New insights into the taxonomy and evolution of Jurassic planktonic foraminifera

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Abstract

Globuligerina glinskikhae nov. sp. Gradstein & Waskowska and Globuligerina waskowskae nov. sp. Gradstein are new species of Jurassic planktonic foraminifera from the Middle Jurassic of Dagestan and Poland. G. glinskikhae nov. sp. with its remarkable ‘protoglobigerine’ test may be an early evolutionary offshoot of Globuligerina oxfordiana (Grigelis). It may be an index taxon for upper Bajocian through Bathonian strata in Eastern Europe and Southwest Asia, and might be recognizable also in thin sections. We consider G. waskowskae nov. sp. to be a possible forerunner of Conoglobigerina helvetojurassica (Hauesler), the first planktonic foraminiferal species with a reticulate wall texture. Currently, is only known from Poland. In some localities, specimens of G. oxfordiana and of G. glinskikhae nov. sp. posses an additional apertural opening, often lacking a rim; its function is enigmatic. The postulated lineage from Jurassic Globuligerina balakhmatovae (Morozova) to Cretaceous Clavihedbergella eocretacea Neagu is refined with the description of Petaloglobigerina simmonsi nov. gen., nov. sp. Gradstein from the Kimmeridgian of Portugal. The evolutionary transition from G. balakhmatovae to P. simmonsi occurs by means of the ontogenic development of a petaloid test, with a pronounced flattening of the whorl with ovate chambers, the last ones often offset and twisted. Jurassic planktonic foraminifera, now known to consist of three genera and 12+ species underwent long periods of stasis, interrupted by late Bajocian, mid-Oxfordian and early Kimmeridgian evolution. The three ‘stasis and root’ taxa G. oxfordiana, G. bathonian and G. balakhmatovae are geographically widespread in lower to mid palaeo-latitudes, and stratigraphically long ranging within the Middle and Late Jurassic. Modern digital microscopes, with co-axial and side LED lighting and excellent image stacking software are important tools in the study of Jurassic planktonic foraminifera, and fast and cost-effective communication tools in modern micropalaeontology.

Keywords: Jurassic, Planktonic foraminifera, Evolution, Biostratigraphy and palaeoecology

Introduction

This study reports on one new genus and three new species of Jurassic planktonic foraminifera. Globuligerina glinskikhae nov. sp. Gradstein & Waskowska and Globuligerina waskowskae nov. sp. Gradstein are new species of Jurassic planktonic foraminifera from the upper Bajocian—lower Bathonian strata of the Khouroukra section in central Dagestan and the middle Bathonian of the Gnaszyn section in the Częstochowa area of Poland. Petaloglobigerina simmonsi nov. gen., nov. sp. Gradstein occurs in the lower Kimmeridgian Tójera Formation in the Montejunto area of central Portugal. All chronostratigraphic assignments are based on well-established local ammonite zonations (Stam 1986). The new taxa improve our understanding of the early evolution in this group of stratigraphically important microfossils.
Material and methods
The Polish, Dagestan and Portuguese outcrop sections 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 1.0 × and 1.6 × objectives) and Nikon (VL100POL) stereo microscopes, good use was made for wall texture determination of the Leica DM 750 M biological microscope with polarizer/analyser and Epi 10 × /0.25 and N Plan L 20 × /0.35 and Plan L 50 × /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.

Taxonomy

_Globuligerina glinskikhae_ nov. sp., Gradstein and Waskowska

Figure 1, 1–7

Description
Test diameter generally in the 100–125 μm range, with 2–3 whorls in a compact trochoid shape. Relatively large, last whorl with three, globular chambers, slowly increasing in size, with the last globular chamber taking up about half of the final whorl. Coiling direction mostly dextral. Sutures depressed, umbilicus tight, aperture a low slit with rim at the base of the last chamber in the umbilical area. Test wall microperforate with numerous small pustules and scattered pore mounds.

The holotype and paratypes are from sample GN 6 in the lower part of the Gnaszyn section of the Częstochowa area of Poland (Gradstein et al. 2017a, Figures 12 and 13). The sample is placed in the _Morrisi_ Ammonite Zone—Middle Bathonian; it is a grey and slightly sandy claystone with numerous bioclasts, mainly of mollusks shells. In the Gnaszyn section, the new species is relatively rare, but many paratype specimens occur in the marine clays of the Khouroukra section of central Dagestan (Gradstein et al. 2017a, Figure 9), particularly in sample 8 of Bed 19, assigned to the _Parkinsonii_ Ammonite Zone, Upper Bajocian.

The new species is named in honour of Dr. Larisa Glin-skikh, Novosibirsk, Russia, who supplied the sample material from Dagestan, and provided valuable stratigraphic information.

The type specimens are stored in the European Micropalaeontology Reference Centre of the MicroPress Europe Foundation at AGH, Krakow, Poland.

Discussion

_Globuligerina glinskikhae_ nov. sp. may be readily distinguished from _Globuligerina oxfordiana_ (Grigelis) because of its tight, three-chambered and highly globular last whorl (Fig. 1, no. 1). _G. oxfordiana_ has four chambers (and only rarely 3.5 or 4.5) in the last whorl with the second chamber in the last whorl characteristically protruding (see Fig. 1, no. 1 and Fig. 1, nos. 2 and 3 for a comparison of the two test shapes). We have not observed morphological intermediates between the two taxa, but consider it likely that _G. glinskikhae_ evolved from _G. oxfordiana_, perhaps during the Bajocian in Dagestan time and then spread to for example Poland, where it is rare in Bathonian strata. We have not observed the new taxon in clay-prone planktonic foraminiferal assemblages from the Middle Jurassic of Portugal or the Grand Banks of Newfoundland, but co-author AW had correspondence with palynology colleague Dr. Elahe Aarei (School of Earth Sciences, Damghan University, Iran) who showed pictures of Bathonian specimens closely resembling _G. glinskikhae_. We failed to obtain Iranian sample material.

Because of its prominent globular chambers, arranged in a large, three chambered last whorl, we consider it feasible to recognize this taxon in thin sections; it maybe a possible index for Upper Bajocian to Bathonian strata.
**Globuligerina waskowskae** Gradstein nov. sp.

**Figure 2**, 1–8

**Description**

Test generally in the 100–150 µm range, with three whorls in a trochoid coil. The relatively small initial whorls stand in contrast to the large, final whorl with four chambers, regularly increasing in size. Our specimen photographs show the relatively flat spiral base of the last whorl. The axis of coiling tilts in the large penultimate chamber, resulting in progressive forward tilting over the umbilicus and culminating in crescentic shape of the other three chambers in the final whorl. Sutures depressed, aperture umbilical, a low and elongate arch to high arched, with a rim. Umbilicus closed. Wall microperforate, with many small pustules and scattered pore mounds.

The holotype and paratypes are from sample GN 6 in the lower part of the Gnaszyn section of the Częstochowa area of Poland (Gradstein et al. 2017a, Figures 12 and 13). The sample is placed in the Morrisi Ammonite Zone—Middle Bathonian; it is a grey and slightly sandy claystone rich in deeper marine epistominids such as *E. mosquensis* Uhlig. If it was without a reticulate wall texture, the Kimmeridgian specimens of *C. helvetojurassica* could readily be assigned to *G. waskowskae* nov. sp.

**Globuligerina oxfordiana** (Grigelis) 1985

**Figure 3**, 1–7

1958 'Globigerina' *oxfordiana* Grigelis, Nauch.Dokl. Vvys.Shk., Geol.-Geogr. Nauki 3, pp. 110–111, text Fig. 1. 1966 *Globigerina oxfordiana* Grigelis. Bignot and Guyader 1966, pp. 105–107, plate 1, Figs. 1–11. 1971 *Globigerina oxfordiana* (Grigelis). Bignot and Guyader 1971, p. 83, plate 1, Figs. 1–4; plate 2, Figs. 3, 4. 2017a. *Globuligerina oxfordiana* (Grigelis). Gradstein et al. 2017a, pp. 235–239, plates 9–14, all images.

**Discussion**

*Globuligerina oxfordiana* is common in many Middle-to-Late Jurassic open marine sedimentary successions, and is relatively well described. Aperture variable in shape, low-to-high arch, generally comma-shaped, with the posterior margin typically set forwards in the umbilicus. The aperture often has a thickened rim around it.

What is not reported in the literature is a peculiar apertural feature of *G. oxfordiana* with an additional opening such that the thickened wall of the apertural rim forms a pillar in the larger, total apertural opening. The feature was observed in specimens from the Middle Jurassic sections in Khouroukra, Dagestan and Gnaszyn, Poland, from the lower Oxfordian of NW France and the lower Kimmeridgian Tojeira Formation, Montejunto, Portugal. The feature is particularly common in the lower Oxfordian section in NW France. Figure 3, nos. 1–7 provides striking examples of this feature, clearly showing that the extra opening has no rim. A speculation is only that this feature of wall resorption leading to the extra apertural opening is linked to sexual reproduction.

Specimens of *G. glinskikhae* nov. sp. from Dagestan rarely show this peculiar feature too. This taxon commonly occurs with *G. oxfordiana* in the same Dagestani samples.
Recently, Apthorpe (2020) showed a similar apertural feature in well-preserved specimens from the Bajocian of NW Australia. The specimens resemble *Globuligerina bathoniana* (Pazdrowa) and *G. oxfordiana*. The feature deserves further study.

Our specimens are stored in the European Micro-palaeontology Reference Centre of the MicroPress Europe Foundation at AGH, Krakow, Poland.

*Petaloglobigerina* nov. gen. Gradstein

Test trochospiral, low spired, final whorl large and often flat with 3.5–4 petaloide and ovate chambers, rarely finger like; chamber periphery may become narrow and pointed, but not imperforate. In larger specimens, individual chambers in the last whorl may slightly twist from the axis of coiling; sutures strongly incised; umbilicus narrow or closed; aperture a narrow slit with rim at base of last chamber in umbilical position. A small and incomplete (half) bulla may be rarely present, covering the aperture. Wall microperforate and densely pustulose, with pustules fusing to form irregular ridges.

The new genus occurs abundantly in samples from the lower Kimmeridgian.

Tojeira Formation, Montejunto area (Estramadura), central Portugal.

Smaller, and likely mostly juvenile specimens in the assemblages have been previously referred to as *Globuligerina balakhmatovae* (Morozova) (Gradstein et al. 2017a, b) with its characteristic four chambers in the low concave last whorl, shaped in a clover-like pattern; aperture is slit and there is no bulla.

*Globuligerina balakhmatovae* represents a single taxon evolutionary branch of Jurassic planktonic foraminifera that has a low spired test and appears not to have changed test shape or wall texture from Bajocian through Kimmeridgian (Gradstein et al. 2018).

Characteristic specimens of *G. balakhmatovae* are illustrated in Fig. 4, nos. 4, 6–11 from the Khouroukra section in Dagestan (Upper Bajocian), which is the type section of the nominate species (Gradstein et al. 2017a).
Similar specimens occur in the Tojeira section (Fig. 4, 2) and in the Bajocian through Oxfordian of the conjugate Grand Banks of Newfoundland (Fig. 4, nos. 1, 3−5), (see also Stam 1986).

It might be tempting to transfer all specimens of this long-ranging species to the new genus Petaloglobigerina, but this awaits a more detailed evaluation of the original types as designated by Morozova and Moskalenko (1961) 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.

Petaloglobigerina simmonsi Gradstein nov. sp.

Figure 5, nos. 1–8

Description

Test generally in the 100−150 μm range, trochospiral, low spired. Final whorl large and often almost flat with 3.5−4 petaloide and ovate chambers, rarely finger-like; chamber periphery may become narrow and even pseudo-keeled, but us not imperforate. In larger specimens, individual chambers in the last whorl may slightly twist from the coiling axis; sutures strongly incised; umbilicus narrow or closed; aperture a narrow slit with rim at base of last chamber in umbilical position. A small and incomplete (half) bulla may be rarely present, shielding the aperture. Wall microperforate and densely pustulose, with pustules fusing to form irregular ridges.

The new species name is in honour of Dr. Mike Simmons, who made major contribution to the understanding of this group of microfossils with his taxonomic study published in 1997 (Simmons et al. 1997).

The type specimens are stored in the European Micropalaeontology Reference Centre of the MicroPress Europe Foundation at AGH, Krakow, Poland.

Discussion

The species is abundantly in samples from the lower Kimmeridgian.

Tojeira Formation, Montejunto area (Estramadura), central Portugal.

Smaller and likely mostly juvenile specimens in the assemblages have been assigned to G. balakhmatovae (Stam 1986; Gradstein et al. 2017a, b) with its characteristic four chambers in the low concave last whorl, shaped in a clover-like pattern; aperture is a slit, and there is no bulla.

We postulate that P. simmonsi nov. gen., nov. sp. shows a morphological transition in its ontogeny from G. balakhmatovae, the latter being its evolutionary ancestor.

There is no stratigraphic record of the P. simmonsi nov. gen., nov. sp. in post (early) Kimmeridgian strata for which we lack sample material with free specimens. Gradstein et al. (2018) proposed the change from specimens, now assigned to P. simmonsi nov. gen., nov. sp. to Clavihedbergella eocretacea Neagu 1975 in the early Berriasian, but more information is essential. In C. eocretacea (http://www.mikrotax.org/pforams/), chambers in the last whorl expand more in size and the apertural position is umbilical extra-umbilical or interiomarginal, not umbilical as in P. simmonsi nov. gen., nov. sp. Aperture is a low arch or slit with a narrow rim in both taxa. Chambers in both taxa may become somewhat elongated and rather flat, and may twist relative to the plane of coiling. In both taxa, four chambers are commonly found in the last whorl. Both taxa also have an ovate chamber shape, with a tendency to a narrow periphery and a rugulose wall texture.

Evolution

Integrating the work of Gradstein et al. (2017b, 2018) with the new taxa described herein provides new insights into the evolution of early planktonic foraminifera.

The study of Wernli (1988) on thin sections from Toarcian limestone samples from the Domuz Dag mountain chain of SE Turkey provided by Poisson (Paris) documents the oldest known occurrence of true planktonic foraminifera. Curiously, this is the only record 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 Görg and 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).

(See figure on next page.)

Fig. 4 Globuligerina balakhmatovae (Morozova). Nos. 1, 4a, b and 5, cuttings sample 8360 ft., Eider well, Grand Banks, Bajocian-Bathonian; wall texture varies from relatively smooth to densely pustulose, with pustules merging into short ridges. No. 2, sample 24/2P, Tojeira Formation, Montejunto, Portugal, lower Kimmeridgian; wall texture coarsely pustulose. No. 3, sswc sample 5000 ft., Bittern well, Grand Banks, Callovian—early Oxfordian; note the coarse pustulose test and oblong chambers, final one becoming pointed. Nos. 6, 7, 8, 9, 10 and 11 side, umbilical and spiral views of co-types of Globuligerina balakhmatovae (Morozova) in the type section for this taxon from sample 8, Parkinsonii Zone, Upper Bajocian, Khouroukra, Dagestan.
Figure 6 depicts this history in a simple stratigraphic column, a figure updated from Gradstein et al. (2017b, 2018).

The Toarcian through Aalenian record is only known from thin sections, and it appears that an often larger and higher spired form similar to *G. bathoniana* and a smaller, lower spired form similar to *G. 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.

As outlined in Fig. 6, we consider that within the Jurassic and earliest Cretaceous four lineages of planktonic foraminifera occur, which for graphic clarity are indicated with green, brown, blue and red stratigraphic lines. Two key taxa, *P. simmonsi* nov. gen., nov. sp. and *G. oxfordiana* are postulated to be ancestral links to Cretaceous taxa.

The ‘green group’ is monotypic and consists of *G. balakhmatovae* evolving in Kimmeridgian time in *P. simmonsi* nov. gen., nov. sp.

The ancestry of *G. 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, including other taxa in the genera *Globuligerina* and *Oberhauserella*.

There is no stratigraphic record of the low-spired *Psimonss* nov. gen., nov. sp. in post (early) Kimmeridgian strata. Based on a general similarity in test morphology, Gradstein et al. (2018) proposed that this taxon might have evolved in *C. eocretacea* in early Berriasian time.

The ‘brown group’ includes *Globuligerina dagestanica* (Morozova), the common species *G. bathoniana* and rare *G. jurassica* (Hofman), 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, *G. jurassica* might be a local and often aberrant variant of *G. dagestanica*; it is not illustrated in Fig. 6.

The ‘blue group’ consists of *Globuligerina avariformis* (Kasimova) and *Conoglobigerina grigeli* (Gradstein), 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 line age is postulated from the compact *G. avariformis* into the equally, or even more compact *C. grigeli*. The latter acquires a reticulate wall sculpture. Its youngest record is Kimmeridgian. We refrain to speculate on the ancestry of *G. avariformis*, our stratigraphic and taxonomic data are insufficient.

The ‘red group’ includes *G. xfordiana*, *G. glinskikhae* nov. sp., *G. tojeiraensis* Gradstein and the inferred lineage from *G. waskowskae* nov. sp. to *C. 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 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 may be seen to strengthen our postulation that *G. oxfordiana* is ancestral to *Favusella hoterivica* (Subbotina). But interestingly, specimens from our four other, widely different localities of Late Bajocian through Early Kimmeridgian age (Grand Banks, Portugal, Poland and Dagestan) show pustulose wall texture only. The close morphological comparison and overlap in wall texture features, makes it viable to consider *G. oxfordiana* to be the ancestor of *F. hoterivica*. In Fig. 6, both taxa are illustrated. To demonstrate that this evolution took place in Tithonian time, as postulated in Fig. 6, wall texture analysis of well-preserved, free specimens is required.

The species *G. tojeiraensis*, with elongated chambers and wide-open umbilicus is known from the Bajocian–Bathonian of Dagestan, the Callovian–Oxfordian of the
| Stage        | Planktonic Foraminifera Ranges |
|-------------|--------------------------------|
| Berriasian  | Clavihedbergella eccentrica    |
|             | Conoglobigerina gulekhenais    |
|             | Favusella hotervica            |
|             | Hedbergella aff. similis       |
| Tithonian   | Petaloglobigerina simmonsi     |
|             | Globuligerina bathoniana       |
|             | Conoglobigerina grigeli        |
|             | Globuligerina oxfordiana       |
|             | Conoglobigerina helvetojurassica |
| Kimmeridgian| "Globuligerina" balakhmatovae  |
|             | Globuligerina dagestanica      |
|             | Globuligerina avariformis      |
|             | ?                              |
|             | ?                              |
|             | ?                              |
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Fig. 6 Stratigraphic ranges and evolution of Jurassic planktonic foraminifera. For details, see text.
Grand Banks of Newfoundland and the Lower Kimmeridgian of Portugal. Its overlap in morphology with G. oxfordiana suggests the latter to be ancestral. The origin of G. oxfordiana itself is shrouded in mystery.

The discovery and description in this study of well-preserved G. waskowskae nov. sp. (Fig. 2), with a test morphology much alike C. 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 C. helvetojurassica, appearing in Middle Oxfordian.

In summary, and as illustrated in Fig. 6, the planktonic foraminifera occurred in Toarcian-Aalenian time (but no free specimens record) and with at least eight taxa in Bajocian-Bathonian. With the subsequent disappearance of two taxa and appearance of four new taxa, the Oxfordian-Kimmeridgian planktonic foraminiferal record consists of six taxa. Giving weight to the acmes of taxa in Portugal, the Kimmeridgian is the time Jurassic planktonic foraminifera flowered. A dramatic faunal change-over, which is not well documented, and not well understood led to the survival of only one taxon, most likely G. oxfordiana, during Tithonian time. During Berriasian time, several new taxa appeared.

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Authors’ contributions
Both FG and AW performed the detailed micropaleontologic analysis, FG wrote most of the manuscript and AW made the plate figures. Both authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

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