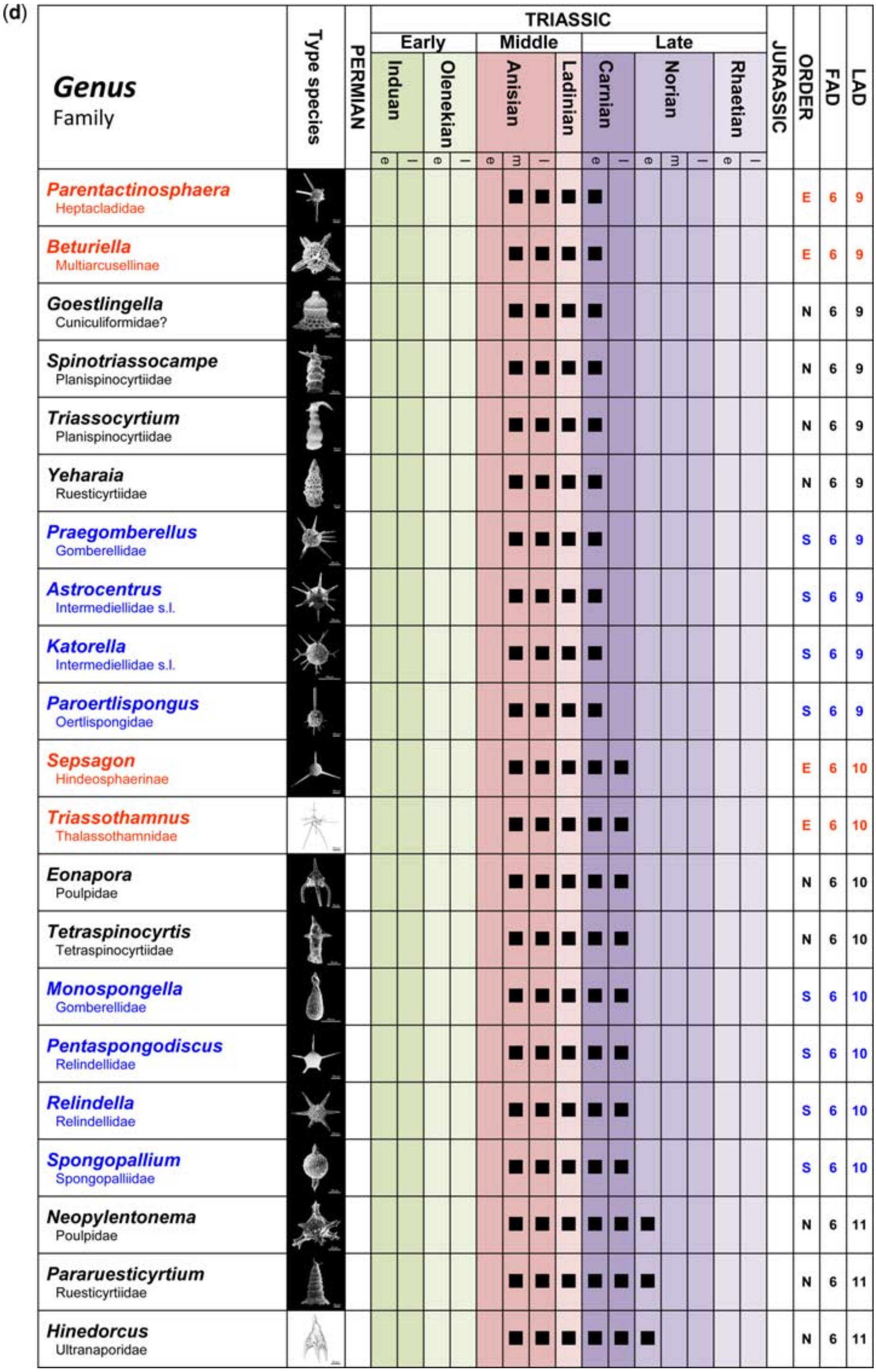
Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Heptacladus Heptacladidae								■	■										E	6	7
Parasepsagon Hindeosphaerinae								■	■										E	6	7
Pentactinocapsa Pentactinocarpidae								■	■										E	6	7
Monicasterix Monicastericidae								■	■										N	6	7
Triassobipedis Poulpidae								■	■										N	6	7
Paratriassocampe Ruesticyrtiidae								■	■										N	6	7
Pseudotriassocampe Ruesticyrtiidae								■	■										N	6	7
Spongolophophaena Spongolophophaenidae								■	■										N	6	7
Spongosilicarmiger Spongosilicarmigeridae								■	■										N	6	7
Baratuna Tripedurnulidae								■	■										N	6	7
Tripedocassis Tripedurnulidae								■	■										N	6	7
Muellericyrtium Ultranaporidae								■	■										N	6	7
Molzaxis Ximolzasinae								■	■										N	6	7
Palaeosemantis Zaldacriinae								■	■										N	6	7
Zaldacria Zaldacriinae								■	■										N	6	7
Patrulius Patruliidae								■	■										S	6	7
Tetratholura Patruliidae								■	■										S	6	7
Nandartia Archaeosemantidae								■	■	■									N	6	8
Nofrema Spongosilicarmigeridae								■	■	■									N	6	8
Tripedurnula Tripedurnulidae								■	■	■									N	6	8
Spongoxystris Spongotortilispinidae								■	■	■									S	6	8

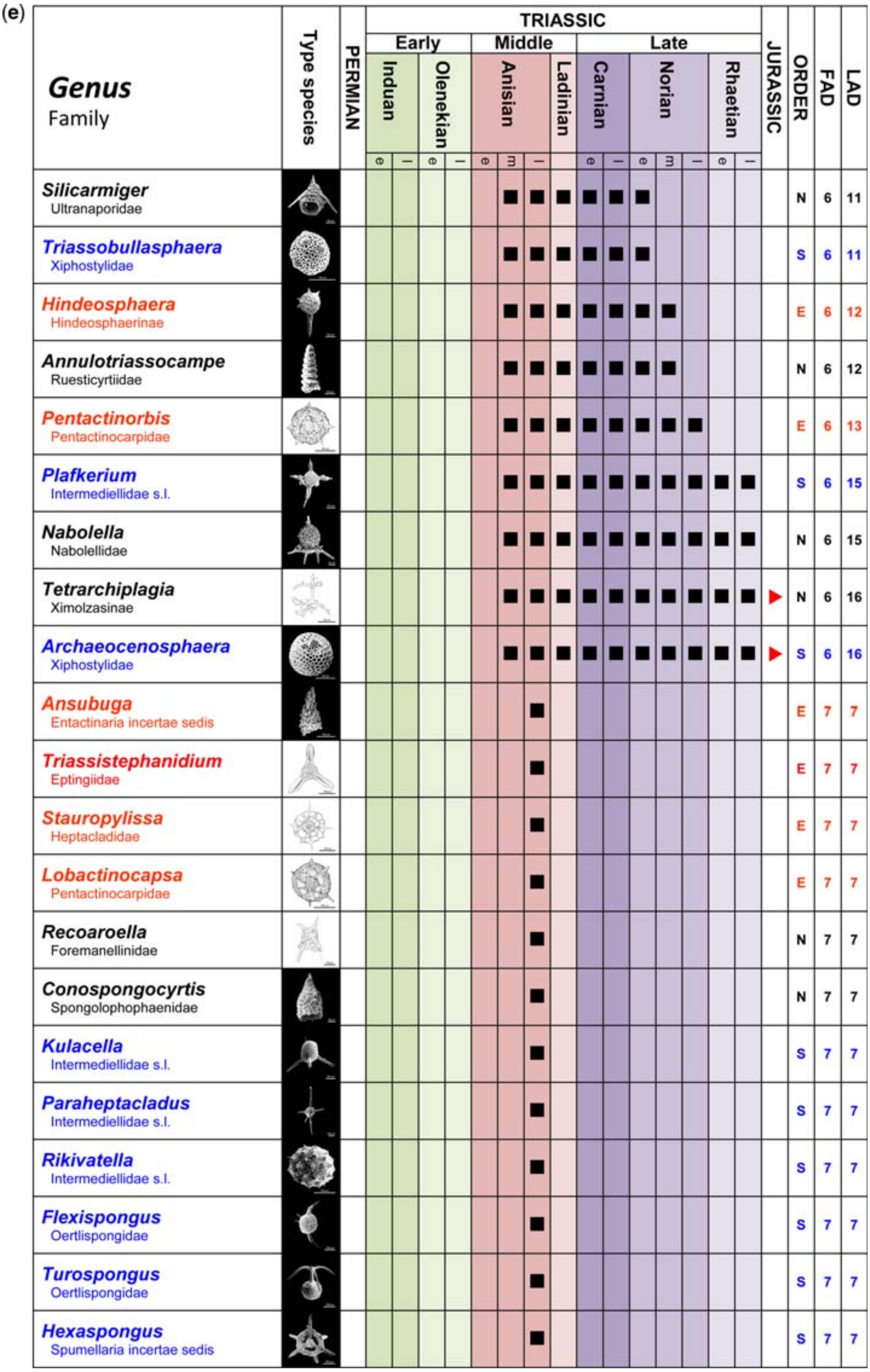
Fig. 3. *Continued.*



(d)

Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Parentactinosphaera Heptacladidae								■	■	■	■								E	6	9
Beturiella Multiarcusellinae								■	■	■	■								E	6	9
Goestlingella Cuniculiformidae?								■	■	■	■								N	6	9
Spinotriassocampe Planispinocyrtiidae								■	■	■	■								N	6	9
Triassocyrtium Planispinocyrtiidae								■	■	■	■								N	6	9
Yeharaia Ruesticyrtiidae								■	■	■	■								N	6	9
Praegomberellus Gomberellidae								■	■	■	■								S	6	9
Astrocentrus Intermediellidae s.l.								■	■	■	■								S	6	9
Katorella Intermediellidae s.l.								■	■	■	■								S	6	9
Paroertlispongus Oertlispongidae								■	■	■	■								S	6	9
Sepsagon Hindeosphaerinae								■	■	■	■	■							E	6	10
Triassothamnus Thalassothamnidae								■	■	■	■	■							E	6	10
Eonapora Poulpidae								■	■	■	■	■							N	6	10
Tetraspinocyrtis Tetraspinocyrtiidae								■	■	■	■	■							N	6	10
Monospongella Gomberellidae								■	■	■	■	■							S	6	10
Pentaspongodiscus Relindellidae								■	■	■	■	■							S	6	10
Relindella Relindellidae								■	■	■	■	■							S	6	10
Spongopallium Spongopalliidae								■	■	■	■	■							S	6	10
Neopylentonema Poulpidae								■	■	■	■	■	■						N	6	11
Pararuesticyrtium Ruesticyrtiidae								■	■	■	■	■	■						N	6	11
Hinedorcus Ultranaporidae								■	■	■	■	■	■						N	6	11

Fig. 3. *Continued.*



(e)

Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Silicarmiger Ultranaporidae								■	■	■	■	■	■						N	6	11
Triassobullasphaera Xiphostylidae								■	■	■	■	■	■						S	6	11
Hindeosphaera Hindeosphaerinae								■	■	■	■	■	■	■					E	6	12
Annulotriassocampe Ruesticyrtiidae								■	■	■	■	■	■	■					N	6	12
Pentactinorbis Pentactinocarpidae								■	■	■	■	■	■	■	■				E	6	13
Plafkerium Intermediellidae s.l.								■	■	■	■	■	■	■	■	■	■		S	6	15
Nabolella Nabolellidae								■	■	■	■	■	■	■	■	■	■		N	6	15
Tetrarchiplagia Ximolzasinae								■	■	■	■	■	■	■	■	■	■	▶	N	6	16
Archaeocenosphaera Xiphostylidae								■	■	■	■	■	■	■	■	■	■	▶	S	6	16
Ansubuga Entactinaria incertae sedis									■										E	7	7
Triassistephanidium Eptingiidae									■										E	7	7
Stauropylissa Heptacladidae									■										E	7	7
Lobactinocapsa Pentactinocarpidae									■										E	7	7
Recoaroella Foremanellinidae									■										N	7	7
Conospongocyrtis Spongolophophaenidae									■										N	7	7
Kulacella Intermediellidae s.l.									■										S	7	7
Paraheptacladus Intermediellidae s.l.									■										S	7	7
Rikivatella Intermediellidae s.l.									■										S	7	7
Flexispongus Oertlispongidae									■										S	7	7
Turospongus Oertlispongidae									■										S	7	7
Hexaspongus Spumellaria incertae sedis									■										S	7	7

Fig. 3. *Continued.*

(f)

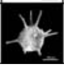
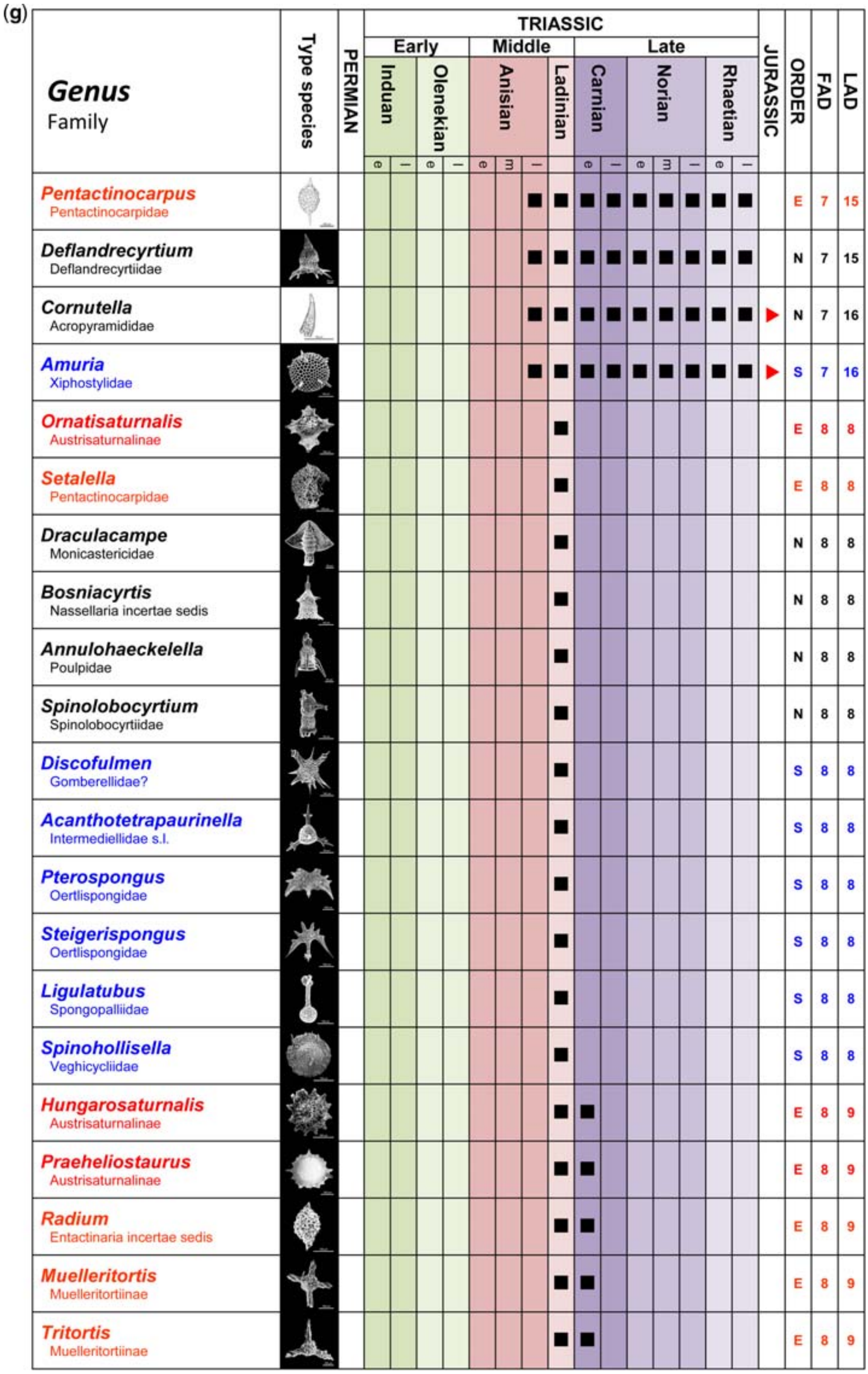
Genus Family	Type species	PERMIAN	TRIASSIC																JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late											
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Annulobulbocyrtium Bulbocyrtiidae									■	■										N	7	8
Foremanellina Foremanellinidae									■	■										N	7	8
Tubotriassocyrtis Monicastericidae									■	■										N	7	8
Ladinocampe Planispinocyrtiidae									■	■										N	7	8
Gomberellus Gomberellidae									■	■										S	7	8
Baumgartneria Oertlispongidae									■	■										S	7	8
Falcispongus Oertlispongidae									■	■										S	7	8
Welirella Centrocubidae									■	■	■									E	7	9
Baloghisphaera Multiarcusellinae									■	■	■									E	7	9
Multiarcusella Multiarcusellinae									■	■	■									E	7	9
Striatotriassocampe Ruesticyrtiidae									■	■	■									N	7	9
Angulopaurinella Intermediellidae s.l.									■	■	■									S	7	9
Oertlispongus Oertlispongidae									■	■	■									S	7	9
Recoarella Relindellidae									■	■	■									S	7	9
Dreyericyrtium Deflandrecyrtiidae									■	■	■	■								N	7	10
Spinomersinella Spinomersinellidae									■	■	■	■								S	7	10
Poulpus Poulpidae									■	■	■	■	■							N	7	11
Vinassaspongus Spongopalliidae									■	■	■	■	■							S	7	11
Tubospongopallium Spongopalliidae									■	■	■	■	■							S	7	11
Pylostephanidium Eptingiidae									■	■	■	■	■	■	■					E	7	13
Triassospongosphaera Intermediellidae s.l.									■	■	■	■	■	■	■					S	7	13

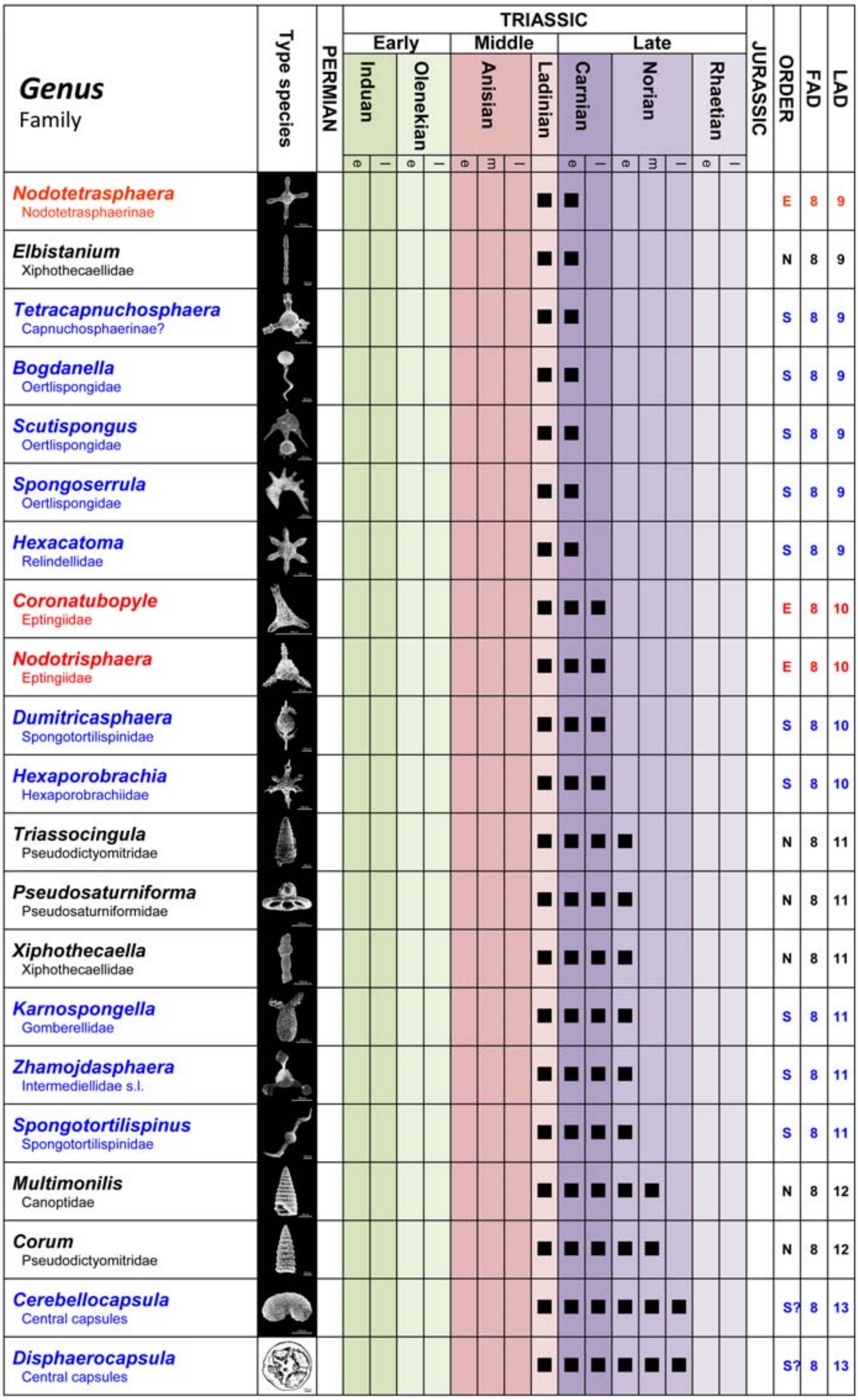
Fig. 3. *Continued.*



Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Pentactinocarpus Pentactinocarpidae									■	■	■	■	■	■	■	■	■		E	7	15
Deflandrecyrtium Deflandrecyrtiidae									■	■	■	■	■	■	■	■	■		N	7	15
Cornutella Acropyramididae									■	■	■	■	■	■	■	■	■	►	N	7	16
Amuria Xiphostylidae									■	■	■	■	■	■	■	■	■	►	S	7	16
Ornatisaturnalis Austrisaturnalinae										■									E	8	8
Setalella Pentactinocarpidae										■									E	8	8
Draculacampe Monicastericidae										■									N	8	8
Bosniacyrtis Nassellaria incertae sedis										■									N	8	8
Annulohaeckelella Poulpidae										■									N	8	8
Spinolobocyrtium Spinolobocyrtiidae										■									N	8	8
Discofulmen Gomberellidae?										■									S	8	8
Acanthotetrapaurinella Intermediellidae s.l.										■									S	8	8
Pterospongus Oertlispongidae										■									S	8	8
Steigerispongus Oertlispongidae										■									S	8	8
Ligulatubus Spongopalliidae										■									S	8	8
Spinohollisella Veghicycliidae										■									S	8	8
Hungarosaturnalis Austrisaturnalinae										■	■								E	8	9
Praeheliostaurus Austrisaturnalinae										■	■								E	8	9
Radium Entactinaria incertae sedis										■	■								E	8	9
Muelleritortis Muelleritortiinae										■	■								E	8	9
Tritortis Muelleritortiinae										■	■								E	8	9

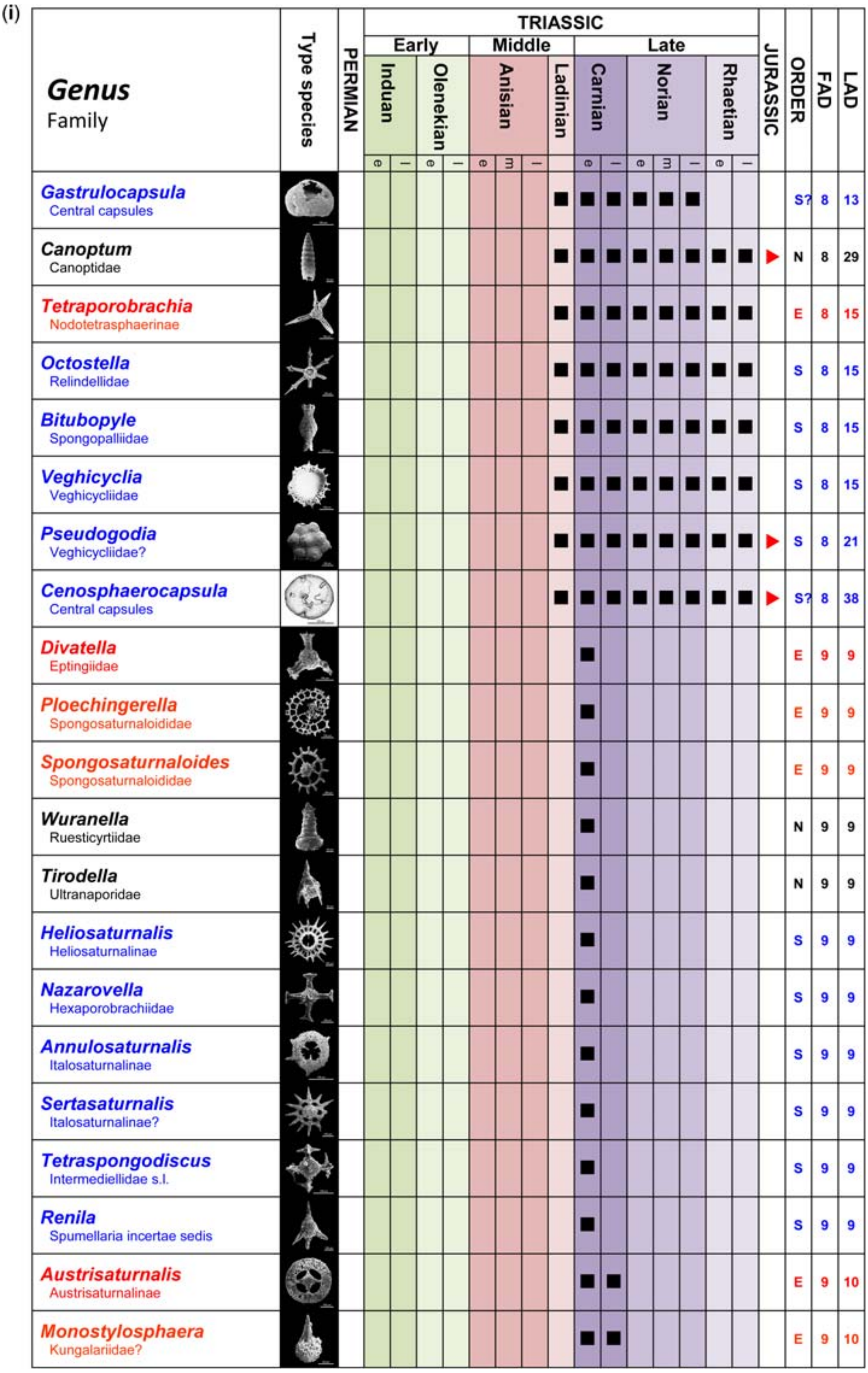
Fig. 3. *Continued.*

(h)



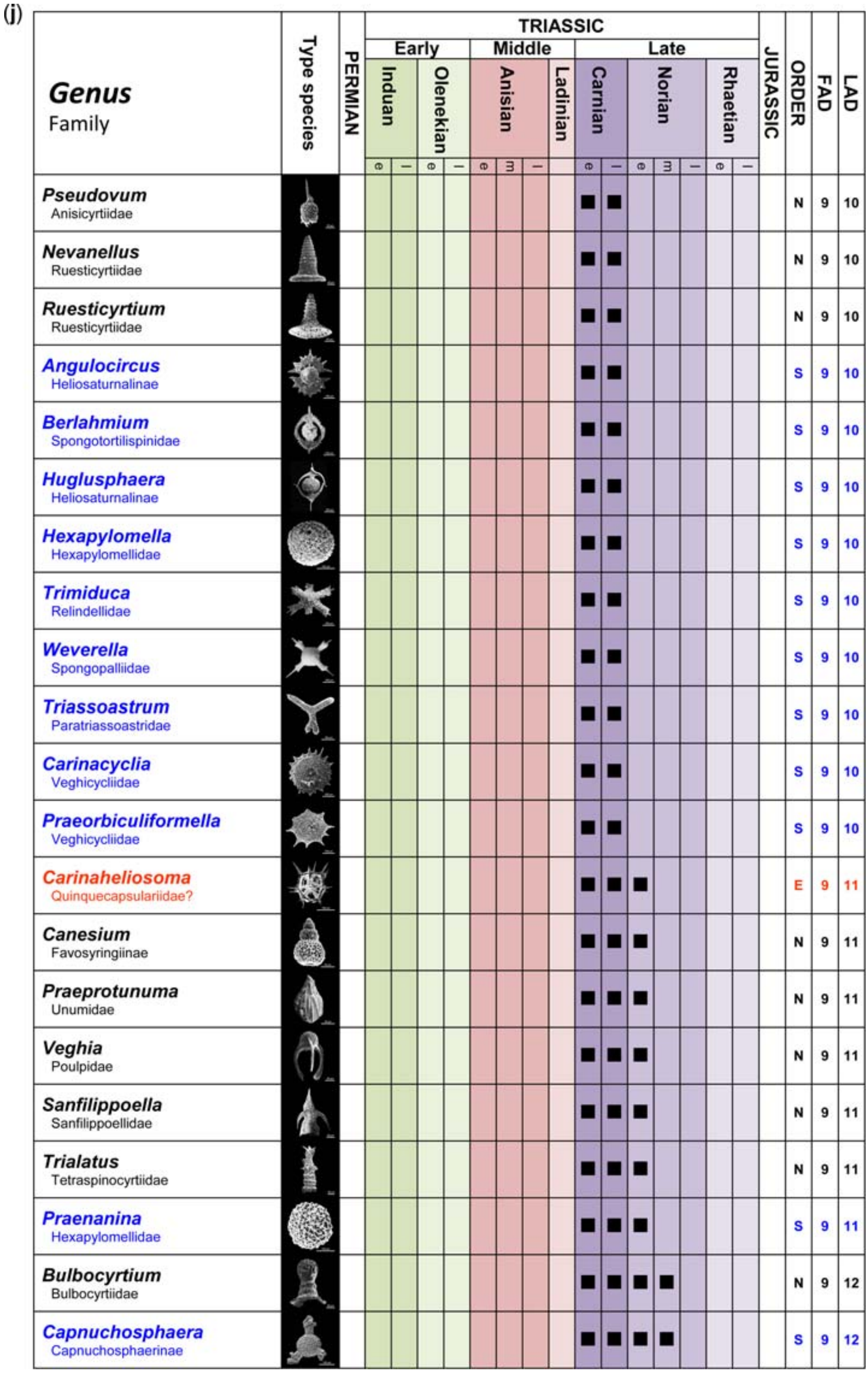
Genus Family	Type species	PERMIAN	TRIASSIC																JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late											
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian						
			e	l	e	l	e	m	l		e	l	e	m	l	e	l					
Nodotetrasphaera Nodotetrasphaerinae										■	■									E	8	9
Elbistanium Xiphothecaellidae										■	■									N	8	9
Tetracapnuchosphaera Capnuchosphaerinae?										■	■									S	8	9
Bogdanella Oertlispongidae										■	■									S	8	9
Scutispongus Oertlispongidae										■	■									S	8	9
Spongoserrula Oertlispongidae										■	■									S	8	9
Hexacatoma Relindellidae										■	■									S	8	9
Coronatubopyle Eptingiidae										■	■	■								E	8	10
Nodotrisphaera Eptingiidae										■	■	■								E	8	10
Dumitricasphaera Spongotortilispinidae										■	■	■								S	8	10
Hexaporobrachia Hexaporobrachiidae										■	■	■								S	8	10
Triassocingula Pseudodictyomitridae										■	■	■	■							N	8	11
Pseudosaturniforma Pseudosaturniformidae										■	■	■	■							N	8	11
Xiphothecaella Xiphothecaellidae										■	■	■	■							N	8	11
Karnospongella Gomberellidae										■	■	■	■							S	8	11
Zhamojdasphaera Intermediellidae s.l.										■	■	■	■							S	8	11
Spongotortilispinus Spongotortilispinidae										■	■	■	■							S	8	11
Multimonilis Canoptidae										■	■	■	■	■						N	8	12
Corum Pseudodictyomitridae										■	■	■	■	■						N	8	12
Cerebellocapsula Central capsules										■	■	■	■	■	■					S?	8	13
Disphaerocapsula Central capsules										■	■	■	■	■	■					S?	8	13

Fig. 3. *Continued.*


(i)

Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Gastrulocapsula Central capsules										■	■	■	■	■	■				S?	8	13
Canoptum Canoptidae										■	■	■	■	■	■	■	■	▶	N	8	29
Tetraporobrachia Nodotetrasphaerinae										■	■	■	■	■	■	■	■		E	8	15
Octostella Relindellidae										■	■	■	■	■	■	■	■		S	8	15
Bitubopyle Spongopalliidae										■	■	■	■	■	■	■	■		S	8	15
Veghicyclia Veghicycliidae										■	■	■	■	■	■	■	■		S	8	15
Pseudogodia Veghicycliidae?										■	■	■	■	■	■	■	■	▶	S	8	21
Cenosphaerocapsula Central capsules										■	■	■	■	■	■	■	■	▶	S?	8	38
Divatella Eptingiidae											■								E	9	9
Ploechingerella Spongosaturnaloididae											■								E	9	9
Spongosaturnaloides Spongosaturnaloididae											■								E	9	9
Wuranella Ruesticyrtiidae											■								N	9	9
Tirodella Ultranaporidae											■								N	9	9
Heliosaturnalis Heliosaturnalinae											■								S	9	9
Nazarovella Hexaporobrachiidae											■								S	9	9
Annulosaturnalis Italosaturnalinae											■								S	9	9
Sertasaturnalis Italosaturnalinae?											■								S	9	9
Tetraspongodiscus Intermediellidae s.l.											■								S	9	9
Renila Spumellaria incertae sedis											■								S	9	9
Austrisaturnalis Austrisaturnalinae											■	■							E	9	10
Monostylosphaera Kungalariidae?											■	■							E	9	10

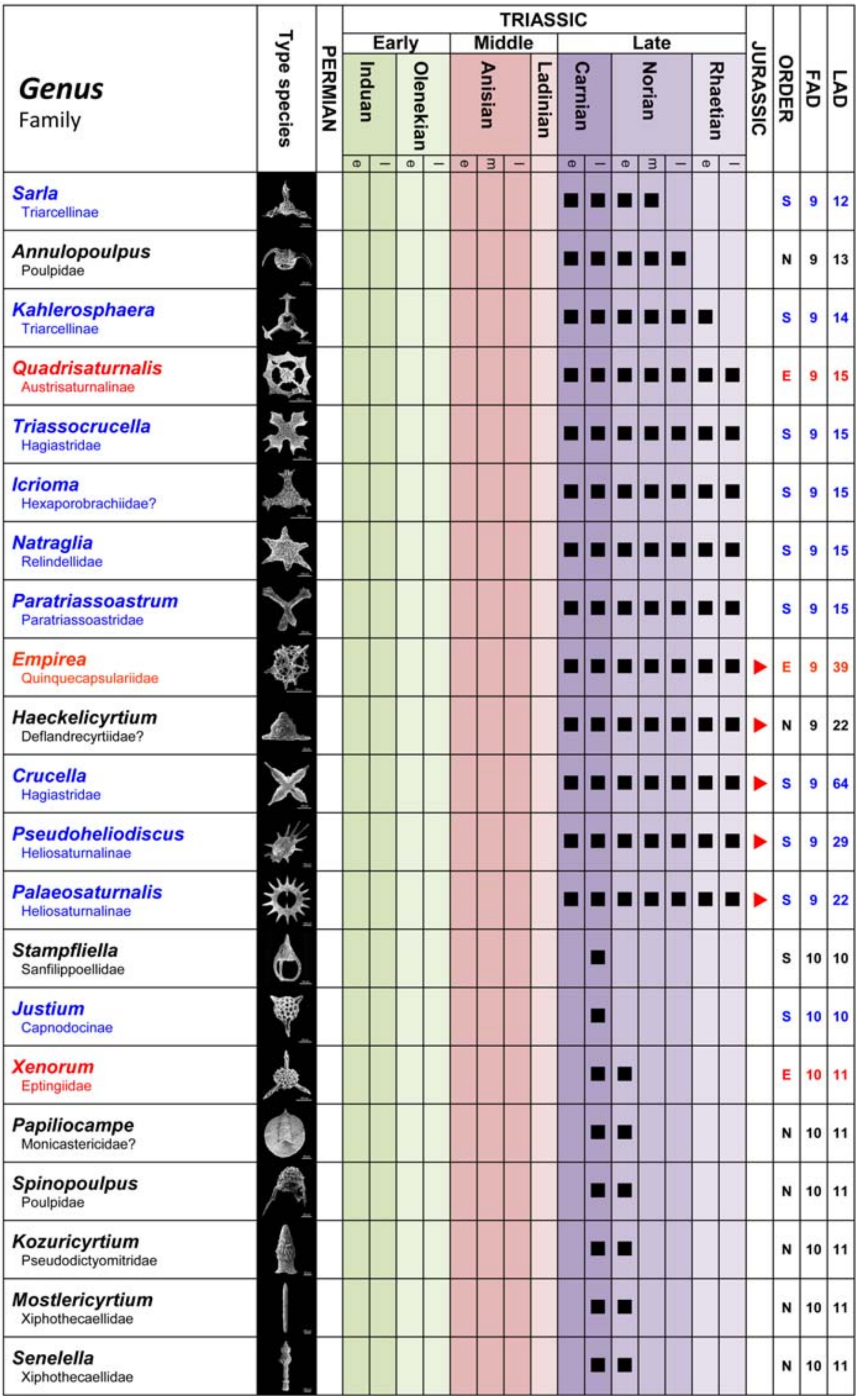
Fig. 3. *Continued.*



Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Pseudovum Anisicyrtiidae											■	■							N	9	10
Nevanellus Ruesticyrtiidae											■	■							N	9	10
Ruesticyrtium Ruesticyrtiidae											■	■							N	9	10
Angulocircus Heliosaturnalinae											■	■							S	9	10
Berlahmium Spongotortilispinidae											■	■							S	9	10
Huglusphaera Heliosaturnalinae											■	■							S	9	10
Hexapylomella Hexapylomellidae											■	■							S	9	10
Trimiduca Relindellidae											■	■							S	9	10
Weverella Spongopalliidae											■	■							S	9	10
Triassoastrum Paratriassoastridae											■	■							S	9	10
Carinacyclia Veghicycliidae											■	■							S	9	10
Praeorbiculiformella Veghicycliidae											■	■							S	9	10
Carinaheliosoma Quinquecapsulariidae?											■	■	■						E	9	11
Canesium Favosyringiinae											■	■	■						N	9	11
Praeprotunuma Unumidae											■	■	■						N	9	11
Veghia Poulpidae											■	■	■						N	9	11
Sanfilippoella Sanfilippoellidae											■	■	■						N	9	11
Trialatus Tetraspinocyrtiidae											■	■	■						N	9	11
Praenanina Hexapylomellidae											■	■	■						S	9	11
Bulbocyrtium Bulbocyrtiidae											■	■	■	■					N	9	12
Capnuchosphaera Capnuchosphaerinae											■	■	■	■					S	9	12

Fig. 3. *Continued.*

(k)



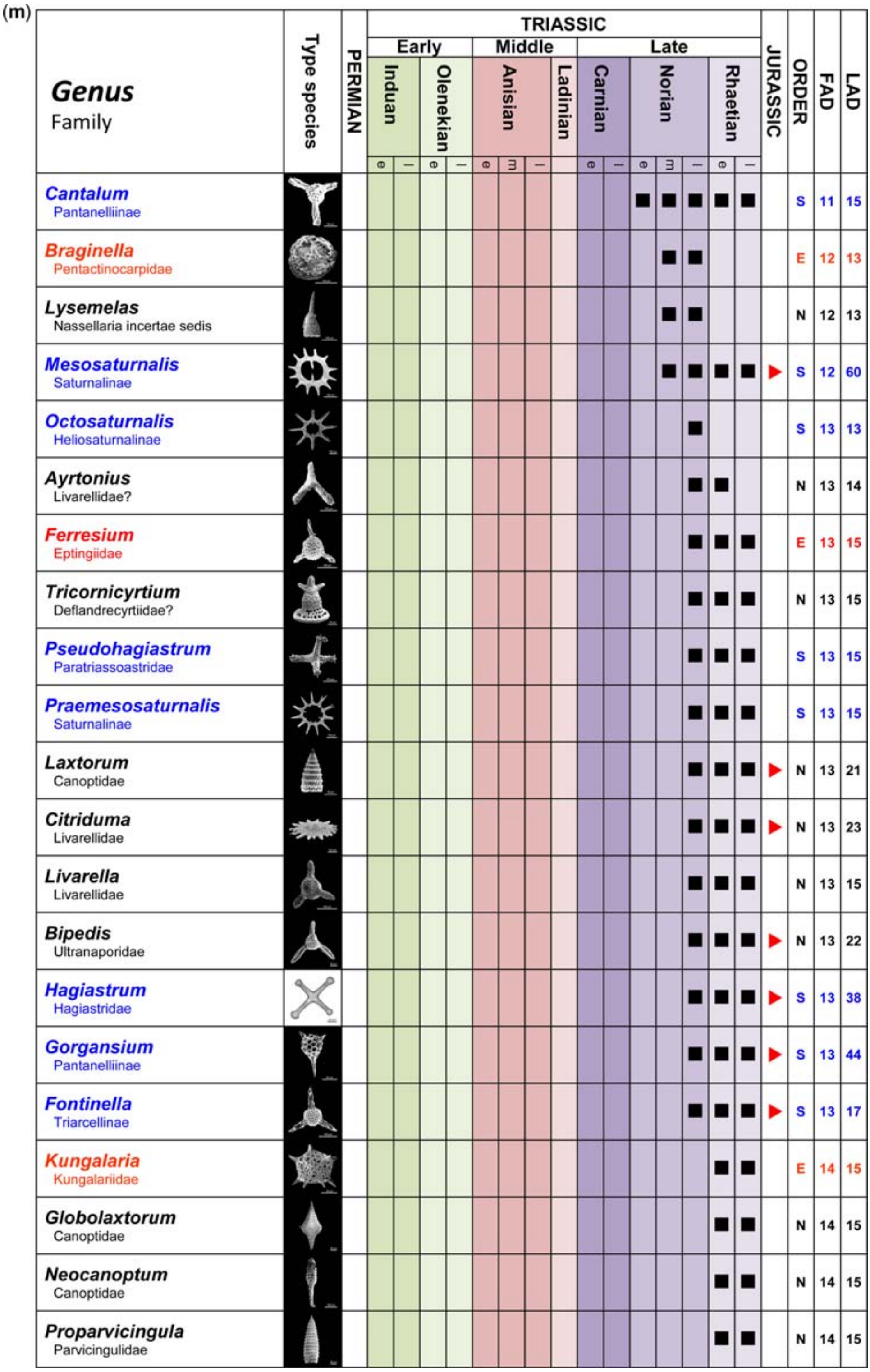
Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Sarla Triarcellinae											■	■	■	■					S	9	12
Annulopoulpus Poulpidae											■	■	■	■	■				N	9	13
Kahlerosphaera Triarcellinae											■	■	■	■	■	■			S	9	14
Quadrisaturnalis Austrisaturnalinae											■	■	■	■	■	■	■		E	9	15
Triassocrucella Hagiastridae											■	■	■	■	■	■	■		S	9	15
Icrioma Hexaporobrachiidae?											■	■	■	■	■	■	■		S	9	15
Natraglia Relindellidae											■	■	■	■	■	■	■		S	9	15
Paratriassoastrum Paratriassoastridae											■	■	■	■	■	■	■		S	9	15
Empirea Quinquecapsulariidae											■	■	■	■	■	■	■	▶	E	9	39
Haeckelicyrtium Deflandrecyrtiidae?											■	■	■	■	■	■	■	▶	N	9	22
Crucella Hagiastridae											■	■	■	■	■	■	■	▶	S	9	64
Pseudoheliodiscus Heliosaturnalinae											■	■	■	■	■	■	■	▶	S	9	29
Palaeosaturnalis Heliosaturnalinae											■	■	■	■	■	■	■	▶	S	9	22
Stampfliella Sanfilippoellidae												■							S	10	10
Justium Capnodocinae												■							S	10	10
Xenorum Eptingiidae												■	■						E	10	11
Papiliocampe Monicastericidae?												■	■						N	10	11
Spinopoulpus Poulpidae												■	■						N	10	11
Kozuricyrtium Pseudodictyomitridae												■	■						N	10	11
Mostlericyrtium Xiphothecaellidae												■	■						N	10	11
Senelella Xiphothecaellidae												■	■						N	10	11

Fig. 3. *Continued.*

(l)

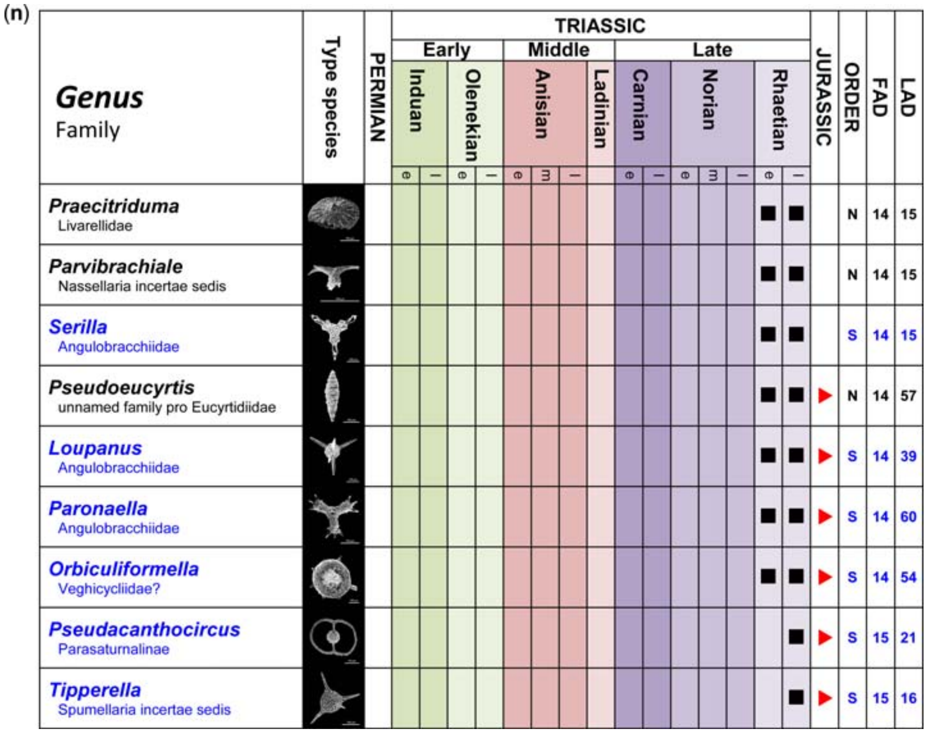
Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Dicapnuchosphaera Capnuchosphaerinae												■	■						S	10	11
Monocapnuchosphaera Capnuchosphaerinae												■	■						S	10	11
Nodocapnuchosphaera Capnuchosphaerinae												■	■						S	10	11
Xipha Nakasekoellidae												■	■	■					N	10	12
Blechschmidtia Heliosaturnalinae												■	■	■					S	10	12
Capnodoce Capnodocinae												■	■	■					S	10	12
Archaeoacanthocircus Heliosaturnalinae												■	■	■					S	10	12
Hetalum Deflandrecyrtiidae?												■	■	■	■				N	10	13
Japonocampe Pseudodictyomitridae												■	■	■	■				N	10	13
Betraccium Pantanelliinae												■	■	■	■	■	■		S	10	15
Spinosicapsa Favosyringiinae												■	■	■	■	■	■	▶	N	10	49
Pantanellium Pantanelliinae												■	■	■	■	■	■	▶	S	10	50
Caphtorocyrtium Planispinocyrtiidae													■						N	11	11
Triarcella Triarcellinae													■						S	11	11
Ellisus Eptingiidae													■	■					E	11	12
Tauridastrum Eptingiidae													■	■					E	11	12
Catoma Nodotetrasphaerinae													■	■					E	11	12
Pachus Pseudodictyomitridae													■	■					N	11	12
Loffa Capnodocinae													■	■					S	11	12
Renzium Capnodocinae													■	■					S	11	12
Triadosphaera Central capsules													■	■	■				S?	11	13

Fig. 3. *Continued.*



Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Cantalum Pantanelliinae													■	■	■	■	■		S	11	15
Braginella Pentactinocarpidae														■	■				E	12	13
Lysemelas Nassellaria incertae sedis														■	■				N	12	13
Mesosaturnalis Saturnalinae														■	■	■	■	▶	S	12	60
Octosaturnalis Heliosaturnalinae															■				S	13	13
Ayrtonius Livarellidae?															■	■			N	13	14
Ferresium Eptingiidae															■	■	■		E	13	15
Tricornicyrtium Deflandrecyrtiidae?															■	■	■		N	13	15
Pseudohagiastrum Paratriassoastridae															■	■	■		S	13	15
Praemesosaturnalis Saturnalinae															■	■	■		S	13	15
Laxtorum Canoptidae															■	■	■	▶	N	13	21
Citriduma Livarellidae															■	■	■	▶	N	13	23
Livarella Livarellidae															■	■	■		N	13	15
Bipedis Ultranaporidae															■	■	■	▶	N	13	22
Hagiastrum Hagiastridae															■	■	■	▶	S	13	38
Gorgansium Pantanelliinae															■	■	■	▶	S	13	44
Fontinella Triarcellinae															■	■	■	▶	S	13	17
Kungalaria Kungalariidae																■	■		E	14	15
Globolaxtorum Canoptidae																■	■		N	14	15
Neocanoptum Canoptidae																■	■		N	14	15
Proparvicingula Parvicingulidae																■	■		N	14	15

Fig. 3. *Continued.*



Genus Family	Type species	PERMIAN	TRIASSIC															JURASSIC	ORDER	FAD	LAD
			Early				Middle				Late										
			Induan		Olenekian		Anisian			Ladinian	Carnian		Norian			Rhaetian					
			e	l	e	l	e	m	l		e	l	e	m	l	e	l				
Praecitriduma Livarellidae																■	■		N	14	15
Parvibrachiale Nassellaria incertae sedis																■	■		N	14	15
Serilla Angulobracchiidae																■	■		S	14	15
Pseudoeucyrtis unnamed family pro Eucyrtidiidae																■	■	▶	N	14	57
Loupanus Angulobracchiidae																■	■	▶	S	14	39
Paronaella Angulobracchiidae																■	■	▶	S	14	60
Orbiculiformella Veghicycliidae?																■	■	▶	S	14	54
Pseudacanthocircus Parasaturnalinae																	■	▶	S	15	21
Tipperella Spumellaria incertae sedis																	■	▶	S	15	16

Fig. 3. *Continued.*

Early Anisian

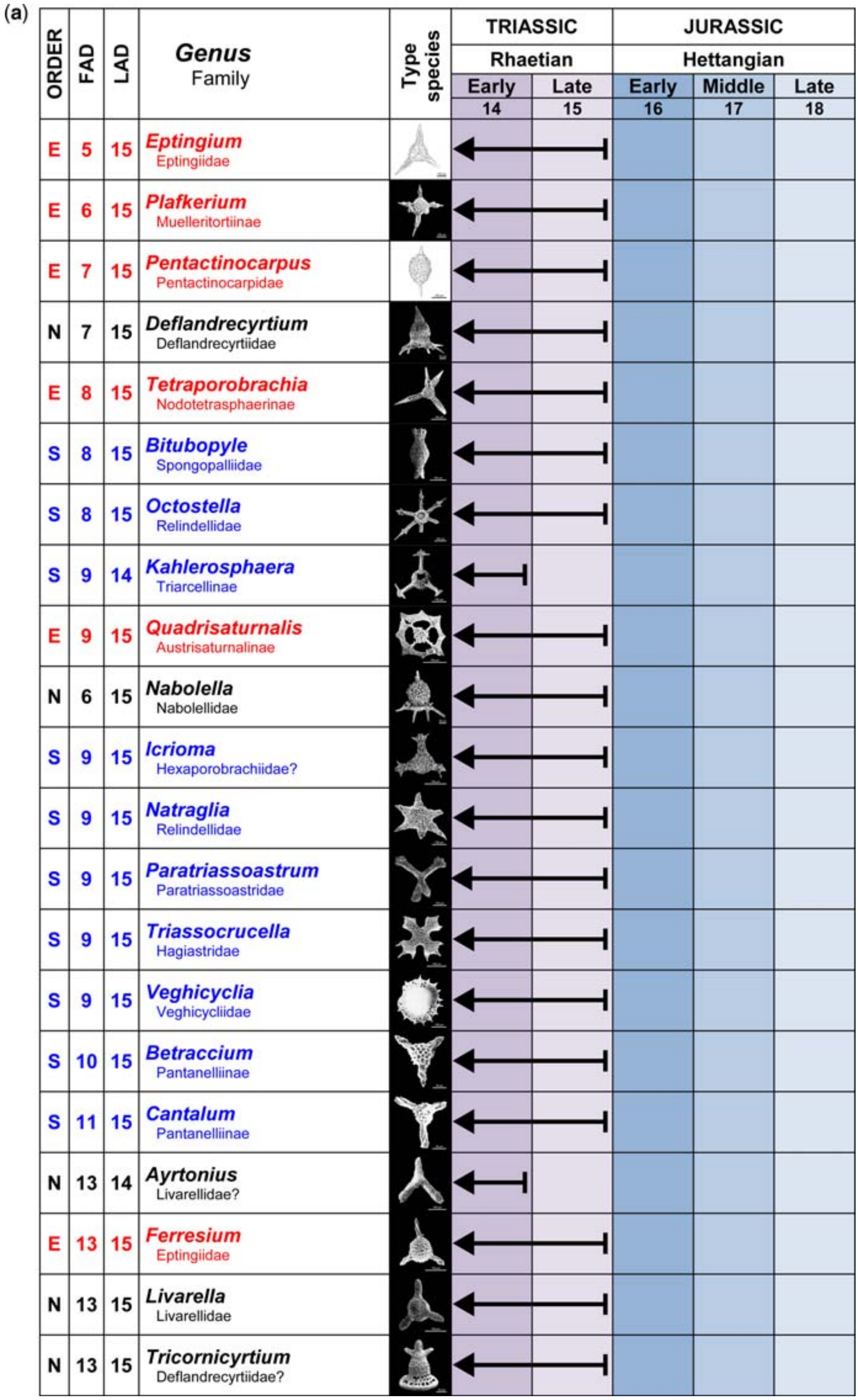
Originations during the Early Anisian are not as well documented as in the Early Triassic, but it is likely that the first appearance of advanced forms of Eptingiidae (*Eptingium* and *Cryptostephanidium*) took place at this time, as well as the origin of two of the most diverse Triassic families of multicyrtid nassellarians: the Planispinocyrtiidae (*Planispinocyrtis*) and Ruesticyrtiidae (*Triassocampe*).

Middle Anisian

The Middle Anisian (Pelsonian and Illyrian) is marked by a huge diversification, especially among nassellarians. It records the first occurrence of many mono- and dicyrtid genera of the families Tripedurnulidae (*Tripedocassis*, *Baratuna* and *Tripedurnula*), Poulpidae (*Triassobipedis*, *Eonapora* and *Neopylentonema*), and the origination of the families Nabolellidae (*Fueloepicyrtis*), Ultranaporidae (*Muellericyrtium*, *Hinedorcus* and *Silicarmiger*) and Spongosilicarmigeridae (*Spongosilicarmiger* and *Nofrema*). The multicyrtids also experienced a large diversification, and new families such as the Tetraspinocyrtidae (*Tetraspinocyrtis*), Monicastericidae (*Monicasterix*) and Bulbocyrtiidae appeared for the first time. Several new generic occurrences include the Ruesticyrtidae (*Paratriassocampe*, *Yeharaia*, *Pararuesticyrtium* and *Annulotriassocampe*) and Planispinocyrtiidae (*Spinotriassocampe* and *Triassocyrtium*).

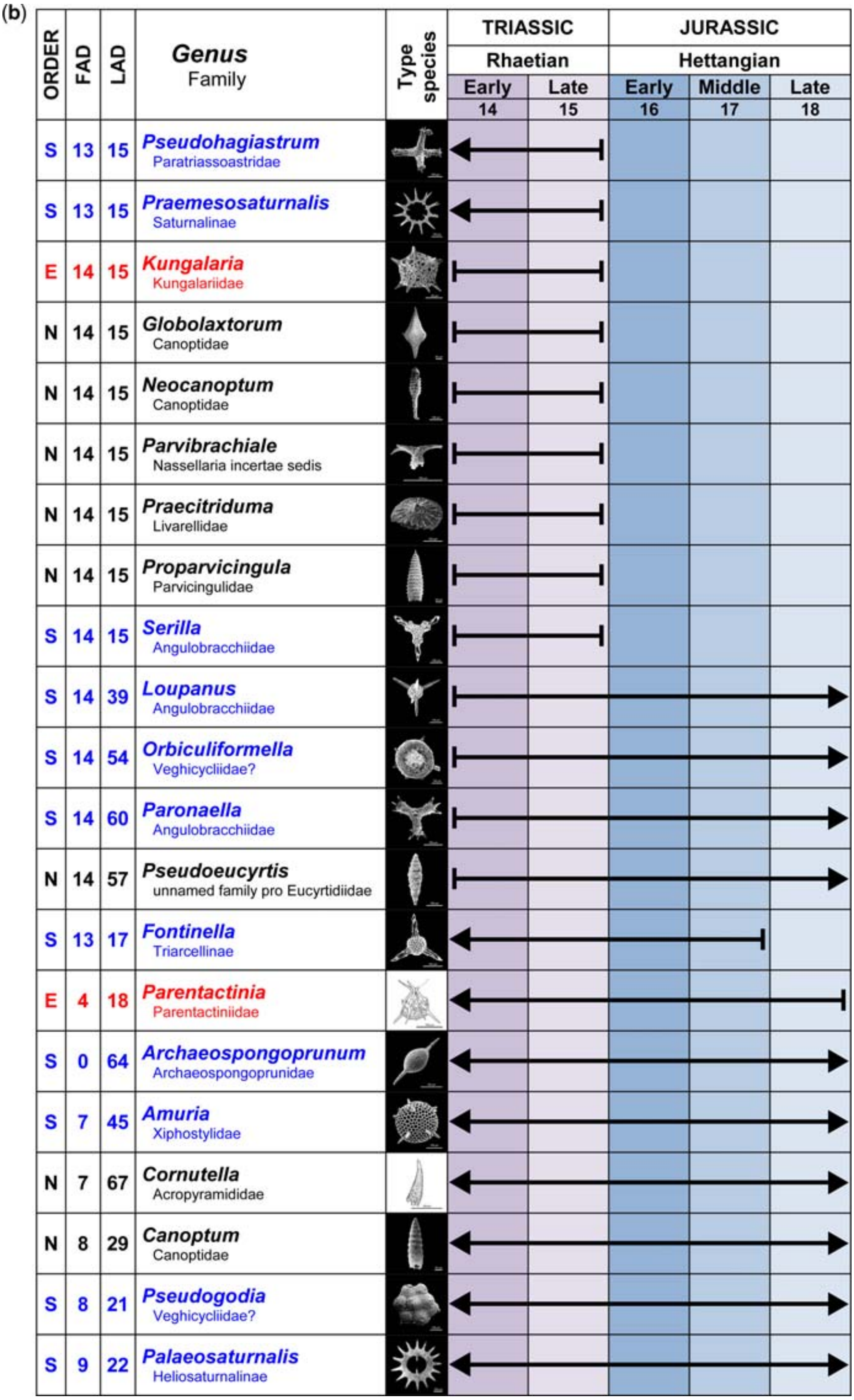
The Middle Anisian was also a period of high diversification in Entactinaria. New families appearing at this time are the Pentactinocarpidae (*Pentactinocapsa* and *Pentactinorbis*) and Heptacladidae (*Pseudosepsagon*, *Heptacladus*, *Parentactinosphaera*, and other undescribed genera) together with the mass-occurrence of the subfamily Hindeosphaerinae (*Parasepsagon*, *Pseudostylosphaera*, *Sepsagon* and *Hindeosphaera*). Spumellarians start to be frequent in the middle Anisian, and while important occurrences are rare, an interesting modification is the initial development of twisted spines in a simple spongy form (*Monospongella*) belonging to the Sponguracea, a superfamily in which this characteristic is extremely common. The Pyloniacea, one of the most important spumellarian groups in both Mesozoic and Cenozoic, appeared during this period; the oldest representative is the genus *Patrulius*.

A word of caution is needed, however, when interpreting the outstanding diversification during the Middle Anisian as this could be an artifact of



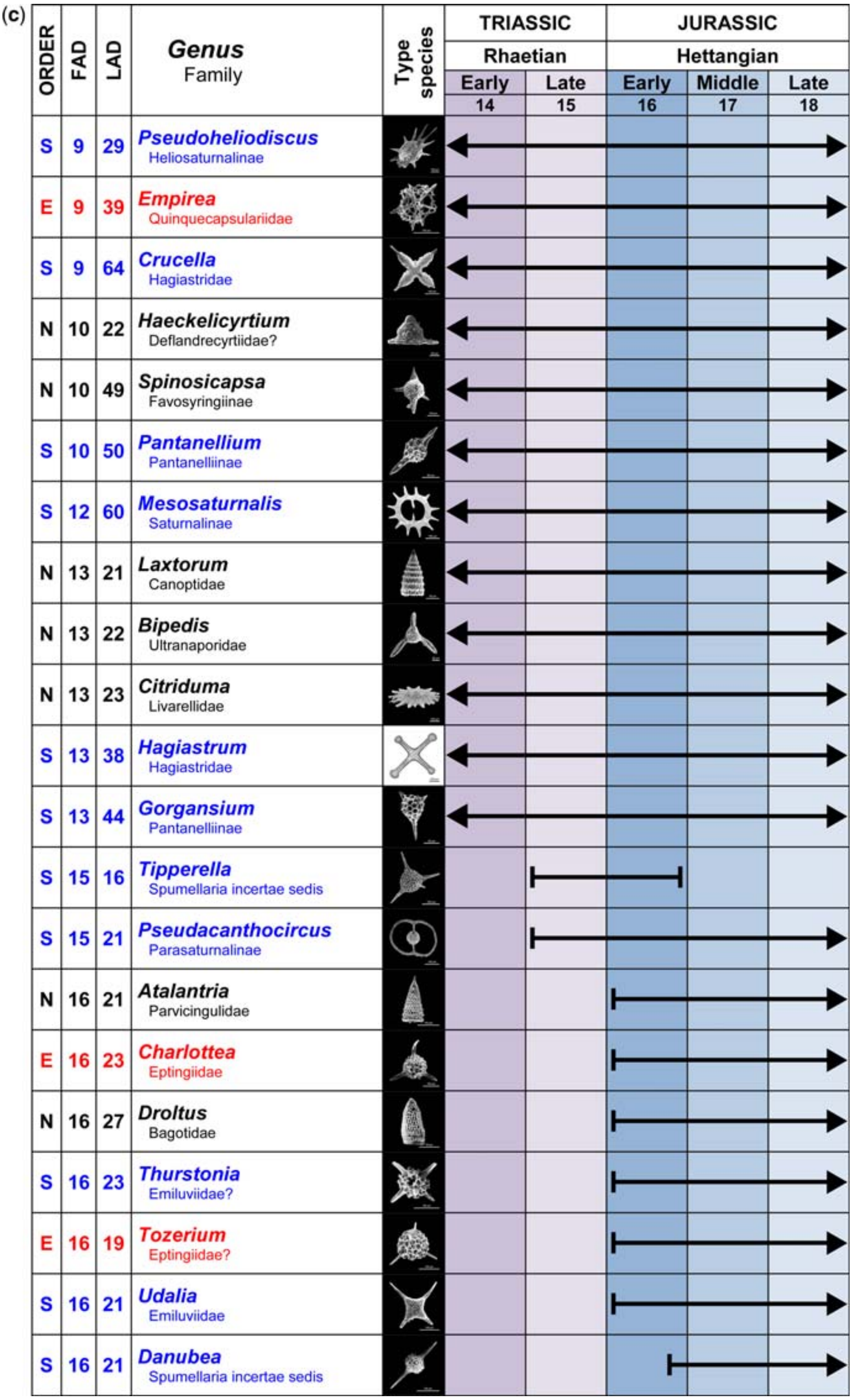
ORDER	FAD	LAD	*Genus* Family
E	5	15	***Eptingium*** Eptingiidae
E	6	15	***Plafkerium*** Muelleritortiinae
E	7	15	***Pentactinocarpus*** Pentactinocarpidae
N	7	15	***Deflandrecyrtium*** Deflandrecyrtiidae
E	8	15	***Tetraporobrachia*** Nodotetrasphaerinae
S	8	15	***Bitubopyle*** Spongopalliidae
S	8	15	***Octostella*** Relindellidae
S	9	14	***Kahlerosphaera*** Triarcellinae
E	9	15	***Quadrisaturnalis*** Austrisaturnalinae
N	6	15	***Nabolella*** Nabolellidae
S	9	15	***Icrioma*** Hexaporobrachiidae?
S	9	15	***Natraglia*** Relindellidae
S	9	15	***Paratriassoastrum*** Paratriassoastridae
S	9	15	***Triassocrucella*** Hagiastridae
S	9	15	***Veghicyclia*** Veghicycliidae
S	10	15	***Betraccium*** Pantanelliinae
S	11	15	***Cantalum*** Pantanelliinae
N	13	14	***Ayrtonius*** Livarellidae?
E	13	15	***Ferresium*** Eptingiidae
N	13	15	***Livarella*** Livarellidae
N	13	15	***Tricornicyrtium*** Deflandrecyrtiidae?

Fig. 4. Faunal spectra at the Triassic–Jurassic boundary. The FAD and LAD numbers refer to stage and substage numbering used in O'Dogherty *et al.* (2009*a, b*). Same letter key as Figure 3.



ORDER	FAD	LAD	Genus Family
S	13	15	*Pseudohagiastrum* Paratriassoastridae
S	13	15	*Praemesosaturnalis* Saturnalinae
E	14	15	*Kungalaria* Kungalariidae
N	14	15	*Globolaxtorum* Canoptidae
N	14	15	*Neocanoptum* Canoptidae
N	14	15	*Parvibrachiale* Nassellaria incertae sedis
N	14	15	*Praecitriduma* Livarellidae
N	14	15	*Proparvicingula* Parvicingulidae
S	14	15	*Serilla* Angulobracchiidae
S	14	39	*Loupanus* Angulobracchiidae
S	14	54	*Orbiculiformella* Veghicycliidae?
S	14	60	*Paronaella* Angulobracchiidae
N	14	57	*Pseudoeucyrtis* unnamed family pro Eucyrtidiidae
S	13	17	*Fontinella* Triarcellinae
E	4	18	*Parentactinia* Parentactiniidae
S	0	64	*Archaeospongoprunum* Archaeospongoprunidae
S	7	45	*Amuria* Xiphostylidae
N	7	67	*Cornutella* Acropyramididae
N	8	29	*Canoptum* Canoptidae
S	8	21	*Pseudogodia* Veghicycliidae?
S	9	22	*Palaeosaturnalis* Heliosaturnalinae

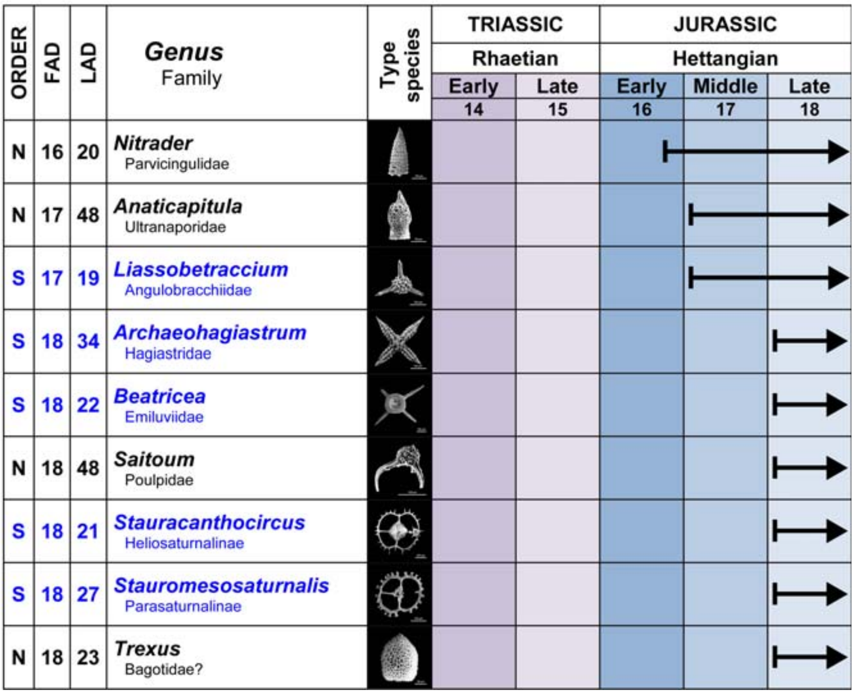
Fig. 4. *Continued.*



ORDER	FAD	LAD	*Genus* Family
S	9	29	*Pseudoheliodiscus* Heliosaturnalinae
E	9	39	*Empirea* Quinquecapsulariidae
S	9	64	*Crucella* Hagiastridae
N	10	22	*Haeckelicyrtium* Deflandrecyrtiidae?
N	10	49	*Spinosicapsa* Favosyringiinae
S	10	50	*Pantanellium* Pantanelliinae
S	12	60	*Mesosaturnalis* Saturnalinae
N	13	21	*Laxtorum* Canoptidae
N	13	22	*Bipedis* Ultranaporidae
N	13	23	*Citriduma* Livarellidae
S	13	38	*Hagiastrum* Hagiastridae
S	13	44	*Gorgansium* Pantanelliinae
S	15	16	*Tipperella* Spumellaria incertae sedis
S	15	21	*Pseudacanthocircus* Parasaturnalinae
N	16	21	*Atalantria* Parvicingulidae
E	16	23	*Charlottea* Eptingiidae
N	16	27	*Droltus* Bagotidae
S	16	23	*Thurstonia* Emiluviidae?
E	16	19	*Tozerium* Eptingiidae?
S	16	21	*Udalia* Emiluviidae
S	16	21	*Danubea* Spumellaria incertae sedis

Fig. 4. *Continued.*

(d)



ORDER	FAD	LAD	Genus Family
N	16	20	***Nitrader*** Parvicingulidae
N	17	48	***Anaticapitula*** Ultranaporidae
S	17	19	***Liassobetraccium*** Angulobracchiidae
S	18	34	***Archaeohagiastrum*** Hagiastridae
S	18	22	***Beatricea*** Emiluviidae
N	18	48	***Saitoum*** Poulpidae
S	18	21	***Stauracanthocircus*** Heliosaturnalinae
S	18	27	***Stauromesosaturnalis*** Parasaturnalinae
N	18	23	***Trexus*** Bagotidae?

Fig. 4. *Continued.*

preservation. Extremely well-preserved Triassic faunas first appear in this interval, for example, the Pelsonian assemblage from Cristian in Romania (Dumitrica 1982*c*, 1991 etc.) and the Illyrian assemblage from Felsöörs in Hungary (Kozur & Mostler 1994). The first occurrences of rare and delicate forms (e.g. *Fueloepicyrtis*, *Tripedocassis*, *Tripedurnula*, *Pentactinocapsa*, *Patrulius*) may also be related to better preservation. The number of resistant genera that newly appear is, nevertheless, extremely high, which indicates that the diversification rate in the middle Anisian was indeed the highest during the Triassic.

Late Anisian

The early late Anisian (starting with the *Reitziites reitzi* Ammonoid Zone) is easily recognized by the occurrence and diversification of the genus *Oertlispongus*; nassellarians reach their maximum diversification during this period. The late Anisian is characterized by the occurrence of the typical scalariform multicyrtid genus *Ladinocampe* and the first nassellarians bearing a skirt-type distal segment (Deflandrecyrtiidae: *Deflandrecyrtium* and *Dreyericyrtium*). The typical dicyrtid *Foremanellina* and the scalariform *Annulobulbocyrtium*, genera characterized by a very large and rounded cephalis, also appear at this time.

Ladinian

The occurrence of heavily ornamented (foliaceous) Oertlispongidae (*Pterospongus*, *Steigerispongus*, *Scutispongus* and *Spongoserrula*) is one of the most important events during the Ladinian. The multicyrtid families Pseudodictyomitridae (*Triassocingula* and *Corum*) and Canoptidae (*Canoptum* and *Multimonilis*) make their first occurrence also. This interval further records an important bloom of Entactinaria bearing strong, twisted spines (*Tritortis* and *Muelleritortis*) and advanced Austrisaturnalinae (*Ornatisaturnalis*, *Hungarosaturnalis*, *Praeheliostaurus*).

Early Carnian

Major changes in the composition of Triassic radiolarian assemblages occurred during the early Carnian (note that a twofold subdivision is used herein for the Carnian, because Cordevolian is considered to be part of the Julian) and a huge turnover, both at the generic and family level (De Wever *et al.* 2006), took place. Generic diversity reaches its maximum extent, especially among spumellarians, and with it came the first blooming of spumellarians bearing twisted spines (*Sarla*, *Spongotortilispinus*), hollow spines (*Capnuchosphaera*), branched spines (*Kahlerosphaera*) and the origin of a particularly common group during the Mesozoic, the true Saturnalidae. The latter are represented by three early branches: the Archaeoacanthocircidae (*Huglusphaera*), Heliosaturnalinae (*Pseudoheliodiscus*) and Italosaturnalinae (*Annulosaturnalis*). However, five genera of the Oertlispongidae went dramatically extinct within this interval. This is remarkable in that the Oertlispongidae are considered the stock of all Triassic Saturnalidae (Kozur & Mostler 1990; Dumitrica & Hungerbühler 2007). The early Carnian also witnessed new morphological organizations within the arm-bearing Pyloniacea, with the appearance of the first genus having four arms, for example, *Triassocrucella*, which can be considered the oldest Hagiastridae. *Hexaporobrachia*, an easily recognized form with six latticed tubular arms also occurs in this interval. In nassellarians, the genus *Praeprotunuma* first appears, as well as the genus *Trialatus*, the last representative of the Tetraspinocyrtiidae. In the Entactinaria, the most interesting innovation is the occurrence of the Spongosaturnaloididae (*Spongosaturnaloides* and *Ploechingerella*), a group very close to the family Eptingiidae that possess a simple or multiple saturnalid type ring. At this time several genera of the Multiarcusellidae (*Austrisaturnalis, Quadrisaturnalis* and *Hungarosaturnalis*) develop a saturnalid-like test with the ring resulting from the junction of cortical arches.

Late Carnian

The Pantanelliidae first appeared during this interval. The genus *Pantanellium* is the oldest representative and represents the main stock from which all the other Mesozoic pantanelliids are derived. The interval also records the first appearance of pantanelliids bearing strongly twisted-spines (*Betraccium*), but these occur only in low latitudes. An interesting form in this group is the genus *Capnodoce*, the first pantanelliid with hollow spines. The Capnuchosphaerinae become very diverse with *Dicapnuchosphaera*, *Monocapnuchosphaera*, and *Nodocapnuchosphaera* appearing at the end of the Carnian. At the early–late Carnian transition the genus *Archaeoacanthocircus* appeared, an easily recognizable primitive saturnalid with a flat and very broad ring bearing four spines. The genus *Xipha* (= *Nakasekoellus*) and *Mostlericyrtium* are two easily recognizable nassellarians appearing at this time also. Only one Entactinaria, the genus *Xenorum*, originated within this interval; it is the first robust Eptingiidae bearing twisted spines.

Early Norian

The Early Norian is marked by severe extinctions affecting many primitive (scalariform) multicyrtid nassellarians (*Triassocampe*, *Pararuesticyrtium*, *Papiliocampe*) and all representatives of the Xiphothecaellidae. *Caphtorocyrtium* is characteristic of the early Norian and is the only known Planispinocyrtiidae to possess a distal skirt-like chamber (quite common in Ruesticyrtiidae) and probably the last multicyrtid genus displaying this morphology, which began in the middle Anisian. Among spumellarians, it is interesting to note the occurrence of the genus *Triarcella*, which develops a saturnalid-like ring by connecting the three carinated main spines.

Middle Norian

This interval records a drastic diversity drop. It is marked by severe extinctions affecting many primitive multicyrtids (Ruesticyrtiidae, Bulbocyrtiidae), and the last representatives of the Capnodocinae and Capnuchosphaeridae families went extinct at this time. Only three new genera appeared, the *incertae sedis* multicyrtid *Lysemelas*, the new Pentactinocarpidae with cortical shell *Braginella* and the new Saturnalinae *Mesosaturnalis.*

Late Norian

New multicyrtid nassellarians displaying typical Jurassic patterns are common in the late Norian. These are represented by two genera of the family Canoptidae (*Canoptum* and *Laxtorum*). The latter first appeared in the late Norian, whereas the former arose in the Ladinian but did not become abundant and diverse until the late Norian; both genera survived the end-Triassic extinction. Following the Carnian, no new families appeared for the remainder of the Triassic with the exception of the Livarellidae, which produced several dicyrtid representatives (*Ayrtonius*, *Citriduma* and *Livarella*). Aside from these, dicyrtids are rarely recorded in the Late Triassic. Another interesting form is the genus *Bipedis*, belonging to the common Jurassic Ultranaporidae. This interval saw the rapid diversification and acme of pantanelliids bearing strongly twisted-spines (*Betraccium*) and of saturnalids with a 3- or 4-bladed ring, for example, the genus *Octosaturnalis*. In general, the late Norian is marked mainly by the appearance of new forms of nassellarians and spumellarians while the Entactinaria are represented only by the appearance of *Ferresium*. This will be a common feature during the Rhaetian where the assemblages are almost entirely dominated by nassellarians and spumellarians.

Early Rhaetian

The base of the Rhaetian is marked by the appearance of new representatives of the Canoptidae

(*Globolaxtorum*, *Neocanoptum* and *Proparvicingula*). The latter genus seems to be the direct ancestor of the Jurassic family of Parvicingulidae because it displays an offset arrangement of pore frames quite close to the family. In spumellarians, a remarkable evolutionary adaptation is noted whereby the genus *Serilla* evolves from *Ferresium* by acquiring concave sides and a strongly triangular test (Carter & Guex 1999). *Orbiculiformella*, a common genus in the Jurassic, also appears at this level.

Late Rhaetian

The end of the Triassic is marked by the extinction of many families (see below). Only two spumellarian genera originate during this interval (*Pseudacanthocircus* and *Tipperella*) and both cross the T/J boundary.

Radiolarians, mass-extinctions and problems at Triassic boundaries

Problems exist with radiolarian faunas at both the base and top of the Triassic. Takemura *et al.* (2007*a*, *b*) have only recently discriminated end-Permian from earliest Triassic radiolarian assemblages, whereas at the top of the Triassic System, few radiolarian zonations cross the Triassic–Jurassic boundary (e.g. Yao *et al.* 1980*a*, *b*; Yao 1982; Yoshida 1986; Sugiyama 1997). Since both boundaries are characterized by severe extinctions related to major ecological perturbations, a thorough evaluation of boundary events is far beyond the scope of this paper. This problem has partly been addressed in recent studies dealing with radiolarian taxonomy as well as short-term changes in diversity and relative abundances (De Wever *et al.* 2006; Carter 2007). The changes in taxonomic structure have been compared to fluctuations in geochemical composition of sediments and to faunal turnovers in other fossil groups (see De Wever *et al.* 2006 for a recent review).

The end of Palaeozoic groups and the collapse of radiolarian diversity

The Permian–Triassic boundary records the greatest extinction known in the fossil record. Radiolarians were severely damaged at all taxonomic levels, and undoubtedly the extinction must have played an important role in the evolutionary history of this group of protists during the Triassic. According to the data reviewed by De Wever *et al.* (2001, 2003, 2006), no new orders of radiolarians appeared after the Permian–Triassic crisis. The only exception might be the Nassellaria, if we consider that Mesozoic nassellarians are not direct descendants of Paleozoic representatives, all of which disappeared by the end of the Carboniferous.

At the family level, the crisis seems to have produced little effect because of the 18 families that existed during the Permian (De Wever *et al.* 2006), 13 cross the critical interval. This is rather different at the generic level, where the end-Permian extinction caused a decrease of more than 50% (Kuwahara & Yao 2001; Umeda 2002; Yao & Kuwahara 1997), although real diversity varies from one author to another. Nevertheless, the decline in generic diversity unquestionably starts in the late Lopingian, but the scope of this faunal turnover is still precarious for two main reasons: (1) the scarcity of papers covering the Permian–Triassic interval (see De Wever *et al.* 2006); and (2) the lack of a taxonomic revision of Late Paleozoic genera.

The scarcity of data is tightly bound to the abrupt disappearance of radiolarian cherts from deep-marine sections of South China, Japan, and Western Canada in the Late Permian (Isozaki 1997). Radiolarians reappeared only in the Spathian following a gap of 7–8 Ma, but the mechanisms responsible for the cessation of siliceous sedimentation are not entirely understood. Logically, the abrupt change in radiolarians is amplified by this lithological turnover, and hence the current information on Early Triassic radiolarians should be considered quite incomplete. The development of a satisfactory common taxonomic system for the Late Permian–Early Triassic is also hampered by a ‘frontier effect’ that occurs equally at major boundaries of the Mesozoic. In other words, the taxonomic criteria used for classification change over the Eras, resulting in a somewhat artificial taxonomy. This evidently results because the groups of authors working on Late Palaeozoic and Early Triassic radiolarians are quite distinct in most cases. In this sense, De Wever *et al.* (2001) stressed the importance of homogenizing the taxonomic criteria used for the Palaeozoic, Mesozoic and Cenozoic, in order to update our biostratigraphic knowledge.

The long Early Triassic recovery

True recovery following the end-Permian extinction does not begin until the middle Anisian when new genera bloom and assemblages become highly diverse. The Middle Triassic was undoubtedly the main epoch for radiolarian radiation. More than a third of the total number of radiolarian families recognized from the Cambrian to Present originated during this important period of plankton radiation (De Wever *et al.* 2006). Similarly, generic diversity starts to increase progressively in the early middle Anisian, and attains a maximum in the early Carnian with the occurrence of more than 135 genera (Fig. 3). However, recovery following the aftermath of the end-Permian extinction is marked by rare occurrences, poor preservation and a paucity of new forms (Sashida 1983, 1991; Sugiyama 1992, 1997; Suzuki *et al.* 2002; Hori *et al.* 2003; Kamata 2007; Kamata *et al.* 2007; Takemura *et al.* 2007*a*, *b*). These faunas mostly contain species of entactinarians (*Entactinia*, *Hegleria*, *Parentactinia*, *Pseudostylosphaera*, *Tiborella*, *Glomeropyle*), some sparse mono- and dicyrtid nassellarians (*Archaeosemantis*, *Hozmadia*, *Tripedocorbis*, *Triassospongocyrtis*), spicular nassellarians (*Archaeosemantis, Verticiplagia*) and rare spumellarians (*Thaisphaera, Pegoxystris*).

Recently, some representatives of Middle Triassic spumellarians belonging to the families Intermediellidae (*Tetrapaurinella*, *Paurinella*), Gomberellidae (*Tamonella*) and Oertlispongidae (*Pararchaeospongoprunum*) have been reported from the uppermost Permian of China (Feng *et al.* 2006); however, they have not been found yet in Lower Triassic material. Kozur *et al.* (1996) and Kozur (1998, 2003*a*) have suggested that the long phase of recovery may be due to immigration from southern high latitude cold waters (less affected than those of high northern and low latitudes) rather than from tropical waters, which would be a faster process. This process would be slow (*c.* 5 Ma; late Induan to early Anisian) because it would require first the adaptation of some elements of the cold water fauna to warm tropical conditions. But, as stressed by De Wever *et al.* (2006), real data neither support nor contradict this interpretation, they are just insufficient at the present time.

The Anisian–Ladinian boundary

The GSSP for the Ladinian Stage has only recently been established (Brack *et al.* 2005). The decision on the boundary ammonoid zone thus postdates all hitherto published radiolarian zonations for the Middle Triassic (Fig. 1). This GSSP was discussed for several decades, and two options were strongly debated. The question was whether to define the base of the Ladinian at the base of the *Reitziites reitzi* Ammonoid Zone or at the base of the *Eoprotrachyceras curionii* Ammonoid Zone. The FAD of *Eoprotrachyceras curionii* (Mojsisovics) was finally approved, and the GSSP was ratified by the IUGS Executive Committee in Spring 2005.

Based on the radiolarian record, Kozur vigorously advocated that the best level for the base of the Ladinian would be the FAD of *Reitziites reitzi* (Böckh) (Kozur & Mostler 1994; Kozur 1995, 2003*a*, *b*). He pointed out that radiation of radiolarian taxa was explosive from the *Paraceratites trinodosus* to the *Reitziites reitzii* zones and consequently, that the resolution of radiolarian biochronology in this interval is as high as that of the ammonites. In contrast to this, no distinct change in the radiolarian fauna is recorded near the base of the *E. curionii* Zone.

Other radolarian researchers mainly followed Kozur's arguments. They agreed that the base of the *Spongosilicarmiger italicus* Radiolarian Zone (corresponding to the *Reiziites reitzi* Ammonoid Zone) is well marked by a major radiolarian turnover. In addition, they favoured this boundary for practical reasons, that is, because the marker species are easy to find even in poorly preserved material. The lineage of Oertlispongidae, a family with a high biochronological value for the Ladinian, diversifies at this level, and the species below and above this boundary have dissolution-resistant spines, which are easy to determine and always common. Consensually, the *Reitziites reitzi* Ammonoid Zone was considered as the base of the Ladinian in radiolarian papers published until 2005 (e.g. Sashida *et al.* 1999; Dumitrica 1999; Feng & Liang 2003; Goričan *et al.* 2005).

The officially accepted GSSP at the base of the *Eoprotrachyceras curionii* Ammonoid Zone lies much higher than the base of the *R. reitzi* Zone and is of crucial importance to Middle Triassic radiolarian dating. First, one has to bear in mind that early Ladinian ages based on radiolarians in literature older than 2005 should be 'translated' to late Anisian. Second, the boundary should be displaced in existing radiolarian zonations. In Figure 1, where the historical review is presented, we retain the early Ladinian in the old sense of this term. In Figure 2 the new position of the Anisian–Ladinian boundary is emphasized. In the range chart of genera (Fig. 3) developed herein, we wanted to preserve the obvious faunistic changes at the base of the *R. reitzi* Zone. For this reason, the Anisian in the range chart consists of three intervals, but the Ladinian is not subdivided. The upper Anisian contains two radiolarian zones formerly attributed to the lower Ladinian; these are the *Spongosilicarmiger italicus* and *Ladinocampe multiperforata* zones. The Ladinian in the range chart basically is equivalent to the *Muelleritortis cochleata* Zone. We note that the base of the Ladinian as now defined is not distinct in the radiolarian fauna. The Anisian–Ladinian boundary is correlated to the upper part of the *Ladinocampe multiperforata* Zone, that is, to the upper part of the *Ladinocampe vicentinensis* Subzone (Kozur 2003*a*, *b*). Because the radiolarian zones do not allow an exact correlation with ammonoid zones at this level and because the stratotype at Bagolino in the Southern Alps (Brack *et al.* 2005) contains no radiolarians, the only usable solution remains to consider the top of the *Ladinocampe multiperforata* Zone as the top of the Anisian.

The Carnian–Norian boundary

The Carnian–Norian boundary (CNB) is one of four Triassic boundaries that are not yet defined. In North America, this boundary traditionally has approximated the base of the Kerri Zone, that is, the level between the Macrolobatus and Kerri zones (Silberling & Tozer 1968), whereas in Tethys the boundary is located between the Spinosus and Jandianus zones (Krystyn *et al.* 2002).

Currently there are no proposals for the Carnian–Norian boundary before the Triassic Subcommission for consideration, but two candidates and at least two levels are under discussion (M. J. Orchard, pers. comm. 2008):

1. The thick hemipelagic limestone succession at Pizzo Mondello, Sicily (Muttoni *et al.* 2001, 2004; Nicora *et al.* 2007) has neither a precise level nor a marker taxon proposed for definition and the magnetostratigraphic marker previously employed as a proxy apparently does not correspond with any significant fossil events. However, Nicora *et al.* (2007) consider the FAD of *Epigondolella quadrata* (= *E. abneptis*) as a possible marker. Most radiolarians illustrated from this section (Nicora *et al.* 2007) are clearly early Norian, with only a few taxa mentioned as Carnian, and depending on where the boundary is eventually placed, some of these could be early Norian also.
2. Orchard (2007*a*, *b*) proposed a section Black Bear Ridge, in the Williston Lake area in north-east British Columbia, for the Carnian–Norian boundary based on the excellent fossil succession. This section contains a continuous outcrop of Ludington and Pardonet formations deposited in a deep marine slope setting on the north-western margin of Pangea and also contains ammonoids (Tozer 1965) and abundant bivalves. A significant bivalve turnover (McRoberts 2007), and a dip in carbon isotopes (Williford *et al.* 2007) are both coincident with the appearance of *Metapolygnathus echinatus* (occurring in both North America and Tethys) and with the ascendance of typical *M. primitius*; this lies close to the base of the traditional Kerri Zone and is favoured as the datum for GSSP definition in Canada. Radiolarians are also expected to play a role in Carnian–Norian boundary studies at Black Bear Ridge as they have previously in the Charlotte Islands (Carter & Orchard 2000). Presently, only one late Carnian collection is known from the Black Bear Ridge area (Carter, pers. comm.), but collections from many localities in the Charlotte Islands provide insight to the boundary interval, as they are linked through *M. echinatus*, which occurs in both areas. A full multi-authored proposal for the section at Black Bear Ridge is expected in 2009.
3. Since the late 1970s, Kozur (1980, 2003*a*, *b*) has advocated the FAD of *Epigondolella quadrata* as a marker for the Carnian–Norian boundary. This taxon is common in Tethys and in the upper part of the Kerri Zone and upper *M. primitius* conodont zone (Orchard 1983) in North America. These ideas are presently cloaked in taxonomic uncertainty since the introduction of several new and transitional taxa and have not lead to a proposal.

Given the uncertainty regarding future definition of the Carnian–Norian boundary, it is difficult at this time to accurately determine radiolarian ranges surrounding this particular level.

Triassic–Jurassic boundary faunas

The Triassic–Jurassic boundary marks a significant palaeontological event in earth history as intense physical and chemical forces affected both terrestrial and marine faunas (Tanner *et al.* 2004). In the seas, conodonts and ceratite ammonoids disappeared almost completely with only a few known holdovers in the earliest Hettangian, bivalves gradually evolved across the boundary, pollen changed significantly (McElwain *et al.*1999) and radiolarians suffered a dramatic extinction that signalled a productivity collapse in the oceans (Ward *et al.* 2001).

Prior to 1989, knowledge of Rhaetian radiolarians was known only from scant reports in Japan (Yao 1982; Yao *et al.* 1980*a*, *b*; Kishida & Sugano 1982; Kishida & Hisada 1986; Yoshida 1986), China (Kojima & Mizutani 1987), Austria (Kozur & Mostler 1981; Kozur 1984), Oregon (Yeh 1989) and New Zealand (Spörli & Aita 1988; Spörli *et al.* 1989) while several collections of probable Hettangian age were known from the Queen Charlotte Islands (Pessagno & Blome 1980; Pessagno & Whalen 1982), east-central Oregon (Pessagno & Blome 1980) and a few taxa were illustrated from Japan (Hori 1990). The impetus for detailed Triassic–Jurassic boundary studies began in 1987 with the finding of long successions of Rhaetian and Hettangian radiolarians dated by co-occurring conodonts and/or ammonites at Kennecott Point and Kunga Island, Queen Charlotte Islands (Carter *et al.* 1989; Carter 1990; Tipper & Carter 1990; Tipper *et al.* 1994). Soon after, many species were described and zonation based on unitary associations led to the establishment of two radiolarian zones for the Rhaetian (Carter 1993) and seven zones for the Hettangian–Sinemurian (Carter *et al.* 1998).

Since that time, Rhaetian faunas have been found around the globe (see review in Carter 2007), and Hettangian faunas are known from the Northern Calcareous Alps (Kozur & Mostler 1990), Hungary (Kozur 1993; Pálfy & Dosztály 2000; Pálfy *et al.* 2007), Italy (Bertinelli *et al.* 2004), Japan (Hori 1992; Sugiyama 1997), Montenegro (Goričan 1994) and southern Turkey (Tekin 1999, 2002). However, earliest Hettangian faunas are still very rare and confirmed only to the Queen Charlotte Islands and Japan (Carter & Hori 2005; Longridge *et al.* 2007*a*, *b*), Montenegro (Goričan 1994) and Peru (Carter 1993). The following discussion of Triassic–Jurassic boundary faunas is based on collections from the Queen Charlotte Islands, as these are the most diverse and completely-documented fauna known and support postulation by Hallam & Wignall (1997) that the best evidence for catastrophic change at the end of the Triassic may come from microfossils.

Rhaetian radiolarian faunas and the end-Triassic extinction

Over 160 described or informal species are present in the diverse Rhaetian fauna of the Queen Charlotte Islands (Carter 1993). Approximately half disappear towards the end of the *Proparvicingula moniliformis* Zone (early Rhaetian), but the others together with newly arising species range upward into the *Globolaxtorum tozeri* Zone (late Rhaetian) and many continue into uppermost beds of the Rhaetian. Then, over the space of less than a metre, nine families, at least 27 genera (Fig. 4), and nearly all Rhaetian species disappeared (Longridge *et al.* 2007*a*, *b*). For radiolarian correlation with ammonite and condont faunas see also Longridge *et al.* (2007 *a*, *b*). A lesser scale pattern of extinctions together with the first appearance of Hettangian taxa (discussed below) has also been observed in Japan, providing evidence that the radiolarian crisis at the end of the Triassic was not local, but rather global in extent (Carter & Hori 2005).

The taxa most severely affected by the extinction were architecturally complex forms, for example, *Eptingium*, *Icrioma*, *Nabolella*, *Paratriassoastrum*, *Pentactinocarpus*, *Praecitriduma*, *Tetraporobrachia*, and short-ranging genera confined to the Rhaetian such as *Serilla*, *Kungalaria* and *Globolaxtorum*. It is note worthy that nearly all forms with highly twisted or spiralling spines disappeared. This morphological characteristic is exceptionally well displayed in Upper Triassic radiolarians, but is not found in Hettangian taxa whose peripheral spines are generally primitive and rod-like. Genera surviving the boundary are typically forms with conservative morphologies such as *Amuria*, *Archaeocenosphaera*, *Canoptum*, *Crucella*, *Orbiculiformella*, *Pantanellium* and *Paronaella*.

Guex (1993, 2001) has postulated that conditions of ecological stress may have contributed to simplification and/or reduced size in protists such as foraminiferans, silicoflagellates and radiolarians. The end-Triassic radiolarian fauna substantiates these ideas, as it is clear from perturbations in geochemical signatures (McRoberts *et al.* 2007; Pálfy *et al.* 2007) that ecological conditions were very unstable at that time. The latest Rhaetian fauna is rife with individuals that are sharply reduced in size and multicyrtid nassellarians having a reduced number of chambers (see also Carter & Guex 1999). This trend is further accentuated in the earliest Hettangian where the fauna is dominated by small-sized spumellarians and rare multicyrtid nassellarians with fewer chambers. This evidence supports O'Dogherty & Guex (2002), who suggested that spumellarians are more extinction-resistant than nassellarians and thus are more likely to dominate post-extinction faunas. Small spumellarians also dominate the recovery fauna following the end-Permian extinction (e.g. Kakuwa 1997, English abstract: p. 76). See also Matsuoka (2007), who assessed feeding mechanisms in living multi-segmented nassellarian radiolarians and determined that the diminishment of available prey may contribute to the rarity of these forms. Should these same feeding modes have existed in the Mesozoic, they too may have played an important role in contributing to the lack of nassellarians during times of ecological stress.

The early Hettangian radiolarian fauna

The low diversity earliest Hettangian fauna is composed of primitive indeterminate spumellarians and entactiniids, rare nassellarians and usually only a single species of a new and/or surviving genus. A few Rhaetian holdovers are present in the very lowest beds but these are always small, rare and disappear quickly. The persistence of these short-ranging holdovers may support ideas that the extinction was rapid, but not instantaneous. This trend is also seen in an exceptionally abundant and well preserved mixed fauna from Kennecott Point in the Queen Charlotte Islands (sample R2, section II in Longridge *et al.* 2007*b*) composed of *c.* 90% Hettangian species and <10% Rhaetian holdovers (Longridge *et al.* 2007*b*). This sample occurs well above Rhaetian faunas and below lowest Hettangian ones that lack Rhaetian holdovers.

Survival faunas have generally been described as producing low diversity, simple forms that are dominated by highly abundant geographically and environmentally widespread species and can also include blooms of opportunistic taxa that thrive only in difficult environmental conditions (Erwin 1998, 2001). The earliest Hettangian radiolarian fauna of the Queen Charlotte Islands is dominated by simple forms with spongy or irregularly latticed meshwork and long, rod-like rather than triradiate and/or twisted spines. Most spherical spumellarians and entactiniids lack definable organized structure, are extremely varied morphologically, and occur with floods of *Archaeocenosphaera laseekensis*, a spherical form with simple hexagonal pore-frames and no spines. *Pantanellium tanuense*, a probable opportunist, is also abundant in all but the very oldest samples. These two species suggest that oceanic productivity may have been restored sufficiently in the earliest Hettangian to allow vast numbers of these simple forms to proliferate. Nassellarians such as *Canoptum merum*, *Droltus hecatensis*, *Bipedis elizabethae* and indeterminate parahsuids are rare and very small. Over time the number of 'indeterminate spherical spumellarians' (possibly short-lived endemics) reduces as the fauna rebuilds. True recovery following the end-Triassic extinction does not begin until the middle–upper Hettangian when new genera appear and assemblages become more diverse.

Approximately 20 genera, most arising in the Carnian, Norian and Rhaetian, survived the end Triassic crisis, and at least six new genera first appear in the lower Hettangian together with other indeterminate forms. Most surviving genera are present in the Hettangian, but others, for example, *Citriduma* and *Gorgansium*, having sporadic distribution, do not reappear until the Pliensbachian; hence their absence in the Hettangian may not be that unusual. Genera barely surviving the extinction have been termed 'Rhaetian holdovers' (Longridge *et al.* 2007*b*) and include *Fontinella*, *Deflandrecyrtium*, *Livarella* and *Proparvicingula*. These genera are probably not true survivors because they are very rare, small in size, and all disappear completely by the middle Hettangian, at least in material from Queen Charlotte Islands. Other surviving genera are present in the Hettangian but disappear before the end of the Lower Jurassic. These include *Haeckelicyrtium, Laxtorum*, *Parentactinia* and *Tipperella*: the latter is abundant in the early Hettangian but gradually disappears as the fauna rebuilds; *Parentactinia* disappears at the end of the Hettangian, *Laxtorum* in the lower Pliensbachian; and *Haeckelicyrtium* is rare in the Hettangian and Sinemurian, common in the Pliensbachian, but unknown thereafter. Still other genera survived to have their major radiation in the Jurassic and Cretaceous, with the most well known being *Canoptum*, *Crucella*, *Orbiculiformella*, *Pantanellium* and *Paronaella*. Finally, the group least affected by events may be the saturnalids; *Mesosaturnalis*, *Palaeosaturnalis*, *Praehexasaturnalis*, *Pseudacanthocircus* and *Pseudoheliodiscus* all survived the end Triassic crisis, and a few species even crossed the boundary, for example, *Pseudacanthocircus troegeri* and *Mesosaturnalis acuminatus*.

Current status of the Triassic–Jurassic boundary

The system boundary between the Triassic–Jurassic has been difficult to define owing partly to sea level fall, which caused widespread gaps in sedimentation and facies breaks at the end of the Triassic (Hallam 1997; Hallam & Wignall 2000), and to the decreasing diversity and/or extinction in fossil groups at this time. Over the past 20 years four candidates where the boundary was present and could be recognized were proposed as Global Stratotype Section and Point (GSSP) for the T–J boundary, and this number was expanded to six in 2007. Ammonites have traditionally been the markers for Jurassic GSSPs, but owing to the rarity of ammonites in the boundary beds, carbon isotope anomalies and radiolarians were also proposed as potential markers. For radiolarians, the section on the southeast side of Kunga Island, Queen Charlotte Islands was proposed by Carter & Tipper (1999) and updated by Longridge *et al.* (2007*a*, *b*). There, the entire Rhaetian to middle/lower upper Hettangian sequence is exposed over a distance of *c.* 150 m with over 70 radiolarian collections documenting the faunal succession. Other proposed localities and their indicators were the New York Canyon area, Nevada [FAD *Psiloceras spelae* (Lucas *et al.* 2007*a*, *b*) and carbon isotopes (McRoberts *et al.* 2007)], St. Audries Bay, Somerset, UK and Larne, Northern Ireland [FAD *Psiloceris planorbis* (Simms & Jeram 2007; Warrington *et al.* 2008, respectively)], and Kuhjoch, Austria (FAD *P.* cf. *spelae*, von Hillebrandt *et al.* 2007).

The task of choosing the best candidate for GSSP was the mandate of the Triassic–Jurassic Boundary Task Group (TJBTG) of the International Subcommission on the Jurassic System (ISJS). In March–April 2008, the FAD of *Psiloceras spelae* was chosen as the marker in the Kuhjoch section, Tyrol, Austria. In June this decision was passed by the voting members of ISJS, and in August, the Ferguson Hill section in Nevada was approved as ASSP (Auxilliary Stratotype Section and Point). Ratification by the International Commission on Stratigraphy (ICS) will comprise the final step in this decision. In the words of G. Bloos, Secretary of the TJBTG, in his final summary to task group members, 'each section will remain an important stratigraphic landmark in the future'. Thus, Kunga Island will remain the standard for the radiolarian succession across the Triassic–Jurassic boundary.

Summary

Usefulness and limitations

During the past 30 years much effort has been paid to the biostratigraphy of Triassic radiolarians, with most publications focusing on faunas from low and middle latitude sequences. A few high latitude assemblages have been described also, but the faunas are much less diverse and the localities few and geographically limited. The main zonal units discussed in this paper (Fig. 2) represent our current knowledge of the biostratigraphy of radiolarians whose applicability and traceability has been tested satisfactorily in numerous geographic areas. The resolution of these zonal schemes is quite satisfactory, but is still less precise than scales based on ammonites and conodonts, especially in intervals devoid of continuous radiolarian-bearing sequences, that is, the Lower Triassic.

But, the future is promising because the numerical and morphological diversity of genera is extremely high through the Triassic as evidenced by the range chart (Fig. 3), which offers a tool hitherto unknown in the biostratigraphy of the group. The range chart, comprised of 282 revised genera, undoubtedly presents some oversimplification because it is shown in entire (rather than partial) stages or substages increments and this implies, falsely, that many first and last occurrences happen at exactly the same time. However, even with these limitations the range chart constitutes a powerful tool for dating at substage resolution.

Future perspectives

More than 1700 species have been formally described for the Triassic. This great taxonomic diversity unquestionably includes a large quantity of synonyms, but also provides an optimal background for refining the resolution of future zonations based on the range of species. But, it is important to emphasize, that the taxonomic approach must also reflect phyletic relationships and not merely external geometric ones as in the Haeckelian system.

Special attention must also be given to critical boundaries (particularly those bounding the Mesozoic) in order to reduce the distortion/disconnection produced by groups of authors working either side of a particular boundary who may employ a distinctly different approach to classification. Improving the common taxonomy around these boundaries will be an active field in the coming years and only possible if, in forthcoming InterRad meetings, new working groups are engaged to do this task. Although the history of Triassic radiolarian research is rather long, many countries remain largely unexplored. New discoveries of extremely rich faunas are still to be expected. The most recent examples of such discoveries are the Tuvalian assemblages from Turkey and Oman (Dumitrica & Hungerbühler 2007; Kozur *et al.* 2007*a*, *b*, *c*; Moix *et al.* 2007), that contain many new genera and species. These new researches will be the key to bringing new resolution to Triassic biostratigraphic scales in the future.

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