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REVIEW PAPER

Dinosaur extinctions related to the Jenkyns Event (early Toarcian, Jurassic)

Extinciones de dinosaurios relacionadas con el Evento Jenkyns (Toarciense inferior, Jurásico)

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Abstract: The early Toarcian Jenkyns Event (~183 Ma) was characterized by a perturbation of the global carbon cycle, global warming, which at continental areas led to intensified chemical weathering, enhanced soils erosion, and intensified wildfires. Warming and acid rain affected diversity and composition of land plant assemblages, caused a loss of forests and thereby impacted on trophic webs. The Jenkyns Event, triggered by volcanic activity of the Karoo-Ferrar Large Igneous Province, changed terrestrial ecosystems, and also affected the dinosaurs. Fossil macroplant assemblages and palynological data reveal reductions in the diversity and richness of plant communities. A substantial loss of land plant biomass and a shift to forests dominated by Cheiropelidiaceae conifers occurred as a consequence of seasonally dry and warm conditions. Major changes occurred to hervivore dinosaurs, with extinction of diverse basal families of Sauropodomorpha ('prosauropods') as well as some basal sauropods. Ornithischian dinosaurs show patchy records; some heterodontosaurids disappeared and the scelidosaurids (Thyreophora) went extinct during the Jenkyns Event. The dominant carnivorous dinosaurs, the Coelophysoidea (Theropoda), died out during the Jenkyns Event. We interpret the Jenkyns Event as a terrestrial crisis for ecosystems, marked especially by floral changes and the extinction of some dinosaur clades, both hervivores and carnivores.

Resumen: El Evento Jenkyns del Toarciense inferior (~183 Ma) se caracterizó en ambientes continentales por una perturbación del ciclo del carbono, un calentamiento global, un aumento de la meteorización, la pérdida de suelos y la proliferación de incendios. El calentamiento y la lluvia ácida afectaron a la diversidad y composición de las asociaciones vegetales, causó la pérdida de masas forestales y tuvo un fuerte impacto en las redes tróficas. El Evento Jenkyns, cuyo detonante fue la intensa actividad volcánica de la Provincia Ígnea de Karoo-Ferrar, cambió los ecosistemas continentales, afectando entre otros a los dinosaurios. Los datos palinológicos y de las asociaciones fósiles de macroplantas muestran una reducción de la diversidad y la riqueza de las comunidades vegetales, especialmente una pérdida de biomasa y la dominancia de coníferas cheirolepidiáceas en los bosques, en un contexto de condiciones cálidas estacionalmente áridas. Pueden observarse cambios importantes entre los dinosaurios herbívoros con la extinción de varias familias basales de sauropodomorfos ("prosaurópodos") y algunos saurópodos basales. Los dinosaurios ornitisquios, pese a su registro más incompleto, muestran la desaparición de algunas especies de heterodontosáuridos y la extinción de la familia Scelidosauridae (Thyreophora) en relación con el Evento Jenkyns. Los dinosaurios carnívoros de la superfamilia Coelophysoidea (Theropoda) también se extinguieron durante el Evento Jenkyns. Por lo tanto, se interpreta que el Evento Jenkyns contituyó una crisis biótica en los ecosistemas continentales de gran importancia, marcada especialmente por cambios en la flora y la extinción de algunos grupos de dinosaurios tanto herbívoros como carnívoros.

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INTRODUCTION

The early Toarcian was characterized by an important environmental change called the Jenkyns Event (*e.g.*, Müller *et al.*, 2017; Reolid *et al.*, 2020, 2021a; Erba *et al.*, 2022), one of the most significant hyperthermal events of the Mesozoic (*e.g.*, García Joral *et al.*, 2011; Korte & Hesselbo, 2011; Suan *et al.*, 2011; Danise *et al.*, 2013; Baghli *et al.*, 2020; Storm *et al.*, 2020; Ruebsam *et al.*, 2020a, 2020b). TEX_{86} palaeothermometry proxies applied to NW Tethys sediments suggest a warming of 5ºC during the Pliensbachian–Toarcian transition and a peak of 10ºC warming during the Jenkyns Event (Ruebsam *et al.*, 2020b). Other processes documented during the Jenkyns Event include: (1) a perturbation of the carbon cycle evidenced as a negative carbon isotopic excursion (**CIE**; *e.g.*, Jenkyns & Clayton, 1986; Kemp *et al.*, 2005; Hesselbo *et al.*, 2007; Ruebsam *et al.*, 2019, 2020a); (2) oxygen depleted conditions in some marine basins, the Toarcian Oceanic Anoxic Event (**T-OAE**; Gill *et al.*, 2011; Fonseca *et al.*, 2018; Izumi *et al.*, 2018; Ruebsam *et al.*, 2018; Suan *et al.*, 2018); (3) a sea-level rise (*e.g.*, Hallam, 1981; Pittet *et al.*, 2014; Haq, 2018; Krencker *et al.*, 2019); and (4) a crisis of marine carbonate productivity (Bucefalo-Palliani *et al.*, 2002; Mattioli *et al.*, 2004) and acidification (Müller *et al.*, 2020; Ettinger *et al.*, 2021).

In the context of environmental change, the early Toarcian is also characterized by a second-order extinction that affected marine ecosystems, including dynoflagellate cysts, foraminifera, ostracods, brachiopods, corals, bivalves, and cephalopods (*e.g.*, Hallam, 1987; Little & Benton, 1995; Harries & Little, 1999; Aberhan & Fürsich, 2000; Macchioni & Cecca, 2002; Vörös, 2002; Arias, 2009, 2013; Dera *et al.*, 2010; García Joral *et al.*, 2011; Caruthers *et al.*, 2014; Baeza-Carratalá *et al.*, 2017; Reolid *et al.*, 2019; Vasseur *et al.*, 2021; Reolid & Ainsworth, 2022). In addition to the extinction, the biotic crisis is also expressed in a decrease of diversity, mainly affecting benthic communities, as well reductions in body size of some taxa (Harries & Little, 1999; Piazza *et al.*, 2020).

Key triggers of the Jenkyns Event include the emission of volcanic CO_2 and thermogenic CH_4 associated with the emplacement of the Karoo-Ferrar Large Igneous Province (**LIP**) and probably the Chon Aike LIP volcanism (Pankhurst & Rapela, 1995), that broadly coincide with the negative CIE (Hesselbo *et al.*, 2007; Moulin *et al.*, 2017; Fantasia *et al.*, 2019; Font *et al.*, 2022; Fig. 1). In addition, the destabilization of marine methane hydrates (Hesselbo *et al.*, 2000; Kemp *et al.*, 2005), intensified wetland methanogenesis (Them *et al.*, 2017a) and deterioration of climate-sensitive reservoir permafrost areas during the global warming (Ruebsam *et al.*, 2019) may have contributed to the increase of greenhouse gases into the atmosphere. We might assume heating and acid rain on land, leading to a loss of forests and soil wash into the sea, together with aridity and sporadic heavy rainfall conditions on land, all features of the standard hyperthermal extinction model (Benton & Newell, 2014; Benton, 2018).

Even though the Jenkyns Event has been mainly studied in marine sediments, it also impacted terrestrial settings, and many authors have identified a displacement of climatic belts with the spread of aridity (Rodrigues *et al.*, 2019; Lu *et al.*, 2020; Font *et al.*, 2022) and enhanced weathering (*e.g.*, Brazier *et al.*, 2015; Montero-Serrano *et al.*, 2015; Percival *et al.*, 2016; Them *et al.*, 2017b). During the Jenkyns Event, global warming also affected continental ecosystems. A decrease of ^{13}C fractionation during photosynthesis in C3 plants, confirms a turn to arid climate for emerged areas of Western Tethys during the Jenkyns Event (Rodrigues *et al.*, 2019, 2021; Ruebsam *et al.*, 2020a). Other changes in terrestrial ecosystems affected diversity and composition of land plant assemblages (Slater *et al.*, 2019; Jin *et al.*, 2020) and an increase of wildfires in some areas (Baker *et al.*, 2017).

Dinosaur faunas underwent remarkable evolutionary changes during the Triassic–Jurassic transition (Benton, 1993; Brusatte *et al.*, 2008a, 2008b; Allen *et al.*, 2019; Klausen *et al.*, 2020; Novas *et al.*, 2021; Langer & Godoy, 2022). Nevertheless, the discontinuous terrestrial fossil record and the lack of consistent age constraints have made it difficult to correlate the fossil records to environmental changes or to major events in floral evolution (Barrett, 2014). In any case, the most studied event that had an impact on dinosaurs is the End Triassic Mass Extinction (**ETME**; Benton, 1993; Brusatte *et al.*, 2010; Allen *et al.*, 2019; Singh *et al.*, 2021) whereas the early Toarcian global change remains little studied (Rauhut *et al.*, 2016; Pol *et al.*, 2020; Reolid *et al.*, 2022).

The purpose of this work is to identify the impact of the Jenkyns Event on terrestrial ecosystems, mainly focused on vegetational changes and dinosaur assemblages. This work is a review of the Early Jurassic record of Sauropodomorpha, Theropoda and Ornithischia with the appearance and last occurrence of some lineages, and we discuss the climatic transformations in continental environments related to the early Toarcian Jenkyns Event.

MATERIALS AND METHODS

Climatic trends (global warming/cooling) were reconstructed from oxygen isotope data measured on belemnite and brachiopod calcitic shells. Boxplots with a step size of 2.5 Myr were considered for the $\delta^{18}O$ data to assess secular climate trends and variability within a 2.5 Myr interval (Supplementary Table 1). The 2.5 Myr step size approximates the temporal resolution and dating inaccuracy of the palaeontological data. Boxplots and smoothing splines were calculated using PAST software (Hammer *et al.*, 2001).

The fossil record of continental vertebrates, is patchy, with large temporal gaps between stratigraphic formations (Benton, 1998; Lloyd *et al.*, 2008; Benson & Butler, 2011; Benton *et al.*, 2011, 2013). Further, much of what we know comes from particular horizons or formations, some of them Fossil-Lagerstätten. In addition, the dating of continental sedimentary formations is often less certain than for marine formations.

Nonetheless, despite suggestions that the amount of error in the data might make large-scale interpretation risky or flawed, we argue instead that the broad story of the history of life as documented in the fossil record is roughly correct (Sepkoski *et al.*, 1981; Benton, 1998). We base this assumption on three lines of evidence, (1) comparisons of cladograms with the fossil record show good correspondence in most cases (Norell & Novacek, 1992; Benton *et al.*, 2000), (2) study of collector curves shows that the application of intense searching by palaeontologists and even the opening up of new territories such as China, does not materially affect the large-scale knowledge of stratigraphic ranges of major clades (Benton, 2008; Benton *et al*., 2013), and (3) Lagerstätten do not necessarily distort the records (Walker *et al*., 2019).

For this study, we include a total of 83 species (17 Ornithischia, 44 Sauropodomorpha and 22 Theropoda) (see Supplementary Table 2) after a detailed review of the taxonomic assignments, updated ages of the lithostratigraphic formations where fossil remains were recovered, and geographic areas.

RESULTS

Early Jurassic climates

The Early Jurassic climate was predominantly humid and warm (Frakes *et al*., 1992), but characterized by high variability, which involved colder and warmer periods (*e.g.*, Dera *et al*., 2011; Korte & Hesselbo, 2011; Korte *et al*., 2015; Ruebsam *et al*., 2019, 2020b). The Early Jurassic interval between the Triassic/Jurassic boundary and the early Toarcian Jenkyns Event is characterized by several smaller carbon-cycle perturbations identified as CIEs (Cramer & Jarvis, 2020; Schoepfer *et al*., 2022). The Sinemurian–Pliensbachian boundary is marked by a negative CIE (Franceschi *et al*., 2019) and the *Ibex* Zone of the lower Pliensbachian is characterized by a positive CIE and warming (Armendáriz *et al*., 2012).

Moreover, differing latitudinal climatic belts developed during the Early Jurassic (*e.g.*, Rees *et al*., 2000; Dera & Donnadieu, 2012; Boucot *et al*., 2013; Philippe *et al*., 2017). High latitudinal areas experienced temperate climate conditions with recurring excursions to warm-temperate, cold-temperate and cold climates (*e.g.*, Zakharov *et al*., 2006; Devyatov *et al*., 2011; Ruebsam & Schwark, 2021). Low-latitude areas along the Tethys margins were located in the tropical to subtropical climate belt with high precipitation rates. Semi-arid to arid conditions prevailed in the interior regions of Laurentia and southern Gondwana (Parrish *et al*., 1982; Rees *et al*., 2000).

During the Sinemurian and earliest Pliensbachian global temperatures continued high with equatorial sea surface temperatures in the range 30–33°C as calculated from the TEX_{86} proxy (Robinson *et al*., 2017). Based on $\delta^{18}O$ from belemnite findings from the UK (Bailey *et al*., 2003), Spain (Rosales *et al*., 2004; Gómez *et al*., 2008) and France (Harazim *et al*., 2013), a cooling and regression has been proposed for the late Pliensbachian. In addition, Tchoumatchenco *et al*. (2008) identified sediments of potentially glacial origin deposited during the times of the *Emaciatum* Zone (upper Pliensbachian) and *Polymorphum* Zone (lower Toarcian) from the Mediterranean Province. During the late Pliensbachian, cooling may have promoted the formation of high-latitudinal glaciation with wider incidence during the latest Pliensbachian to earliest Toarcian (Dera *et al*., 2011; Ruebsam *et al*., 2019; Ruebsam & Schwark, 2021; Fleischmann *et al*., 2022). The end Pliensbachian is characterized by a sea-level drop with subsequent flooding and a negative CIE related to the Pliensbachian–Toarcian boundary event (Bodin *et al*., 2016; Al-Suwaidi *et al*., 2022; Fleischmann *et al*., 2022). The negative CIE of the Pliensbachian–Toarcian boundary and the related palaeoenvironmental changes have been attributed to an early phase of Karoo-Ferrar LIP magmatism (Percival *et al*., 2015, 2016; Fig. 1).

According to Ruebsam *et al*. (2020b), latest Pliensbachian to early Toarcian equatorial sea surface temperatures varied between 22 and 32°C, attesting to extremely variable and contrasting climatic conditions. Subsequently, the sea water temperatures at low latitudes increased by about 10°C during the Jenkyns Event related to the carbon cycle perturbation (lower *Serpentinum–Levisoni* ammonite Zone; Ruebsam *et al*., 2020b; Fernández *et al*., 2021). Studies from oxygen isotopes indicate that temperatures continued high during the middle and late Toarcian (Dera *et al*., 2011; Korte *et al*., 2015).

Vegetation record

Palynological analyses indicate that the Triassic–Jurassic fern spike was followed by dominance of the Cheirolepidiaceae conifers during the Hettangian and early Sinemurian in China, Australia, New Zealand and Europe (Akikuni *et al*., 2010; Bonis *et al*., 2010; Diéguez *et al*., 2010; de Jersey & McKellar, 2013; Gravendyck *et al*., 2020; Li *et al*., 2020). In the Sichuan Basin (China) the lowermost Jurassic is characterized by high abundance of fern palynomorphs, and progressive increase of conifers, mainly Cheirolepidiaceae and Pinaceae (Li *et al*., 2020). The palynological record of the lowest Jurassic in North Germany is characterized by dominant conifer forests composed of Pinaceae, Podocarpaceae and Cheirolepidiaceae with abundant Selaginellales (Gravendyck *et al*., 2020).

The Pliensbachian in the European record is characterized by palynological assemblages indicative of high-diversity forests, dominated by a mixture of bisaccate pollen-producing conifers and seed-ferns accompanied by spore-producing mosses (bryophytes) and club mosses (lycophytes) (Slater *et al*., 2019; Danise *et al*., 2021). Increased proportions of spore-producing mosses (bryophytes) and clubmosses (lycophytes) indicate relatively wetter conditions on land during the Pliensbachian (Slater *et al*., 2019). In South America, the record of the pre-Toarcian plant assemblages of the Cañadón Asfalto Basin (Argentina) consists of diverse sphenophytes, dipteridacean ferns, conifers, cycads, seed-ferns, and bennetitaleans, collectively suggesting humid climates (Escapa *et al*., 2008; Choo *et al*., 2016). The beginning of the Toarcian is characterized by a decrease in diversity and richness of palynological assemblages with an increase in abundance of cycads (*Chasmatosporites* spp.) and a drop in bisaccate pollen-producing conifers and seed-ferns (Pieńkowski *et al*., 2016; Slater *et al*., 2019).

At the onset of the Jenkyns Event identified by the negative CIE, land plants suffered a major drop in diversity and richness (Slater *et al*., 2019; Danise *et al*., 2021; Fig. 1). Poorly diversified forests dominated by Cheirolepidiaceae (represented by *Classopollis* spp.) and cycads replaced the previous forests of bisaccate pollen-producing conifers and seed ferns.

Land plant communities during the middle–late Toarcian, after the Jenkyns Event, presented low diversity in Europe and South America, with dominance of the conifer families Cheirolepidiaceae, Cupressaceae and Araucariacea (Escapa *et al*., 2008; Olivera *et al*., 2015; Choo *et al*., 2016; Deng *et al*., 2018; Slater *et al*., 2019), together indicating seasonally dry and warm conditions.

Therefore, the increase of warm -and drought- adapted plants through the Jenkyns Event, suggests a warmer and drier climate than in the Pliensbachian with strong seasonality favouring drought-adapted plants. These conditions persisted during the middle and late Toarcian with the abundance of xerophytic and thermophilic plant groups in both the southern hemisphere (Escapa *et al*., 2008; Olivera *et al*., 2015; Choo *et al*., 2016; Pol *et al*., 2020) and northern hemisphere (Deng *et al*., 2018; Slater *et al*., 2019).

Dinosaur assemblages

Sauropodomorpha. After the extinction of most of the basal Sauropodomorpha, members of Plateosauridae and Melanorosauridae, and some genera of basal sauropods (Brusatte *et al*., 2010; McPhee *et al*., 2017; Novas *et al*., 2021; Reolid *et al*., 2022) at the end of the Triassic, the beginning of the Jurassic is characterized by the first occurrence of many taxa. During the earliest Jurassic new basal sauropodomorphs (‘prosauropods’) such as Massospondylidae and Anchisauria, radiated from Hettangian to Pliensbachian (Fig. 2) with sizes ranging from 1.5 m in *Ignavusaurus* to 9 m in *Lufengosaurus* in the case of Massospondylidae (Barrett *et al*., 2005; Knoll, 2010) and from 2.4 m in *Anchisaurus* to 10 m in *Jingshanosaurus* in the case of Anchisauria (Galton & Upchurch, 2004; Yates, 2004).

Basal Sauropoda diversified at the beginning of the Jurassic (*e.g.*, *Ammosaurus*, *Antetonitrus*, *Ledumahadi*, *Pulanesaura, Yizhousaurus*) with sizes ranging from 2.5 m in *Ammosaurus* to 12 m in *Ledumahadi* (Brusatte *et al*., 2010; McPhee *et al*., 2017, 2018).

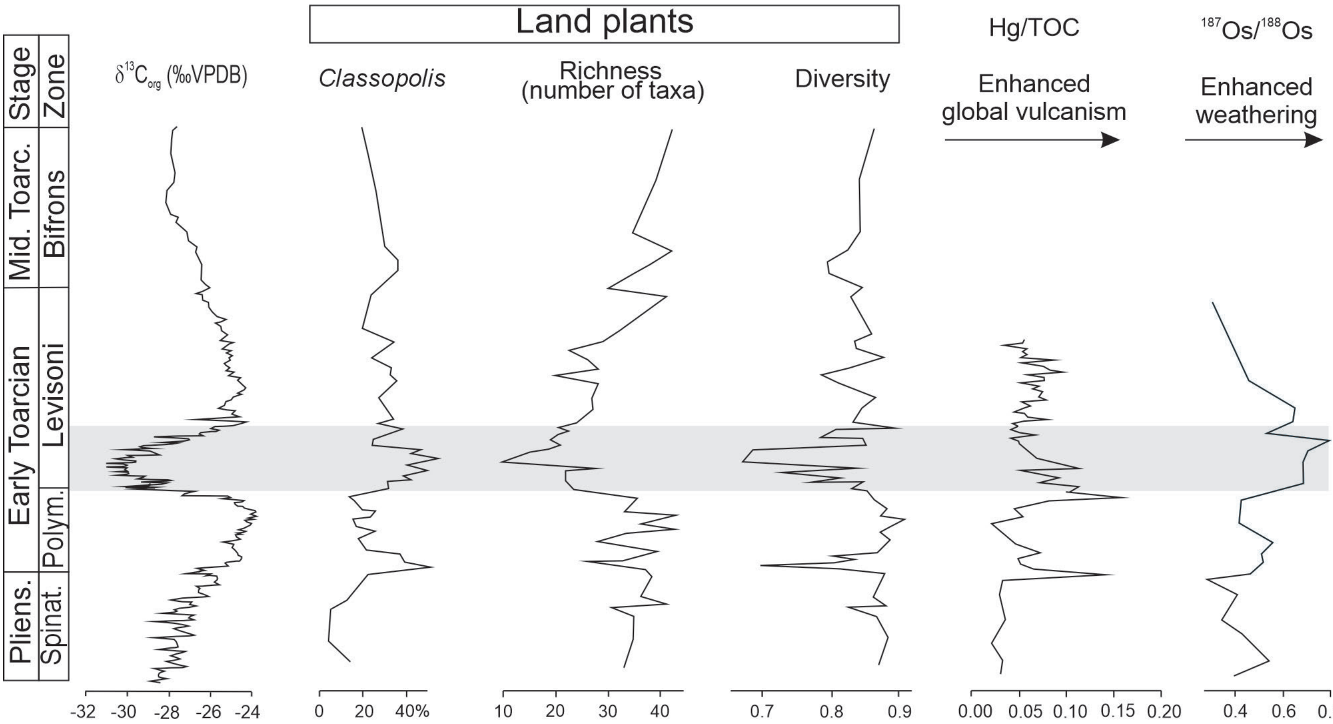

Figure 1. Different proxies of environmental conditions during the latest Pliensbachian to middle Toarcian in the British sedimentary basins (Cardigan Bay Basin and the Cleveland Basin). Comparison of the $\delta^{13}C$ from organic matter of the Mochras borehole, Cardigan Bay Basin (Xu *et al*., 2018a; Storm *et al*., 2020), percentage of *Classopolis* spp. (Cheirolepidiacea conifer), richness and diversity (H-index) of land plants from Yorkshire, Cleveland Basin (Slater *et al*., 2019), Hg/TOC values from the Mochras borehole as a proxy of global vulcanism (Percival *et al*., 2016) and $^{187}Os/^{188}Os$ ratio from the Mochras borehole as a proxy of continental weathering (Percival *et al*., 2016). Enhanced global vulcanism is relatively early with respect to the Jenkyns Event (grey band) with maximum values coinciding with the onset of the negative CIE and subsequent changes in the land plant community and continental weathering. Note that the Pliensbachian–Toarcian boundary coincides with a volcanic event and changes in the land plants.

Moreover, *Tonganosaurus*, the first eusauropod (Family Mamenchisauridae) is recorded in the Hettangian of the Yimen Formation (China; Li *et al*., 2010). However, Eusauropoda diversified during the Middle Jurassic (Pol *et al*., 2020; Reolid *et al*., 2022).

The earliest Jurassic was a time for geographic dispersion of sauropodomorphs that extended north of the palaeoequator and are recorded from North America (*Ammosaurus*, *Anchisaurus*, *Sarahsaurus*, *Seitaad*) and Asia (*Irisosaurus*, *Jingshanosaurus*, *Lufengosaurus*, *Xingxiulong*, *Xixiposaurus*, *Yimenosaurus*, *Yizhousaurus*, *Yunnanosaurus*) (*e.g.*, Bai *et al*., 1990; Yates, 2010; Rowe *et al*., 2011; Wang *et al*., 2017a; Peyre de Fabrègues *et al*., 2020).

The beginning of the Toarcian constitutes the extinction boundary for the last basal sauropodomorphs (‘prosauropods’), including Anchisauria and Massospondylidae, even though they were diverse during the Sinemurian and Pliensbachian (Fig. 2).

Basal Sauropoda were also affected but some of them survived the Jenkyns Event in Europe with *Ohmdenosaurus* (Wild, 1978), in Africa with *Vulcanodon* (Cooper, 1984) and *Tazoudasaurus* (Allain *et al*., 2004), in India with *Barapasaurus* (Jain *et al*., 1975), and in Asia with *Isanosaurus*, *Gongxianosaurus*, *Sanpasaurus* and *Zizhongosaurus* (Hou *et al*., 1976; Buffetaut *et al*., 2000; Yaonan & Wang, 2000; McPhee *et al*., 2016) (Fig. 2). However, basal Sauropoda disappeared before the Aalenian (Middle Jurassic; Figs. 2 and 3), with the exception of *Archaeodontosaurus*, a possible basal sauropod from the Bathonian of Madagascar (Buffetaut, 2005).

After the Jenkyns Event, Eusauropoda diversified (Fig. 3) with records of the genera *Bagualia*, *Patagosaurus, Volkheimeria* from South America, *Spinophorosaurus* from Africa, and *Nebulasaurus* from Asia (Remes *et al*., 2009; Xing *et al*., 2015; Pol *et al*., 2020; Reolid *et al*., 2022).

Ornithischia. The other group of herbivorous dinosaurs, the ornithischians, diversified after the End Triassic Mass Extinction, at the beginning of the Jurassic in South Gondwana with the appearance of new genera corresponding to the Family Heterodontosauridae (*Abrictosaurus*, *Heterodontosaurus*, and *Pegomastax*; Thulborn, 1974; Sereno, 2012), but also with the origin of the Family Fabrosauridae (Africa; *Fabrosaurus* and *Lesothosaurus*; Butler, 2005; Butler *et al*., 2008) composed of small bipedal forms (Figs. 2, 3) generally < 2 m long. The clade Thyreophora, characterized by parallel rows of keeled dermal armour scutes or bony plates (osteoderms) on the dorsal surface of the body debuted in the Early Jurassic (Fig. 3). They were represented by the Family Scelidosauridae, which originated and diversified during the Early Jurassic in Laurasia (‘*Lusitanosaurus*’, *Scelidosaurus*, and *Emausaurus* from Europe, *Laquintasaura* from Central America, *Scutellosaurus* from North America, and *Yuxisaurus* and *‘Bienosaurus’* from Asia) (Lapparent & Zbyszewski, 1957; Colbert, 1981; Haubold, 1990; Dong, 2001; Baron *et al*., 2016). Scelidosaurids were quadrupedal and had heavily built bodies (in some cases reaching 4 m long), but probably *Scutellosaurus* and *Emausaurus* were bipedal forms (Riguetti *et al*., 2022). However, in the phylogenetic analyses of Maidment (2010), Raven and Maidment (2017) and Norman (2021), *Scutellosaurus*, *Emausaurus* and *Scelidosaurus* are regarded as successive basal thyreophorans (see also Thompson *et al*., 2012), so Family Scelidosauridae would then be a paraphyletic group.

The first genus of Neornithischia, *Stormbergia*, appeared during the Hettangian–Sinemurian in South Gondwana (South Africa and Lesotho; Butler, 2005).

Theropoda. As for the sauropodomorphs, theropods extended and diversified during the Early Jurassic. The dominant early Jurassic theropods were Coelophysoidea with the families Coelophysidae (*Coelophysis*, *Megapnosaurus*, *Panguraptor*, and *Sarcosaurus*) and Dilophosauridae (*Dilophosaurus*, *Dracovenator*, and *Shuangbaisaurus*) (Figs. 2, 3). Both families colonized Africa (*Megapnosaurus*, *Dracovenator*) and Asia (*Panguraptor*, *Shuangbaisaurus*) during the Hettangian and Sinemurian (Yates, 2006; You *et al*., 2014; Wang *et al*., 2017b). The dilophosaurids occupied the top of the trophic chain, with *Dracovenator* and *Dilophosaurus* (5–6.5 m and 270–390 kg; Therrien & Henderson, 2007; Reolid *et al*., 2021b) being among the largest theropods in the Early Jurassic. However, Marsh and Rowe (2020) proposed that *Dilophosaurus* is a stem-averostran theropod rather than a member of Coelophysoidea.

In addition to coelophysoids, new theropod groups appeared during the earliest Jurassic, including stem-averostran *Tachiraptor* (Langer *et al*., 2014), basal forms of Ceratosauria (*Saltriovenator*; Dal Sasso *et al*., 2018) and Tetanurae (*Dracoraptor*, *Sinosaurus*, *Kayentavenator*, and *Cryolophosaurus*) (Fig. 2). They were robuster forms than coelophysoids (*Saltriovenator zanellai* and *Cryolophosaurus ellioti* reached more than 6.5 m; Smith *et al*., 2007; Dal Sasso *et al*., 2018).

The beginning of the Toarcian represented a major break in the evolution of theropods. The coelophysoids disappeared during the Toarcian (Figs. 2, 3). However, new basal Ceratosauria are recorded in the Toarcian such as *Dandakosaurus* from India (Yadagiri, 1982) and *Berberosaurus* from Morocco (Allain *et al*., 2007). After the Jenkyns Event, during the late Toarcian, the first allosauroids (*Asfaltovenator*; Metriacanthosauridae) and the first megalosauroids (*Condorraptor* and *Piatnitzkysaurus*; Piatnitzkysauridae) are recorded in South America (Rauhut, 2005; Carrano *et al*., 2012; Rauhut & Pol, 2019) (Fig. 2).

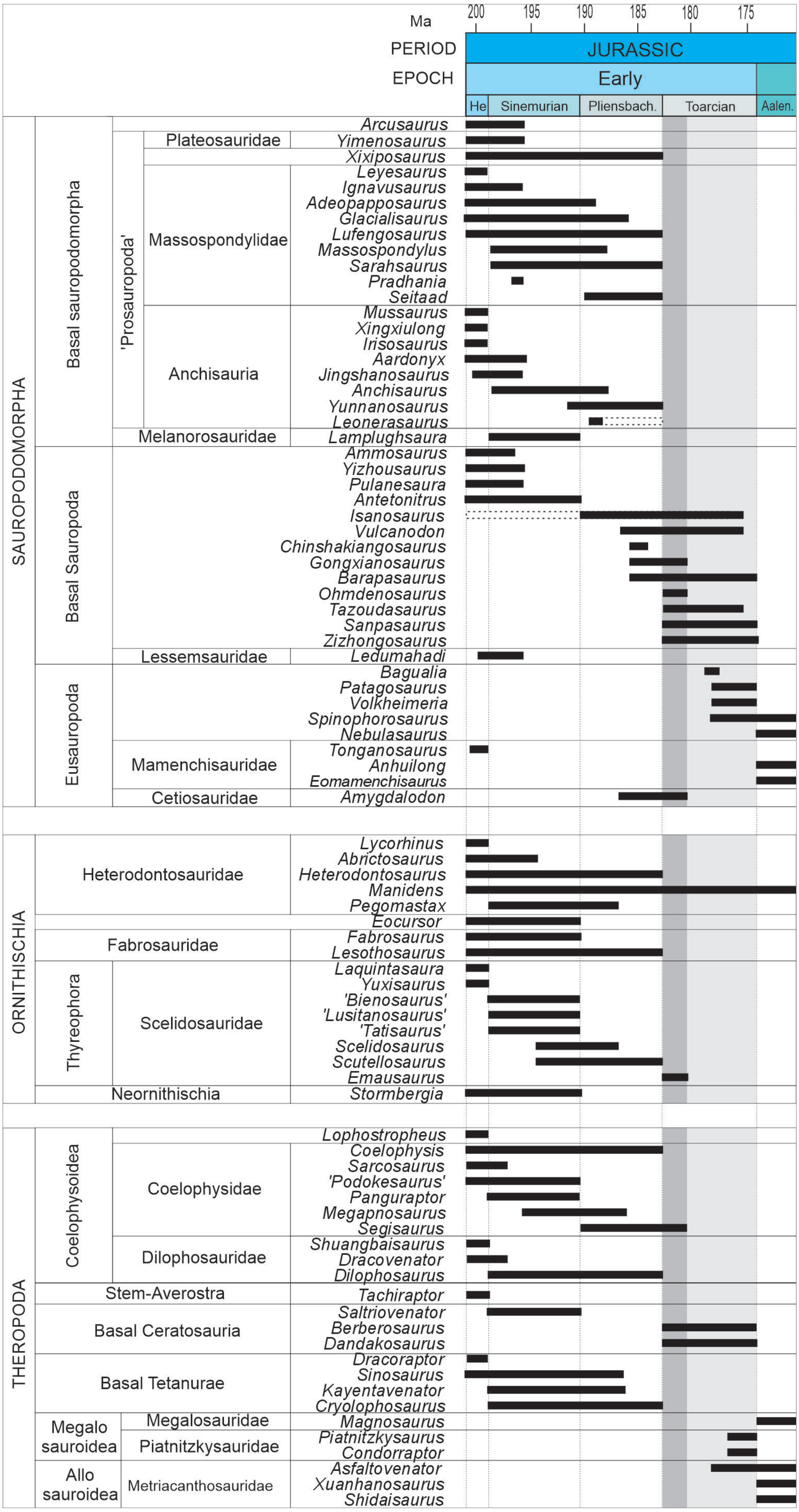

Figure 2. Distribution of genera of sauropodomorphs, ornithischians and theropods from Hettangian to Aalenian. The early Toarcian biotic crisis associated with the Jenkyns Event, is indicated with a dark grey bar. Note that many dinosaur taxa disappear during the Jenkyns Event or after that but before the Aalenian stage.

DISCUSSION

Early Jurassic diversification of dinosaurs

The Triassic–Jurassic transition is characterized by severe environmental stress in the ocean and on land, as well as enhanced atmospheric CO_2 concentrations (McElwain *et al*., 1999; Cohen & Coe, 2007; Michalík *et al*., 2007; Whiteside *et al*., 2010). The volcanic activity of the Central Atlantic Magmatic Province (**CAMP**) caused a massive input of greenhouse gases into the atmosphere that triggered global warming (4 to 5°C; McElwain *et al*., 1999; Schoepfer *et al*., 2022) and mass extinction both on land and sea (Whiteside *et al*., 2010). Acid rain was generated by the CAMP eruptions, as well as increased wildfires and the resulting extensive deforestation probably caused by warmer and drier climates (Blackburn *et al*., 2013; Thibodeau *et al*., 2016; Percival *et al*., 2017; Pole *et al*., 2018; Alipour *et al*., 2021; Zhang *et al*., 2022).

At the end of the Rhaetian, crurotarsan archosaurs suffered substantial extinction and only the crocodylomorph lineage persisted (Brusatte *et al*., 2008a; Benton *et al*., 2014). Herbivores such as dicynodonts (Therapsida) and aetosaurs (Crurotarsi) and carnivores such as poposauroids (Crurotarsi) and phytosaurs disappeared at the end of the Triassic (Benton *et al*., 2014). Among dinosaurs, both sauropodomorphs and theropods were affected by the extinction (Benton, 1993; Brusatte *et al*., 2010; Singh *et al*., 2021; Reolid *et al*., 2022).

After the ETME, an evolutionary radiation of dinosaurs occurred and dinosaurs became the most successful group of terrestrial vertebrates during the Jurassic and Cretaceous, occupying many different ecological niches and exhibiting a wide range of adaptations (Lloyd *et al*., 2008; Brusatte *et al*., 2010; Langer *et al*., 2010; Benton *et al*., 2014). However, Brusatte *et al*. (2008b, 2010) and Benton *et al*. (2014) indicated that the extinction of competitor groups such as crurotarsan archosaurs at the end of the Triassic was not met with an explosion of dinosaurs in terms of morphological disparity.

The Early Jurassic is characterized by a progressive increase of diversity and presence of plants indicative of more humid conditions and the development of a more pronounced latitudinal climate gradient (Rees *et al*., 2000; Escapa *et al*., 2008; Choo *et al*., 2016; Philippe *et al*., 2017; Slater *et al*., 2019; Gravendyck *et al*., 2020).

Early Jurassic sauropodomorphs prospered according to the recovery of primary producers. Most of their key adaptations such as huge size, quadrupedal locomotion and graviportal specializations, continued into the Early Jurassic. The basal sauropods were the same size as the largest basal sauropodomorphs and shared the same habitats (Apaldetti *et al*., 2018). Basal sauropods and basal sauropodomorphs (‘prosauropods’) probably avoided competition for trophic resources through specializations in masticatory apparatus such as U-shaped jaws, spatulate tooth crowns with small denticles and the presence of a lateral plate on the dentary (Barrett & Upchurch, 2007; Yates *et al*., 2010).

Herbivorous ornithischians during the earliest Jurassic were globally distributed and relatively diverse and abundant. The heterodontosaurids diversified and other families originated such as fabrosaurids and scelidosaurids (Thyreophora). The diversification of ornithischians may be related to the end-Triassic extinction of several herbivore groups that left empty ecological niches to occupy (Olsen *et al*., 2002; Butler *et al*., 2007; Brusatte *et al*., 2008b).

In the case of carnivorous dinosaurs, the Early Jurassic theropods were much more diverse and showed an increased variability of morphologies compared to the Late Triassic. The proliferation of theropods drove the colonization of all continents and increases in size in many new taxa. The coelophysoids (Dilophosauridae and Coelophysidae) dominated during the earliest Jurassic (Brusatte *et al*., 2010; Fig. 3), and basal forms of Ceratosauria and Tetanurae appeared (Smith *et al*., 2007; Dal Sasso *et al*., 2018), being robust carnivores characterized by larger body sizes and more disparate morphology.

The extinction of many carnivores (rauisuchians, phytosaurs and ornithosuchids) at the end of the Triassic surely favoured the evolutionary radiation of theropods and the colonization of new territories during the Early Jurassic (Olsen *et al*., 2002; Brusatte *et al*., 2008b, 2010; Benton *et al*., 2014). Reolid *et al*. (2022) point out that the diversification of theropods (taxonomic and morphological) during the Early Jurassic indicates specializations for different prey and ecological niches related to the diversification of sauropodomophs and ornithischians.

The early Toarcian global warming

Even though the record of Toarcian continental vertebrates is poor, it is clear that some clades of herbivores and carnivores disappeared during the Toarcian biotic crisis (Figs. 2, 3). During the Pliensbachian–Toarcian transition and during the Jenkyns Event, 83% of genera of sauropodomorphs disappeared (10 of 12 genera), accounting for all families of ‘prosauropods’ (Massospondylidae and Anchisauria). Some basal Sauropoda survived into the early Toarcian (*e.g.*, *Barapasaurus*, *Gongxianosaurus, Isanosaurus*, *Ohmdenosaurus***,** *Sanpasaurus*, *Tazoudasaurus*, *Vulcanodon*, and *Zizhongosaurus*; Jain *et al*., 1975; Hou *et al*., 1976; Wild, 1978; Cooper, 1984; Buffetaut *et al*., 2000; Yaonan & Wang, 2000; Allain *et al*., 2004; McPhee *et al*., 2016). But these taxa disappeared before the Aalenian (Fig. 2).

Among the ornithischians, Pliensbachian species disappear, but new genera of Fabrosauridae and Heterodontosauridae are recorded during the Middle Jurassic. In the case of the thyreophorans of the Family Scelidosauridae, the early Toarcian marks their extinction (Fig. 3).

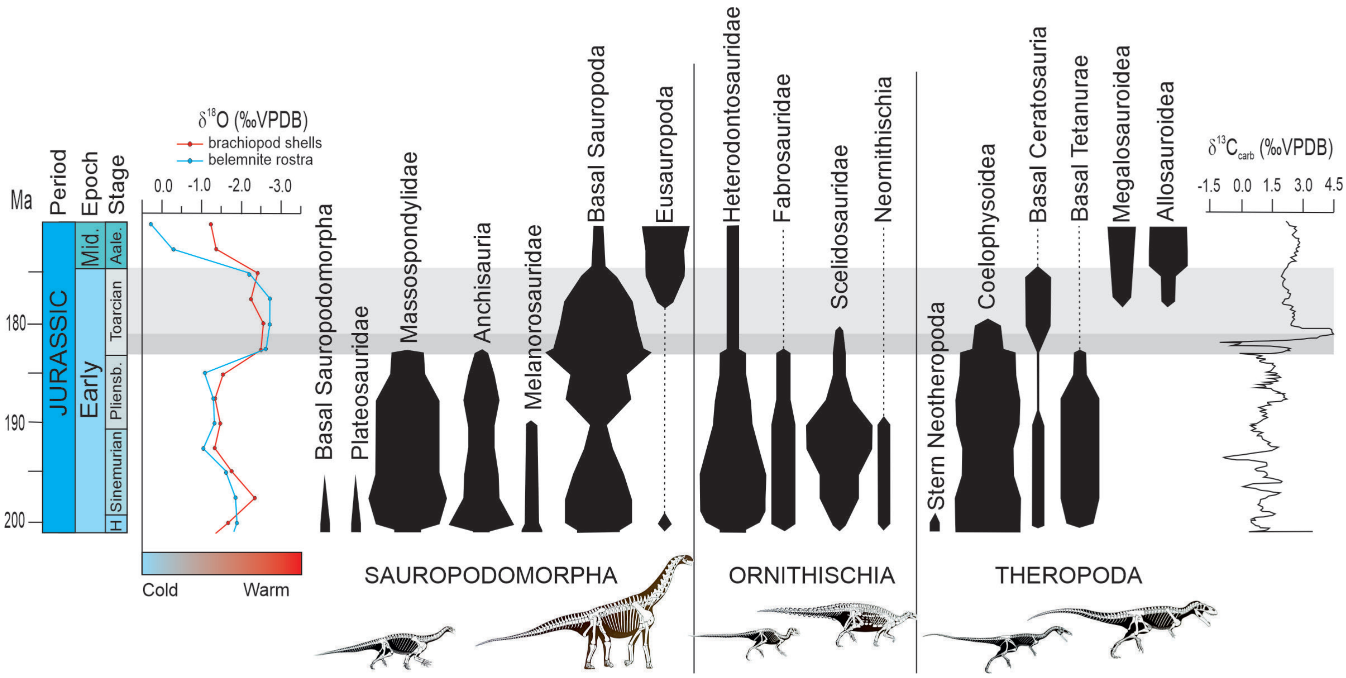

Figure 3. Comparison of the distribution of the main clades of dinosaurs from Hettangian to Aalenian with temperature fluctuations as inferred from $\delta^{18}O$ values (box plots show oxygen isotope data in a 2.5 Myr window) and the composite global $\delta^{13}C$ curve from carbonate by Schoepfer *et al.* (2022) for the Hettangian–Toarcian and by Bartolini *et al.* (1999) for the Aalenian. The width of the bars is proportional to the number of genera. The Jenkyns Event constituted an important biotic crisis with a major role in dinosaur evolution with extinctions and subsequent radiations of new taxa.

Changes in vegetation, the primary producers in trophic chains in terrestrial ecosystems, triggered the extinction of herbivores and the consequent extinction of some carnivores. Land plants suffered a major loss in richness and diversity at the onset of the negative CIE that characterized the Jenkyns Event (Deng *et al.*, 2018; Slater *et al.*, 2019; Danise *et al.*, 2021; Fig. 1). Enhanced weathering, lost of soils and loss of richness of vegetation advanced in parallel with environmental deterioration (Fig. 1). Analyses of spore-pollen assemblages from both hemispheres show that vegetation shifted from a Pliensbachian high-diversity assemblage with conifers, seed ferns and lycophytes, to an early Toarcian low-diversity assemblage dominated by Cheirolepidiacea conifers, and minority cycads, Araucariaceae and Cupressaceae (Escapa *et al.*, 2008; Olivera *et al.*, 2015; Choo *et al.*, 2016; Slater *et al.*, 2019; Danise *et al.*, 2021). Cheirolepidiaceae are interpreted as xerophytic and thermophilous trees of subtropical-tropical climates, and some cheirolepidaceans were coastal shrubs that tolerated seasonally dry and warm conditions (Alvin, 1982; Tosolini *et al.*, 2015), having characteristics typical of disaster taxa that dominate disturbed ecosystems after crises.

As for the carnivores, Pliensbachian theropods were severely affected with the extinction of many taxa during the early Toarcian (*Coelophysis*, *Cryolophosaurus*, *Dilophosaurus*, '*Podokesaurus*', *Segisaurus*). Coelophysoids disappeared in the early Toarcian, probably affected by the extinction of many of their potential prey (Figs. 2, 3). Only two basal ceratosaurians (*Berberosaurus* and *Dandakosaurus*) have been recorded in the lower Toarcian (Fig. 2).

The effects of volcanogenic global warming were hostile for both marine and continental ecosystems of the Early Jurassic (*e.g.*, Little & Benton, 1995; Harries & Little, 1999; Piazza *et al.*, 2020; Pol *et al.*, 2020; Reolid *et al.*, 2022). The early stages of Karoo-Ferrar LIP volcanism occurred at the Pliensbachian–Toarcian boundary (Them *et al.*, 2018; Xu *et al.*, 2018b) and coincided with the initial shift in land plant communities (Slater *et al.*, 2019) and a temperature fluctuation about 5°C warming followed by 8°C cooling in the middle *Polymorphum* (*Tenuicostatum*) ammonite Zone. The main impact on land plant communities recorded at the start of the negative CIE contemporaneous with the main activity phase of the Karoo-Ferrar LIP (Sell *et al.*, 2014; Burgess *et al.*, 2015; Moulin *et al.*, 2017; Them *et al.*, 2018; Font *et al.*, 2022; Ruhl *et al.*, 2022; Fig. 1) and Chon Aike LIP volcanism (Pankhurst & Rapela, 1995) was accompanied by about 10°C warming (Ruebsam *et al.*, 2020b) and enhanced continental weathering (Percival *et al.*, 2016; Them *et al.*, 2017b; Fig. 1). Consequently, during the early Toarcian, drastic climate fluctuations profoundly impacted on continental ecosystems causing a biotic crisis with shifts in flora and fauna.

CONCLUSIONS

The early Toarcian Jenkyns Event was characterized in terrestrial environments by global warming, perturbation of the carbon cycle, enhanced weathering and wildfires. This event profoundly affected the course of dinosaurian evolution. We might expect that heating, arid conditions, and potential acid rain on land should lead to a loss of diversity and plant biomass and would affect the rest of the trophic web.

Early Jurassic (pre-Toarcian) plant assemblages were dominated by conifers (mainly Cheirolepidiaceae and Pinaceae) and ferns with large fronds. Cycadophytes, ginkgophytes, and bennetitaleans and seed-ferns also were common, whereas bryophytes and lycophytes were more abundant in high latitude regions. The plant distribution indicates well-established climatic belts. At this time, sauropodomorphs dominated the herbivore guild and diversified. The basal sauropodomorphs (‘prosauropods’) Massospondylidae and Anchisauria radiated from Hettangian to Pliensbachian. Basal Sauropoda also diversified in the Early Jurassic.

Ornithischians, the other main group of hervivorous dinosaurs, diversified in the Early Jurassic in Gondwana with the radiation of Heterodontosauridae and the origin of Fabrosauridae. The new Suborder Thyreophora, represented by the Family Scelidosauridae, diversified in Laurasia.

Among theropods, Coelophysoidea (families Coelophysidae and Dilophosauridae) dominated during the Hettangian and Sinemurian and extended from North America and Europe to Asia and Africa. In addition, some basal forms of Ceratosauria and Tetanurae appeared in the Early Jurassic.

The beginning of the Toarcian is characterized by decreased diversity and richness of land-plant assemblages. Low-diversity forests were dominated by xerophytic, thermophilic conifers such as Cheirolepidiaceae, indicating seasonally dry and warm conditions. Climatic and vegetation changes drove the extinction of all basal sauropodomorph ‘prosauropods’, at the base of the Toarcian and the basal Sauropoda surviving the Jenkyns Event disappeared during the middle and late Toarcian. The ornithischian armored dinosaurs, Scelidosauridae, died out during the Toarcian. Carnivorous theropods Coelophysidae and Dilophosauridae, which were dominant in Jurassic pre-Toarcian, disappeared with the Jenkyns Event.

Consequently, we recognize the Jenkyns Event as an important biotic crisis for terrestrial ecosystems, affecting plants and dinosaurs. More studies on dinosaurs, but also in other continental tetrapods and in arthropods will help to understand the impact of the Jenkyns Event in the Mesozoic life history.

Supplementary information. The article has two tables as supplementary data available at the Spanish Journal of Palaeontology web-site (https://sepaleontologia.es/spanish-journal-palaeontology/) linked to the corresponding contribution. The information provided by the author has not being copy edited or substantially formatted.

Supplementary Table 1. Data base of dinosaur species from Hettangian (Early Jurassic) to early Aalenian (Middle Jurassic) with taxonomic assignments, updated ages of the lithostratigraphic formations where fossil remains were recovered and geographic areas.

Supplementary Table 2. Data base of δ^{18}O from shells for the Hettangian to Toarcian (Early Jurassic) including average, variance and standard deviation.

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