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## Evolutionary patterns and palaeobiogeography of Pliensbachian and Toarcian (Early Jurassic) Radiolaria



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### ABSTRACT

Recent studies on the global distribution of Pliensbachian and Toarcian polycystine radiolarians allowed us to examine faunal turnovers and the biogeography through this critical time interval around a major ecologic and biotic crisis. The analysis is based on the distribution of 167 species belonging to 69 genera. Significant variations in the ratio between the number of originating and extinct species have been recognized. During the early Early Pliensbachian FADs greatly exceeded LADs and the maximum diversity was reached in the late Early Pliensbachian. The trend then reversed with the number of LADs exceeding FADs throughout the Late Pliensbachian and Early Toarcian (extinction interval). Recovery started in the Middle and Late Toarcian, when the number of FADs again surpassed the number of LADs.

Three differing evolutionary patterns are observed amongst radiolarian genera through the studied time interval. The largest group diversified rapidly in the Early Pliensbachian and experienced higher extinction rates in the Late Pliensbachian and Early Toarcian; a second group exhibited no major changes; and a third group of mainly spongy spumellarians was successful during the extinction interval. The overall trend of radiolarian diversity is in a fairly good agreement with that of other marine faunas (ammonites and also ben-thos), but shows an inverse correlation with diversity trends of phytoplankton.

Correlation with concomitant environmental changes indicates that radiolarian radiation/extinction rates were not consistently linked with temperature fluctuations or sea-level changes. It is also evident that the diversity decrease started well before the Early Toarcian negative  $\delta^{13}$ C peak and the Oceanic Anoxic Event (OAE). The extinction interval corresponds well to the duration of a short-term anomaly in the strontium-isotope record, including the rapid decrease of  $^{87}$ Sr/ $^{86}$ Sr values in the Late Pliensbachian as well as the rapid increase in the Early Toarcian. This coincidence supports the hypothesis that the predominance of extinctions over originations was caused by a series of climate and environmental changes related to intensified magmatic activity.

Some distinct biogeographic differences have been observed. Generic differences are most strongly displayed by the presence or absence of a particular genus or by changes in abundance while species differences range from greater variability to having completely different species in separate palaeolatitudinal realms. Two groups of genera are distinguished: those that are common to abundant in the Tethys (low latitudes) and rare to absent in mid to high latitudes, and those common to abundant in mid to high latitudes and rare to absent in the Tethys.

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#### 1. Introduction

The late Early Jurassic (Pliensbachian and Toarcian) was a period of intense and widespread change in the marine physical environment that strongly affected both neritic and pelagic biotic communities. The

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palaeoceanographic events include eustatic sea-level changes (Hag et al., 1987; Hallam, 1988), severe climatic oscillations (Guex et al., 2001; Bailey et al., 2003; van de Schootbrugge et al., 2005) and global anoxia (Jenkyns, 1988). Extinction events took place across the Late Pliensbachian and Toarcian (Hallam, 1986, 1987; Little and Benton, 1995; Little, 1996; Harries and Little, 1999) and have been well documented world-wide in several groups of marine organisms such as ammonites (O'Dogherty et al., 2000; Guex et al., 2001; Macchioni and Cecca, 2002; Cecca and Macchioni, 2004; Dera et al., 2010; Sandoval et al., 2012; Caruthers et al., 2013), benthic foraminifers (Septfontaine et al., 1991; Nikitenko and Mickey, 2004; Ruban and Tyszka, 2005; Caruthers et al., 2013), bivalves (Aberhan and Fürsich, 1996; Aberhan and Baumiller, 2003), ostracods (Arias, 2009; Gómez and Arias, 2010), brachipods (Vörös, 2002; Ruban, 2004; García Joral et al., 2011) and cnidarians (Lathuilière and Marchal, 2009). The elevated extinction levels were not an instantaneous event but characterized a protracted interval that spanned several ammonite zones around the Pliensbachian-Toarcian boundary (Little and Benton, 1995). The concomitant flood basalt volcanism of the Karoo-Ferrar large igneous province (LIP) in southern Gondwana is often regarded as the prime cause of environmental perturbations and consequent biotic crises (Pálfy and Smith, 2000; Guex et al., 2001; Wignall, 2001; Courtillot and Renne, 2003; Morard et al., 2003; Caruthers et al., 2013).

The Pliensbachian-Toarcian radiolarian faunal turnover was first recognized in the 1990s from oceanic successions in Japan (Hori, 1993a, 1997). Knowledge of late Early Jurassic radiolarians was still rather incomplete at that time and the precise succession of radiolarian events, their magnitude, exact timing and global correlativity was unknown. Existing radiolarian zonations (Pessagno et al., 1987b; Carter et al., 1988; Hori, 1990) were local, of low resolution and included a relatively small number of taxa. In order to construct a global radiolarian zonation for the Pliensbachian, Toarcian and Aalenian a joint international project was initiated under the framework of InterRad (International Association of Radiolarists). The first step was to establish a set of clearly defined and updated taxonomic species to be used in construction of the zonation. The resulting catalogue (Goričan et al., 2006) included the systematics of 274 species and 13 subspecies each with an up-to-date synonymy, original and subsequent definitions, remarks, and data on geographic distribution. Secondly, a comprehensive dataset from sections around the world was produced. This dataset was used to establish a global Unitary Association (UA) radiolarian zonation (Carter et al., 2010). The zonation established nine zones for the Pliensbachian to Aalenian interval and presented the stratigraphic ranges of 197 species from low and middle to high palaeolatitudes. Well-preserved faunas from continuous stratigraphic sections in Haida Gwaii (Queen Charlotte Islands) provided the most detailed record for the studied interval, and allowed correlation of the radiolarian zones with North American ammonite zones or assemblages.

Here we use the established zonation for further analysis of spatiotemporal relationships among radiolarian faunas for the Pliensbachian– Toarcian interval. The primary aim of the present study is to clarify radiolarian evolutionary rates through this time interval, and to examine these relationships with global environmental conditions and with the evolutionary pattern of other marine organisms. Secondly, we aim to identify faunal differences between low and middle to high latitude assemblages.

#### 2. Material and methods

#### 2.1. The Pliensbachian-Toarcian radiolarian dataset

The Pliensbachian to Aalenian zonation (Carter et al., 2010) was based on data from 220 samples from measured sections plus some individual samples from Haida Gwaii, British Columbia (BC), Williston Lake, north-eastern BC, east-central Oregon, Baja California Sur, southern Spain, Austria, Slovenia, Turkey, Oman, Japan and Argentina (Fig. 1). The



**Fig. 1.** Pliensbachian–Toarcian palaeogeographic map with localities included in the zonation of Carter et al. (2010). The map according to Sandoval et al. (2012) as modified from Dera et al. (2009). 1–Haida Gwaii (Queen Charlotte Islands); 2–Northeastern British Columbia; 3–East-central Oregon; 4–Baja California Sur; 5–Betic Cordillera, Spain; 6–Northern Calcareous Alps, Austria; 7–Julian Alps, Slovenia; 8–Gümüslu Allochthon, Turkey; 9–Al Aridh Group of the Hawasina Nappes, Oman; 10–Mino Terrane, Japan; 11–Neuquén Basin, Argentina.

total dataset included the occurrence of 197 species. Only the stratigraphically useful species were included in the computations: we eliminated those that were either rare, long ranging or non-diagnostic with wide limits of variability and others that occur sporadically because their skeletons are very delicate and are rarely preserved.

The large quantity of data was integrated into the global radiolarian range chart based on the Unitary Association (UA) method of Guex (1977, 1991). The calculation was produced with the UA-Graph computer program (Hammer et al., 2008) and the resulting protoreferential consisted of 41 successive UAs (Fig. 2). The first and the last UAs represent the Upper Sinemurian and the Lower Bajocian respectively. The remaining 39 UAs were merged in zones according to prominent radiolarian faunal breaks and ammonite data, mostly from sections located in Haida Gwaii. Nine Unitary Association Zones (UAZ) were defined: four Lower Pliensbachian, one Upper Pliensbachian, one Lower Toarcian, one Middle–Upper Toarcian, and two Aalenian. These zones are defined by UA alone and are equivalent to concurrent range zones.

The zonation includes three stages: Pliensbachian, Toarcian and Aalenian. However, the data on the Aalenian are too scarce to allow a reliable interpretation of faunal turnovers. The Aalenian contains only the most stratigraphically important species that have already been used for biostratigraphy in previous works. For the Aalenian, the primary goal of the Carter et al. (2010) zonation was to show the ranges of species originating in the Toarcian and to correlate the new Aalenian zones with the zones established by Baumgartner et al. (1995). Several species, even those that first appear in the Aalenian may have been neglected. For this reason, only the Pliensbachian

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