

The planktonic foraminifera of the Jurassic. Part II: Stratigraphy, palaeoecology and palaeobiogeography

Felix Gradstein¹ · Andrew Gale² · Ludmila Kopaevich³ · Anna Waskowska⁴ · Algimantas Grigelis⁵ · Larisa Glinskikh⁶ · Ágnes Görög⁷

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Abstract The stratigraphy, palaeoecology and palaeobiogeography are outlined for two genera and ten species of Jurassic planktonic foraminifera described in Gradstein et al. (Swiss J Palaeontol 2017. doi:10.1007/s13358-017-0131-z). The two genera are *Globuligerina* and *Conoglobigerina*. *Globuligerina* probably appeared in late Toarcian (late Early Jurassic) and *Conoglobigerina* first occurred in Middle Oxfordian (early Late Jurassic). Within the two genera ten species are defined, including from older to younger: *Globuligerina dagestanica* (Morozova), *G. avariformis* (Kasimova), *G. balakhmatovae* (Morozova), *G. oxfordiana* (Grigelis), *G. bathoniana* (Pazdrowa), *G. jurassica* (Hofman), *G. oxfordiana* (Grigelis) *calloviensis* Kuznetsova emended, *G. tojeiraensis* Gradstein, *Conoglobigerina helvetojurassica* (Haeusler), *C. grigelisi* Gradstein and *C. gulekhensis* (Gorbachik and Poroshina).

Globuligerina balakhmatovae, *G. oxfordiana* and *G. bathoniana* are longer ranging, although there are subtle evolutionary trends in these taxa that may refine stratigraphic usage. Other taxa have shorter stratigraphic ranges. Using stratigraphic trends, test morphology and wall texture changes, the species are tentatively assembled in four evolutionary groups, termed A–D, and in six zones from Late Toarcian through Tithonian. The greater species diversity and possibly also specimen abundance took place in the Kimmeridgian, a time of high global sea level and greenhouse palaeoclimatic conditions. Jurassic planktonic foraminifera preferred marine continental margin conditions instead of the distal open ocean and spread from offshore Eastern Canada to offshore Western Australia along the margins of the Tethys Ocean. The group did not venture into austral or boreal realms, likely reasons why migration probably failed to the west coasts of South and North America.

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✉ Felix Gradstein
felix.gradstein@gmail.com

- ¹ Natural History Museum, University of Oslo, 0318 Oslo, Norway
- ² SEES, University of Portsmouth, Portsmouth PO1 3QL, UK
- ³ Leninskie Gory, Geological Faculty, Lomonosov Moscow State University, GSP-1, Moscow 119991, Russian Federation
- ⁴ AGH Akademia Górniczo-Hutnicza, al. Mickiewicza 30, 30-059 Kraków, Poland
- ⁵ Academy of Sciences, Vilnius, Lithuania
- ⁶ Trofimuk Institute, Ac. Koptyug av. 3, Novosibirsk 630090, Russia
- ⁷ Paleontological Department Eötvös, Loránd University, Budapest 1117, Hungary

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Introduction

This study attempts to synthesize the stratigraphy, palaeoecology and palaeobiogeography of the Jurassic planktonic foraminifera, using the taxonomic–stratigraphic information outlined in Gradstein et al. (2017).

Table 1 shows the geographic distribution of taxa dealt with from the literature and in our sampling (for free specimens), and Fig. 1 shows the stratigraphic distribution of the taxa. The conjugate Jurassic basins of the Grand Banks of Newfoundland and Portugal, including Galicia

Table 1 Geographic distribution of Jurassic planktonic foraminifera studied from our sample material, and the literature

	E Canada, Grand Banks	NW Atlantic, DSDP SITE 534	Portugal, Galicia Bank	UK, Dorset	France	Switzerland, Italy	Hungary, Bulgaria	Poland, Germany	Baltic, S Sweden	W Russia	Crimea, Caucasus	Dagestan, Turkmenistan, Azerbaijan	Turkey	NE Africa, Middle East	NW Australia, Exmouth Plateau
<i>C. gulekhensis</i>	?									X	X				
<i>C. grigelisi</i>	X	X		X											
<i>G. tojeiraensis</i>	X	X			X										
<i>C. helvetojurassica</i>		X		X	X										
<i>G. oxfordiana calloviensis</i>										X			X		
<i>G. oxfordiana</i>	X	X	X	X	X	X	X	X	X	X	X	X	?	X	X
<i>G. bathoniana</i>	X	X			X	X	X			X		?	X	X	
<i>G. dagestanica</i>						X					X				
<i>G. balakhmatovae</i>	X	X		X			X				X				
<i>G. avariformis</i>		?			?						X	?			
<i>G. jurassica</i>	?	?			?					X					

Bank, together contain the stratigraphically longest and taxonomically most complete record, with 5 or 6 taxa confirmed from Bajocian through Tithonian; Crimea and Russia follow after. Sampling wise the record is very fragmented, with long series of continuous samples that are almost barren of Jurassic planktonic foraminifera. An exception is the 70-m-thick Tojeira Formation, Early Kimmeridgian of Portugal, where the taxa are common to abundant throughout. Details are in Gradstein et al. (2017).

For this chapter, A. Görög contributes a detailed palaeobiogeographic reconstruction for the early Middle Jurassic of planktonic foraminifera at a much higher scale of resolution than the global overview on the stratigraphic charts and Scotese maps discussed below. This detailed information was first outlined by Görög and Wernli (2003), using both data from thin-sections and samples with free specimens.

Stratigraphy and evolutionary trends

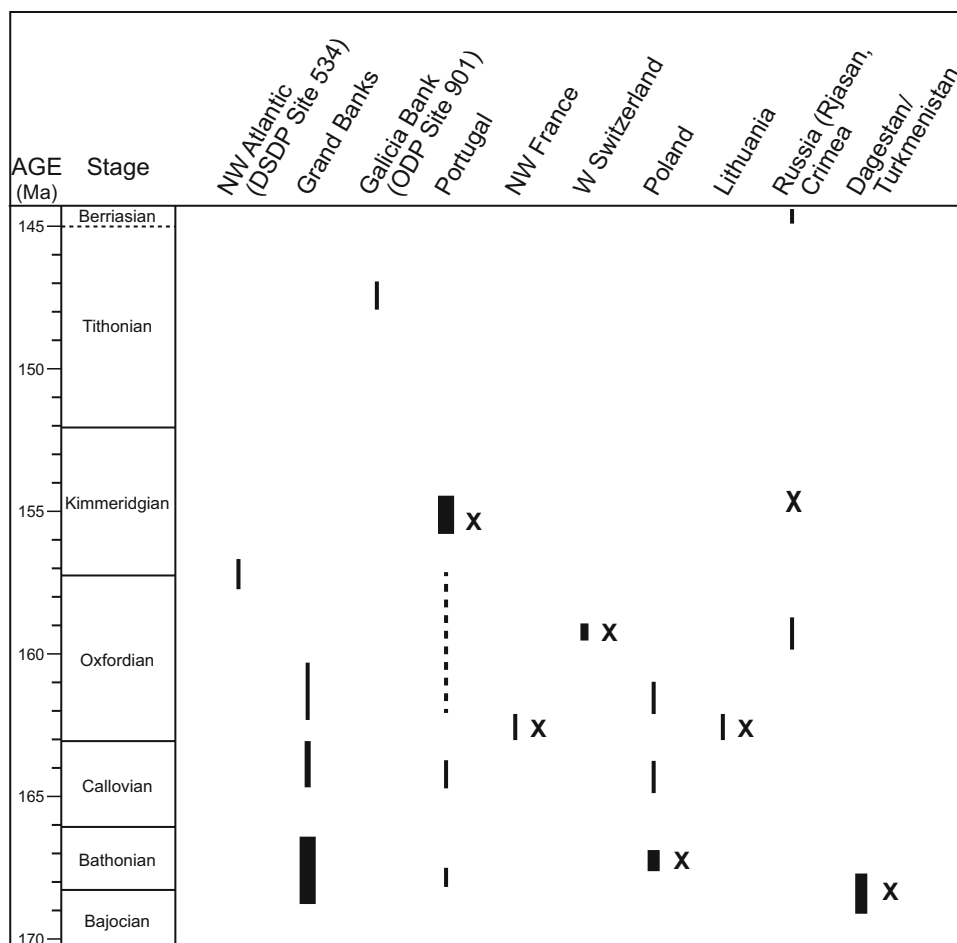
Stratigraphy

The Jurassic Period has a duration slightly over 55 myr, from ~201 to ~145 Ma, and is subdivided into 11 stages. Figure 2 provides a concise stratigraphic overview of the

Period with stage durations, main markers for the global boundary stratotype sections (GSSP), planktonic foraminiferal events as taken from the stratigraphic range chart of Fig. 3 and schematic curves for coastal onlap, eustatic sea level, and geochemical markers (Ogg et al. 2016). We will refer back to Fig. 2 when discussing palaeoecology and palaeobiogeography.

The Middle Jurassic stages Aalenian, Bajocian, Bathonian and Callovian from 174 to 163 Ma are short, each with duration between 2 and 3 myr. The Middle Jurassic with a duration of 11 myr is much shorter than the over 18-myr-long Late Jurassic. If we consider the original study of Wernli (1988) on thin-sections from limestone samples in the Domuz Dag mountain chain of Turkey to document the oldest known occurrence of planktonic foraminifera, this major calcareous marine microplankton group appeared in the geologic record in the Toarcian around 180 Ma ago. If we consider the study by Görög and Wernli (2004) on Tithonian age samples from Hungary as one of the youngest ones in the Jurassic, the Jurassic planktonic foraminifera range from Late Toarcian (*Bifrons*–*Variabilis* Zones) through Late Tithonian (*C. alpina* calpionellid Zone). The poorly known and rare *Conoglobigerina gulekhensis*, together with *Conoglobigerina helvetojurassica* and *Globuligerina tojeiraensis* might qualify as the ‘missing links’ between Jurassic and Cretaceous taxa, but this requires more data on

Fig. 1 Stratigraphic distribution of Jurassic planktonic foraminifera in the localities studied. A *thicker bar* means many specimens, and an *x* refers to species type locality



their taxonomy, geography and stratigraphy. At the same time, it should be stressed that there is only a single study (Wernli 1988) on Jurassic planktonic foraminifera in Lower Jurassic (Toarcian) strata. It is desirable to independently verify the sampling and stratigraphic–micropalaeontologic analysis and also obtain Jurassic planktonic foraminifera from other Toarcian localities, preferably as free specimens.

It should be investigated if the explosion of nannofossils in the Tithonian and the demise of Jurassic planktonic foraminifera are causally related.

Below, we will return to what is known about the origin and evolution of planktonic foraminifera, but first we will have a look at the stratigraphic range chart of Fig. 3. The Toarcian through Aalenian record is only known from thin-sections, and although it is suggestive to consider that a higher spired form like *G. bathoniana* and a smaller, lower spired form like *G. oxfordiana* occur in these thin-sections, this needs documentation with well-preserved free specimens. Test size difference, like smaller Toarcian and larger, or thicker and thinner Aalenian specimens (Wernli 1988; Görög and Wernli 2004) in itself are not taxonomic feature and, in our view have more to do with growth conditions in optimal or suboptimal environments,

selective sediment sorting, water masses and vertical biota distribution and other hard-to-quantify factors in fossil material. These test features should be carefully studied to clarify potential palaeoecologic trends.

Evolution

As outlined in Fig. 3, we distinguish four main groups of taxa, which for simplicity sake are denoted with the letters A, B, C and D.

The A group is monotypic and consists of *Globuligerina balakmatovae*. It has a rather flat test shape, a tendency to ovate and flattened chambers, rarely an imperforate peripheral band, a slit aperture only and no bulla. This morphology is not seen in other *Globuligerina* taxa. Bajocian type illustrations show globular chamber shape to be more common than observed in younger strata, with Kimmeridgian chambers often becoming ovoid and more rugulose (Gradstein et al. 2017; plates 1, 2 and 3). These might be evolutionary features.

The evolutionary relationship of *G. balakhmatovae* is not clear. A possible morphological transition exists to *Oberhauserella* aff. *parocula* described by Wernli and

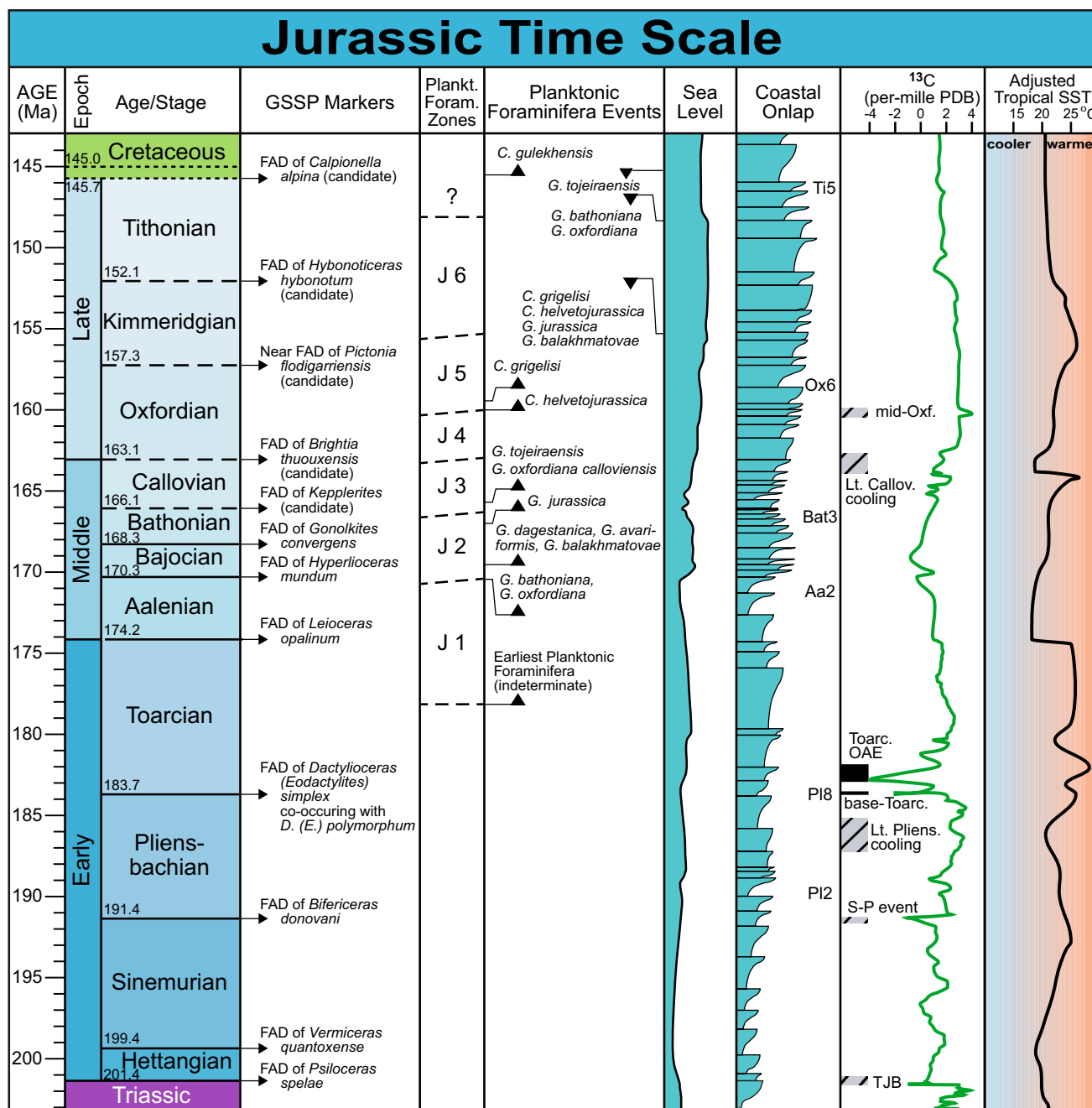


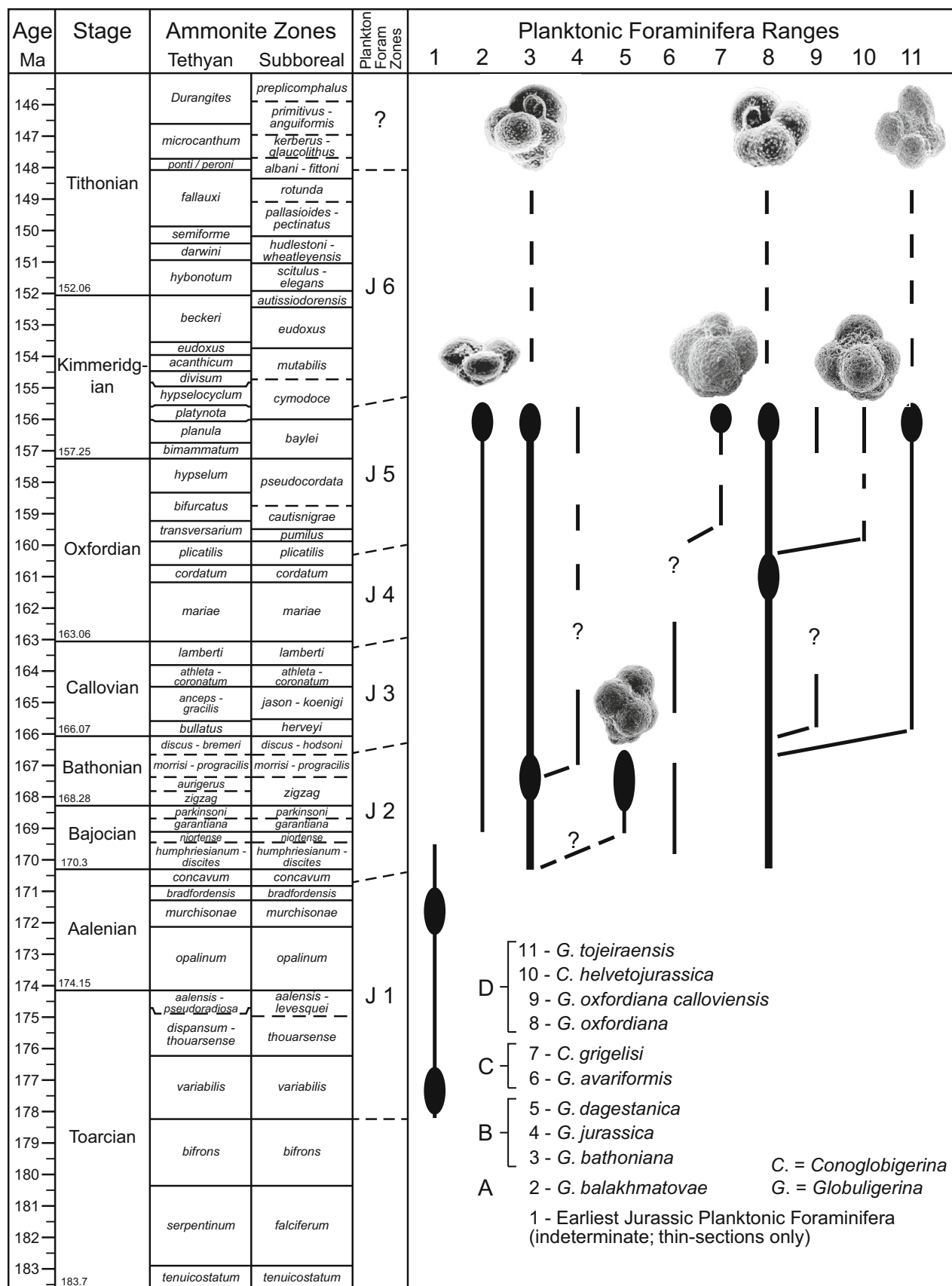
Fig. 2 The Jurassic geologic time scale 2016 (after Ogg et al. 2016) with Jurassic planktonic foraminifera events, using the stratigraphic ranges in Fig. 3. We consider these events to be tentative and open to

revision using stratigraphic ranges data from more sections, particularly in Toarcian–Aalenian and Kimmeridgian–Tithonian intervals

Görög (2007) from SE France, but this requires to refine our knowledge on the stratigraphic appearance of both taxa. If *Globuligerina balakhmatovae* is a single species evolutionary stock, it is taxonomically meaningful to provide a new genus name for it. The name might honour its original author or other key events in its taxonomic and sampling history. But first, a more detailed study of the wall texture should be undertaken, relative to other taxa in the genus *Globuligerina*.

Fig. 3 Stratigraphic range chart of Jurassic planktonic foraminifera using a subdivision in evolutionary groups A–D. We consider the stratigraphic ranges to be tentative and open to revision using information from more sections with planktonic foraminifera, particularly in Toarcian–Aalenian and Kimmeridgian–Tithonian intervals

The B group includes *Globuligerina dagestanica*, the common species *G. bathoniana* and rare *G. jurassica*, all higher spired trochoid morphotypes with an arch to looped aperture and commonly a bulla. If the latter taxon would be



lumped under the first one listed, we can distinguish a taxon with a more symmetrical and regular trochospire with 4 chambers in the last whorl (*bathoniana* type) and a more irregular (or sometimes triangular) trochospire with 3, 3–4 or 4 chambers in the last whorl (*dagestanica* type).

Although it is possible to clearly recognize *G. dagestanica* in its type-region, its occurrence outside this area, particularly in the Jura Mountains needs study (Wernli and Görög 2007). The stratigraphic range of *G. jurassica* is poorly understood, since gerontic specimens of other higher spired forms can agree with its taxonomic description. Both taxa might probably relate to *G. bathoniana*, but since we do not know the detailed morphology of this taxon prior to the Bajocian, it is not possible at this time to assume it to be their ancestor. The morphological variability of *G. dagestanica* is a puzzling feature for evolution, given that *G. bathoniana* shows much more limited morphologic variation, if we exclude its gerontic specimens.

Globuligerina bathoniana also get higher spired through time; no wall texture trend was observed in this taxon.

The C group consists of *Globuligerina avariformis* and *Conoglobigerina grigeli*, both of which do not have a geographically widespread record. The taxa typically have a last whorl that strongly embraces earlier ones, such that the test almost appears involute. An evolutionary lineage is postulated from the compact *G. avariformis* into the equally, or even more compact *Conoglobigerina grigeli*. The latter acquires a reticulate wall sculpture. Its youngest record is Kimmeridgian. The ancestry of *G. avariformis* we refrain from speculating on.

The D group includes *Globuligerina oxfordiana*, *G. tojeiraensis* and *Conoglobigerina helvetojurassica*. These are low-to-medium high-spired morphotypes, with spherical-globular or radially somewhat elongated chambers, narrow to wide umbilicus, large last whorl and arch to looped aperture with lip. In well-preserved and typical *G. oxfordiana* the looped aperture is very slightly offset from the umbilicus. A stratigraphic trend exists to a more reticulate wall texture and the umbilicus opens up.

The ancestor of *Conoglobigerina helvetojurassica*, a species known from the Middle Oxfordian of Switzerland and the Kimmeridgian of Portugal, is postulated to be *Globuligerina oxfordiana*. Morphological intermediates between the two taxa are present, with the last large whorl, nicely ball-shaped chambers and acquisition of a strongly reticulate wall texture being typical features of *Conoglobigerina helvetojurassica*.

The species *Globuligerina tojeiraensis*, with elongated chambers and wide-open umbilicus is known from the Callovian–Oxfordian of the Grand Banks, the Lower Kimmeridgian of Portugal and with isolated specimens from the Tithonian of Galicia Bank, offshore Portugal. Its

overlap in morphology with *G. oxfordiana* suggests the latter to be ancestor. The origin of *G. oxfordiana* is shrouded in mystery.

The origin of the reticulate *Conoglobigerina gulekensis* is not understood; it may sprout from the *oxfordiana*–*helvetojurassica* lineage which itself may have given rise to *Favusella hoterivica* (Subbotina), (Görög and Wernli 2003; Gradstein 2017a). A bend in the coiling axis is common to *C. gulekensis* and *C. helvetojurassica*. Since *Globuligerina bathoniana* did not evolve its wall texture, *Conoglobigerina gulekensis* unlikely evolved from this higher trochoid taxon.

Above summary brings us back to the origin of the planktonic foraminifera. Clemence and von Hillebrandt (2014) recently presented a detailed and thoughtful study on the origin of Jurassic planktonic foraminifera. The Oberhauserellidae (particularly the transitional form *Praegubkinella racemosa*) have been considered as the benthic ancestor stock of Jurassic planktonic foraminifera (e.g. *Conoglobigerina* and *Globuligerina*, see Hart 2003). A close link exists between the distribution and abundance of *Oberhauserella* and *Praegubkinella* taxa and major environmental stress conditions, such as marine oxygen depletion near the Tr–J boundary and in the Early Toarcian. It is not clear if this link is really a palaeoecologic one. Also and more important, benthic *Praegubkinella* is closer in building plan (with toothplate, and inner built foramen, but no tubercles or pseudo muricae) to benthic *Reinholdella* than to *Globuligerina*. *Praegubkinella* evolved from *Reinholdella* in Early Jurassic time. The authors conclude that a direct evolutionary line between both groups cannot be demonstrated.

We add that a taxonomic and stratigraphic study of *Oberhauserella* is desirable in strata where *Globuligerina* also appears. Currently, we have a single detailed study for the Bajocian–Bathonian of France where we may consider that oberhauserellids might have evolved in *Globuligerina* (see Wernli and Görög 2007). This issue needs detailed study, probably also using Micro CT, thin-sectioning and conventional high-resolution SEM imaging.

In the Early Jurassic we find shallow marine Early Toarcian sections with *Oberhauserella*, and a pelagic marine Late Toarcian section in Turkey, with what appears to be *Globuligerina* spp. Hence, there is a gap in the Toarcian of at least 3–5 myr with no information on Jurassic planktonic foraminifera. No data exist that suggest an evolutionary-taxonomic link in the Early Jurassic between *Oberhauserella* and *Globuligerina*.

Although planktonic foraminifera are commonly present in Portuguese sections from Bajocian through Kimmeridgian age (with test size often in the 100–150 µm range), there is not a trace of this biota in Portuguese Lower Jurassic sections (Exton and Gradstein 1984; Rita et al.

2016). Despite extensive sampling and study the same is true for the long stratigraphic well sections, offshore Eastern Canada. Intensive study of relevant sections in Morocco and Turkey is desirable to expand the pioneering information on Toarcian through Bajocian material collected and studied by Wernli (1987, 1988).

With our current knowledge, the origin of Jurassic planktonic foraminifera is shrouded in mystery.

Biostratigraphic scheme

Using our stratigraphically extensive and geographically widespread information on the Jurassic planktonic foraminifera, it is possible to come up with a simplified and tentative biostratigraphic scheme. The user should bear in mind that the rather scattered occurrence, both geographically and stratigraphically makes biostratigraphy with Jurassic planktonic foraminifers difficult. The zonal summary below takes into account our observed first and last occurrences, but stays away from assigning links to ammonite zones. More research is desirable to create a solid biostratigraphy with this, still rather enigmatic group of microfossils.

Stratigraphically upwards in time the following events and acmes may be tentatively recognized (Fig. 3):

Zone J1—Appearance of Jurassic planktonic foraminifera; higher and lower sized tests present; late Toarcian through Aalenian.

Zone J2—Appearance and consistent presence of *Globuligerina oxfordiana* and *G. bathoniana*, with local geographic presence of *G. balakhmatovae*, *G. dagestanica* and *G. avariformis*; Bajocian through Bathonian.

Zone J3—Appearance of *Globuligerina oxfordiana calloviensis* and *G. tojeiraensis*—Callovian

Zone J4—Consistent presence of *Globuligerina oxfordiana* with local geographic appearance of tests with reticulate wall texture on some chambers—early through middle Oxfordian.

Zone J5—Appearance of the genus *Conoglobuligerina* with *C. helvetojurassica* and *C. grigelisi*, with locally common occurrence of *Globuligerina balakhmatovae*, *G. oxfordiana*, *G. bathoniana* and *G. tojeiraensis*—middle Oxfordian through early Kimmeridgian.

Zone J6—Last occurrence of *Globuligerina oxfordiana*, *G. bathoniana* and *G. tojeiraensis*—late Kimmeridgian (?) through part of late Tithonian.

Palaeoecology and palaeobiogeography

The following summary is after Ogg and Hinnov (2012). The Jurassic is commonly considered as an interval of sustained warmth, without any well-documented glacial periods. Oxygen isotope records of oceanic temperature

trends are patchy and heavily biased towards records from Europe and Russia. Glendonite occurrences are observed in high-latitude settings during a few Jurassic intervals. From these proxies it appears that the average climates were an overall warm period (lighter O-18 values) from Hettangian through a peak in Toarcian, but with a possible cold (glendonite-rich) interval during late Pliensbachian and an early Toarcian greenhouse episode, coinciding with a major carbon isotope excursion (see the Toarcian Oceanic Anoxic Event in Fig. 2). Cooler temperatures in Aalenian culminated in a peak in glendonite abundance in Bajocian, but rare or no occurrences after in the Jurassic. No cold-climate markers are found to support a postulated ‘cold-snap’ and glacial induced sea-level regression at the transition from Callovian to Oxfordian, although middle Callovian may have been an intermediate climate optimum, followed by a relative cooling. No glendonites are reported from Late Jurassic, during which there is trend towards more equitable climate—the Boreal/Tethyan temperature difference of ca. 7–9 °C in the middle Oxfordian decreases during the end of the Jurassic. Greenhouse conditions reached a maximum during Kimmeridgian (widespread petroleum source rock), coinciding with a peak in global sea level.

Atmospheric carbon dioxide levels were at least four times the present level, potentially creating the relatively shallow CCD in the oceans. An explosion in productivity in calcareous (nanno-) plankton during the Tithonian, especially the robust nannoconid types, contributed to lowering of the CCD and onset of chalk (‘creta’) deposits that characterize the Lower Cretaceous in all ocean basins. A decrease in pCO₂ during the Tithonian may have been a major factor in this evolutionary surge of calcified plankton. It is not understood if this also led to the demise of Jurassic planktonic foraminifera.

So far this succinct summary does not provide clues why planktonic foraminifera developed. However, running ahead of the argument to be made below that Jurassic planktonic foraminifera are ‘coastal’ facing an oceanic realm, one might argue that during Bajocian time colder climatic conditions provided palaeoceanographic gradients and stress to yield niches for evolutionary development in the species lineages of *G. oxfordiana* and *G. bathoniana*. There is no evidence that the Toarcian OAE (Fig. 2) provided the trigger for planktonic foraminiferal evolution, occurring several million years before the first occurrence of these taxa.

Görög and Wernli (2003) wrote that the widespread occurrence in deeper water strata of Bajocian thick-walled planktonic foraminifera might be due to calcitic overgrowth in deeper water living forms. The authors postulated that smaller forms were surface dwellers and large ones inhabited deeper water environments. A stratigraphic–

palaeoecologic distribution model of Jurassic planktonic foraminiferal morphotypes is postulated, with thick-walled forms in deeper marine and stratigraphically older deposits. A link is indicated between abundance, large-sized tests, and sometimes thick-walled Jurassic planktonic foraminifera and deeper water (Tethys) conditions. Tethyan associations have specimens up to 400 μm in size, and often >70% abundance in assemblages with high-, medium- and low-spired taxa, like *G. bathoniana* types and *G. oxfordiana*. Epicontinental settings yield mostly smaller sized tests <220 μm , have a lower abundance in microfossil assemblages and a higher species variety.

An alternative explanation for the abundance of larger and thicker test assemblages might be that the smaller and thinner aragonite tests all but dissolved in deeper water below the relatively shallow aragonite carbonate depth (ACD).

Figure 4 is a good example of a detailed palaeobiogeographic map of Görög and Wernli (2003) for the Aalenian–Bajocian interval, with a majority of the sites of Bajocian age. The actual map base is from Atlas Tethys Palaeoenvironmental Maps of Dercourt et al. (1993), which maps show palaeoenvironmental and palaeoceanographic settings. Thicker-walled and larger ‘protoglobigerinids’ (a foraminiferal term frequently used by these authors) occupy carbonate-rich Tethys, and thin-shelled assemblages are typical for shallower marine terrigenous facies, adjoining Tethys.

Stam (1986) provided evidence from geologic transects in Portugal that flatter *G. balakhmatovae* prefers a deeper marine habitat than higher spired *G. bathoniana*. Maximum palaeo waterdepth postulated was 250 m.

If we focus only on assemblages with free specimens of Jurassic planktonic foraminifera, it is striking that no record exists of these taxa in truly distal open marine, deep water deposits, cored by the Deep Sea Drilling Projects (DSDP) and International Ocean Drilling Projects (IODP) in Atlantic, proto-Indian and Pacific oceans. An early summary of these finding is in Gradstein (1983). The few, poorly preserved specimens of *G. oxfordiana* in Late Jurassic abyssal sediments of DSDP Site 534 are likely the result of gravity flow deposition, with the species coming from the marine realm along the continental margin, off-shore USA.

We assign palaeoecologic weight to the abundant and diverse record of planktonic taxa in Middle and Upper Jurassic sediments on the Grand Banks of Newfoundland and in Portugal, prior to seafloor spreading in that segment of the North Atlantic Ocean. The Grand Banks and Portugal were separated by a continental seaway, less than 400 km wide prior to seafloor spreading in mid Cretaceous time. The palaeowater depth of the marine strata in these two areas was likely not over 250 m (Gradstein 1976; Stam

1986). The Montejunto Basin in Portugal with the Tojeira shales was a marine half graben not more than 50 km wide (see fig. 5 in Gradstein et al. 2017). Both thin and small and thicker and larger sized tests are present.

The palaeogeographic maps of Scotese on Figs. 5 and 6 help to explain the distribution of Jurassic planktonic foraminifera. Starting with oceanization of the central North Atlantic in Middle Jurassic time, recorded in DSDP Site 534 (Gradstein 1983; Riegraf and Luterbacher 1989) the Atlantic Ocean steadily widened, but no gateway for biota exchange existed to the Pacific prior to Cretaceous time. Planktonic foraminifera locally (!) thrived in Eastern Canadian, South and Central European and some West Asian marine basins and are not typical for the (dark blue coloured) Tethys Ocean. Obducted Jurassic Tethyan Ocean strata may locally have abundant planktonic foraminifera as outlined by Görög and Wernli (2003), but to our knowledge, none of these deposits are truly distal oceanic.

Another clue to the observation that Jurassic planktonic foraminifera are found along Tethys continental margins is provided by the fact that Jurassic planktonic foraminifera have not been described from Pacific Ocean marine strata, and neither from the extensive Jurassic basins along the west coasts of South and North America.

The Bajocian of the Exmouth Plateau, Northwestern Australia and the Bajocian of Grand Banks, Eastern Canada, both yield Jurassic planktonic assemblages. Assuming that the Jurassic planktonic foraminifera originated in the Toarcian–Aalenian of the Middle East (using the findings of Wernli 1988) two migrations may have taken place, one to the west- and northwest, and one to the southeast, following the margins (but not the wide-open sea) of the Tethys ocean. Hence, the spectacular find on the Exmouth Plateau in Australia is not surprising (Apthorpe, unpublished; see Gradstein 2017b).

Since the Jurassic planktonic foraminifera likely did not invade the ‘high seas’, migration around the southern tip of Gondwana to the west coast of S. America was unlikely. It also meant migration outside the Tethyan to sub-Tethyan belt, was unlikely. This might be further investigated by detailed analysis of Jurassic marine strata of western S. America (Peru, Chile) to confirm that Jurassic planktonic foraminifera do not occur there.

The fact that global sea level in Late Jurassic rose by 80+ or more metres relative to present height (Figs. 5, 6) may explain the widespread European distribution of the planktonics during this time.

So far, we have not dwelled on the observation that microperforate foraminifera are known with a benthic and a planktonic habitat. The milestone study by Darling et al. (2009) showed that the living, triserial planktonic foraminifer *Streptochilus globigerus* is genetically the same

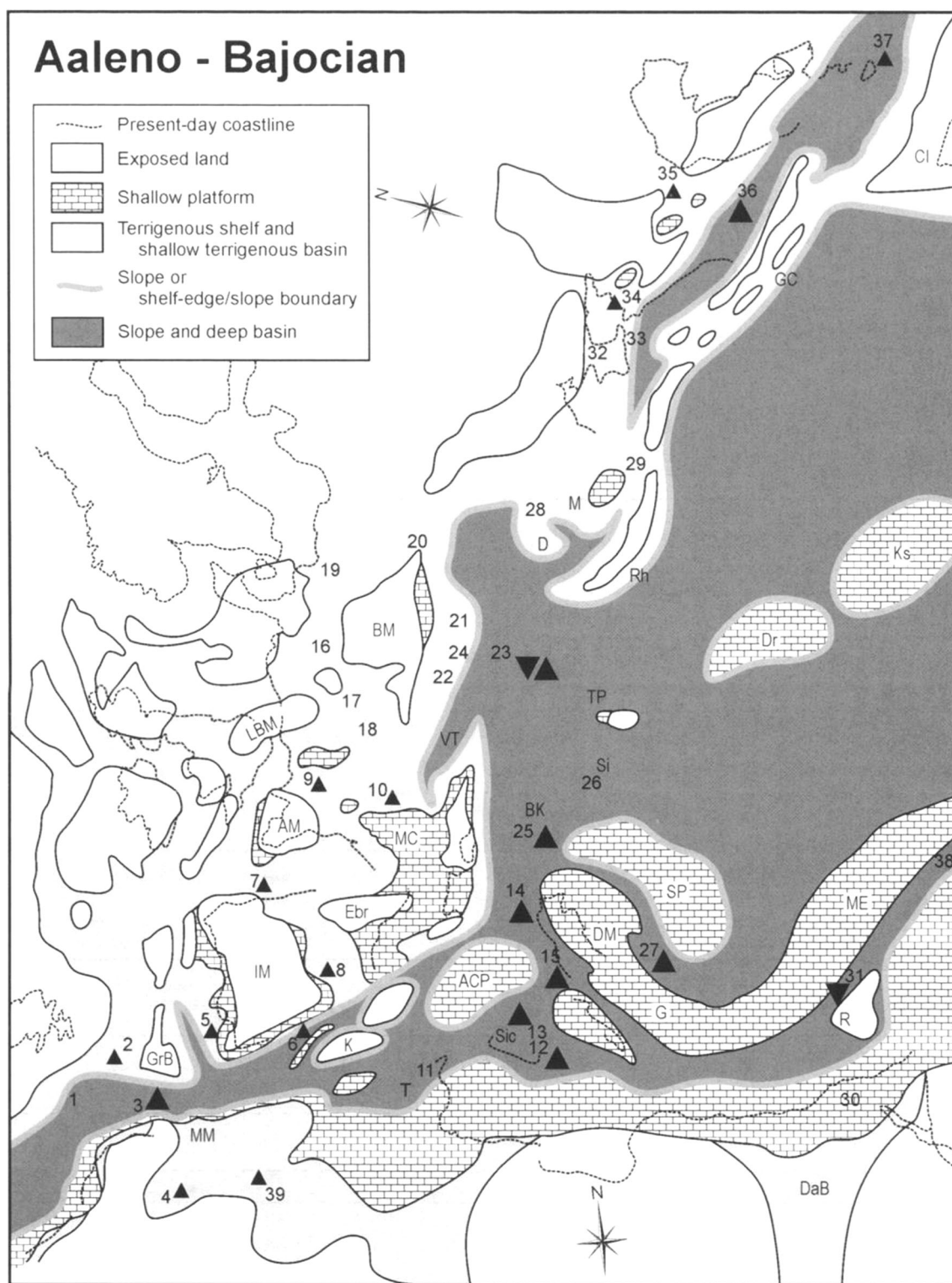


Fig. 4 Palaeogeographical distribution of protoglobigerinids in Aaleno-Bajocian time. The *numbers* refer to the localities listed in Görög and Wernli (2003). *Fat upright triangles* refer to Bajocian age assemblages with thick- and thin-walled specimens; *inverted triangles*

refer to the same for the Aalenian. *Small upright triangles* refer to assemblages with thin-shelled specimens, more or less restricted to shallow marine terrigenous facies

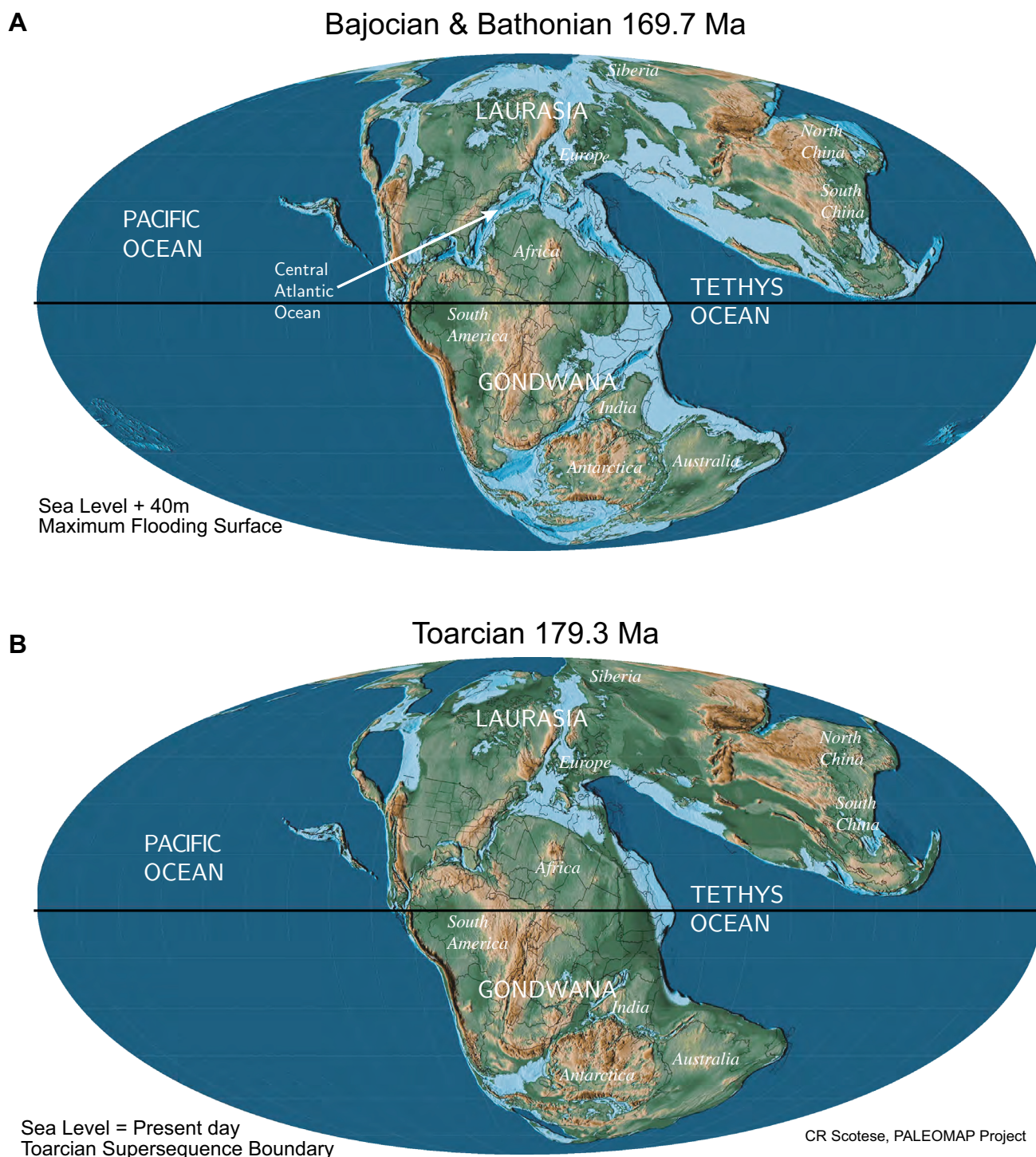


Fig. 5 Toarcian and Bajocian–Bathonian global palaeogeographic reconstructions from Scotese (2014, Paleomap Project)

species as the benthic *Bolivina variabilis*. It shows a potential genetic capacity of benthic foraminifera to overcome major palaeoceanographic upheavals that suddenly modified their biotope. The study also mentions that the living triserial planktonic foraminifer *Gallitellia vivans* had a benthic ancestor in the Miocene.

If we extrapolate this dual habitat to the Jurassic, we hypothesize that aragonitic benthic organisms will not have found a suitable life environment on the deep ocean floor. This situation may be a factor in the preferred distribution of this biota in the South European and East Asian marine basins ‘facing’ Tethys.

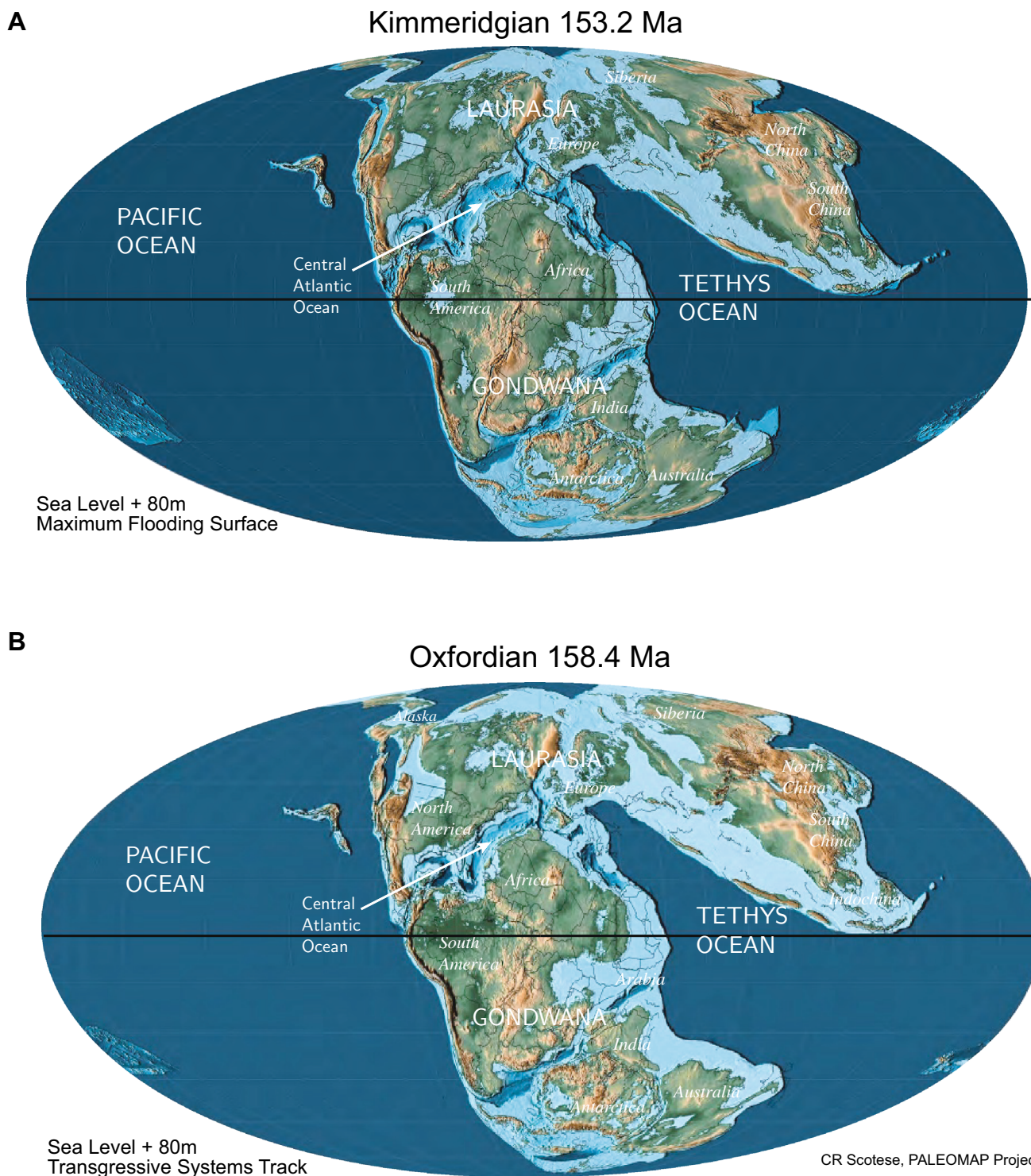


Fig. 6 Oxfordian and Kimmeridgian global palaeogeographic reconstructions from Scotese (2014, Paleomap Project). Global sea level is drawn 80 m over the present height

Although no finds have been reported on potential benthic siblings of Jurassic planktonic foraminifera, we mention the strange life form, figured on plate 17 in Gradstein et al. (2017) of what might possibly be a sessile

stage of a *G. helvetojurassica* in the shallow marine Oxfordian strata of Switzerland. This find, discussed under the taxonomic description of this taxon, needs more detailed analysis. It shows an involute concavo-convex

trochoid test. The final whorl has 4 or 4.5 chambers and a flattened side opposite the last whorl. The flattened side might indicate that the test was attached, hence Jurassic planktonic foraminifera possibly included taxa that were meroplanktonic.

Conclusions

An overview is provided of the stratigraphy, palaeoecology and palaeogeography of Jurassic planktonic foraminifera using stratigraphic series of sediment samples from Canada, Portugal, France, Switzerland, Poland, Lithuania, Russia and Dagestan.

The aragonitic test limits fossilization and may partially account for the scattered stratigraphic and palaeogeographic distribution. The group is known from Middle Toarcian through Tithonian, from ~180 to ~145 Ma; its origin is unknown and there is a lack of studies on pre-Bajocian assemblages. It should be investigated if the explosive abundance of nannofossils in Tithonian and the demise of Jurassic planktonic foraminifera are causally related. The transition from Jurassic to Cretaceous taxa is not understood.

Using stratigraphic trends, test morphology and wall texture changes, the species are tentatively assembled into four evolutionary groups, termed A–D.

The A group is monotypic and consists exclusively of one species, *G. balakhmatovae*, late Bajocian through early Kimmeridgian. A trend exists to larger size, more ovate chamber shape and rougher pustulose wall texture. *Oberhauserella* aff. *parocula* from the Bajocian through Bathonian of the French Jura Mountains may be related.

The B group includes *Globuligerina dagestanica*, the common species *G. bathoniana* and *G. jurassica*. *G. dagestanica* is confined to Bajocian–Bathonian strata in its type area. Middle and Late Jurassic *G. bathoniana* may become higher spired through time. The phylogeny in this group is not clear.

The C group consists of *Globuligerina avariformis* and *Conoglobigerina grigelisi*. An evolutionary trend is postulated to more reticulate wall texture; the oldest record is Bathonian and the youngest record Kimmeridgian.

The D group includes the Middle and Late Jurassic *Globuligerina oxfordiana*, *G. tojeiraensis* and *Conoglobigerina helvetojurassica*. The latter two probably evolved from *G. oxfordiana* with a trend to a reticulate wall texture and wider umbilicus in *C. helvetojurassica* and a trend to radially extended chambers in *G. tojeiraensis*. Both taxa also have a more flaring last whorl compared to *G. oxfordiana*. The origin of *G. oxfordiana* is shrouded in mystery.

The origin of *Conoglobigerina gulekhensis* is not understood; it maybe a side branch of the *oxfordiana*–*helvetojurassica* lineage. *Favusella hoterivica* (Subbotina) may also have originated from *C. helvetojurassica*.

Using our stratigraphically extensive and geographically widespread information on the Jurassic planktonic foraminifera it is possible to come up with a tentative biostratigraphic scheme. The user should bear in mind that the rather scattered occurrences of taxa, both geographically and stratigraphically, makes biostratigraphy with Jurassic planktonic foraminifera difficult and tentative at best.

Zone J1—Appearance of Jurassic planktonic foraminifera; higher and lower sized tests present; late Toarcian through Aalenian.

Zone J2—Appearance and consistent presence of *Globuligerina oxfordiana* and *G. bathoniana*, with local geographic presence of *G. balakhmatovae*, *G. dagestanica* and *G. avariformis*; Bajocian through Bathonian.

Zone J3—Appearance of *Globuligerina oxfordiana calloviensis* and *G. tojeiraensis*—Callovian

Zone J4—Consistent presence of *Globuligerina oxfordiana* with local geographic appearance of tests with reticulate wall texture on some chambers—early through middle Oxfordian.

Zone J5—Appearance of the genus *Conoglobigerina* with *C. helvetojurassica* and *C. grigelisi* and locally common occurrence of *Globuligerina balakhmatovae*, *G. oxfordiana*, *G. bathoniana* and *G. tojeiraensis*—middle Oxfordian through early Kimmeridgian.

Zone J6—Last occurrence of *Globuligerina oxfordiana*, *G. bathoniana* and *G. tojeiraensis*—late Kimmeridgian (?) through part of late Tithonian.

Greatest species diversity and possibly also specimen abundance took place in the Kimmeridgian, a time of high global sea level and greenhouse palaeoclimatic conditions.

Jurassic planktonic foraminifera preferred marine continental margin conditions instead of the distal open ocean and spread from offshore Eastern Canada to offshore Western Australia along the margins of the Tethys Ocean. The group did not venture in austral or boreal realms, likely reasons why migration probably failed to the west coasts of South and North America.

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