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The first 40 million years of planktonic foraminifera

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Abstract

We provide a biochronology of Jurassic planktonic foramininfera, using first order linkage to ammonite and nannofossil stratigraphy and geochronology. This enigmatic and understudied group of microfossils occurred from middle Toarcian through Tithonian time, from ~180 to ~143 Ma; its origin is unknown. There are three genera: *Globuligerin*a, *Conoglobigeri*na and *Petaloglobigerina*. The genus *Globuligerina*, with a smooth to pustulose test surface texture appeared in Toarcian (late Early Jurassic) and *Conoglobigerina*, with a rough reticulate test surface texture in Oxfordian (early Late Jurassic) time. The genus *Petaloglobigerina*, with a petaloid last whorl and one or more twisted and claviform chambers evolved in early Kimmeridgian time from *Globuligerina balakhmatovae*. We recognize stratigraphic events from eleven species across four evolutionary lineages, calibrated to Geologic Time Scale 2020. A dramatic faunal change over, which is not well documented led to the survival of only one taxon, most likely *Gobuligerina oxfordiana* in the Tithonian. During the Berriasian several new taxa appeared.

Keywords: Planktonic foraminifera, Jurassic, evolution, biochronology.

Introduction

We provide a tentative biochronology of Jurassic planktonic foramininfera, using their taxonomy, stratigraphy, paleoecology and paleogeography with first order linkage to ammonite and nannofossil stratigraphy and geochronology. The study uses bio-chronostratigraphic information summarized in the section called 'Stratigraphic Inventory' on this enigmatic and understudied group of microorganisms. For one, studies on the earliest (Toarcian) record in this group are wanting, and there is no information on evolutionary transition in Tithonian time to Cretaceous planktonic foraminifera.

The summary below takes from our recent studies (Gradstein et al., 2017a; Gradstein & Waskowska, in press). The Jurassic planktonic foraminifera were microperforate and probably all aragonitic in test composition, in equilibrium with Jurassic high-magnesium calcite seawater. The aragonitic test limits fossilization and may partially account for the scattered stratigraphic and paleogeographic distribution. We have not found evidence for dimorphism and asume reproduction was sexual as in recent planktonic foraminifera. The group occurred from middle Toarcian through Tithonian time, from ~180 to ~143 Ma; its origin is unknown. The earliest record is from one locality in Turkey only, suggestive of the isolated population concept in evolution. The literature record since 1881 counts fewer than 100 publications.

Coiling mode, chamber configuration in the last whorl, wall texture and intraspecific variation in aperture shape are key taxonomic features; it precludes use of thin-sections for taxonomy. Some taxa have pore mounds and all but one may have a 'kummer-form' last chamber (bulla). Wall texture underwent evolutionary change from smooth and pustulose to reticulate and honey combed. Creating a rougher wall surface texture is a biological measure to enhance drag and flotation, likely advantageous to Jurassic planktonic foraminifera.

There are three genera: *Globuligerin*a, *Conoglobigeri*na and *Petaloglobigerina*. *Globuligerina*, with a smooth to pustulose wall surface texture appeared in Toarcian (late Early Jurassic) and *Conoglobigerina,* with a rough reticulate wall surface texture in Oxfordian (early Late Jurassic) time. *Petaloglobigerina*, with a petaloid last whorl and one or more twisted and claviform chambers evolved in Kimmeridgian time from *Globuligerina balakhmatovae*. A dozen stratigraphic events are recognized across four evolutionary lineages, calibrated to Geologic Time Scale 2020 (Gradstein et al., 2020). The Jurassic planktonic foraminifera preferred marine continental margin conditions along the margins of the Tethys Ocean.

Principles of biochronology

Biostratigraphic correlation is not necessarily time correlation. It may approximate time-correlation, or it may be the identification of the same biofacies and potentially be diachronous, because comparable fossil record in samples some distance apart, does not imply synchronicity of deposition.

The above conservative statement comes from the International Stratigraphic Guide (Salvador (ed.), 1994: 65-66). The Guide recognizes (and sparsely defines) units and principles of biostratigraphy, but does not recognize and define biochronology. The most likely reason is that the latter is a predictive interpretation, and not an observation and description of fossil correlation. In its formal stratigraphic presentation the Guide has no place for biochronology, since the latter resolutely bypasses zones, stages and chronostratigraphy on its way to geochronology.

Biochronology avoids the classical concept of zones (and stages), in favour of ‘the organisation of geologic time according to the irreversible process of evolution in the organic continuum’ (Berggren and Van Couvering, 1978: 39). The authors lament that the essential desire to extend correlation in time, mistakenly is an activity in stratigraphy, whereas it properly is an exercise in geochronology. *Biochronology attempts to rank, order and scale fossil events and fossil ranges in linear time, and scale regional stratigraphies with isochrons*

Despite not being honoured by the International Stratigraphic Guide, biochronology is really what a great many paleontologists and stratigraphers are after. Many studies aim to generate an optimum network of fossil correlations, thought to embody a reliable and high-resolution isochronous time (lines) framework. Linking such a network with magnetochrons, stable and unstable isotope determinations, and cyclothems, albeit in danger of inviting circular reasoning, creates a geochronologic correlation framework.

Paleontologic events

The key to biochronology and its building blocks are fossil events. A fossil or paleontological event is the presence of a taxon in its time context, derived from its position in a rock sequence. Most commonly used are First Appearance and Last Appearance Datum’s (FAD and LAD). Since the first or last appearance datums may be difficult to recognize or distinguish where specimen numbers dwindle or get obscured by ‘noise’ (like reworking of fossil tests), it can be advantageous to substitute with first and last consistent (or common) appearances. A first or last appearance datum is consistent when such stratigraphic range endpoints are part of an observed continuous stratigraphic range (Fig.1).

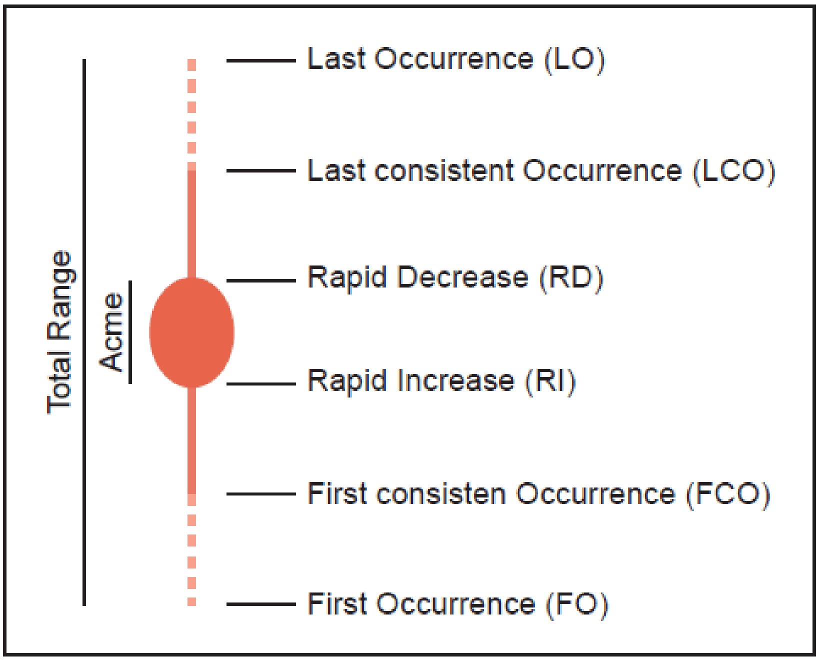

Figure 1. Terminology of biostratigraphic events along the total stratigraphic range of a single taxon. The first and last consistent occurrence may coincide with the first and last common occurrence; the rapid increase and rapid decrease encapsulate the acme of the taxon. Instead of First or Last Occurrence, First or Last Appearance is frequently used. The former is more a chronostratigraphic term, and the latter a geochronologic one.

If the fossil record encountered in stratigraphic sections that we want to correlate and calibrate in time would be ubiquitous and perfect, *i.e*. if only time would control the appearance, range and disappearance of taxa, then biostratigraphy would be a straightforward exercise. The science of biochronology, as developed for the evolutionary first and last occurrence datums of ocean plankton, in conjunction with geomagnetic reversals in Deep Sea Drilling Sites, would be a matter of systematic book keeping on a worldwide scale, only constrained by taxonomic deliberations. Unfortunately, the paleontological record is highly imperfect, and its noise may call for more intricate, or even murky biostratigraphic decision making (for example when absence of occurrence is an argument) that detracts from the validity of a potential biochronologic framework.

Factors bearing on the quality of the fossil record are in Figure 2. Together, these uncertainty factors are as follows:

1. Quality and quantity of sampling
2. Specimen frequency of fossil taxa
3. Confidence of taxonomic identification
4. Influence of environmental change on the stratigraphic range of taxa
5. Differential rate of taxon evolution in different parts of the world
6. Time lag in migration of taxa, where correlation is over large distances, or across major environmental barriers.

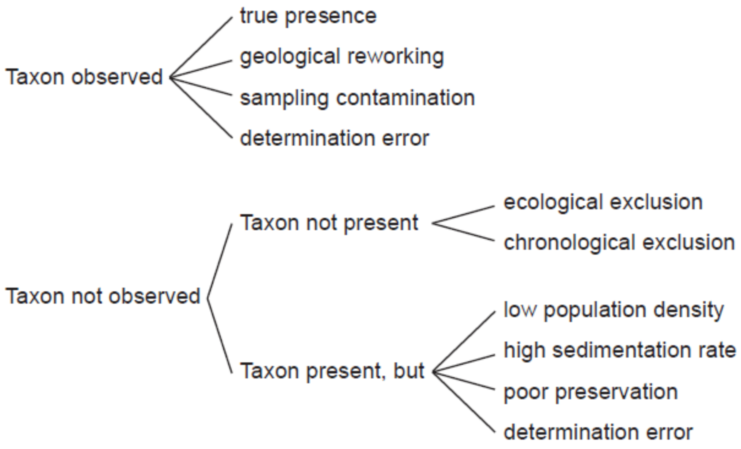

Figure 2. Sampling factors bearing on the quality of the paleontologic event record. With Jurassic planktonic foraminifera the state of preservation, either aragonitic (which is the original composition of the test) or calcitic plays a role, and so does the rate of sedimentation. For details, see text.

A more extensive description of these factors is in Gradstein *et al*. (1985).

If significant diachroneity is observed for bioevents, *e.g.*, by plotting them against magnetochrons or stable isotope spikes in two or more sections, than a numerical method or graphic illustration should be devised to quantify the error bar on bioevent correlations. As a matter of routine latitudinal or environmental shifts in event calibrations should be taken into account.

Material and methods

The Polish, Dagestan and Portuguese outcrop sections and offshore eastern Canada well sections and were described with great stratigraphic detail and with complete geographic notations in Gradstein et al. (2017a). Sample numbers used in the current study refer to the notations and stratigraphic sections in this literature reference.

In addition to standard Leica (M205C with PLANAPO 1.0x and 1.6x objectives) and Nikon (VL100POL) stereo microscopes, good use was made for wall texture determination of the Leica DM 750M biological microscope with polarizer/analyser and Epi 10x/0.25 and N Plan L 20x/0.35 and Plan L50x/0.50 objectives. Both objectives have long distances between objective and specimen and allow optimum incident light illumination. Digital optical images were obtained efficiently with the Deltapix M12ZS digital microscope with 1.25, 2.5 and 4.16 objectives and Insight stacking software. SEM images were obtained with the FEI QUANTA 200 FEG scanning microscope at the Laboratory of Phase, Structural, Textural and Geochemical Analyses of the Faculty Geology, Geophysics and Environmental Protection at AGH, Krakow, Poland.

Stratigraphic inventory

Below we describe in stratigraphic order, from Toarcian through Berriasian-early Valanginian our sample material with planktonic foraminifera as free tests from washed sample residues. The listing of these 25+

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localities worldwide also includes critical literature references with planktonic assemblages from which we do not have specimens or sample material (indicated with a small x). Figure 3 shows the majority of localities from which Jurassic planktonic foraminifera are known (Gradstein et al., 2017b), including the key ones on which the current analysis is based. The zonal and age assignments, as derived from ammonite or nannofossil zonations follow the chronostratigraphic subdivisions of the Jurassic and earliest Cretaceous stages in Ogg et al. (2016), Hesselbo et al. (2020) and Gale et al. (2020. Note that the early, middle and late subdivision of stages is not formalized and open to change.

Figure 3. Occurrence of Jurassic planktonic foraminifera in the Tethyan - sub Tethyan marine belt. Reference to the localities is after Gradstein et al. (2017b, c) and this study.

Middle Toarcian, SW Turkey (x)

Bifrons – *Variabilis* Zones, thin-sections, *Globuligerina* spp.; tests on average 150µm (Wernli, 1988).

Early Aalenian, SW Turkey (x)

Opalinum Zone, thin-sections, *Globuligerin*a spp., (thick walled), tests on average 250µm (Wernli, 1988).

Early Bajocian, Morocco (RIF) (x)

Sauzi Zone, *Globuligerina* spp., tests on average 280-300µm, maximally 340µm (Wernli, 1987).

Early Bajocian, NW Australia (x)

Study and locality: Small clay samples from marine dredges acquired along the NW Australian Continental Margin, facing the Argo Abyssal Plain of Tethys contain about 75+ fragile and small, aragonitic planktonic foraminifera.

Age: Early Bajocian, using nannofossils and dinoflagellates.

Microfossil assemblage: *Globuligerina oxfordiana, G.bathoniana* and a species that maybe endemic to this region. The assemblage needs comparative study.

Reference: Apthorpe (2020).

Middle Bajocian, Hungary (x)

Study and locality: Hard "Ammonitico Rosso" limestone of Som Hill, Bakony Mountains yielded a diversified and rich planktonic foraminifera assemblage, using weak acidisation to disengage the tests from the limestone matrix. The acidisation does not preserve wall textures of the test, necessary to differentiate genera.

Zones and age: *Humphriesianum* and *Niortens*e Zones, middle Bajocian.

Assemblage: The planktonic assemblage is diverse and dominated by large specimens, often reaching 400µm in diameter, including *Globuligerina* aff. *dagestanica*, *Globuligerina oxfordiana* (medium and large forms), *Globuligerina* aff. *bathoniana* (large form), and *Globuligerina avariformis.*

Reference: Wernli & Görög (1999).

Middle Bajocian, France (x)

Study and locality: Find of Jurassic planktonic foraminifera in the type section of the Bajocian Stage, France.

Zone: *Humphriesianum* Zone, middle Bajocian.

Assemblage: Poorly preserved *Globuligerina oxfordiana* in a biomicrite with ferriginous oolites, attesting to the shallow marine nature of the sediment.

Reference: Bignot & Janin (1984).

Late Bajocian, Azerbijan (x)

G.K. Kasimova and D.G. Aliyeva in 1984 briefly described *Conoglobigerina avariformis* Kasimova from the Bajocian of Azerbaijan. The holotype illustrations are drawings without wall sculpture information, but a metatype illustrated in Simmons et al. (1997) has short pseudomurical ridges.

Late Bajocian-Early Bathonian, Dagestan (Russia)

Study and locality: In 1961, V.G. Morozova and T.A. Moskalenko for the first time described a rich Jurassic '*Globigerina*' biofacies, with abundant free specimens of several taxa. The assemblage occurs in fine grained, bathyal shales near the villages of Gunib and Chokh, Central Dagestan, NE Caucasus. The Gunib section has geographic coordinates 42^0 23′16N:46^0 57′ 40E, and the Chock section 42^0 19′ 18N:47^0 1′ 57E.

Zones and Age: *Parkinsonii* and *Zigza*g Zones, late Bajocian- early Bathonian. **Assemblage**: *Globuligerina dagestanica*, *Globuligerina balakhmatovae* and *Globuligerina oxfordiana*. The planktonic assemblage is associated with epistominids and discorbids.

Through the courtesy and cooperation of Temirbekova Umuhayabat Temirbekovna (Makhachkala, Dagestan) we obtained Jurassic planktonic specimens from the type sections near Gunib and Chokh in Central Dagestan. This allowed us to study topotype specimens. Through the courtesy of co-author Ludmila Kopaevich we also obtained micropaleontology slides with planktonic foraminifera of the Gunib and Chokh sections from the Gorbachik collection in Moscow.

References: Morozova & Moskalenko (1961); Gradstein et al. (2017a).

Late Bajocian-Early Bathonian, Dagestan (Russia)

Study and locality: Co-author LG participated in 2015 in a field trip to a nearby and stratigraphically identical section (42^0 9$'$ 23N:47^0 7$'$ 60E) to Gunib and Chokh. This means that the Jurassic planktonic foraminifera in it are essentially topotypes of those described first by Morozova and Moskalenko (1961). The stratigraphic levels in this new section ХУРУКРА (Khouroukra) were studied and sampled together with specialists in ammonite and belemnites, and described in Cherkashin et al. (2015, in Russian, where the Khouroukra section is described on p. 66-68 and shown in their photograph 24). The studied part of the Khouroukra section includes the lower and middle subformation of the Tsudakhar Formation.

The lower subformation shows interbedded light gray siltstones and sandstones. The middle subformation consists of a dark gray claystones, with interbeds of siltstones, rare sandstones, with siderite concretions. There are rare and thin (0.10-0.15 m) interbeds of calcareous rocks.

Zones and age: *Parkinsonii* and *Zigzag* Zones, **l**ate Bajocian - early Bathonian.

Assemblage: Gastropodes, ostracodes and a relatively rich and diversified benthonic foraminifera assemblage with *Hyperammina, Trochammina, Reophax, Ophthalmidium, Ichthyolaria, Dentalina, Lenticulina, Oberhauserella, Epistomina* and *Discorbis* (*D. paraspis*), together with planktonic foraminifera. The latter are well preserved and common to abundant, and include *Globuligerina dagestanica*, *Globuligerina oxfordiana, Globuligerina glinskikhae* and *Globuligerina balakhmatovae.*

References: Gradstein et al. (2017a); Gradstein & Waskowska (in press).

Bajocian-Bathonian-Callovian, Grand Banks, offshore eastern Canada

Study and stratigraphy: From 1970 until 1995 senior author FG was professionally involved with the biostratigraphy of the sedimentary wedge along the continental margin of eastern Canada.

Zones and age: *Garantella-*, *Globuligerina bathoniana-* and *Reinholdella crebra* var. Zones, Bajocian through Callovian.

Microfossil assemblages: In side-wall-cores (swc) and cuttings (cts) samples between 10600 and 6230 feet in the Eider M-75 well *Globuligerina bathoniana* and *Globuligerina oxfordiana* occur in abundance, and *Globuligerina balakhmatovae* is common. Preservation of the calcite tests is excellent. The same three species also occur in the same stratigraphic interval in the Murre G-67 and Cormorant N-83 wells. In swc's at 5000 and 5350 feet in the Bittern M-62 well, assigned to the *Reinholdella crebra* var Zone (Callovian) *Globuligerina tojeiraensis* occurs with few specimens together with a small and compact globigerinid form tentatively determined as *Conoglobigerina grigelisi*. Deeper in the same well assigned to the *Globuligerina bathoniana* Zone (Bathonian) occur *Globuligerina balakhmatovae* and *Globuligerina bathoniana*.

References: Gradstein (1976), Stam (1986), Gradstein et al. (2017a).

Middle Bathonian, Portugal

Rare specimens of *Globuligerina bathoniana* occur in the shallow marine sedimens of middle Bathonian age in the Brenha Road section, Mondego area, Portugal (Stam, 1986).

Middle Bathonian, Poland

Study and locality: In 1969, Olga Pazdrowa published 'Bathonian Globigerina from Poland', (Pazdrowa, 1969). The taxon *Globigerina bathoniana* was described with about 150 well-preserved specimens from the ore-bearing clays of Ogrodzieniec, Zawiercie County, Southern Poland at 50^0 27' N and 19^0 31' E. Author FG received from Olga Pazdrowa a foraminiferal assemblage from Ogrodzieniec, including the globigerinid taxon. Later, he undertook self micropaleontological sampling of the strata in the Ogrodzieniec claypit; these samples were used in the PhD. study by Stam (1986). Now, the Ogrodzieniec quarry has been partly filled in and made inaccessible (but see below).

Zone and age: *Morris*i Zone, middle Bathonian.

Assemblage: The local foraminiferal assemblage is diverse, and from the list of taxa received from Olga Pazdrowa includes: *Garantella ornata*, *Reinholdella crebra*, *Epistomina regularis*, *E. costifera*, *E. nuda*, *Paleomiliolina czestochowiensis*, *Ophtalmidium agglutinans*, *O. carinatum*, *Paalzowella pazdroae*, *Spirillina radiata* and *Conorboides paulus*. According to Pazdrowa (1969) the Jurassic planktonic foraminifera lived in a shallow marine basin with siliciclastic sedimentation. We interpret this paleo environment as probably deep neritic, using the evidence from epistominids with Jurassic planktonic foraminifera from other basins (Stam, 1986).

References: Pazdrowa (1969); Stam (1986); Gradstein et al. (2017a).

Middle Bathonian, Poland

Study and locality: After the Ogrodzienie quarry became non-existent (see above), co-author AW undertook fieldwork and sampling of the same *Morissi* ammonite Zone in the Gnaszyn iron ore quarry in the southern part of Kraków-Silesia. The Gnaszyn (Gnaszyńscy) quarry (coordinates: N$50^0$48' 11.4" E$19^0$02' 31.9") is located in the SW.Częstochowa city area of the Gnaszyn district. The 25 m thick section of dark shales represents the higher part of the Częstochowa ore-bearing clay formation being locally 140m thick. The monotonous, strongly bioturbated black or dark greyish siltstones and claystones are rich in bioclasts, occasionally with different amount of sandy admixture. It contains seven levels of sphaerosideritic concentrations (N-T horizons).

Zone and age: *Morrisi* Zone – middle Bathonian.

Fossil assemblage: There is a diverse and rich fossil fauna with ammonites, belemnites, bivalves, scaphopods, gastropods, foraminifers, echinoderms and shark teeths, as well as trace fossils, calcareous nannoplankton, pollen, sphoromorphs, dinoflagellates and driftwoods. Benthic foraminifera include are dominated by Ceratobuliminidae and Vaginulinidae, and smaller numbers of agglutinated taxa.

The Jurassic planktonic foraminifera bearing GN-6 sample was taken in the lower part of the Gnaszyn section. This is a grey and slightly sandy claystone with numerous bioclasts, mainly of mollusks shells. The sample is rich in very well preserved, aragonitic planktonic foraminifera with *Globuligerina oxfordiana* and fewer *Globuligerina bathoniana, Globuligerina glinskhikae* and *Globuligerina waskowskae.*

References: Smoleń (2012); Gedl et al. (2012); Gradstein et al. (2017a); Gradstein & Waskowska (in press).

Middle Callovian, Portugal

Study and locality: Along the Mareta Beach section in southern Portugal, thick and well bedded calcareous shales crop out, locally with thin sand layers with ripple marks, load and flute casts, and upwards in the beach section with more marls and limestones. The shales and marls have common *Bositria.*

Zone and Age: Bordalo da Rocha (1976) assigned a late Bajocian through Callovian age to the lithological unit, using a detailed ammonite zonation.

Micropaleontologic assemblage: Middle Jurassic foraminiferal paleoecology and Jurassic planktonic foraminifera in the Mareta Beach section were investigated by Stam (1986). In sample 31 (*Coronatum* Zone, middle Callovian), the author recognized rare *Globuligerina bathoniana.* The neritic setting of the Callovian strata, with few epistominids, does not lend itself to find Jurassic planktonic foraminifera in abundance.

References: Bordalo da Rocha (1976); Stam (1986); Gradstein et al. (2017a).

Early Oxfordian, NW France

Study and locality: In 1966, G. Bignot and J. Guyader discovered several dozen small specimens of *Globuligerina oxfordiana* (Grigelis) in the clays of Villers, Le Havre, Normandy, Northwest France.

Zone, stage and microfossil assemblage: The level is lower Oxfordian, *Mariae* Zone, about 6m below the *Cordatum* zone with ferruginous oolites. Jurassic planktonic foraminifera are from a low energy, shallow marine embayment, connected to open sea. Using the paleo waterdepth model of Stam (1986) the species lived in a shallow marine environment, not exceeding 150m in paleo waterdepth (Samsom et al., 1992). G. Bignot kindly donated *Globuligerina oxfordiana* specimens to Gradstein for comparison to Grand Banks specimens.

References: Bignot & Guyader (1966); Stam (1986), Gradstein et al. (2017a), Gradstein & Waskowska (in press).

Middle Oxfordian, Switzerland

Study: In April 2016, author Gradstein visited the Natural History Museum in Basel, Switzerland to study type slides listed to contain *Globigerina helvetojurassica* Haeusler, and also sample the nearby Eisengraben Section to obtain fresh microfossil material containing this species. The museum type slides did not contain suitably preserved specimens of this taxon, and are unrecognizable, but topotypes of this taxon were successfully sampled, under the expert guidance of W. Etter and M. Knappertsbusch.

Locality: The Eisengraben Section, ca 35km NW of Zuerich in Canton Aargau, Switzerland is the type section of the Birmenstorfer Schichten, *Tranversarium* Zone, middle Oxfordian. The section has coordinates 651 600/264 070 on Schweizerische Landeskarte 1:25000, Blatt 1069, Frick (reference figure 4 in Oesterle, 1969).

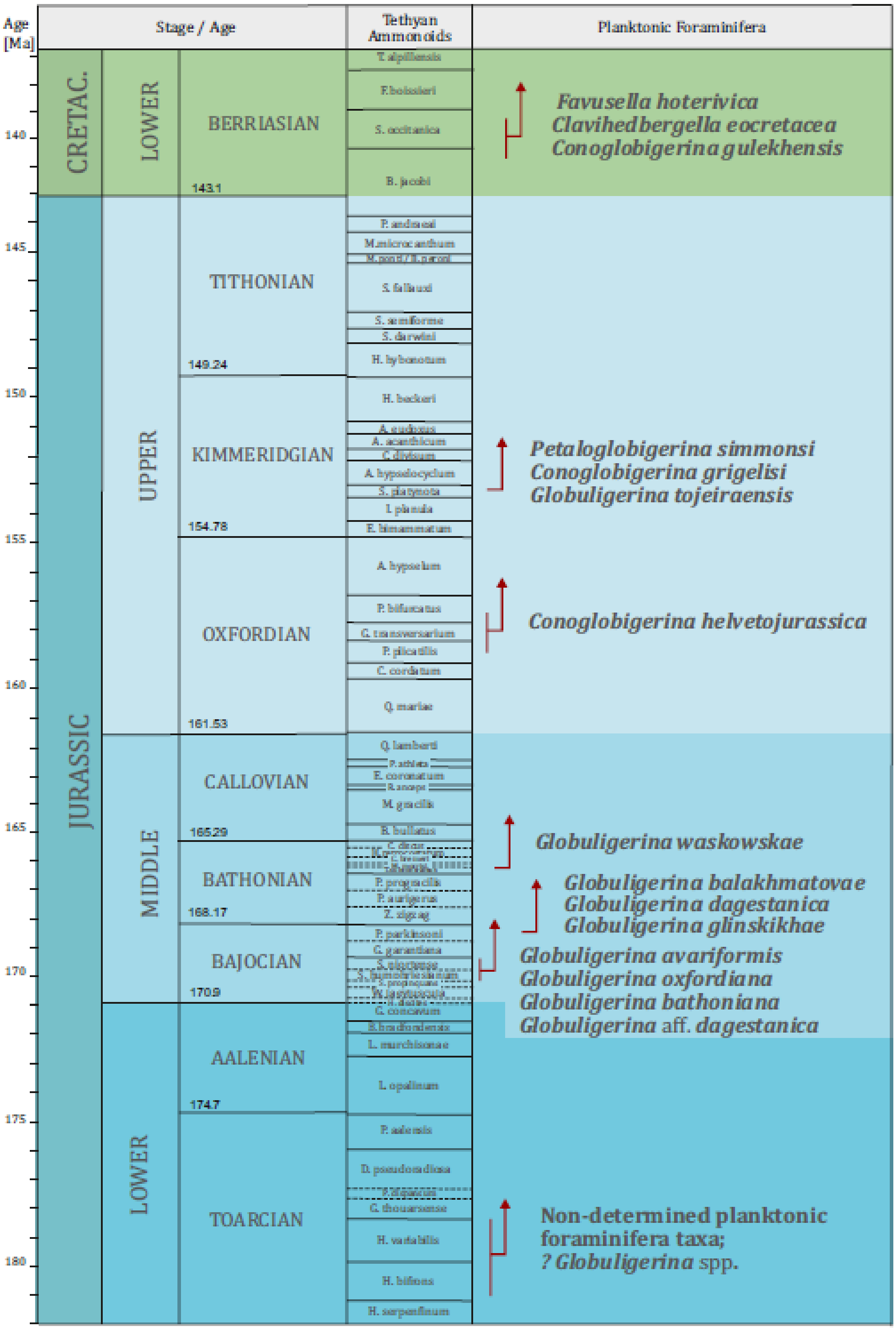

Figure 4. First Appearance Datum (FAD) of species of Jurassic planktonic foraminifera, calibrated to ammonite and nannofossil stratigraphy, as outlined in the text. Event level uncertainty beyond the duration of the ammonite zone(s) in which FAD's were determined is not taken into account in this study.

Zone-stage: *Transversarium* Zone, middle Oxfordian.

Microfossil assemblage: Directly below level 4 in the Eisengraben Section, samples with common and well-preserved specimens were obtained that we consider to be topotypes of *Conoglobigerina helvetojurassica* (Haeusler). Also, rare specimens were obtained of small sized *Globuligerina bathoniana* and *G.oxfordiana*.

Level 4 top has many agglutinated taxa, but hardly any planktonic specimens. Sample 4 mid, at the level of Stam's sample with '*helvetojurassica*' has best preserved specimens, and also includes well-preserved benthics belonging in *Bigenerina, Textularia, Ophthalmidium, Ammodiscus, Glomospira, Trochammina, Haplophragmoides, Dentalina, Nodosaria, Lenticulina* plus some indeterminate taxa. Micro gastropods also occur. Small limonitic concretions are common; small glauconite lumps also occur, testifying to a likely neritic mode of deposition. There are no epistominid benthic taxa.

Micropaleontology slides of Oesterle (1986) in the Basel Museum from the the Birmenstorfer type section contain 50+ of many more (often broken) specimens which we studied that show the same test moulds of crystallized carbonate fragments. The peculiar preservation is the result of a rigorous processing technique (likely a form of acetolysis). At least five morphotypes may be distinguished, which, despite poor preservation, can easily be assigned to the species *Globuligerina* aff. *oxfordiana*, *Globuligerina* aff. *bathoniana, Globuligerina* aff. *jurassica* (with an elongated, high spired and irregularly trochospiral test), *Globuligerina aff. balakhmatovae*, *Globuligerina* aff. *tojeiraensis* (with slightly elongated last chamber) and *Conoglobigerina* aff. *grigelisi.* However, the latter might be *Globuligerina* aff. *avariformis*, since we cannot determine wall texture. For sampling details and plates with SEM illustrations of all planktonic taxa, including the topotypes of *Conoglobigerina helvetojurassica* see Gradstein (2017).

References: Oesterle (1969); Gradstein et al. (2017a).

Oxfordian, Lithuania and Russia

Study and localities: A brief description is provided of the type localities of *Globuligerina oxfordiana* based on the author's (A. Grigelis) notes made on boreholes during his field work in Lithuania in 1956, and in the Nikitino region of central Russia in 1977. Microfaunal remnants were picked by the author after standard sediment disintegration and hand-sieving procedure. The shallow burial at the Oxfordian localities accounts for excellent preservation of the *Globuligerina oxfordiana* taxon.

Geologically, the Lithuanian area belongs to the Precambrian East European Craton. Relatively thin Mesozoic sedimentary strata underly Quaternary surface deposits. Marine Jurassic is distributed in the western-south-western part of Lithuania, with thickness changing from less than 30m in the northwest to 250m in the southwest, against the border with Poland.

Microfossil assemblage: Holo- and paratypes of *Globuligerina oxfordiana* come from dark claystone and dark siltstone in borehole Jotija (Jotija village), Sakiai District, Lithuania at 143m below surface in sample 10, lower Oxfordian (type specimens are provided by A. Grigelis on Plate 12 in Gradstein et al., 2017a). In the original description it is not indicated on which evidence geological age is assigned, but the foraminiferal assemblage contains *Spirophthalmidium birmenstorfense, Lenticulina brueckmanni, L. comptala, Vaginulina flabellata, Trocholina transversarii, Epistomina volgensis, E. brueckmanni* and *Epistominoides* sp. GPS coordinates of the borehole site are 55º02'17N:23º11'42E.

Well-preserved specimens of *Globuligerina oxfordiana* also occur in dark, micaceous silty clay in the interval of 55 – 66 m in borehole Lyduvenai, Raseiniai District, Lithuania. GPS coordinates of this site are 55º30'29N:23º04'59E. The type level contains the ammonite *Cardioceras tenuicostatum* Nikitin (early Oxfordian) and the foraminifera *Epistomina volgensis*, *Epistomina intermedia* and *Lenticulina brueckmanni*.

In Central Russia, well preserved specimens of this taxon (as assigned by Grigelis) also occur in sample 801 in the Shatriche-2 outcrop at the Nikitino settlement on the river Oka, Ryazan District. The actual outcrop is on high right bank of River Oka, ca 2.5 km below the confluence with River Pronya, at outskirt of village Shatriche, in a river washout called "Durnyanki". The sampled sediments are assigned to the middle to late Oxfordian, but no specific fossil information is provided. Type specimens of this species provided by A.Grigelis on Plate 12 in Gradstein et al. (2017a).

References: Grigelis (1958); Gradstein et al. (2017a).

Oxfordian, Poland

Study and locality: A prominent *Globuligerina* limestone in Poland occurs in the Pieniny Klippen Belt (PKB). Co-author AW obtained hard limestone samples of Oxfordian age from the isolated Obłazowa Klippe block in Nowa Biała village (coordinates: N49^{0}25' 42,4", E 20^0 07' 35,5").

Micropaleontologic assemblage: Thin-sections show that *Globuligerina oxfordiana* is abundant and rock-forming, and *Globuligerina bathoniana* is rare.

References: Birkenmajer (1977, 1986); Wierzbowski et al. (1999); Gradstein et al. (2017a).

Oxfordian, Blake Bahama Basin, North Atlantic Ocean

Study: Deep Sea Drilling Site (DSDP) 534, on the landward side of marine Jurassic Magnetic Quiet Zone (JQZ), in the Blake-Bahama Basin, established a Middle Jurassic (Bathonian-Callovian) age for the opening of the N. Atlantic Ocean (Sheridan, Gradstein et al., 1983).

Microfossil assemblage: The site cored abyssal (>2.7 km paleo waterdepth) Jurassic sediments with well preserved and common benthic foraminifera, nannofossils, radiolarians and dinoflagellates. It failed to find in situ Jurassic planktonic foraminifera. Rare, small and poorly preserved *Globuligerina* aff. *oxfordiana* specimens in Core 110 of Oxfordian age, are interpreted as transported with gravity flows from shallower strata. DSDP Leg 11, Site 105, drilled in this region in1972, in this region yielded similar observation.

References: Gradstein (1983); Luterbacher (1972).

Early Kimmeridgian, Portugal

Study: Between 1978 and 2016, author FMG with colleagues and students undertook several stratigraphic surveys and sampling in road outcrops, mountain sections and beach cliffs with Jurassic marine strata in Central and South Portugal. The research was part of a stratigraphic study of the Grand Banks of Newfoundland and its conjugate basin. The Grand Banks and Portugese Jurassic basins were conjugate, prior to mid-Cretaceous oceanisation of this segment of the North Atlantic.

Over the years, several stratigraphers and paleontologists generously provided guidance in the field, and assisted with analysis of ammonites and microfossils collected. These specialists included: R. Mouterde and C. Ruget Perrot (University of Lyon, France), M.M. Ramalho (Geological Survey, Lisbon), R.B. da Rocha (New University of Lisbon), C. Wilson (Open University, UK), T.P. Poulton (GSC, Calgary, Canada), A. Gale and H. Turner (University of Portsmouth, UK) and D. Watkins (Department of Earth and Atmospheric Sciences, University, Lincoln, Nebraska, USA).

Locality: Several sections in the marly Tojeira Formation, over 70m thick, in hills near the hamlet of Ramada and the villages of Pereiro, Tojeira an Vila Verde dos Francos, Montejunto area, Estramadura, west central Portugal. Details are in Gradstein et al. (2017a).

doi:10.20944/preprints202012.0319.v1

Zone-stage: *Platynota – Hypselocyclu*m Zones, early Kimmeridgian

Microfossil assemblage: The Tojeira Formation is rich in fairly well preserved planktonic foraminifera and a very large collection of specimens was made, with seven taxa described. The taxa include *Globuligerina oxfordiana, Globuligerina bathoniana, Globuligerina tojeiraensis, Globuligerina balakhmatovae, Petaloglobigerina simmonsi, Conoglobigerina grigelisi* and *Conoglobigerina helvetojurassica.* Planktonic foraminiferal tests are calcitic, nor aragonitic. Th*e* Portugese Jurassic planktonic foraminifera occur together with a rich epistominid assemblage, also found in Grand Banks sections with *Pseudolamarckina rjasanensis*, *Epistomina mosquensis* and *Epistomina uhligi*. Agglutinated foraminiferal taxa and micro-gastropods are common; the calcareous benthic foraminifera *Discorbis paraspis* and *Discorbis scutiliformis* are rare. The benthic foraminiferal assemblage is only known from deeper neritic and bathyal settings (Stam, 1986).

References: Stam (1986), Agterberg et al. (1989), Gradstein et al. (2017a), Turner et al. (2017) and Gradstein & Waskowska (in press).

Middle Kimmeridgian, Portugal

Study and locality: In 1978, as part of the extensive Tojeira Formation sampling (see above), Rogerio Bordalo da Rocha (Lisbon) kindly guided author FG and students to two dark shales outcrops, one along the road just outside Villa Verde dos Francos and another one outside Pereiro, both in the Montejunto area. The fossiliferous shales with ammonites and *Bositria* are of the Abadia Formation, that overly the Tojeira Formation and underly thick-bedded conglomeratic sands. In the Montejunto area, the Abadia Formation, with shales, sands, conglomerates and olistolithic limestone blocks reach a thickness of over 1km.

Zone and age: Middle Kimmeridgian, according ammonite studies of the Portugese Geological Survey.

Micropaleontologic assemblage: Our samples 4/1 and 25/1 have large size benthic foraminifera with *Epistomina stellicostata, E.volgensis and E.uhligi*. The first two taxa do not occur in the underlying Tojeira Formation, and have their first, regional stratigraphic occurrence in these two samples. In correlation with eastern Canada, this benthic foraminiferal assemblage is Kimmeridgian-Tithonian in age.

Planktonic foraminifera include *Globuligerina bathoniana* (abundant), common *Globuligerina oxfordiana*, rare *Globuligerina tojeiraensis*, rare *Petaloglobigerina simmonsi* and rare *Conoglobigerina grigelisi*. No *Conoglobigerina helvetojurassica* was observed, a species common in the upper part of the underlying Tojeira Formation. Some *Globuligerina oxfordiana* specimens have a reticulate wall texture, a feature taken up in the section on Evolution.

References: Ascoli et al. (1984); Stam (1986), Williamson & Stam (1988).

Tithonian, Hungary (x)

Study: Co-**a**uthor AW and colleagues in 2019 visited the Paprét-árok profile in the Gerecse mountains of Hungary. This locality is described with outcrop details and a Tithonian planktonic foraminiferal assemblage in Görög & Wernli (2004). It turns out the locality does not exist, and its publication and description are based solely on archival data. The locality originally was a railway cut.

Locality: Paprét-árok, Gerecse Mts, Hungary.

Lithology and Zone-Age: In the Paprét-árok profile the succession begins with red radiolarite (Lókút Radiolarite Formation) of Middle Jurassic - Kimmeridgian age. It is followed upwards with a massive and hard bank about 75 cm in thickness, grey, pink and purple in colour. This massive bank is subdivided in five beds numbered 6 to 2, from the base to the top: Beds 6-7 belong to the *Beckeri* and the *Hybonotum* Zones, Bed 5 questionably to the *Darwini* Zone and Bed 4 questionably to the *Fallauxi* Zone, all considered early Tithonian in age. Limestone Beds 3 and 2 are not zoned, but considered as probably late Tithonian in age. Above this massive limestone bank occur grey marl and breccia layers, belonging to the Lower Cretaceous Bersek Marl Formation.

Microfossil assemblage: 'Protoglobigerinids' are described from bed 5 ? *Darwin*i Zone using thin sections and free specimens obtained with weak acetic acid. The authors consider the planktonic foraminiferal assemblage to be monospecific, with a species transitional between *Globuligerina oxfordiana* and *Favusella hoterivica*, but no pore features and wall texture can be determined, making the interpretation tentative. Stratigraphically higher-up, it states that the same section might yield Berriasian planktonic foraminifera, but none are listed.

Reference: Görög & Wernli (2004).

Tithonian-Valanginian, North Africa

Other localities: There is a meagre record of unspecified planktonic foraminifera in thin sections from Tethyan limestones of Tithonian through Valanginian age in N. Africa and Central Europe (Görög & Wernli, 2004).

Early Berriasian, Crimea

Study: For our study of Mesozoic planktonic foraminifera, Ludmila Kopaevich (Moscow) obtained samples from the Tonas River Basin in E. Crimea, Russia. The hard marly sediment interval is assigned to the *Jacobi* ammonite Zone, early Berriasian, not far above the Jurassic-Cretaceous boundary. The Tonas River Basin is a locality from which Gorbachik and Poroshina (1979) described *Globuligerina caucasica* and *Globuligerina gulekhensis*.

Locality, with coordinates: Outcrop 2km south of the village Krasnoselivka in the Tonas Basin, Crimea, Russia. Geographic coordinates are 44.927712_N, 34.634905_E.

Zones, stage: Calcareous nannofossil Zone CC2, late early to middle Berriasian;

Ammonites of the *Jacobi* and *Grandis* subzones of the *Jacobi* Zone of early Berriasian age. Benthic foraminifera of the *Protopeneroplis ultragranulatus—Siphoninella antiqua* Zone and a younger one—*Quadratina tonassica—Siphoninella antiqua* Zone.

Microfossil assemblage: Fairly well-preserved benthic foraminifera, with *Epistomina stellicostata*, *E. volgensis* and *E. uhligi*, *Lamarckina* sp., common *Neobulimina* sp., *Patellina* sp., *Lenticulina* spp., several nodosariid taxa, *Bigenerina* sp., *Spiroplectammina* spp., *Textularia* sp., *Trochammina* sp.

Sample Cr1 contains about 100 specimens of planktonic foraminifera taxa, all microperforate, including with frequent specimens *Favusella hoterivica* (Subbotina), with common specimens *Clavihedbergella eocretacea* Neagu and *Conoglobigerina gulekhensis* (Gorbachik and Poroshina) and with less than 10 specimens each of the taxa *Hedbergella* aff. *similis* (Longoria), ?*Favusella* sp., *Hedbergella* aff. *handousi* Salaj and ? *Globuligerina* sp.

Only *Conoglobigerina gulekhensis* (Gorbachik and Poroshina) was previously known from Berriasian strata, and this only from two regions, Crimea and Azerbaijan. *Favusella hoterivica* (Subbotina) with certainty only is known from Valanginian through Aptian marine strata, and the other taxa only from Valanginian, Hauterivian or even younger stratigraphic intervals. All taxa are of Tethyan or sub-Tethyan origin.

Note: As outlined in some detail in the geological history study by Nikishin et al. (2017), the Crimea region underwent late Berriasian vertical movements,

leading to a regional unconformity with erosion and karstification of underlying strata. The Krasnoselivka section preserves non-karstified Berriasian limestones, subject of our study.

References: Arkadiev et al. (2005); Gorbachik and Poroshina (1979); Gradstein et al. (2018).

Berriasian - early Valanginian, Scotian Shelf, offshore eastern Canada

Study: In 2019, author FG studied foraminifera in micropaleontology slides and washed residues (65-250µm) from exploration well samples stored with the Geological Survey of Canada, Bedford Institute of Canada, Dartmouth, N.S., Canada.

Locality: Exploration wells with interval studied: Oneida O-25, 8630-9460'below casing point at 6876'; Onondaga E-84, 11730-11810', below casing point at 8121'; Glenelg J-48, 4165-4155m, below casing point at 4134m.

Zone, stage: Using dinoflagellates and benthic foraminifera, the studied interval is assigned a Berrisian – early Valanginian age.

Microfossil assemblage: In total about 50 specimens of *Favusella hoterivica* were obtained, many pyritized and with good wall texture details. Some questionable *Conoglobuligerina* aff. *gulekhensis* were found, but preservation is insufficient to provide reliable identification. Benthic foraminifera include *Lenticulina busnardoi*, *Epistomina minireticulata*, *E.stellicostata*, *Neobulimina* sp, *Discorbis* aff. *valdendisensis*, *Discorbis* sp., agglutinated indet. Micro gastropods are common to abundant, as they are in the Kimmeridgian Tojeira Formation in Portugal.

References: Ascoli (1976); Wernli et al. (1995); Bars et al. (1979).

Berriasian-early Valanginian, North Mexico (x)

Study: North Mexico calpionellid publication with thin sections.

Locality: Taraises Formation, north Mexico

Zone, stage: Calpionellid assemblages assigned to Berriasian-early Valanginian.

Microfossil assemblage: Poor thin-section illustrations of *Conoglobigerina gulekhensis*, *Caucasella hoterivica*, *Compactogerina* sp. and *Gorbachikella* sp. by Omaña et al. (2017) from Berriasian-early Valanginian limestones of the Taraises Formation in north Mexico. The images are non-determinate, but the illustration on Figure 5c of Omaña et al. (2017) likely is *Favusella hoterivica*. The type of the monotypic genus *Compactogerina* is coarse perforate and belongs to Neogene *Neogloboquadrina pachyderma* (Gradstein et al., 2017a, b). Lourdes Omaña kindly communicated to Gradstein (May 2018) that it is currently not advised to visit the Mexican site due to drugs-related violence.

Reference: Omaña et al. (2017), and personal communication with the author.

Biochronology

The Jurassic planktonic foraminifera are subdivided in three genera and eleven species, including *Globuligerina oxfordiana* (Grigelis), *Gobuligerina glinskikhi* (Gradstein & Waskowska), *Gobuligerina bathoniana* (Pazdrowa), *Globuligerina dagestanica* (Morozova), *Globuligerina balakhmatovae* (Morozova), *Globuligerina* *avariformis* (Kasimova), *Globuligerina waskowskae* Gradstein, *Globuligerina tojeiraensis* Gradstein, *Conoglobigerina helvetojurassica* (Haeusler), *Conoglobigerina grigelisi* Gradstein *and Petaloglobigerina simmonsi* Gradstein. In addition, for evolutionary insight we include here the three Berriasian species *Favusella hoterivica* (Subbotina), *Clavihedbergella eocretacea* Neagu, and *Conoglobuligerina gulekhensis* (Gorbachik & Poroshina).

Plates 1 through 5 provide light microscope and SEM images of the Jurassic species, grouped by gross morphologic similarity between taxa. Plate 6 shows two key Berrisian planktonic foraminifera, descendants of Jurassic species as postulated in Gradstein et al. (2018).

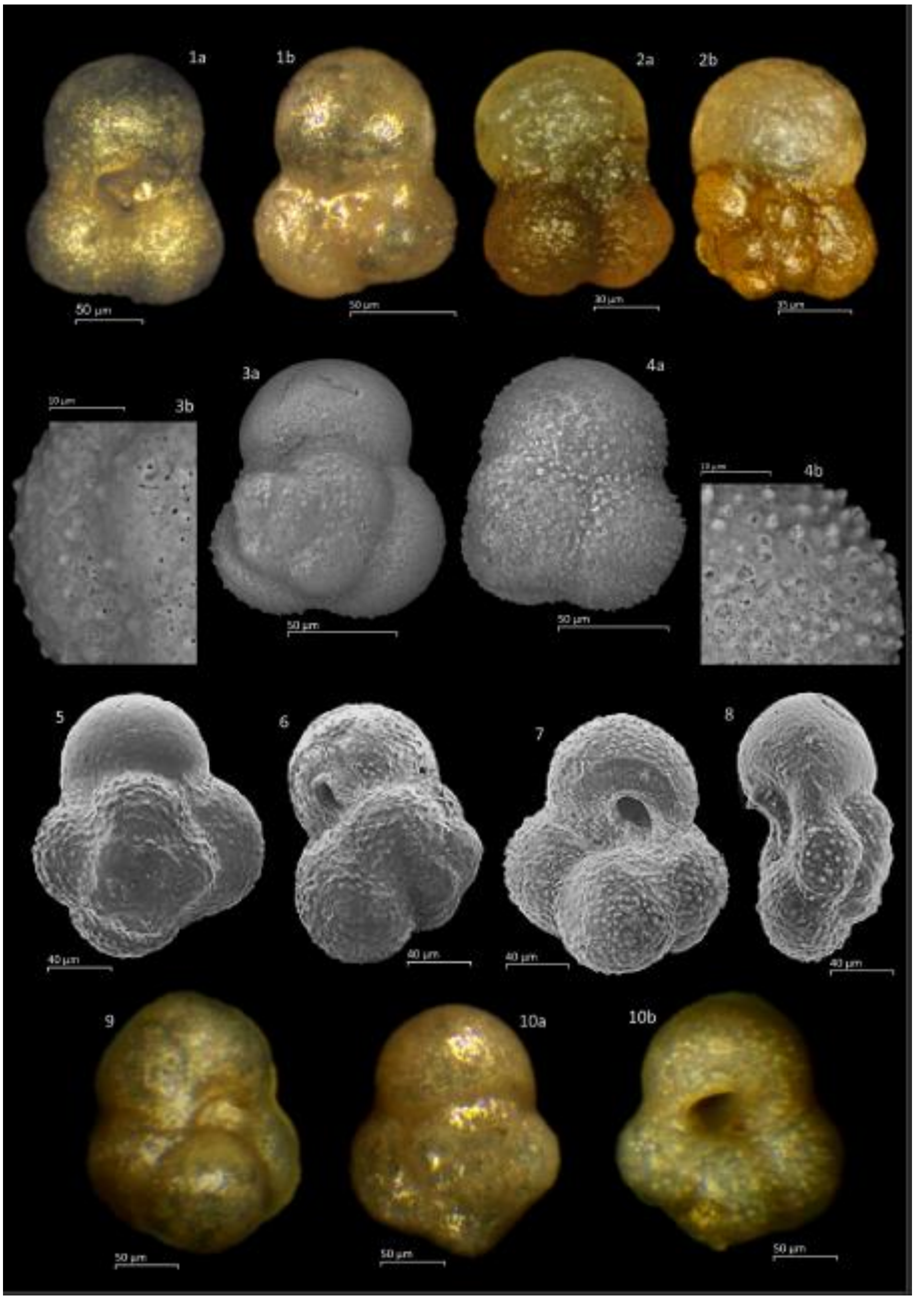

Plate 1. *Globuligerina glinskikhae* Gradstein and Waskowska. Figs. 1a, b – holotype, sample 6, *Morrisi* Ammonite Zone, Middle Bathonian, Gnaszyn, Poland. Figs. 2a, b - paratype, sample 8, *Parkinsoni* Zone, Upper

Bajocian, Khouroukra, Dagestan. Figs. 3a, b and 4a, b – paratypes, sample 6, *Morrisi* Zone, Middle Bathonian, Poland; note the microperforate and pustulose wall with scattered pore mounds.

Globuligerina oxfordiana (Grigelis). Figs. 5 - 7, Oxfordian of Upper Volga, Russia. Fig. 8, Mariae Zone, Lower Oxfordian near Le Havre, France (Figs. 5-8 from Gradstein et al., 2017b). Figs. 9 and 10a, b, sample 6, *Morrisi* Zone, Middle Bathonian, Poland

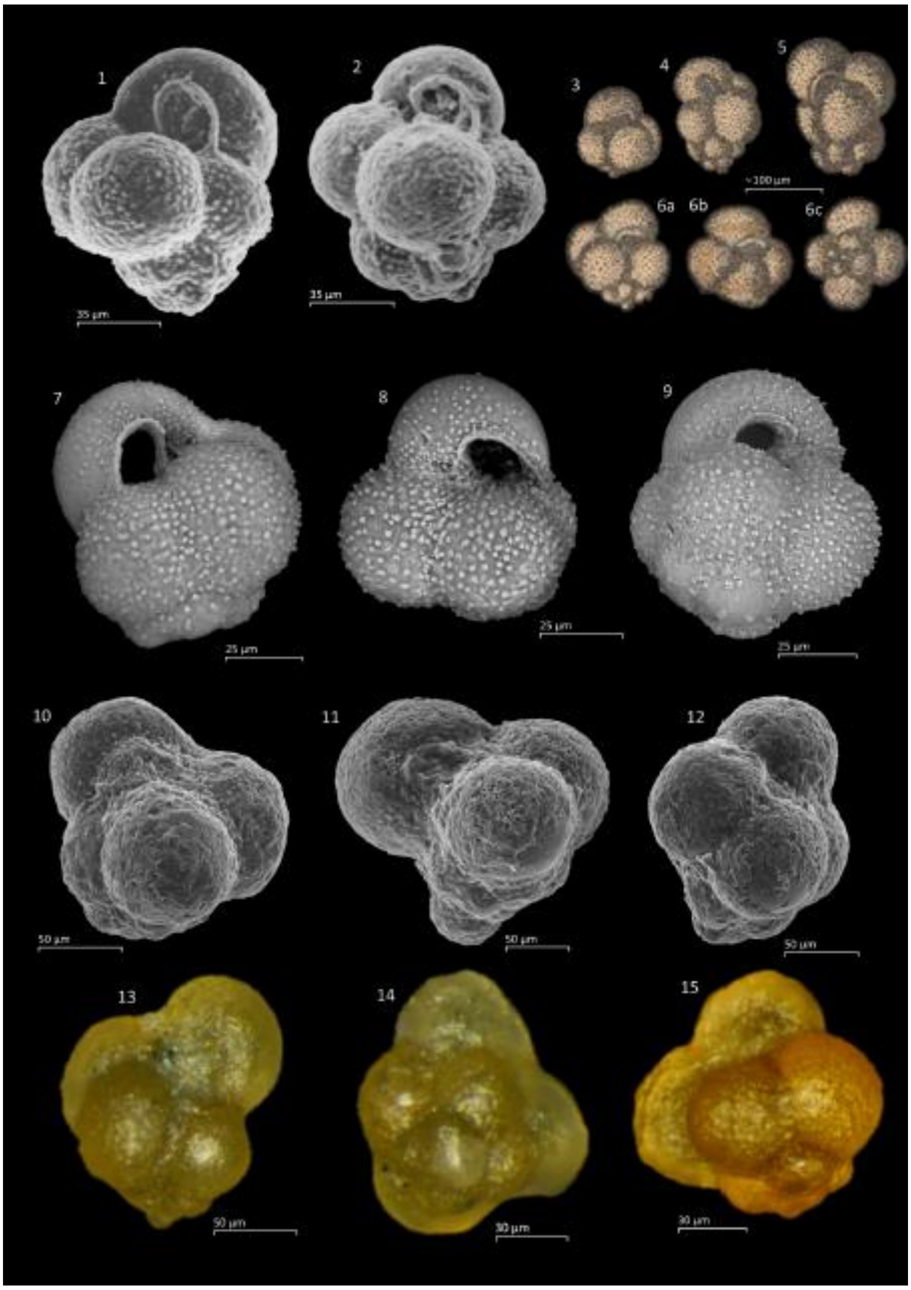

Plate 2. *Globuligerina bathoniana* (Paszdrowa). Figs 1, 2, Eider M-75 well, cts. 8260-8290’, *Garantella* spp. Zone, Bajocian-Bathonian, Grand Banks, Canada. Figs 3-6, re-illustration of Bathonian type species drawings provided by Olga Pazdrowa to Felix Gradstein. Specimen height 140-180µm. Figs 7- 9, sample 6, Morrisi Zone, Middle Bathonian, Gnaszyn, Poland.

Globuligerina dagestanica (Morozova). Figs 10-13, topotype specimens from samples 8 and 9, Khouroukra section, Late Bajocian, Dagestan.

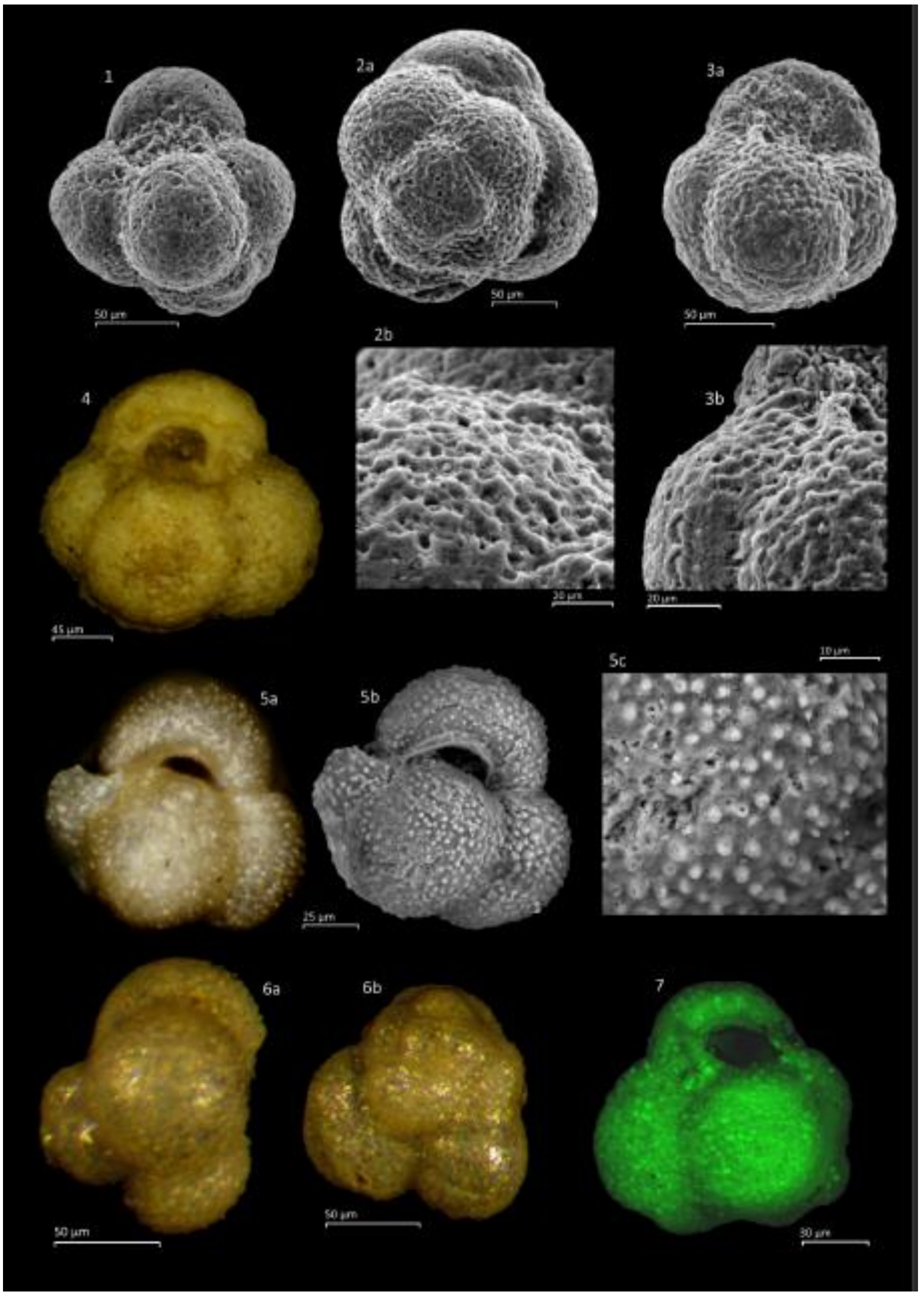

Plate 3. *Conoglobuligerina helvetojurassica* (Haeusler). Figs 1-3, holotype and paratype specimens from sample 4mid, Eisengraben Section, Birmerstorfer Schichten, *Transversarius* Zone, Middle Oxfordian, Canton Aargau, Swizerland; note reticulate wall texture. Fig. 4, sample 24/2P, Tojeira Formation, Lower Kimmeridgian, Montejunto, Portugal.

Globuligerina waskowskae Gradstein. Figs. 5a-7, holotype and paratype specimens, sample 6, *Morrisi* Zone, Middle Bathonian, Gnaszyn, Poland; note microperforate wall with small, regularly distributed pustules, many with pore mounds.

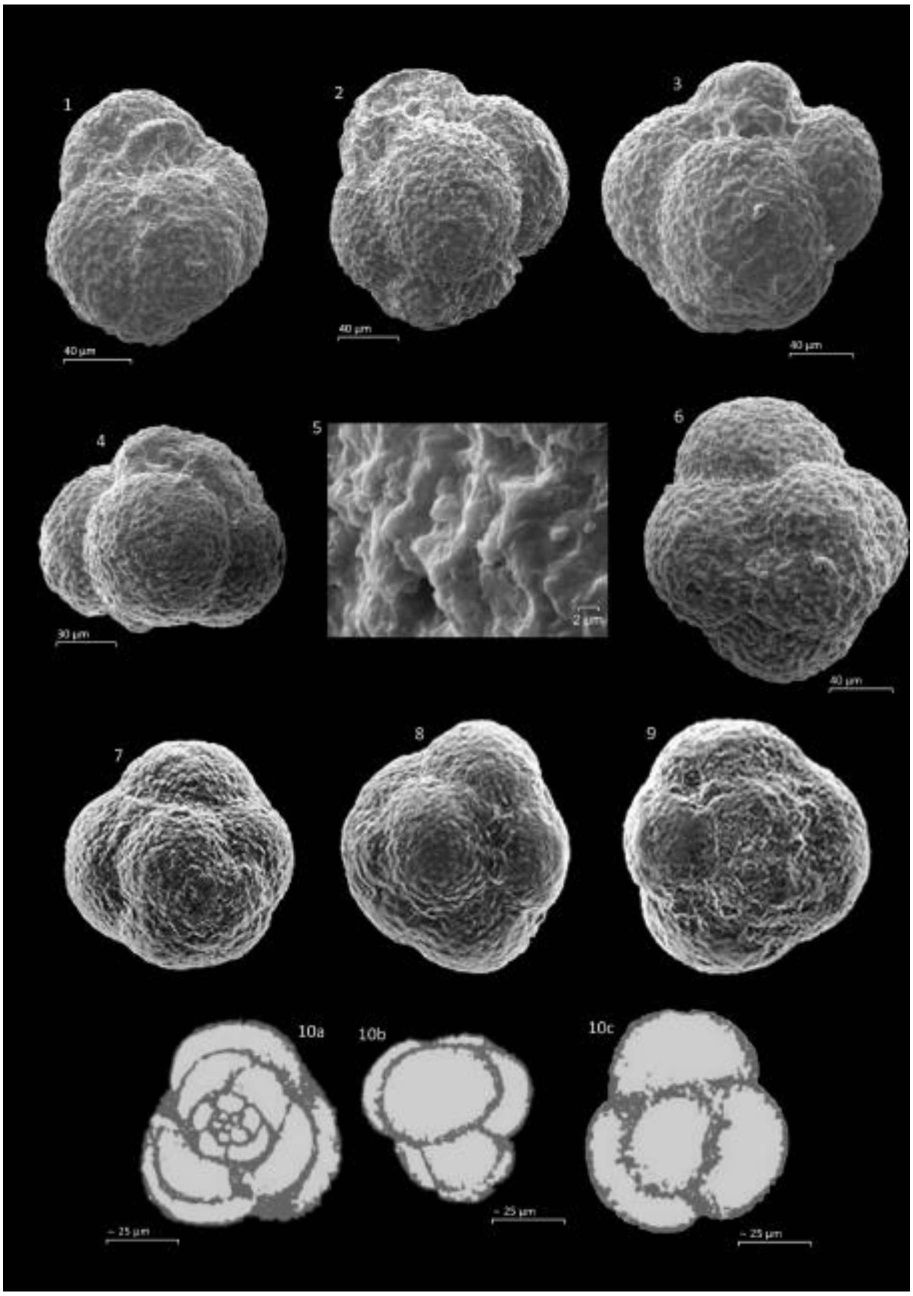

Plate 4. *Conoglobigerina grigelisi* (Gradstein). Figs. 1-6, holotype and paratype specimens in sample 24/2P, Tojeira Formation, Lower Kimmeridgian, Montejunto, Portugal.

Globuligerina avariformis (Kasimova). Figs. 7-9. Upper Bajocian, Negramkoye Gorge, Aras River, Nakhichevan, Azerbijan; metatypes donated by Dr. Kasimova to the Natural History Museum, London, diameter of 320 µm may be an error. Figs. 10a-c, holotype drawing by Kasimova and Aliyeva (1984), x90.

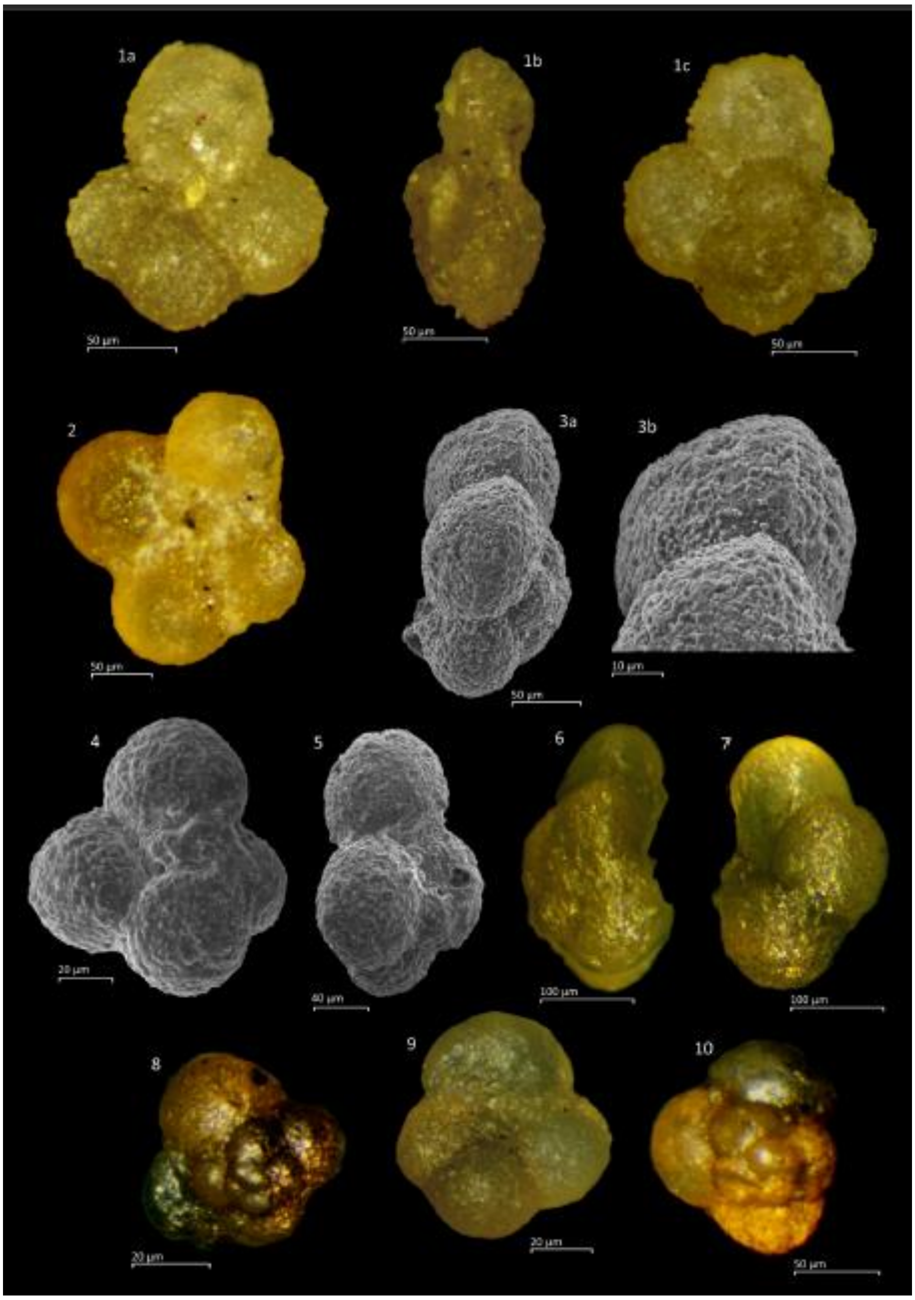

Plate 5. *Petaloglobigerina simmonsi* Gradstein. Figs. 1, 2, holotype and paratype specimens, sample 10, section 1, Tojeira Formation, lower Kimmeridgian, Montejunto, Portugal. Fig. 3, paratype specimen, sample 6-28, upper Tojeira Fm., lower Kimmeridgian, Montejunto, Portugal; note the four chambered last whorl with pointed periphery and the densely pustulose wall texture.

Globuligerina balakhmatovae (Morozova). Fig. 3, cuttings sample 8360’, Eider well, Grand Banks, Bajocian-Bathonian; wall texture densely pustulose, with pustules merging into short ridges. Fig. 4, sample 24/2P, Tojeira Formation, Montejunto, Portugal, lower Kimmeridgian; wall texture coarsely pustulose. Figs. 5 – 9, side, umbilical and spiral views of topotypes of *Globuligerina balakhmatovae* (Morozova), sample 8, *Parkinsonii* Zone, Upper Bajocian, Khouroukra, Dagestan.

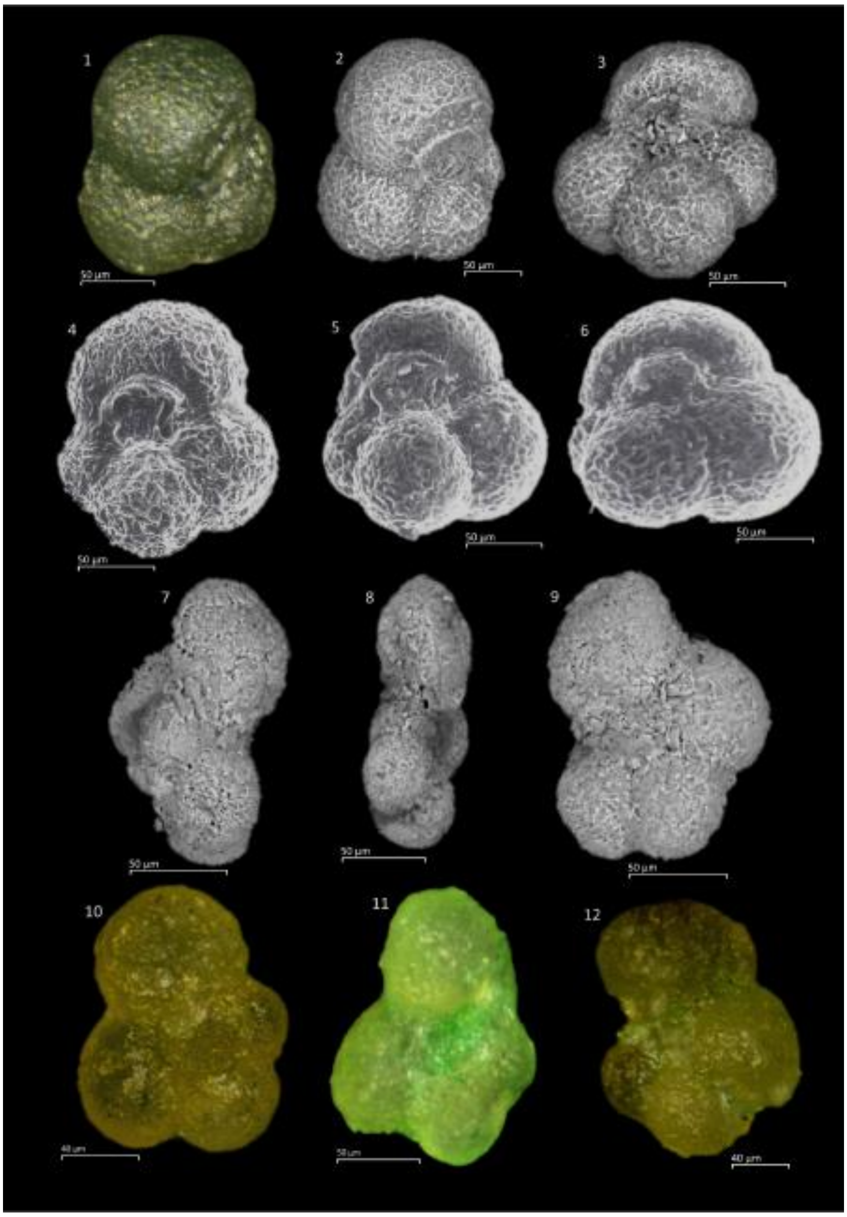

Plate 6. *Favusella hoterivica* (Subbotina). Figs. 1 – 6, Oneida 0-25 well, cts 8760 - 9460', Berriasian, E. Canada (Figs. 4 – 6 from Plate II in Wernli et al. 1995, with permission from the authors).

Clavihedbergella eocretacea (Neagu). Figs. 7 – 12, sample Cr1 of Berriasian age, Krasnoselivka section, Crimea, Russia.

Globuligerina, with a smooth to pustulose test surface texture appeared in Toarcian (late Early Jurassic) time, and *Conoglobigerina*, with a rough reticulate test surface texture in Oxfordian (early Late Jurassic) time. *Petaloglobigerina*, with a petaloid last whorl and one or more twisted and claviform chambers evolved in early Kimmeridgian time from *Globuligerina balakhmatovae*.

Table 1 list the oldest age level of formally described Jurassic planktonic foraminifera species, and Figure 4 depicts the FAD of genera and species in a simple stratigraphic column, calibrated to ammonite and nannofossil stratigraphy, as outlined below. The biochronology uses the GTS2020 geochronologic scale. Event age uncertainty beyond the duration of the ammonite zone(s) in which FAD's were determined is not touched upon on in this study.

From older to younger the FAD's in Ma of the genera are:

Globuligerina – FAD ~ 180 Ma (see below)
Conoglobigerina - FAD ~ 158 Ma
Pentaloglobigerina – FAD ~ 153 Ma

Form older to younger the FAD's in Ma of the species are:

? Globuligerina oxfordiana ~ 180 Ma (see below)
? Gobuligerina bathoniana ~ 180 Ma (see below)
Globuligerina avariformis ~ 169 Ma
Globuligerina oxfordiana ~ 169 Ma
Globuligerina bathoniana ~ 169 Ma
Globuligerina balakhmatovae ~ 169 Ma
Globuligerina dagestanica ~168 Ma
Globuligerina glinskikhi ~ 168 Ma
Globuligerina waskowskae ~166 Ma
Conoglobigerina helvetojurassica ~158 Ma
Globuligerina tojeiraensis ~ 153 (168) Ma (see below)
Conoglobigerina grigelisi ~ 153 (163) Ma (see below)
Petaloglobigerina simmonsi ~152 Ma
Favusella hoterivica ~142 Ma
Clavihedbergella eocretacea ~142 Ma
Conoglobuligerina gulekhensis ~ 142 Ma

The study of Wernli (1988) on thin-sections from Toarcian limestone samples in the Domuz Dag mountain chain of SE Turkey provided by A. Poisson (Paris) from his thesis (Poisson, 1977) documents the oldest known occurrence of planktonic foraminifera. Curiously, this is the only record in the whole world of this oldest known assemblage. Hence, planktonic foraminifera appeared in the Toarcian around 180 Ma ago. The youngest Jurassic occurrence of this group is documented by Görög & Wernli (2004) describing a single taxon of planktonic foraminifera (extracted with acetic acid) in Tithonian age samples from Hungary. Hence, Jurassic planktonic foraminifera range from Late Toarcian (*Bifrons- Variabilis* ammonite Zones) through Late Tithonian (*C. alpina* calpionellid Zone).

Unfortunately, the Toarcian through Aalenian record is only known from thin-sections, but we consider that an often larger and higher spired form similar to *Gobuligerina bathoniana* and a smaller, lower spired form similar to *Globuligerina oxfordiana* occur in these thin-sections. This needs better documentation with well-preserved free specimens. Test size difference in itself may not be a taxonomic feature, and often has more to do with growth conditions in optimal or sub-optimal environments, selective sediment sorting, water masses and vertical biota distribution, and other hard to evaluate factors in fossil material.

The LAD's of these taxa is not known, but all Jurassic species have disappeared before Cretaceous (143 Ma). If the genus *Conoglobigerina* disappeared prior to or early during Tithonian time, the Berriasian- early Valanginian species *Conoglobigerina gulekhensis* should get a new genus name.

From the stratigraphic record outlined in the 'Stratigraphic inventory' chapter it is clear that *Globuligerina oxfordiana*, *Globuligerina bathoniana and Globuligerina balakhmatovae* have a long stratigraphic range, spanning several stages for 20 myr or more. *Conoglobigerina helvetojurassica* has a much shorter stratigraphic range, spanning two stages for 10 myr or more. The single observation that the regionally restricted *Conoglobigerina grigelisi* appears in Callovian –Oxfordian strata on the Grand Banks means its common presence in the Kimmeridgian of Portugal is not an FAD event. The regionally restricted species *Globuligerina dagestanica*, *Globuligerina glinskikhae*, *Globuligerina avariformis* and *Globuligerina waskowskae* may have been stratigraphically short-lived. A special case is *Globuligerina tojeiraensis*, first described by us from the Kimmeridgian of central Portugal. Here it is consistently present in long series of consecutive samples, with a stable and unique test morphology and with frequent specimens. Comparable tests occur with few specimens in Middle Jurassic samples from Dagestan and Poland, and might be aberrant *Globuligerina oxfordiana* rather than *Globuligerina tojeiraensis.*

Evolutionary lineages

As outlined in Figure 5 we consider that within the Jurassic and earliest Cretaceous four lineages of planktonic foraminifera occur, which for graphic clarity are shown with green, brown, blue and red stratigraphic lines. Two taxa, *Petaloglobigerina simmonsi* and *Globuligerina oxfordiana* are postulated to be ancestral links to Cretaceous taxa (Gradstein et al., 2018).

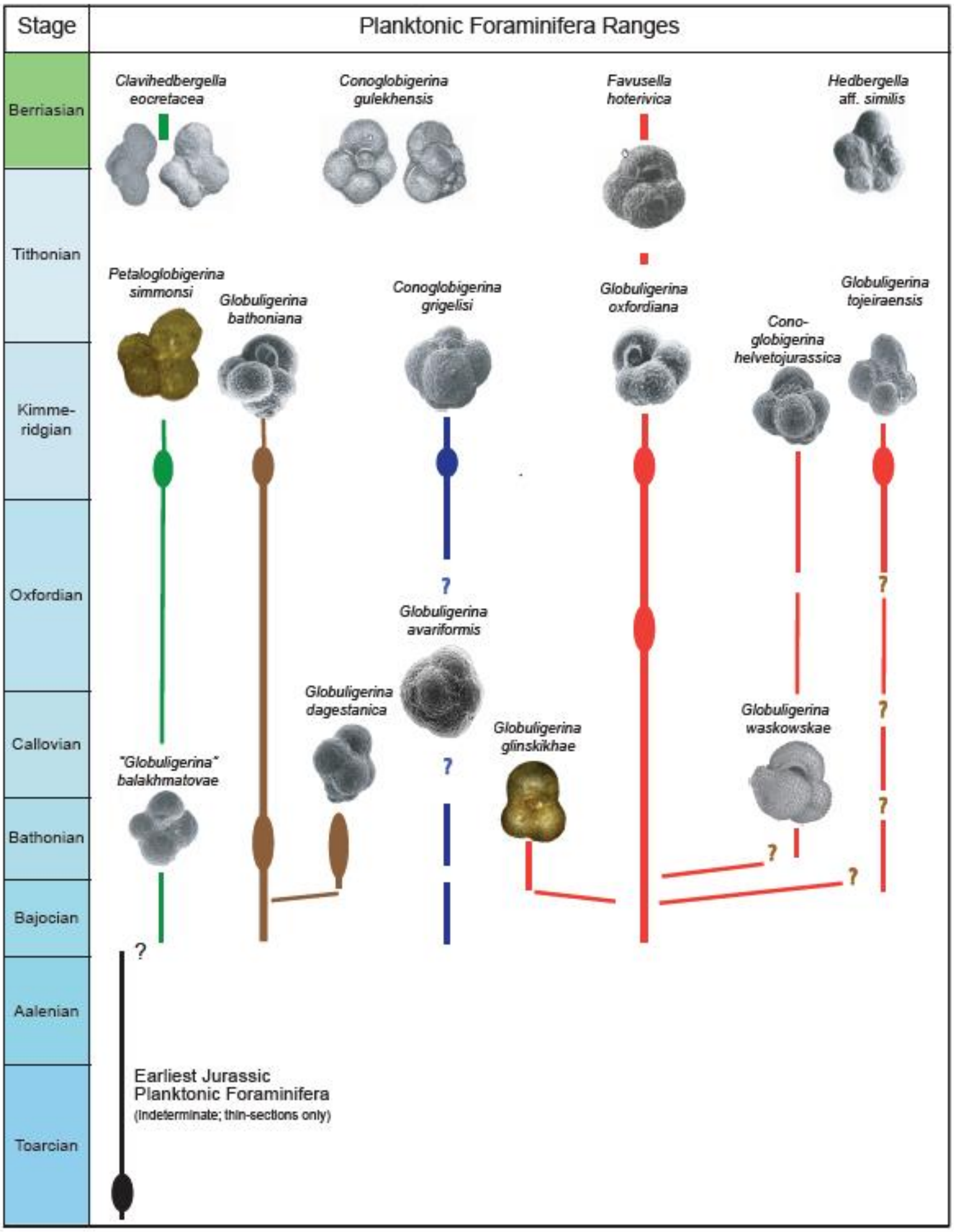

Figure 5. Stratigraphic ranges and evolution of Jurassic planktonic foraminifera. For details, see text

The 'green group' is monotypic and consists of *Globuligerina balakhmatovae* evolving during Kimmeridgian time in *Petaloglobigerina simmonsi*.

The ancestry of *Globuligerina balakhmatovae* is not clear. A possible morphological transition exists to *Oberhauserella* aff. *parocula* described by Wernli and Görög (2007) from SE France, but this requires refinement of our knowledge on the stratigraphic appearance and test morphology of both taxa. A detailed study of wall textures should be undertaken.

Based on a general similarity in test morphology Gradstein et al. (2018) proposed that the Kimmeridgian *Globuligerina balakhmatovae* (now assigned to *Petaloglobigerina simmonsi*) might have evolved in *Clavihedbergella eocretacea* in early Berriasian time. It might be tempting to transfer all specimens of this long-ranging species *Globuligerina balakhmatovae* to the new genus *Petaloglobigerina*, but this awaits a more detailed evaluation of the original types as designated by Morozova & Moskalenko (1981) and re-illustrated in Simmons et al. (1997). For example, the holotype, (but not the paratypes) of *G.balakhmatovae* appears to fall outside the common *G.balakhmatovae* morphology as we observe it; the holotype test is more inflated and chambers are not petaloide or ovate.

The 'brown group' includes *Globuligerina dagestanica* (Morozova) and the common species *Globuligerina bathoniana*, all higher spired trochoid morphotypes with an arch to looped aperture and commonly a bulla. Essentially, we can distinguish one taxon with a more symmetrical and regular trochospire with four chambers in the last whorl (*bathoniana* type), and another taxon with more irregular (or sometimes triangular) trochospire with 3, 3-4 or 4 chambers in the last whorl (*dagestanica* type). In our opinion, *Globuligerina jurassica* (Hofman) might be a local and often aberrant variant of *Globuligerina dagestanica*.

The 'blue group' consists of *Globuligerina avariformis* (Kasimova) and *Conoglobigerina grigelisi* (Gradstein), both of which do not have a geographically widespread record. The two species typically have a last whorl that strongly embraces earlier ones, such that the test almost appears involute. An evolutionary line age is postulated from the compact *Globuligerina avariformis* into the equally, or even more compact *Conoglobigerina grigelisi*. The latter acquires a reticulate wall sculpture. Its youngest record is middle Kimmeridgian. One issue, common to other Jurassic planktonic foraminiferal species is that we do not have a continuously stratigraphic record leading from one species to the other species. We refrain to speculate on the ancestry of *Globuligerina avariformis*. The stratigraphic and taxonomic data are insufficient.

The 'red group' includes *Globuligerina oxfordiana*, *Globuligerina glinskikhae*, *Globuligerina tojeiraensis* and the inferred lineage from *Globuligerina waskowskae* to *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 *Globuligerina oxfordiana* the looped aperture is very slightly offset from the umbilicus. A stratigraphic trend exists in this taxon to a more reticulate wall texture with the umbilicus opening up.
Gorbachik (1983) showed the onset of reticulation on older chamber of a specimen of this species; this is clearly an ontogenetic feature in rare specimens of some assemblages. If ontogeny recapitulates evolution, this wall texture change strengthens our postulation that Jurassic *Globuligerina oxford*iana is ancestral to Cretaceous *Favusella hoterivica* (Subbotina). The close morphological comparison and overlap in wall texture features, makes it viable to consider *Globuligerina oxfordiana* to be the ancestor of *Favusella hoterivica*. Both taxa are

illustrated in Figure 5. It is interesting, as listed above that reticulate *Globuligerina oxfordiana* occur in the Middle Kimmeridgian of Portugal.

The species *Globuligerina tojeiraensis,* with elongated chambers and wide-open umbilicus is known from the Bajocian-Bathonian of Dagestan, the Callovian-Oxfordian of the Grand Banks of Newfoundland and the Kimmeridgian of Portugal. Its overlap in morphology with *Globuligerina oxfordiana* suggests the latter to be ancestral. The origin of *Globuligerina oxfordiana* itself is shrouded in mystery.

The discovery and description in Gradstein & Waskowska (in press) of well-preserved *Globuligerina waskowskae* with a test morphology much alike *Conoglobigerina helvetojurassica* makes it attractive to consider the former taxon to be ancestral. The principal new feature in this evolution is the distinctive reticulate wall texture of *Conoglobigerina helvetojurassica*, appearing in Middle Oxfordian.

In summary, and as illustrated in Figure 5 the planktonic foraminifera appeared during Toarcian time (but no free specimens record) and occurred with at least eight taxa in Bajocian-Bathonian. The Oxfordian – Kimmeridgian planktonic foraminiferal record consists of six taxa. Giving weight to the acmes of taxa, the Kimmeridgian is the time Jurassic planktonic foraminifera flowered. A dramatic faunal change-over, which is not well documented led to the survival of only one taxon, most likely *Gobuligerina oxfordiana* in the Tithonian. During the Berriasian several new taxa appeared.

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