Swiss Journal of Palaeontology
https://doi.org/10.1007/s13358-018-0175-8

REGULAR RESEARCH ARTICLE

Berriasian planktonic foraminifera and calcareous nannofossils from Crimea Mountains, with reference to microfossil evolution

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Received: 26 July 2018 / Accepted: 22 October 2018

Abstract

A Berriasian age planktonic foraminifera assemblage from a section near the village of Krasnoselivka in the Tonas River Basin, Crimea contains *Favusella hoterivica* (Subbotina), ?*Favusella* sp., *Conoglobigerina gulekhensis* (Gorbachik and Poroshina), *Lilliputinella eocretacea* (Neagu), *Lilliputinella* aff. *similis* (Longoria), *Hedbergella* aff. *handousi* Salaj and ? *Globuligerina* sp. Specimens are poorly preserved, but test morphology, aperture and key wall texture features are recognizable. Age assignment is based on a diverse and well-preserved calcareous nannofossils assemblage of upper zone CC2 and ammonites (*Jacobi* Zone). The nannfossils indicate an open marine environment of Tethyan affinity. Several of the planktonic foraminiferal taxa were not previously described from pre-Valanginian or Hauterivian strata. XRD analysis of the tests of benthic and planktonic foraminifera and micro-gastropods shows these to be calcitic in composition, also of those benthic and planktonic foraminifera that were deemed to be originally aragonitic in composition, indicating diagenetic changes in carbonate fractions. From detailed comparison to Jurassic planktonic foraminifera, two lineages are proposed from Late Jurassic into earliest Cretaceous: *Globuligerina oxfordiana* (Grigelis) to *Favusella hoterivica* (Subbotina) and *Globuligerina balakhmatovae* (Morozova) to *Lilliputinella eocretacea* (Neagu). The first lineage is a gradual change in wall sculpture from rugulose to reticulate and the second one a change to a lower spire, more ovate chambers of which the last one may be much larger in size and shift of the aperture out of the umbilicus. The meagre evolution of early planktonic foraminifera from Toarcian through Tithonian with only two genera and fewer than ten species does not follow the evolutionary diversity pattern of nannofossils and dinoflagellates. Tithonian appears to be a bottleneck for planktonic foraminifera, with a sparse record and virtual extinction. The so-called *Globigerina oxfordiana* from the Tithonian in ODP Site 901 on Galicia Bank (Collins et al. Proceeding Deep Sea Drilling Project Science Research 149:193–201, 1996) is of Miocene age.

Keywords Berriasian · Planktonic foraminifera · Nannofossils · Evolution · Palaeobiogeography

Introduction

This study reports on seven species of planktonic foraminifera and 20 species of calcareous nannofossils from the Berriasian of Crimea. Local chronostratigraphy is based on key ammonite and nannofossil taxa. The nannofossils are well preserved, but not the relatively small-sized and calcitic (not aragonitic) planktonic foraminifera. The latter appear to have undergone some test dissolution but taxonomic identification is feasible. Benthic foraminifera in the same sample are better preserved, probably a result of a thicker and less porous wall. The poorly known distribution of Berriasian and also of Jurassic planktonic foraminifera is addressed, and a hypothesis outlined on the evolution of two of the taxa.

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Material

The Crimean sample, provided by co-author Kopaevich, and reported on with *G. gulekhensis* in Gradstein et al. (2017a), is numbered Cr1, and is from a locality situated in the Tonas River Basin, 2 km south of the village of Krasnoselivka (Fig. 1). Geographic coordinates are 44.927712°N, 34.634905°E. Here, along the local road sedimentary strata are exposed assigned to a stratigraphic interval across the Jurassic-Cretaceous boundary. In the outcrop section marly limestones, assigned to upper Tithonian, stratigraphically upward change abruptly into a rhythmic alternation of shales, sandstones and limestones. Figure 2 shows part of the sedimentary section near Krasnoselivka, covering an interval assigned to the Berriasian (Arkad'ev et al. 2005). 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.

Arkad'ev et al. (2005) reports a diverse macro fauna from the sedimentary strata, including the ammonites *Berriasella jacobi* Mazenot and *Pseudosubplanites grandis* (Mazenot). The ammonites are characteristic for the *Jacobi* and *Grandis* subzones of the *Jacobi* Zone of early Berriasian age (Ogg et al. 2016). Arkadiev et al. (op.cit) also cites benthic foraminifera from the same sediments, assigned to two zones of early Berriasian age: an older one—*Protopeneroplis ultragranulatus*—*Siphoninella antiqua* and a younger one—*Quadratina tonassica*—*Siphoninella antiqua* (Gorbachik and Poroshina 1979).

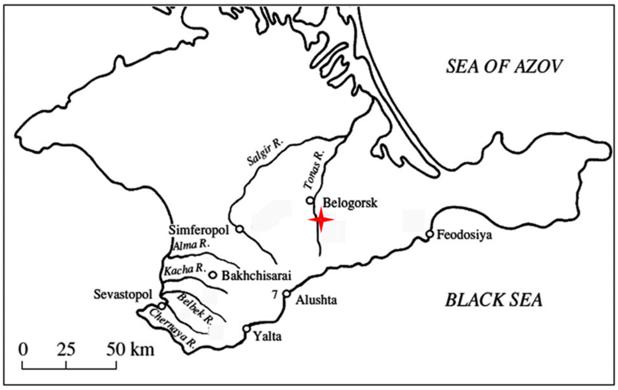


Fig. 1 Locality of sample Cr1 in the Tonas River Basin section, 2 km south of the village of Krasnoselivka, Crimea. Section at red star with geographic coordinates 44.927712°N, 34.634905°E (figure modified after Arkad'ev et al. 2005)

Fig. 2 The Krasnoselivka section; for location see Fig. 1 (Photograph taken by L. Kopaevich)

Previous literature

Savelieva et al. (2017) in a detailed study of foraminifera in a Crimean section across the Berriasian–Valanginian boundary did not encounter either epistominid benthic foraminifera or planktonic foraminifera. The common presence of lenticulinid-nodosariid taxa suggests the environment was (too ?) shallow marine.

Literature on free specimens of Berriasian planktonic foraminifera is virtually non-existent. Gorbachik and Poroshina (1979) described *Conoglobigerina gulekhensis* from the early Berriasian–early Valanginian of SE Caucasus, E. Crimea and Azerbaijan. Wernli et al. (1995) provided information on the record of *Favusella hoterivica* from Berriasian–Valanginian age strata, offshore eastern Canada (see our section on Taxonomy).

Gradstein et al. (2017a) described *Globuligerina gulekhensis* (Gorbachik and Poroshina) from Berriasian strata of Crimea.

Görög and Wernli (2004) studied 'protoglobigerinids' in thin sections and as isolated-free specimens using acetic acid, from a Tithonian limestone near Paprét-árok, Gerecse Mountains, Hungary. The authors consider the assemblage to be monospecific, with specimens transitional between *Globuligerina oxfordiana* and *Favusella hoterivica,* but no pore features and wall texture can be determined. The same section also should yield Berriasian planktonics. It is our understanding that the locality in Hungary no longer exists.

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. There are poor illustrations in thin sections of *Conoglobigerina gulekhensis, Caucasella hoterivica, Compactogerina* sp. and *Gorbachikella* sp. by Omaña et al. (2017) from limestones of the Taraises Formation in north

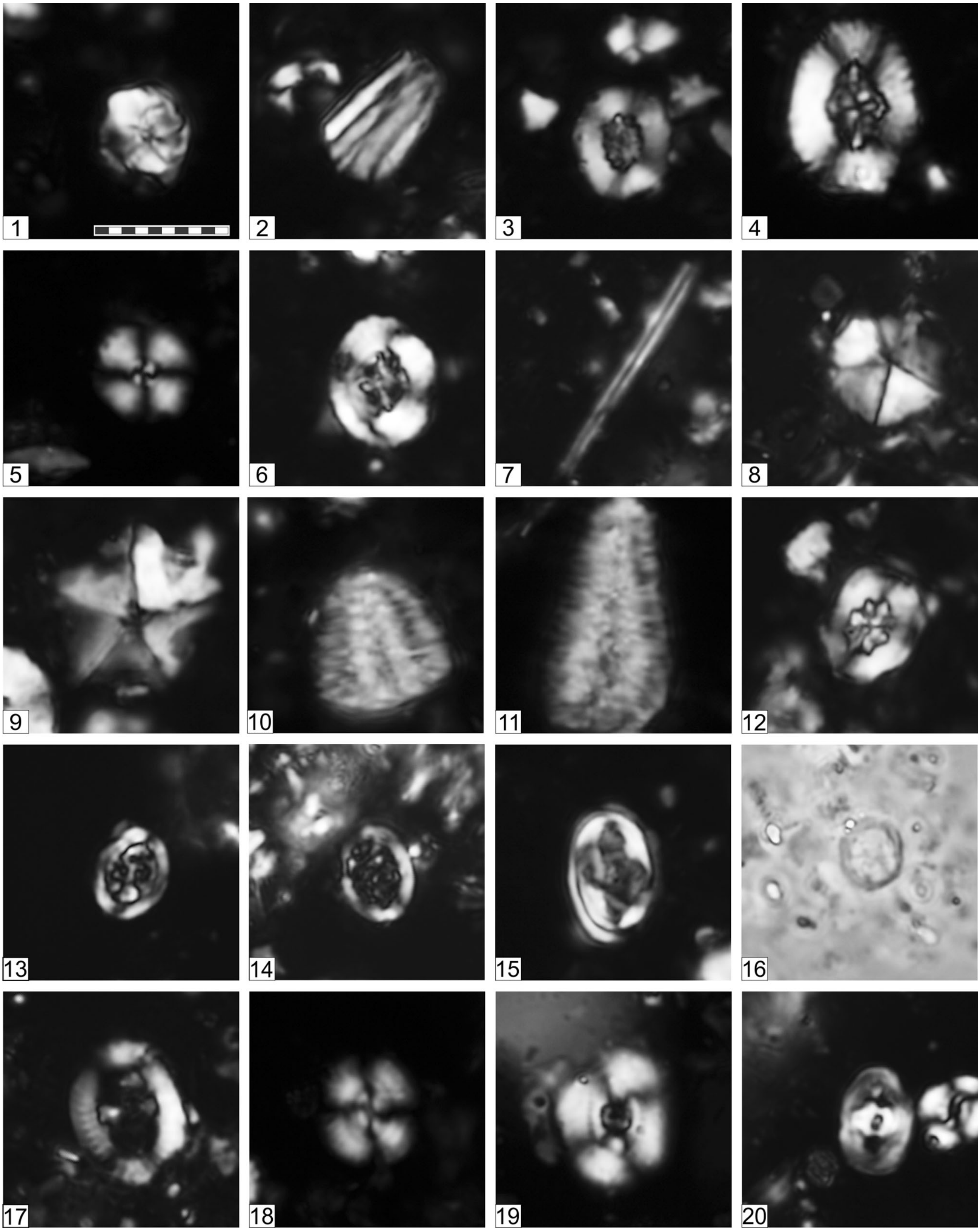
Mexico. The image on their Fig. 5c from specimens in the Taraises Formation likely is *Favusella hoterivica*, but other images are non-determinate. The type of the monotypic genus *Compactogerina* is coarse perforate and belongs to Neogene *Neogloboquadrina pachyderma* (Gradstein 2017a, b). Lourdes Omaña kindly communicated to Gradstein (May 2018) that it is currently not advised to visit the Mexican site due to drugs-related violence.

Calcareous nannofossils

The sample Cr1 yielded a diverse nannoflora, described by co-authors Watkins and Perez. All specimens encountered in the first 100 fields of view (FOV) were counted and the census tabulated in Table 1. More than 400 additional FOV were surveyed to identify additional taxa not encountered in the census count. Figure 3 illustrates some of the characteristic taxa including those with biostratigraphic significance. Calcareous nannofossils in this sample are

Table 1 Nannofossil count in sample Cr1, Krasnoselivka section, Crimea

Taxon	Number of Specimens	Abundance (%)
Assipetra infracretacea	4	0.5
Bidiscus ignotus	4	0.5
Biscutum ubiquens	11	1.3
Conusphaera mexicana mexicana	2	0.2
Cretarhabdus crenulatus	16	1.8
Cretarhabdus madingleyensis	1	0.1
Cretarhabdus surirellus	3	0.3
Cruciellipsis cuvillerii	1	0.1
Cyclagelosphaera margerelii	108	12.3
Cylcagelosphaera deflandrei	3	0.3
Diazmolithus lehmanii	2	0.2
Ethmorhabdus hauterivicus	5	0.6
Helenea chiastia	13	1.5
Helenea staurolithina	1	0.1
Lithraphidites carniolensis	5	0.6
Manivitella pemmatoidea	1	0.1
Micrantholithus hoschulzii	3	0.3
Micrantholithus obtusus	3	0.3
nannoconus steinmannii minor	69	7.9
Nannoconus steinmannii steinmannii	14	1.6
Retecapsa angustiforata	7	0.8
Retecapsa octoradiata	1	0.1
Rhagodiscus adinfinitus	3	0.3
Rhagodiscus asper	17	1.9
Rhagodiscus nebulosus	2	0.2
Rotelapillus crenulatus	10	1.1
Speetonia colligata	2	0.2
Staurolithites crux	3	0.3
Tubodiscus frankiae	1	0.1
Watznaueria barnesiae	510	58.1
Watznaueria britannica	5	0.6
Watznaueria fossacincta	7	0.8
Watznaueria manivitiae	9	1.0
Zeugrhabdotus cooperii	3	0.3
Zeugrhabdotius embergerii	2	0.2
Zeugrhabdotus erectus	5	0.6
Zeugrhabdotus (small)	22	2.5
Total count	878	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◀**Fig. 3** Calcareous nannofossils from sample Cr1, Krasnoselivka section, Crimea. All images in cross-polarized light except 16 (plain light). Scale bar in 1 = 10 micrometers; magnification approximately 2250×. 1, *Assipetra infracretacea*, (Thierstein, 1973) Roth, 1973. 2, *Conusphaera mexicana mexicana* Trejo, 1969. 3, *Cretarhabdus crenulatus* Bramlette & Martini, 1964. 4, *Cruciellipsis cuvillierii* (Manivit, 1966) Thierstein, 1971. 5, *Cyclagelosphaera margarelii* Noël, 1965. 6, *Helenea chiastia* Worsley, 1971. 7, *Lithraphidites carniolensis* Deflandre, 1963. 8, *Micrantholithus hoschulzi* (Reinhardt, 1966) Thierstein, 1971. 9, *Micrantholithus obtusus* Stradner, 1963. 10, *Nannoconus steinmannii minor* (Kamptner, 1931) Deres and Achéritéguy, 1980. 11, *Nannoconus steinmannii steinmannii* Kamptner, 1931. 12, *Retecapsa angustiforata* Black, 1971. 13, *Rhagodiscus adinfinitus* Bown, 2005. 14, *Rhagodiscus nebulosus* Bralower *in* Bralower et al., 1989. 15, *Rhagodiscus asper* (Stradner, 1963) Reinhardt, 1967. 16, *Rotelapillus crenulatus* (Stover, 1966) Perch-Nielsen, 1984. 17, *Speetonia colligata* Black, 1971. 18, *Watznaueria barnesiae* (Black in Black & Barnes, 1959) Perch-Nielsen, 1968. 19, *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964. 20, *Zeugrhabdotus erectus* (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965

common and moderately preserved, with most taxa being reliably identifiable. The sample is placed in the calcareous nannofossil Zone CC2, late early to middle Berriasian, based on the presence of *Retecapsa angustiforata*, *Nannoconus steinmannii steinmanniii*, *Lithraphidites carniolensis* and *Rhagodiscus nebulosus*, without *Calcicalathina oblongata*. The presence of *R. nebulosus* indicates the upper part of CC2; however, the absence of *Percivalia fenestrata* suggests that this interval is not in the uppermost part of CC2. The age of this sample is placed around 143 Ma based on age assignments in Ogg et al. (2016). The sample is strongly dominated by *Watznaueria barnesiae* (ca. 59%), with *Cyclagelosphaera margarelii* an important secondary taxa with about 18% of the assemblage. The *Nannoconus steinmannii* plexus (*N.s. steinmannii* and *N.s. minor*) comprise approximately 10% of the assemblage. The presence of several other characteristic Lower Cretaceous taxa (*Cruciellipsis cuvillierii*, *Speetonia colligata*, *Micrantholithus obtusus* and *M. hoschulzii*), together with the dominance by *W. barnesiae* and the common occurrence of nannoconids, indicates an open marine environment of Tethyan affinity.

Mineralogy of foraminifera

As part of a larger study on the wall composition and wall structure of Jurassic and Cretaceous foraminifera, co-author Friis analysed planktonic and benthic foraminiferal tests and a micro-gastropod from Crimean sample Cr1 for mineralogy.

The mineralogy of individual specimens was investigated by X-ray diffraction method. A single specimen was mounted with oil in a cryo-loop, which was placed in a Kappa geometry Rigaku Synergy-S diffractometer equipped with a HyPix-6000HE detector. The equipment is housed in the Natural History Museum of the University of Oslo. A PhotoJet Cu-micro source operating at 50 kV and 1 mA was used in all experiments, and acquisition time varied between 15 and 40 s. For mineral identification of the specimens, a standard Gandolfi movement was achieved by a combination of standard Phi and Omega movements. The data were collected in both positive and negative Theta ranges and collapsed into a two-dimensional diagram using the CrysAlis Pro V.39 software. Subsequently, the data were imported into Bruker's EVA where search and match were performed for identification. Figure 4 shows the diffractograms for five specimens in sample Cr1, all of which indicate a calcitic test. Minor additional peaks are contribution from quartz and clay minerals and no evidence of aragonite was observed in any of the tested specimens.

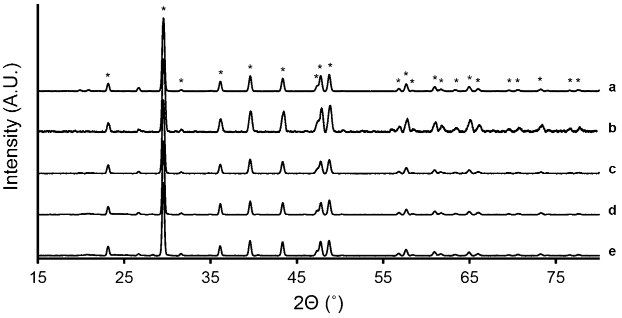


Fig. 4 X-ray diffractograms of a micro-gastropod (a), benthic foraminifera *Lamarckina* (b) and *Epistomina stellicostata* (c) and planktonic foraminifera *Lilliputinella eocretacea* (d) and *Favusella hoterivica* (e). The asterisks denote peaks originating from calcite

Thus, all planktonic tests are calcitic in test composition, as are a micro-gastropod, and benthic foraminifer tests of *Epistomina* sp. and *Lamarckina* sp. The latter three are deemed to originally have had an aragonitic test. Hence, the Rigaku Synergy-S diffractometer test for aragonite in the planktonics and benthics is inconclusive, likely due to post-sedimentary diagenesis. A slightly coarse crystalline test structure is observed which may relate to diagenesis from burial, prior to exhumation.

Benthic foraminifera

The Berrisian sample Cr1 from the Krasnoselivka section contains a diversified assemblage of quite well-preserved benthic foraminifera, among which we identified: *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., *Haplophragmoides* sp. and agglutinated benthic foraminifera indet. Such assemblage indicates deep neritic to upper bathyal marine conditions, a palaeoenvironment where also planktonic foraminifera and nannofossils normally may be expected. This palaeoenviroment interpretation is in agreement with Arkad'ev et al. (2005), which authors estimate the deposits to be indicative of a deep neritic or upper bathyal palaeoenvironment. It also agrees with the (above cited) record in our sample of the nannofossil taxa *Cruciellipsis cuvillierii*, *Speetonia colligata*, *Micrantholithus obtusus* and *M. hoschulzii*, which together with the dominance by *W. barnesiae* and the common occurrence of nannoconids indicate an open marine environment of Tethyan affinity.

Planktonic foraminifera

Re-processing and re-analysis during 2017 and 2018 of sample Cr1 from the Krasnoselivka section recovered several taxa of planktonic foraminifera. Laboratory methodology to extract the small size (65–125 micron) planktonic foraminifera included weak acidisation (yielding many specimens but limited wall texture information), glauber salt fragmentation of sediment and freezing/heating in rapid alternation. The latter method provided the best preservation of foraminiferal tests.

Over 100 specimens of small size (65–125 micron) were recovered; test morphology, test preservation and wall texture were studied using a Leica M205C optical microscope, a Deltapix Modus M12ZS digital microscope (see www.deltapix.com) and the scanning electron microscope imaging fascility of AGH University, Krakow, Poland. Both optical microscopes are capable of one micron resolution with suitable illumination.

An important issue is the actual state of preservation of the planktonic tests, which leaves to be desired. Benthic foraminifera in the sample are quite well preserved with calcitic or agglutinated walls (see the section on mineralogy), and so are the nannofossils. Utilization of a Zeiss XRadia micro-CT scanner (by S. Kendall and D. N. Schmidt of the University of Bristol, UK and the senior author) on selected specimens shows the tests not to be moulds, but in fact have thin walls intact, although earliest chambers are missing (due to dissolution?). The study of selected tests in translucent light with the Leica M2005C and Deltapix M12ZS microscopes confirms that the tests are translucent. We consider that fragile test walls got corroded and that in the walls merging may have taken place of original crystals to larger lumps. Nevertheless, some trace of the original wall texture is discernible and identification of the (non aff.) taxa is positive. The valuable study by Coccioni and Premoli Silva (1994) from the Lower Cretaceous of Rio Argos (Spain) also encountered the obstacle of poorly preserved tests, but yielded new taxonomic and stratigraphic information.

Gradstein et al. (2017a) listed from sample Cr1 rare *Globuligerina gulekhensis* and some indeterminate specimens, one of which is almost planispiral. The current study reports seven planktonic foraminifera taxa in sample Cr1, all microperforate, including with frequent specimens *Favusella hoterivica* (Subbotina), with common specimens *Lilliputinella eocretacea* (Neagu) and *Conoglobigerina gulekhensis* (Gorbachik and Poroshina) and with less than 10 specimens each of the taxa *Lilliputinella* aff. *similis* (Longoria), ?*Favusella* sp., *Hedbergella* aff. *handousi* Salaj and ? *Globuligerina* sp. The record of isolated specimens of ? *Favusella* sp. is not dealt with.

As will be discussed in some detail below, only *Conoglobigerina gulekhensis* (Gorbachik and Poroshina) was known previously from Berriasian strata, and this only from two regions, Crimea and Azerbaijan. *Favusella hoterivica* (Subbotina) with certainty only was 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.

In current literature, the generic and species taxonomy of pre-Aptian planktonic foraminifera lacks standardization and there is no published atlas by the Mesozoic Planktonic Foraminifera Working Group. Rather than trying to improve upon the taxonomy of Lower Cretaceous planktonic foraminifera, which taxonomy lacks agreement on hierarchy of test morphology and insight in evolutionary relationship of taxa, we have taken a conservative approach. In this, we mean that no effort has been made to 'get to the bottom of' junior and senior synonymy issues in species, or the validity of generic and species names. These issues require study of a large collection of well-preserved specimens, in samples from many pre-Aptian and particularly Berriasian sites.

Principal literature consulted includes:

1. The original definition of the taxa recognized, as available in http://www.mikrotax.org/pforams/ for all but *Clavihedbergella eocretacea* Neagu.
2. Neagu (1975, in French) for the latter taxon.
3. The excellent publications by Coccioni and Premoli Silva (1994) on a diverse (albeit poorly preserved) Valanginian–Hauterivian assemblage of southern Spain, and by Butt (1979) on a diverse Hauterivian/Barremian through Aptian assemblage in DSDP Site 397, Leg 47A offshore Morocco.
4. The monograph on Jurassic *Conoglobigerina* and *Globuligerina* in Gradstein (2017a, b) and Gradstein et al. (2017a, b).

5. The excellent (not published) teaching atlas on Cretaceous Planktonic Foraminifera Taxonomy and Biostratigraphy by M.R. Petrizzo (and the Mesozoic Planktonic Foraminifera Working Group), which uses balanced information from research projects currently underway.

Other literature consulted for specific issues includes Gorbachik and Poroshina (1979), Wernli et al. (1995), Görög and Wernli (2003, 2004, 2013), and Huber and Leckie (2011).

Below, we will deal with the taxonomy of the observed taxa, starting with *Conoglobigerina gulekhensis* (Gorbachik and Poroshina), originally described from the Berriasian–early Valanginian of Azerbaijan and the Berriasian of the Tonas Basin, Crimea.

Conoglobigerina gulekhensis (Gorbachik and Poroshina) 1979

Figure 5, 1–12

1979 *Globuligerina gulekhensis* Gorbachik and Poroshina: 286–288, Fig. 1a–c.

1979 *Globuligerina caucasica* Gorbachik and Poroshina: 288, Figs. 2a–3, 3a–d.

1997 *Conoglobigerina gulekhensis* (Gorbachik and Poroshina), in Simmons et al.: 24, 25, pl. 2.6, Figs. 13–15.

Non 1997 *Conoglobigerina caucasica* (Gorbachik and Poroshina), in Simmons et al.: 24, pl. 2.6, Figs. 9–12.

Original description

Test small, no more than 0.25 micron in diameter, high trochoidal; test contour subquadratic, prominently lobate. The spire forming the initial whorl is often slightly displaced relative to the center of the ultimate whorl and sharply delineated from the surface. Peripheral margin broad and round. The test consists of 12–13 chambers forming the 2.5 to three whorls of a spiral. Chambers of initial whorls spherical or ellipsoidal, closely appressed. The size of the chambers increases gradually in each whorl; the chambers of different whorls differ appreciably in size. Septal sutures deepened, straight. Umbilicus small and narrow. Aperture opening in umbilicus, arcuate, with barely apparent lip. Test walls finely perforate; the surface appears smooth under the binocular microscope at a magnification of 96×, but distinctly expressed cancellate ornamentation is seen with the scanning electron microscope (at magnifications of 1000 and 3000×). Cells of cancellate ornamentation are irregularly tetragonal, separated by comparatively broad, high, smooth varices. The cells reach a size of 2 µm. Pores round or oval, mainly located within the cells, but sometimes also on the varices. Pores of two orders are seen; small ones measuring about 0.33 µm, and large ones measuring up to 1 µm. Small pores predominate. Test diameter varies between 0.15 and 0.25 micron and the height is 0.6 or 0.7 of the width; these measurements are for type specimens.

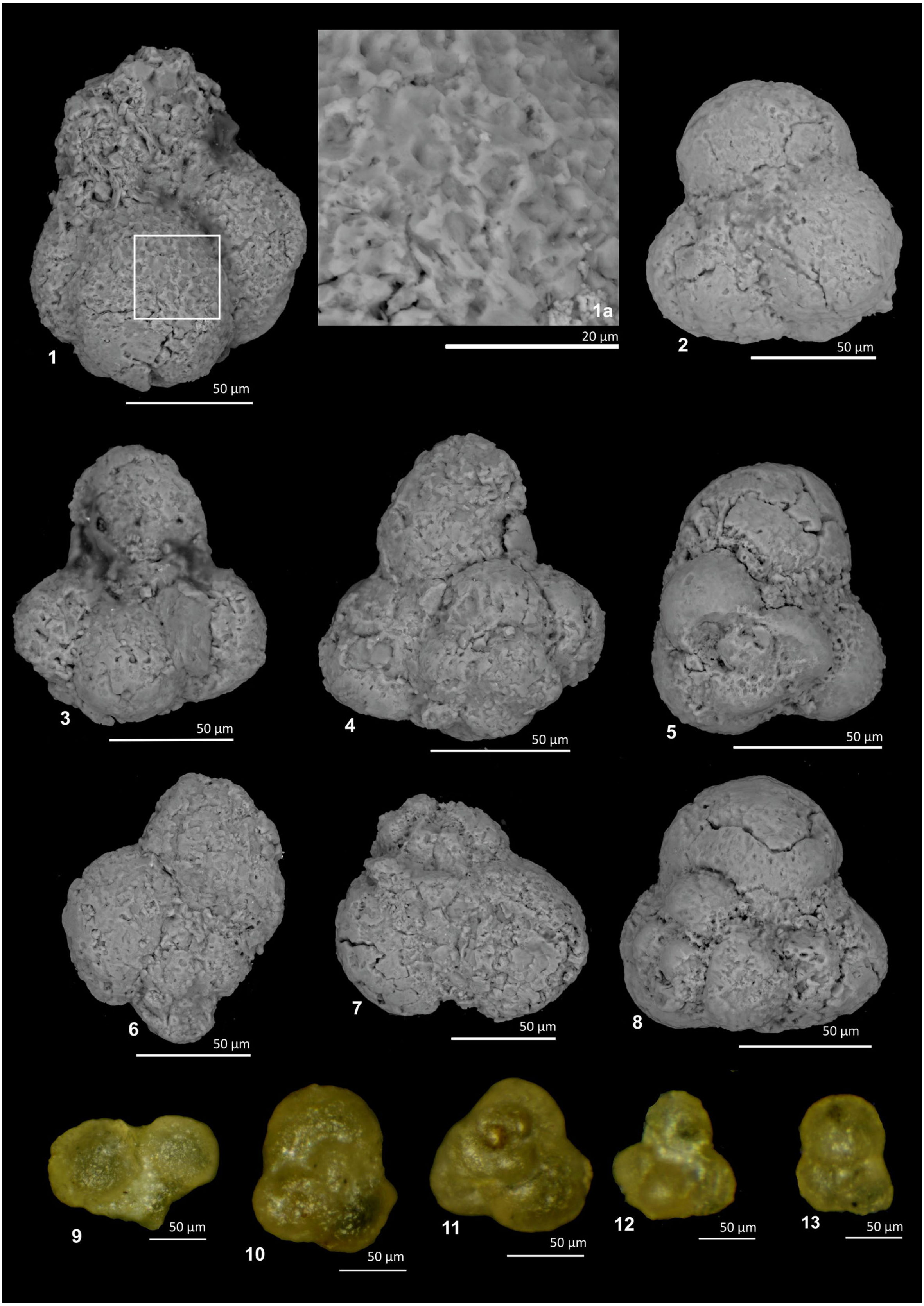
Discussion

Sofar the outstanding diagnosis of Gorbachik and Poroshina (1979) in the English translation of their (originally in Russian) study in the Palaeontology Journal of the American Geological Institute. The description is based on study of about 80 specimens from the Berriasian of Azerbaijan. Test variation is in height and shape of the test and number of chambers in the whorls. The test can be conical in shape, often bluntly conical, and the last whorl may contain three chambers only. This is as observed for most of our Crimean specimens which have a tiny and pointed initial test with two whorls and a large final whorl with three chambers. The original observation that the spire of the first whorls often is slightly displaced relative to the center of the ultimate whorl, and sharply delineated from the test surface, is confirmed and easily recognized, for example in the optical photography images on Figs. 5, 9 and 10.

The Tonas River Basin is listed as co-locality from which Gorbachik and Poroshina (1979) described *Globuligerina caucasica* and *G. gulekhensis*. The principal difference between the two contemporary taxa is a higher spire and more convex spiral side of *G. gulekhensis*. The considerable variation in height of spire and convexity does not warrant this taxonomic splitting; hence all specimens in the assemblage are considered to be variants of one species (Gradstein et al. 2017a).

Although poorly visible on our topotypic specimens on Plate 19 in Gradstein et al. (2017a) from the Tonas River Basin, the reticulate wall texture is clear under suitable magnification. The reticulate wall ornamentation suggests that *Conoglobigerina gulekhensis* is related to *Conoglobigerina* in the Jurassic and to *Favusella* in the Cretaceous. Hence, it is tempting to consider that *C. gulekhensis* evolved from *Globuligerina oxfordiana* like *Favusella hoterivica* did. This subject is taken up below in the section discussing evolution.

Curiously, the metatypes re-illustrated from Simmons et al. (1997) on Plate 19, nos. 6–7 in Gradstein et al. (2017a) show little sign of reticulation. These specimens that were originally assigned to *C. caucasica* both by Gorbachik and Poroshina (1979) and by Simmons et al. (1997) readily might be named *Globuligerina tojeiraensis* Gradstein. Hence, this species might extend from Kimmeridgian into Berriasian, but this is not clearly confirmed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◀**Fig. 5** 1–12, *Conoglobigerina gulekhensis* (Gorbachik and Poroshina) 1979 from sample Cr1, Berriasian, Krasnoselivka section, Crimea, Russia. Specimens typically show a narrow initial spire composed of two whorls and a last and flaring whorl with three (common) or four chambers in the last whorl. The initial narrow spire often is under an angle with the coiling axis of the last whorl (as seen to some extent in the SEM images 4 and 8 and optical photographs 9 and 10). Wall texture is reticulate as seen in 1a

with our data from sample Cr1 (see our listing of ? *Globuligerina* sp.).

Wernli et al. (1995) claimed that *Favusella hoterivica* in Berriasian–Valanginian of former SE Russia, which broadly includes the region with our sample Cr1, were wrongly identified as *Conoglobigerina gulekhensis*. No specific and detailed information was provided that the local taxon is a junior synonym of *Favusella hoterivica*, and we refute the argument. In our Krasnoselivka assemblage, *F. hoteri*vica and *Conoglobigerina gulekhensis* are morphologically different, as described in detail. In particular, Favu*sella hoterivica* has the second chamber in the last whorl of four chambers markedly sticking up, whereas *Conoglobigerina gulekhensis* often has a higher spire, a coiling axis that clearly changes angle and wider last whorl.

Gorbachik and Poroshina (1979) list a diverse benthic foraminiferal assemblage from the Azerbaijan samples with numerous epistominids and ceratobuliminids.

Stratigraphic range

Described by Gorbachik and Poroshina (1979) from early Berriasian–early Valanginian of SE Caucasus, E. Crimea and Azerbaijan. There is currently no record of this taxon outside its narrow (Tethyan) belt in the greater Caucasian Mountains area. Wernli et al. (1995) reported that T. Gorbachik considered *Favusella hoterivica* from the Berriasian of the Scotian Shelf, E. Canada to be *Conoglobigerina gulekhensis*, an interpretation that may have been more inspired by Berriasian age specimens in eastern Canadian offshore wells than by their morphology. Closely reading the arguments by Wernli et al. (1995) on a potential Berriasian age of the taxon in samples of wells Onondaga E-84, Oneida O-25 and Gabriel C-60 leaves the possibility that specimens are of Valanginian age. All well intervals are dated as of Berriasian–Valanginian age and stage boundaries are not clearly delineated. No physical well record or lithology was provided for the critical intervals in these wells to ascertain that the record is stratigraphically continuous. Calpionellids are wanting in the so-called Berrisian age and shallow marine well samples, and dinoflagellates were listed only for Valanginian strata.

Favusella hoterivica (Subbotina 1953)

Figure 6, 1–10.

1953 *Globigerina hoterivica* Subbotina: 50, pl. 1, Figs. 1–4.

1978 'Globigerina' hoterivica Subbotina, in Gradstein, 622, pl 9, Figs. 9–15.

1979 *Hedbergella hoterivica* (Subbotina), in Butt, pl.3, Figs. 1–7; pl.4, Figs. 1–6.

1995 *Favusella hoterivica* (Subbotina), in Wernli et al., pl. 2, 1–16, pl. 3, 1–9, pl.4.

Non 2013 *Favusella hoterivica* (Subbotina), in Görög and Wernli: 286, Figs. 5.1–5.7.

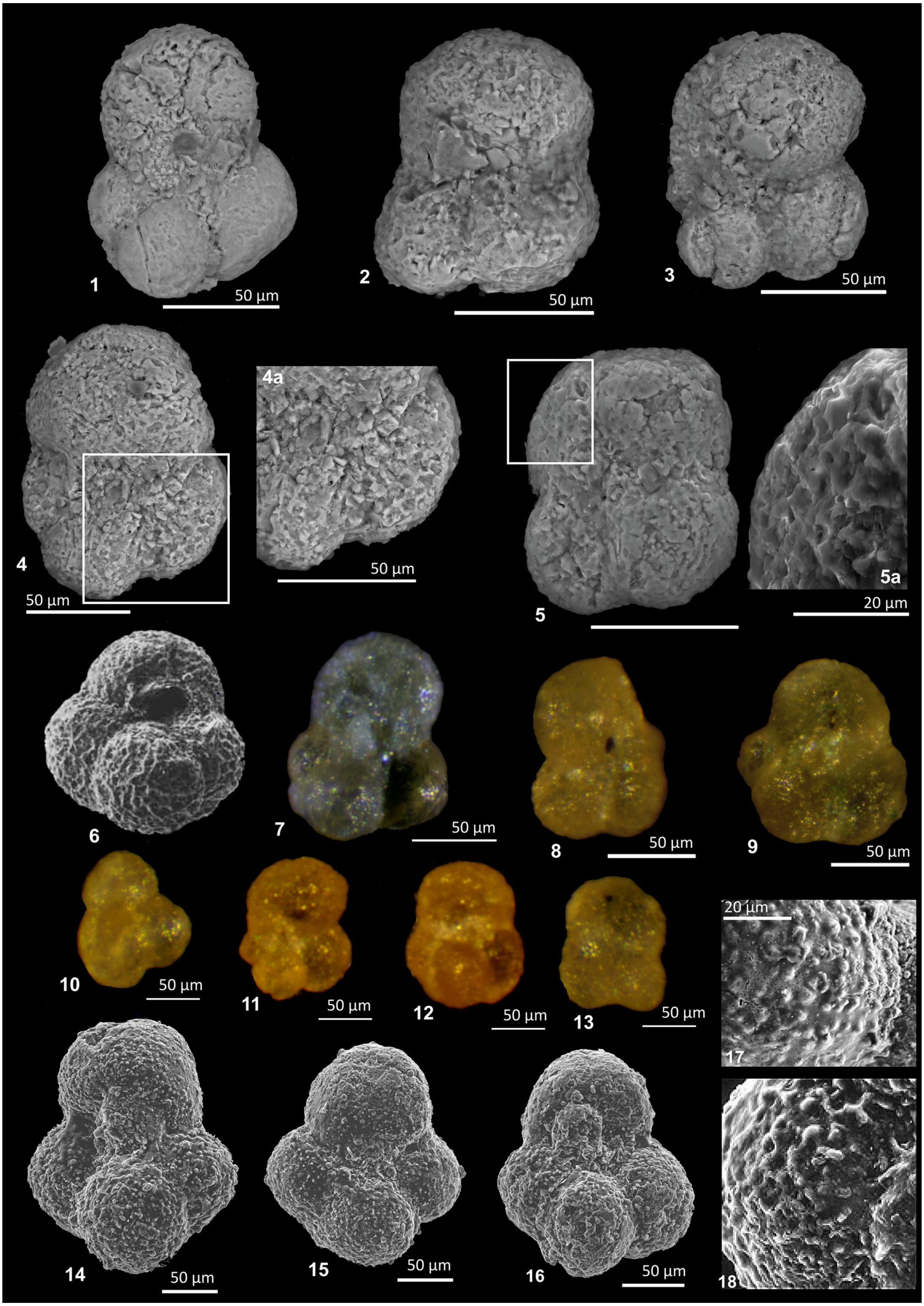
Original description

Test small, strongly convex, turret shaped, consisting of three whorls; there are 4–5 highly inflated rounded chambers in the final whorl; these chambers are closely adjacent to one another so that the whole test looks like a disorganized accumulation of spherical chambers. The chambers grow very uniform in size. The sutures are short, slightly curved, almost straight. The umbilical aperture is a large slit in the extra-umbilical area. The aperture has a small raised lip. Wall smooth, finely porous. Greatest diameter 150 micron, greatest thickness 100 micron.

Discussion

A strongly convex test, disorganized chamber accumulation and smooth wall do not fit with the current identity of the genus species, but given that optical microscopy is challenging with this small-sized taxon, the original description is considered incomplete. A study of the types in VNIGRI might be of use, in which respect we mention that Grigelis and Gorbachik (1980) illustrate a specimen in the collection of L.A. Poroshina from the Hauterivian of Azerbaijan; unfortunately, it lacks reticulate sculpture.

A more informative description of *Favusella hoterivica* was provided by Coccioni and Premoli Silva (1994), as follows: Test very small to small, globigeriniform, trochospiral with intial spire moderately elevated; 2–2.5 whorls of globular chambers; 3.5–4 chambers in the last whorl; increasing rapidly in size, except for the last chamber which displays almost the same size as the penultimate one; equatorial periphery compact, slightly lobate; sutures radial and depressed on both sides; umbilicus very small to absent; aperture umbilical, as a very low arch, possibly bordered by a very thin lip; wall surface moderately favolate, typical of the genus. Diameter 70–168 micron and thickness 34–96 micron.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◀**Fig. 6** 1–15, *Favusella hoterivi*ca from sample Cr1 of Berriasian age in the Krasnoselivka section, Crimea, Russia and *Globuligerina oxfordiana* from the upper Tojeira Fm of Kimmeridgian age in the Montejunto section, Portugal. Note the typically 'lifted up' second chamber in the last whorl of both taxa. 1–5, *Favusella hoterivica* (Subbotina). Note arched aperture and strongly reticulate wall texture. For comparison, Fig. 6 illustrates well-preserved *Favusella hoterivica* with arched aperture with rim and strongly reticulate wall texture from DSDP Site 397, Hauterivian, offshore Morocco (Butt 1979). 7–10 Show *Favusella hoterivica* from sample Cr1, Crimea in optical photography with arched aperture, and the typical 'sticking up' of the third but last chamber. 11–15, *Globuligerina oxfordiana* (Grigelis) from the Kimmeridgian of the Upper Tojeira Fm, Montejunto, Portugal (Gradstein et al. 2017a), ancestor to *Favusella hoterivica* (Subbotina). Note the commonly observed rugulose wall texture in *Globuligerina oxfordiana* (Grigelis) in 14 and the rarely observed reticulate wall texture in 15 (from tiny but typical *G. oxfordiana* specimens in the Oxfordian of Normandy, France, collection Gradstein)

Coccioni and Premoli Silva (1994) reported 3, 3.5 or 4 chambers in the last whorl, overall test shape from almost rectangular to more triangular–quadrangular, and aperture low to higher arch. A bulla may be present. This description closely agrees with the variation in our assemblage, harbouring over 50 small specimens. Close inspection of the axis of coiling shows that it may change angle from the earlier to the last whorl, with the earlier 2–2.5 whorls being positioned almost sideways from the last whorl. In this sense, *F. hoterivica* resembles the mode of coiling of *Conoglobigerina gulekhensis*, which warrants more detailed study of these taxa from several localities to determine in more detail to what extent the test morphology of the two taxa overlaps. Among the specimens in our sample Cr1, several show a looped aperture, as commonly found in *Globuligerina oxfordiana*. A bulla-like last chamber is common. Wall texture is poorly preserved but reticulate, as seen on Fig. 6, 1a.

Favusella hoterivica is widely reported and easily recognized. Although not explicitly mentioned, a majority of our specimens and images of tests in the literature quoted show a feature that also is typical of *Globuligerina oxfordiana*, i.e., the second chamber of the last whorl markedly sticks up, relative to chambers one and three in that whorl. The feature is not obvious in small specimens with only 3–3.5 chambers in the last whorl.

Using the above criteria and rugulose wall texture, the specimen from the Kimmeridgian of France as illustrated by Görög and Wernli (2013) on their Fig. 5, 1a, b, and reported as *Favusella hoterivica*, here is assigned to *Globuligerina oxfordiana.* Specimens 2 through 7 in this same Fig. 5, with a stunted and compact test that strongly embraces its early whorls and a strongly reticulate wall texture, belong to *Conoglobuligerina grigelisi* Gradstein. The acidized tests of Tithonian age specimens from Hungary, assigned by Görög and Wernli (2004) to either *Favusella hoterivica* or *Globuligerina oxfordiana*, lack wall texture features and (unfortunately) cannot be taken into account here. In this context, it is worth mentioning that the Tithonian age core samples on Galicia Bank, offshore Portugal (Collins et al. 1996) reported with *Globuligerina oxfordiana* and *G. bathoniana* only contain a Neogene planktonic taxon (see section below on the Galicia Bank record).

A well-documented record of *Favusella hoterivica* from the sedimentary continental margin, offshore eastern Canada (Wernli et al. 1995) already was touched upon when discussing *Conoglobuligerina gulekhensis*. Specimens illustrated are identical to the Hauterivian–Barremian age ones illustrated by Butt (1979) from the conjugate margin, offshore Morocco (see Fig. 6, 6).

Stratigraphic and palaeogeographic range

Type area is along the Psish River, Krassnodar Kray, Northern Caucasus, former USSR. The type level is Hauterivian and the holotype is in the VNIGRI collection, no. 5166, St.Petersburgh. The species occurs in Berriasian through lower Aptian strata and is reported widely in Tethyan to sub-Tethyan marine facies along continental margins. It is not an oceanic taxon, but it is reported on Blake Nose, at the edge of the Blake Plateau off Florida in bathyal hemipelagic sediments of Barremian age (Gradstein 1978), and in bathyal sediments of Hauterivian-Barremian age, off Morocco (Butt 1979).

Lilliputinella eocretacea (Neagu) 1975

Figure 7, 1–14a

1975 *Clavihedbergella eocretacea* Neagu: 112–113, pl. 89, Figs. 1–10.

1979 *Hedbergella* aff. *simplex* (Morrow), in Butt:, pl. 3, Figs. 11, 12.

1994 *Clavihedbergella eocretacea* Neagu, in Coccioni and Premoli Silva: 669–670, Fig. 9, 10–18.

Description

The Mikrotax internet site does not show the original description (in French), reason why it is printed here in our English translation: Test small, consisting of a very low trochospiral, showing 2–2.5 whorls of which the last one has 4–4.5–5 chambers. Chambers globular with deeply incised and straight sutures; the last 3–4 chambers become oval, elongated or more sharply pointed. Umbilicus wide and shallow, sometimes touching the remains of apertural lips of chambers. Aperture weakly arched, interiomarginal–extra-umbilical with narrow lip, especially towards the umbilicus.

The SEM images of types on the Mikrotax internet site show the wall texture to be relatively smooth and finely rugulose. *Lilliputinella* is a microperforate taxon.

Neagu (1975) lists the type specimens to be mostly over 250 micron in diameter, whereas Coccioni and Premoli Silva (1994) record specimens to be between 106 and 265 micron wide and 40–142 micron thick. The specimens in our sample Cr1 fit in the lower end of the size range.

A good description of the taxon also is provided by Coccioni and Premoli Silva (1994): Test small, flat to low trochospiral, 2–2.5 whorls with predominantly 4 chambers to a maximum of 4.75 chambers in the last whorl. Chambers of the last whorls initially subglobular, then the last 2–3 tending to become elongated radially, occasionally pointed; equatorial periphery strongly lobate to substellate; sutures straight and radial on both sides; umbilicus rather large and shallow; aperture umbilical to extra-umbilical as a low arch with thin lip; original wall surface not preserved.

Coccioni and Premoli Silva (1994) record a large variability related to the degree of elongation of the last chambers and consequently to the degree of lobation of the equatorial periphery.

Stratigraphic range

Prior to the current study, *Lilliputinella eocretacea* was known from strata as old as Hauterivian (Coccioni and Premoli Silva 1994). The updated stratigraphic range is Berriasian through early Aptian. Given the relatively small size of the Crimean specimens, it is possibly that the test size increases stratigraphically upwards. The type specimens are from Barremian strata in Romania.

Lilliputinella aff. *similis* (Longoria)

Figure 8, 1, 2, 2a.

1974 *Hedbergella similis* Longoria: 68, 69, pl. 16, Figs. 11–21.

1994 *Hedbergella simil*is, in Coccioni and Premoli Silva: 6678, 679, Fig. 13, 1–9.

Original description Medium sized, test as with genus; formed by 2–3 whorls; peripheral margin elongate, strongly lobate; 5–6 chambers in the last whorl, increasing in size as added; chambers ovate to elongate on both spiral and umbilical sides, ovoid in peripheral view; sutures radial, slightly curved, depressed on both umbilical and spiral sides; umbilicus wide, shallow; relict apertures often observed on spiral side.

Fig. 7 1–14a, *Lilliputinella eocretacea* (Neagu) 1975 from sample ▶ Cr1, Berriasian, Krasnoselivka section, Crimea, Russia. 2, 7–10 and 12 are optical photographs. SEM images in 3 and 13 show the low to almost flat spire and sometimes pointed periphery; 4a shows the small initial spire and much expended last whorl; in 6a pustules may connect to short ridges and in 14a wall texture pustules are dense and 'spiky'. Aperture is extra-umbilical to interiomarginal and slit-shaped with rim, as seen in 2

Emended description Test medium sized, low trochospirally coiled; 5–6 chambers in the outer whorl, increasing slowly and gradually in size as added; chambers initially globular to subglobular, the last two or, exceptionally three tending to become slightly radially elongate, the final one may be more elongate in some specimens; chambers round at their end; spiral side low; peripheral outline ovoid, lobate; sutures straight to slightly curved on both spiral and umbilical sides; umbilicus rather wide and shallow; aperture as a low extra-umbilical arch reaching the periphery. Wall smooth and finely perforate.

So far, what is provided as description on the Mikrotax internet site. In sample Cr1, few specimens only occur; these are nearly planispiral and flat. Some show minor elongation of the last chamber. The last whorl contains 4.5 or 5 chambers. We tentatively link the specimens to the taxon described originally by Longoria (1974), which in general shows more pronounced chamber elongation.

Stratigraphic range

Originally reported from Barremian and Aptian. A larger assemblage of specimens is warranted to extend the range of this taxon with certainty back in time into Berriasian.

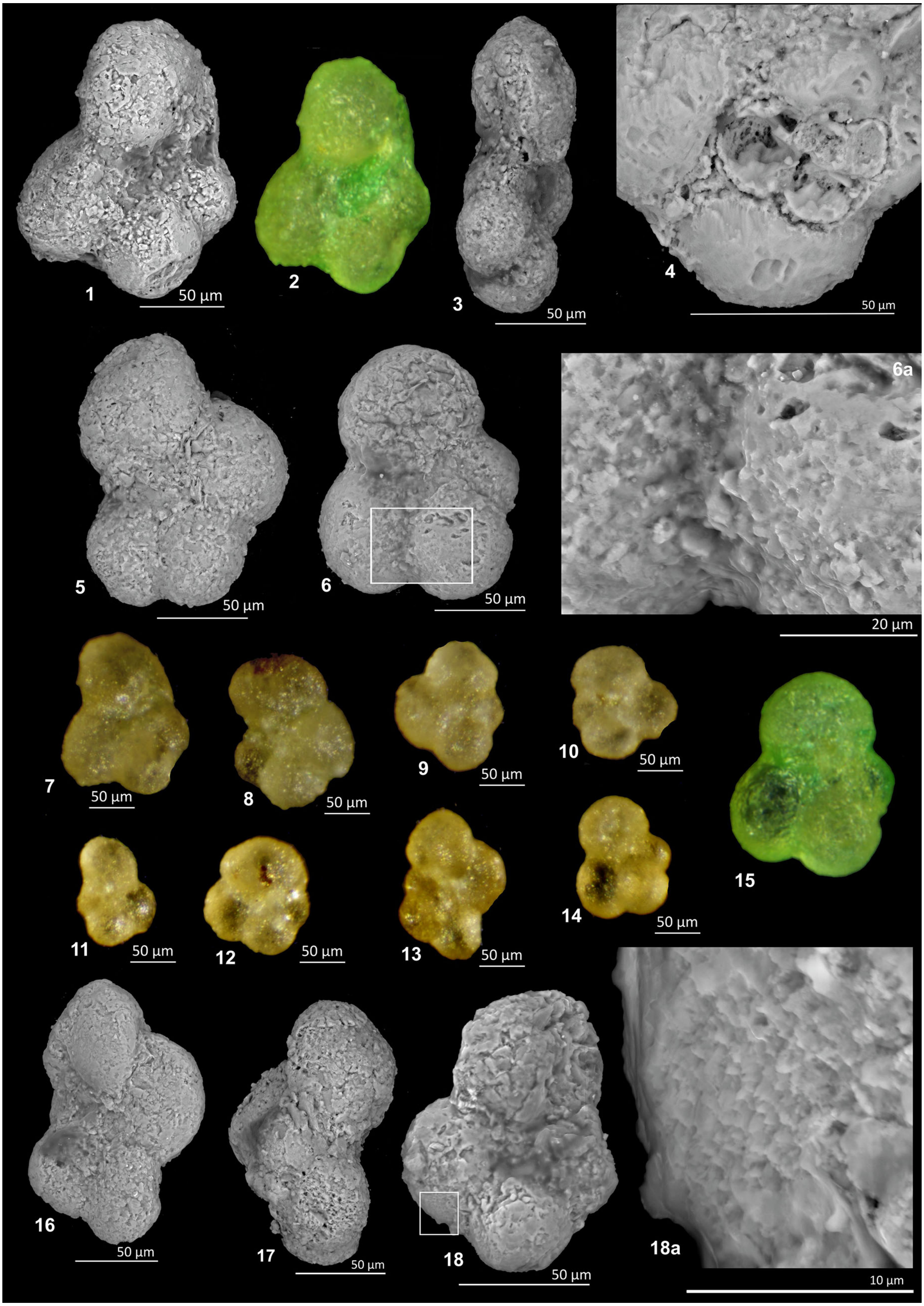
Hedbergella aff. *handousi* Salaj

Figure 8, 3, 4, 4a

1984 *Caucasella* aff. *handousi* Salaj, 592, Fig. 2a–c.

Original description Test small. Coiled in a very low to planar trochospire consisting of 2.5 whorls; peripheral margin quadrate lobate; four chambers in the last whorl, increasing quadrally in sizes as added; chambers globular, somewhat ovoidal on both spiral and umbilical sides, separated by deeply incised sutures; chambers typical ovoidal in peripheral view; sutures radial, slightly curved on both spiral and umbilical sides; wall fine-perforate, surface smooth; primary aperture highly arcuate, extra-umbilical-umbilical bordered by an imperforate flap; umbilicus circular, deep.

Emended description Test small to medium, coiled on a low trochospire; 2–2.5 whorls; 4–4.5 chambers in the outer whorl increasing rather rapidly but fairly gradually in size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as added; chambers globular to subglobular, laterally slightly compressed except the last globular one; equatorial periphery cross-shaped, lobate; sutures depressed, radial mainly straight; umbilical area medium sized and shallow; aperture as a low to medium arch bordered by a lip. Wall smooth, finely perforate.

So far, the excellent diagnosis was available from the Mikrotax internet site on planktonic foraminifera. The few specimens from sample Cr1 likely belong to above taxon.

Stratigraphic range

The species originally was described from the Early Hauterivian of Tunisia. Petrizzo (2015) also shows a stratigraphic range in Valanginian strata. The range now likely extends back into Berriasian.

? *Globuligerina* sp.

Figure 8, 5–7.

Description Specimens show a compact, low-spired test with four chambers in the last whorl, which increase slightly in size. Umbilicus is narrow. Figure 8, 5 shows a flattened apertural face and fairly high arched (and possibly looped) aperture with rim. Specimens are small (less than 125 micron) and rare. Typical specimens of *Globuligerina tojeiraensis* Gradstein have a wider umbilicus and somewhat stretched last chamber, but the current record might fit in the variation of this taxon.

Galicia Bank record of *Globuligerina oxfordiana* (Grigelis)

In this section, we discuss that so-called *Globigerina oxfordiana* from the Tithonian in ODP Site 901 on Galicia Bank (Collins et al. 1996) is of Miocene age. Gradstein et al. (2017a) studied the original record of Jurassic planktonic foraminifera reported by Collins et al. (1996) from the Tithonian in ODP Site 901 on the Iberian Abyssal Plain. The authors assigned the interval a neritic palaeo water depth in an oxygen minimum zone. Some epistominids were observed and small and poorly preserved Jurassic planktonic foraminifera were reported at several cored levels. A number of reportedly reasonably preserved individuals were assigned to *Globuligerina oxfordiana* and *G. bathoniana,* using the taxonomy of Stam (1986).

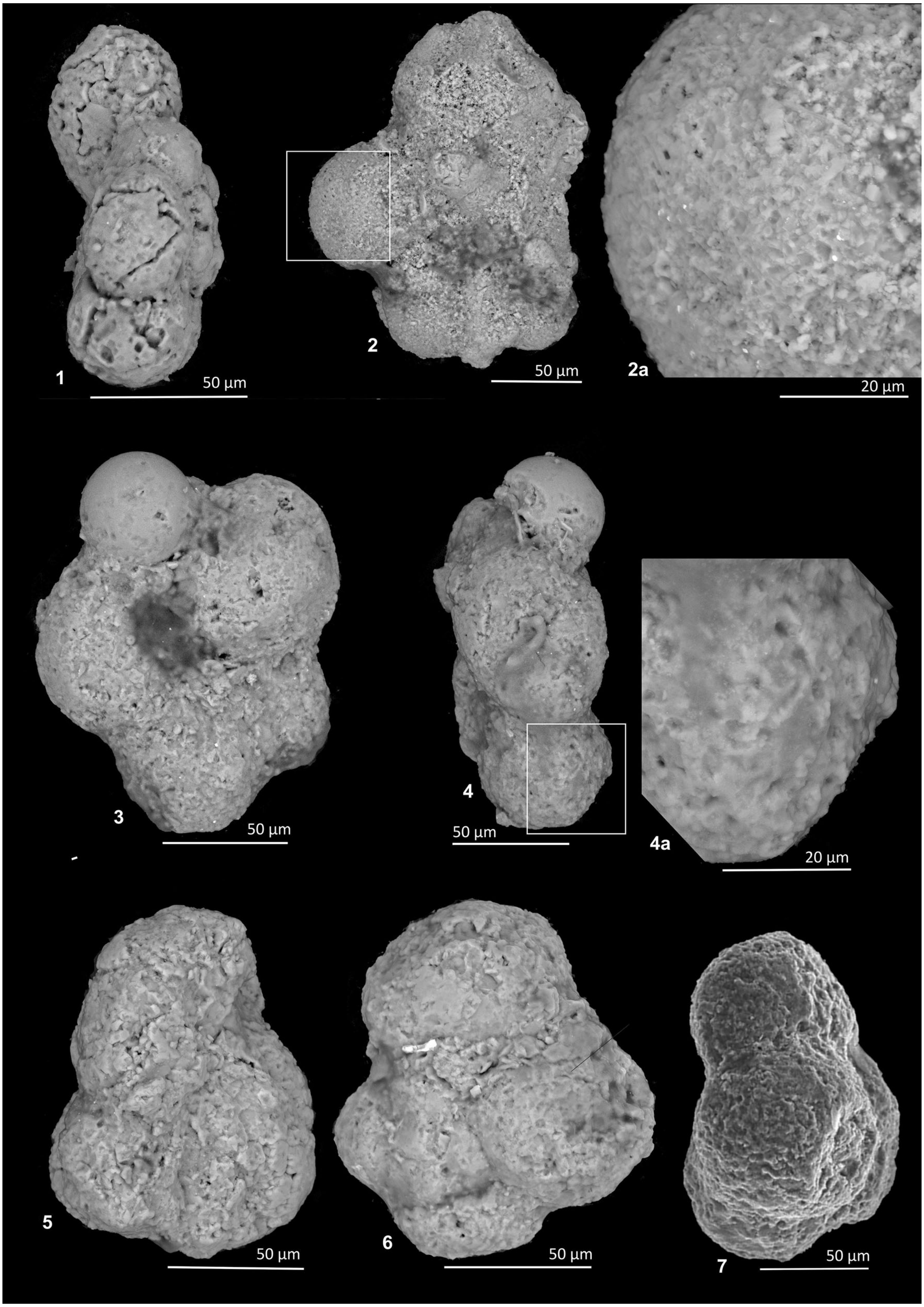
Courtesy of the ODP cores Repository in Bremen, Germany. Gradstein et al. (2017a) obtained three new samples of this interval in Site 901 (149–901A, 3R1, 74–75.5 cm; 5R1, 142/144 cm and 6R1, 6/7.5 cm). The 5 and 6R samples suggest possible mass flow deposits with well-sorted angular quartz grains and abundant fibrous woody fragments. Sample 3R1 is a mudstone. Other than a few *Spirrilina*, *Frondicularia* and *Marginulina*, no foraminifera were observed. The assemblage is likely shallow marine.

In November 2016, Gradstein visited Dalhousie University, Halifax, N.S., Canada to study the microfossil slides with Jurassic planktonic foraminifera of Collins et al. (1996). No slides were located, only the small and washed residues of cores 3 and 5. The latter had been picked for foraminifera, likely reason for the paucity of specimens obtained by us. *Globuligerina bathoniana* reported by Collins et al. (1996) was not found. In sample 5R1-142–144 cm, several poorly preserved and compact specimens were obtained from the so-called *G. oxfordiana* and two poorly preserved specimens tentatively assigned to *Globuligerina tojeiraensis* Gradstein, with wide umbilicus and flaring, slender chambers in the last whorl. A dozen small, well preserved and delicate specimens of a low trochospiral (?) benthic foraminifer are odd in this sample (not reported by Collins et al. 1996; ? contaminants).

For the current project, the *Globuligerina oxfordiana* specimens we found on Galicia Bank were studied, using the SEM fascility at AGH. Specimens are unusually well preserved and show an odd type of pustulose wall texture not prior observed on Jurassic or earliest Cretaceous specimens and two type of pores. The majority of pores are less than 1.5 micron, with scattered few larger than 9 micron. The aperture is a narrow and extra-umbilical slit. This type and position of the aperture is unknown from any Jurassic planktonics. A critical issue is the presence of very well-preserved Neogene nannofossils attached to or in some of the shells.

D. Watkins assigns these very well-preserved nannofossil specimens to be of Neogene age. Hence, we conclude that the Tithonian record on Galicia Bank does not yield in situ planktonic foraminifera. The find explains the pristine benthic specimens deemed contaminants. Specimens tentatively assigned by Gradstein et al. (2017a) to *Globuligerina tojeiraensis* are too poorly preserved, also with SEM imaging, to firmly conclude on taxonomic status.

Fig. 8 1, 2 and 2a, *Lilliputinella* aff. *similis* (Longoria), 1974, from ▶ sample Cr1, Berriasian, Krasnoselivka section, Crimea, Russia. Note lobate periphery, 5 (or even more ?) chambers in the last whorl, slight elongation of chambers, flat spire and densely pustulose wall texture. 3, 4 and 4a, *Hedbergella* aff. *handousi* Salaj, 1984; test is flat, the four chambers in the last whorl regularly increase in size, slit aperture and densely pustule wall texture; the helmet-like bulla has an unusual position. 5–7 ? *Globuligerina* sp.; specimens show a compact, low-spired test with four chambers in the last whorl, which increase slightly in size; 5 shows a flattened apertural face and fairly high arched (and possibly looped) aperture with rim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Diversity through time and evolution

In this section, we will look into the change in planktonic taxa composition from Jurassic into Cretaceous and consider evolution. We make use of details provided by Gradstein et al. (2017b) on this group in the Jurassic and our new data on earliest Cretaceous planktonic foraminifera (see Table 2).

The study of Wernli (1988) on thin sections from limestone samples provided by A. Poisson (Paris) to R. Wernli from the Domuz Dag mountain chain of SE Turkey documents the oldest known occurrence of planktonic foraminifera. Curiously, this is the only record of this oldest known assemblage. Hence, planktonic foraminifera appeared in the Toarcian around 178 Ma ago. The youngest occurrence of this group is documented by Görög 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). Adding now to this record the Crimean early Berriasian planktonic foraminifera, we are looking at about 36 myr of evolutionary history.

Figure 10 depicts this history in a simple stratigraphic column, a figure modified and expanded from Gradstein et al. (2017b). Before we get in details of what we know (and do not know) of the transition from Jurassic into Cretaceous planktonic foraminifera, the Jurassic planktonic foraminiferal history and biozonation are re-iterated from the literature cited.

The Toarcian through Aalenian record is only known from thin sections, and although it is suggestive to consider that an often larger and 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 in itself is not a taxonomic feature and 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. Test features should be carefully studied in a quantitative mode to clarify potential palaeoecologic trends.

As outlined in Fig. 10, we consider in Jurassic and earliest Cretaceous four lineages, which for graphic clarity are indicated with green, brown, blue and red stratigraphic lines. Two key Jurasssic taxa, *Globuligerina balakhmatovae* and *G. oxfordiana,* are postulated to link to Cretaceous taxa. For this reason, their species description is re-iterated from Gradstein et al. (2017a) and the evolutionary hypothesis dealt with below.

Table 2 Planktonic foraminifera in the Kimmeridgian of Portugal, the Tithonian of Hungary and the Berriasian of Crimea; for details see text

	Globuligerina balakhmatovae	Globuligerina oxfordiana	Globuligerina tojeiraensis	Globuligerina bathoniana	Conoglobigerina grigelisi	Conoglobigerina gulekhensis	Favusella hoterivica	? Favusella sp.	Lilliputinella eocretacea	Lilliputinella aff. similis	Hedbergella aff. handousi	? Globuligerina sp.
Berriasian—Crimea						o	o	x	o	x	x	x
Tithonian—Hungary		? o										
Kimmeridgian—Portugal	o	o	o	o	o							

o frequent to abundant, *x* rare to common

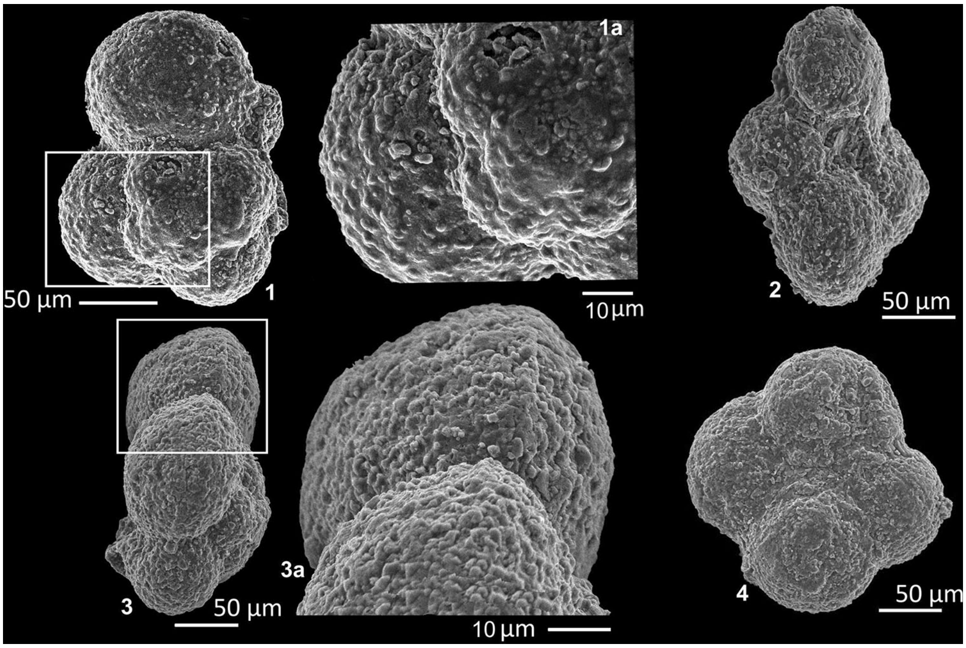


Fig. 9 1–4, *Globuligerina balakhmatovae* (Morozova), 1961 from the upper Tojeira Fm., Kimmeridgian, Montejunto, Portugal. Note the rather symmetrical four chambered last whorl, the sometimes pointed periphery, a low arched, umbilical aperture (in 2) and the densely pustule wall texture. For details, see text

The '**green group**' is monotypic and consists of *Globuligerina balakhmatovae* (Fig. 9, 1–4). Test is small, less than 150 µm and has a low spiral; it consists of two whorls, the first small one with four, rarely three to five chambers and the final, much larger and wider one with four chambers; *H*/*D* ratio about 0.5. Chambers mostly globular, rounded, but in the last whorl may become slightly compressed along their height (flattened), giving an ovate chamber shape. Last whorl chambers wide in an equatorial sense, petaloid and often resembling a 'clover-like flower'. Umbilicus slightly open. Sutures between the chambers weakly depressed, straight in the last whorl. Specimens have no bulla. In Grand Banks and Portuguese samples, rare specimens occur with an imperforate peripheral band (Stam 1986; Gradstein et al. 2017a), aperture small, a half circle arch or low arch, with narrow rim; wall microperforate, surface shiny or matte, smooth to finely pustulose in Middle Jurassic strata and may become coarse pustulose with fused ridges in Kimmeridgian sediments.

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 to refine our knowledge on the stratigraphic appearance and test morphology of both taxa. A detailed study of the wall textures should be undertaken, relative also to other taxa in the genera *Globuligerina* and *Oberhauserella*.

There is no stratigraphic record of the low-spired *Globuligerina balakhmatovae* in post (early) Kimmeridgian strata. A change from this long ranging, morphologically relatively stable taxon to *Lilliputinella eocretacea* in early Berriasian time is proposed here, but more information is required. The two taxa are illustrated in Figs. 8 and 9. Note that in *L. eocretacea* chambers in the last whorl expand more in size and the apertural position is umbilical extra-umbilical or interiomarginal, not umbilical as in *Globuligerina balakhmatovae.* 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 also may twist relative to the plane of coiling. Chambers in both taxa vary from 3.5 to 5, and commonly 4 in the last whorl. Both taxa show also ovate chamber shape, with a tendency to a narrow periphery and a rugulose wall texture. Lack of a diversified, possibly multi taxa (?) assemblage of Tithonian age with free specimens hampers ancestor–descendant investigation.

The '**brown 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. Essentially, we can distinguish one taxon with a more symmetrical and regular trochospire with 4 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 opnion, *G. jurassica* might be a local and often aberrant variant of *G.dagestanica*.

The '**blue group**' consists of *Globuligerina avariformis* and *Conoglobigerina grigelisi*, 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 *Conoglobigerina grigelisi.*

The latter acquires a reticulate wall sculpture. Its youngest record is Kimmeridgian. The ancestry of *G. avariformis* we refrain from to speculate on, our data are insufficient.

The '**red 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 taxon description of *G.oxfordiana* in Gradstein (2017a) is quoted below, and a set of images for this evolutionary important taxon is shown in Fig. 6, 14–18:

Relatively low trochospiral, with an H/D ratio of 0.3–0.8 or even 1; spherical chambers, 3.5–4 in the last whorl. Equatorial periphery varies from fairly lobulated circular to fairly lobulated oval. Last whorl only slightly elevated above previous whorl. Second chamber and final chamber in last whorl typically 'sticking up', relatively to the first and third chambers in the last whorl. Sutures depressed, mostly straight. 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. In exceptionally well-preserved specimens, a small triangular flap may be seen to extend from the lower lip into the umbilicus. A smooth to slightly pustulose bulla, with one aperture, is frequently present, obscuring the primary aperture.

The test wall is microperforate, with pores of ca 1 µm in diameter. Wall surface is densely sculptured with different modes:

(1) By cone-like blunt pustules (pseudomuricae) with diameter of 1–4 µm pointed in centre by a small raise with micro-pore (pore mound).
(2) By porous pustules joining into short irregular ridges.
(3) By ridges joining in a reticulate pattern.

Already 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. In our material, coarse rugulose texture and also reticulation are visible in Fig. 6, 14–18 of specimens from the Oxfordian of Lithuania and France (re-illustrated from Gradstein et al. 2017a, Plates 11 and 12). If ontogeny recapitulates evolution, the local wall texture change may be seen to strengthen our postulate that *G. oxford*iana is both ancestor to *Conoglobigerina helvetojurassica* (see discussion under this taxon in Gradstein et al. 2017a) and to *Favusella hoterivica*. But interestingly, specimens from four other, widely different localities of Late Bajocian through Early Kimmeridgian age show rugulose wall texture only.

The species *Globuligerina tojeiraensis* with elongated chambers and wide-open umbilicus is known from the Callovian–Oxfordian of the Grand Banks and the Lower Kimmeridgian of Portugal. Its overlap in morphology with *G. oxfordiana* suggests the latter to be ancestor. The origin of *G. oxfordiana* itself in late Early Jurassic strata is shrouded in mystery.

The close morphological comparison and overlap in wall texture features make it attractive to consider *Globuligerina oxfordiana* to be the ancestor of *Favusella hoterivica.* In Fig. 6, both taxa are illustrated 'side by side'. If this evolution already took place in Tithonian time, wall texture analysis of well-preserved, free specimens from Tithonian outcrops is required.

The origin of the reticulate *Conoglobigerina gulekhensis* is not understood; it may sprout from the *oxfordiana-helvetojurassica* lineage. A bend in coiling axis is common to *C. gulekhensis* and *C. helvetojurassica*, but the latter taxon is not known in strata younger than Early Kimmeridgian. Since specimens of *C.gulekhensis* and *Favusella hoterivica* in our sample Cr1 appear to share the feature of a bend in the axis of coiling, a detailed comparison of this feature plus the wall texture may shed light on phylogeny. *Globuligerina bathoniana* over its long stratigraphic range did not show variation in wall texture or axis of coiling and often has a looped aperture. *Conoglobigerina gulekhensis* unlikely evolved from this higher spired taxon.

In summary, and as clearly visualized in Figs. 10 and 11, the planktonic foraminifera harboured two taxa in Toarcian-Aalenian (but no free specimens record currently exists) and six new ones in Bajocian–Bathonian. This makes for eight taxa during Bajocian–Bathonian time. With the subsequent disappearance of two taxa and appearance of four new taxa, the Oxfordian–Kimmeridgian also harboured eight taxa. Counting subspecies, possible range extensions from Middle Jurassic and giving weight to acmes, the Kimmeridgian is the time Jurassic planktonic foraminifera flowered. A dramatic change over, which is not well documented and not understood, led to the survival of only one taxon, likely *Globuligerina oxfordiana,* during Tithonian time. During Berriasian time, several new taxa appeared. We do not find solid evidence that Jurassic taxa 'crossed the Period boundary'. In terms of genus/species turnover, changes happened during Bajocian/Bathonian, Oxfordian/Kimmeridgian and Berriasian times. This strongly contrasts with dinoflagellate and nannofossil species diversity trends (Bown et al. 2004; Olde et al. 2015). These two micro-planktonic organisms show a steady expansion in number of taxa, with only a minor decline for dinoflagellates in earliest Cretaceous. The latter

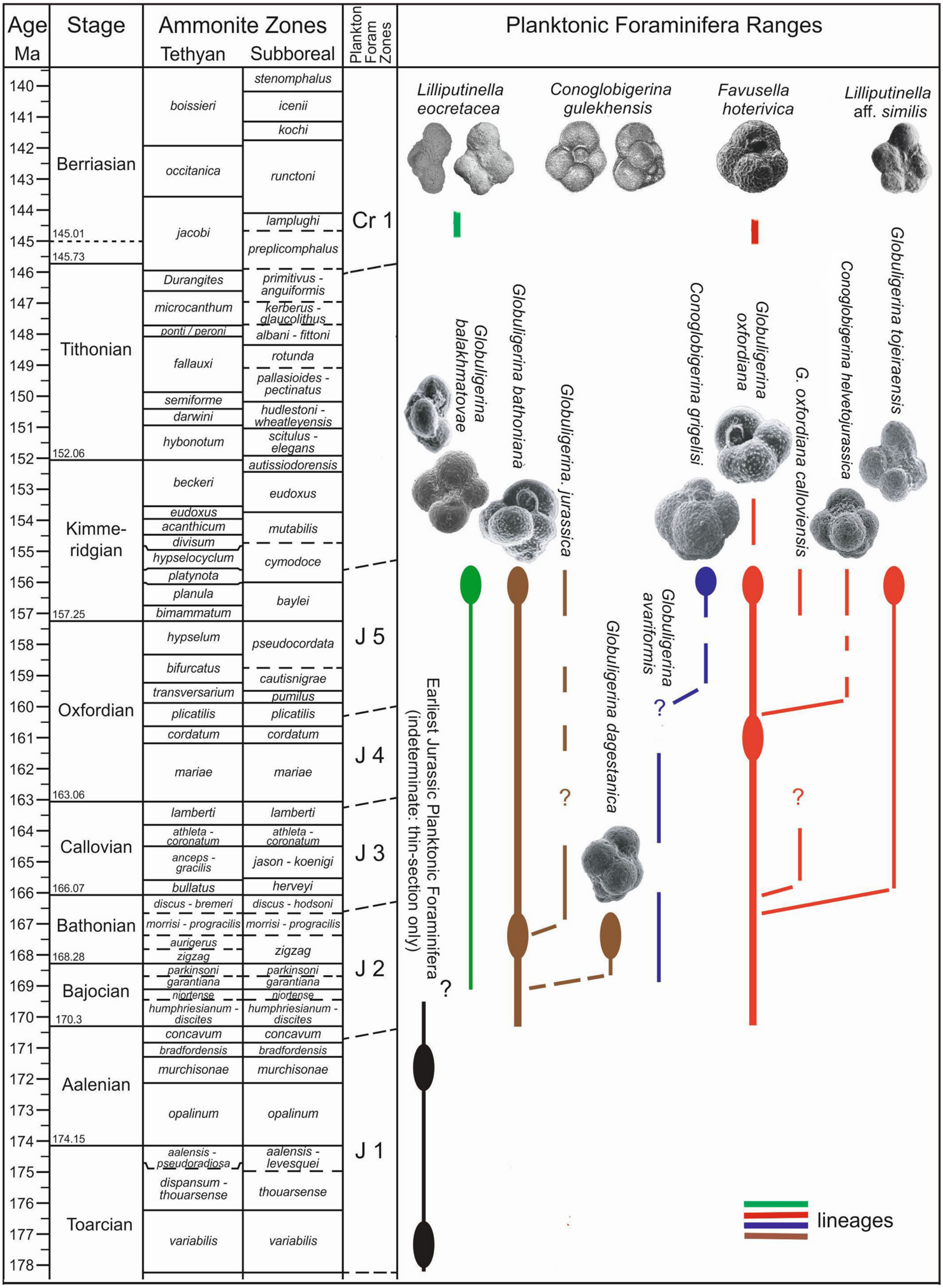


Fig. 10 Stratigraphic ranges and postulated evolutionary development of Jurassic and Berriasian planktonic foraminifera. For details, see text

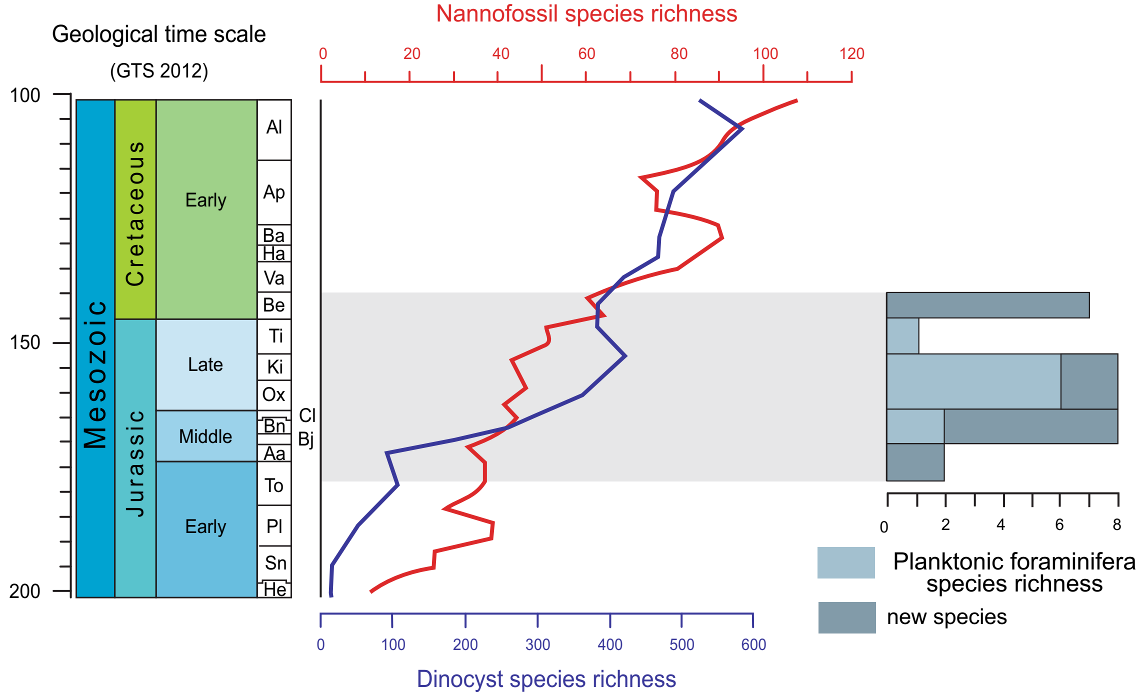


Fig. 11 Taxonomic diversity (species richness) of nannofossils and dinoflagellates in Jurassic through Early Cretaceous time (after Olde et al. 2015 and Bown et al. 2004). To the right, the (meagre) taxonomic diversity of Jurassic planktonic foraminifera from Jurassic into Berriasian is plotted as number of taxa identified. For details, see text

may be due eustatic low sealevel, diminishing coastal niches.

An explosion in productivity of calcareous (nanno-) plankton during the Tithonian, especially the robust nannoconid types, contributed to lowering of the Calcium Carbonate Compensation (CCD) level and onset of chalk ('creta') deposits that characterize the Lower Cretaceous in all ocean basins.

Biostratigraphic scheme

Using our information on Jurassic and earliest Cretaceous 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 difficult. The zonal summary below takes into account our observed first and last occurrences, but stays away from assigning links to ammonite or nannofossil zones. More research is desirable to create biostratigraphy with this, still rather enigmatic group of microfossils.

Stratigraphically upwards in time the following events and acmes may be tentatively recognized through Jurassic and earliest Cretaceous, which expands the Jurassic stratigraphic scheme originally proposed by Gradstein et al. (2017b; Fig. 10):

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 to frequent occurrence of *Globuligerina balakhmatovae, G. oxfordiana, G. bathoniana* and *G. tojeiraensis*—middle Oxfordian through early Kimmeridgian
Zone Cr1	Appearance of *Favusella hoterivica, Conoglobigerina gulekhensis, Lilliputinella eocretacea, L.* aff. *similis* and *Hedbergella* aff. *handousi*

Samples with a continuous record of planktonic foraminifera from deeper marine sections like Krasnoselivka are needed to document and better understand this unique earliest Cretaceous record.

Palaeoecology and palaeobiogeography

Stam (1986) in his large doctorate study involving the planktonic foraminifera of the Grand Banks and Portugal, provided evidence from geologic transects that the flatter-shaped *G. balakhmatovae* preferred a deeper marine habitat than the higher spired *G. bathoniana*. Maximum palaeo waterdepth was postulated near 250 m.

If we focus on assemblages with free specimens of Jurassic through Berriasian 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 (1978). 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, offshore USA. There is an outstanding record of nannofossils in Tithonian through Berriasian deep marine, pelagic sediments of the Blake Bahama Formation in the North Atlantic. Curiously, planktonic foraminifera are absent from this open marine, oceanic facies.

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 palaeo-water depth of the marine strata in these two areas was likely not over 250 m (Gradstein 1978; 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. 2017a). Both thin and small and thicker and larger sized tests of the same species of planktonic foraminifera are present.

The palaeogeographic maps of Chris Scotese on Fig. 12a–c show distribution of Jurassic and Earliest Cretaceous planktonic foraminifera. Starting with oceanisation of the central North Atlantic in Middle Jurassic time, recorded in DSDP Site 534 (Gradstein 1978), 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.

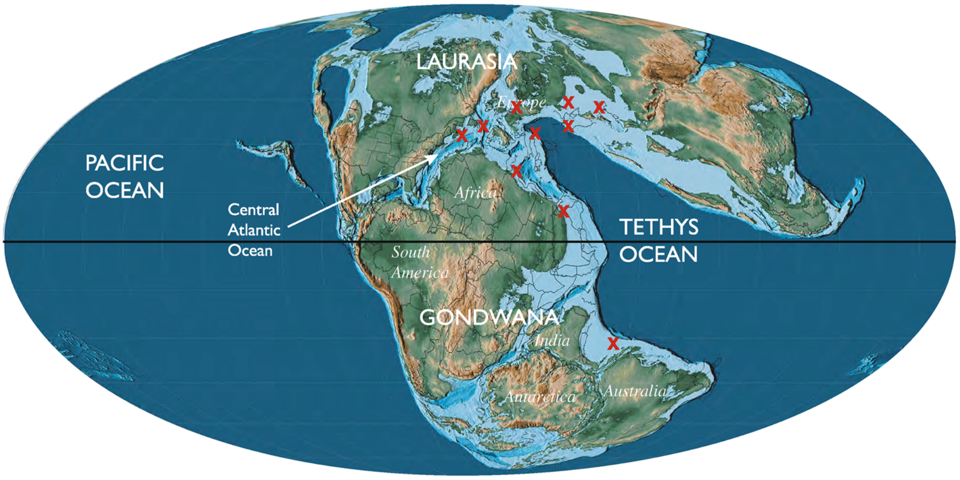
The core of occurrences is in SW Asia, North Africa, Central and SW Europe and offshore East Canada. Assuming that the Jurassic planktonic foraminifera originated in the Toarcian-Aalenian of the Middle East (based on the finding in SW Turkey of Wernli 1988), two migrations may have taken place, one west- and northwest over, and one east over, following the margins (but not the wide-open sea) of the Tethys ocean. Hence, the spectacular find of very well-preserved Middle Jurassic planktonic foraminifera on the Exmouth Plateau in Australia is not surprising (Apthorpe 2003; Apthorpe, unpublished; see also Gradstein 2017b). The Exmouth Plateau is the most southeasterly site where Jurassic planktonic foraminifera have been reported. The westernmost record is in the Haynesville Formation of Oxfordian age, western Gulf of Mexico (R. Campbell, pers. comm. to Gradstein 2017a, b). Detailed study (with free specimens and not in thin sections) of the briefly documented record of Berriasian planktonic taxa from the Taraises Fm., NW Mexico (Omaña et al. 2017) might assist to place this record also on the map of Fig. 12c (see Previous Literature).

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 and Berriasian marine strata of western S. America (Peru, Chile) to confirm that Jurassic planktonic foraminifera do not occur there.

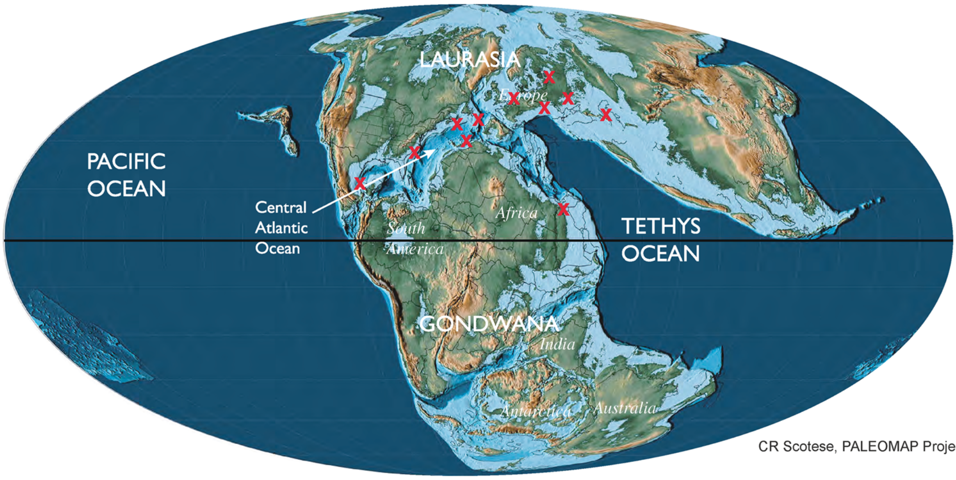
The fact that global sealevel in Late Jurassic rose by 80+ or more meters relative to present height may explain the widespread European distribution of the planktonics during this time.

The Berriasian distribution map of Fig. 12c dramatically illustrates the drastic shrinkage in geographic realm of planktonic foraminifera, still limited as before to hemipelagic, continental margin basins. It was not until Aptian time that planktonic foraminifera invaded truly pelagic, wide ocean realms.

(a) Bajocian - Bathonian (170 Ma)

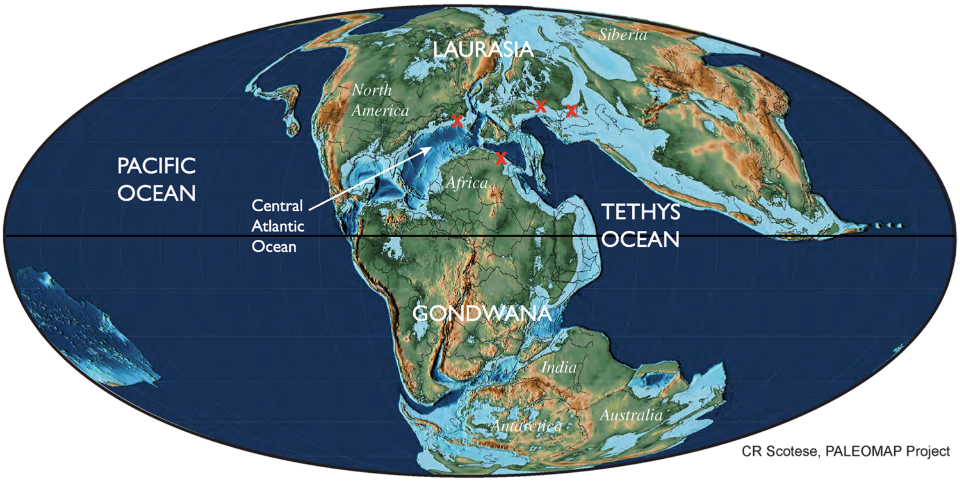


(b) Oxfordian - Kimmeridgian (155 Ma)



CR Scotese, PALEOMAP Project

(c) Berriasian 142 Ma



CR Scotese, PALEOMAP Project

Fig. 12 Bajocian through Berriasian palaeogeographic maps showing the approximate distribution (red crosses) of Jurassic and earliest Cretaceous planktonic foraminifera through time. For details, see text (courtesy Chris Scotese)

Conclusions

A Berriasian age planktonic foraminifera assemblage from a section near the village of Krasnoselivka in the Tonas River Basin, Crimea contains *Favusella hoterivica* (Subbotina), ? *Favusella* sp., *Conoglobigerina gulekhensis* (Gorbachik and Poroshina), *Lilliputinella eocretacea* (Neagu), *Lilliputinella* aff. *similis* (Longoria), *Hedbergella* aff. *handousi* Salaj and ? *Globuligerina* sp. Although specimens are poorly preserved, test morphology, shape and position of the aperture and key wall texture features are recognizable. Age assignment is based on a diverse and well-preserved calcareous nannofossil assemblage of upper zone CC2 and ammonites (*Jacobi* Zone). *Lilliputinella eocretacea*, *Lilliputinella* aff. *similis* and *Hedbergella* aff. *handousi* were not previously described from early pre-Valanginian or Hauterivian strata. XRD analysis of the tests of benthic and planktonic foraminifera and micro-gastropods shows these to be calcitic in composition, also ones that were deemed to be originally aragonitic, indicating diagenetic changes in carbonate fractions. From detailed comparison to Jurassic planktonic foraminifera, two lineages are proposed from Late Jurassic into earliest Cretaceous: *Globuligerina oxfordiana* (Grigelis) to *Favusella hoterivica* (Subbotina) and *Globuligerina balakhmatovae* (Morozova) to *Lilliputinella eocretacea* (Neagu). It is possible that *Conoglobigerina gulekhensis* also descended from *Globuligerina oxfordiana*. The meagre evolution of early planktonic foraminifera from Toarcian through Tithonian, with only two genera and fewer than ten species does not follow the evolutionary diversity pattern of nannofossils and dinoflagellates. Tithonian appears to be a bottleneck for planktonic foraminifera, with a sparse record and virtual extinction of taxa. The so-called *Globigerina oxfordiana* from the Tithonian in ODP Site 901 on Galicia Bank (Collins et al. 1996) is of Miocene age. Detailed study of the 60–125 micron fraction of the well-preserved free specimens of shelly microfossils in marls or marly limestones in both Tithonian and Berriasian (Tethyan or sub-Tethyan) outcrop strata may shine more light on this poorly understood record of planktonic foraminifera transitional between Jurassic and Cretaceous.

Acknowledgements The palaeogeographic maps were kindly provided by Chris Scotese (Colorado, USA). We acknowledge with thanks assistance to this study and publication by Michael Krobicki (AGH, Krakow, Poland), Alexandra Durek and Adam Gawel (AGH, Krakow, Poland), Steen Oersted (Deltapix, Denmark), Andrew Gale (Portsmouth, UK), Wolfgang Kuhnt (Bremen, Germany), Rob Fensome and Bill McMillan (Dartmouth, NS, Canada), Robert Campbell (Shell, Houston), Mark Leckie (Amherst, USA), Brian Huber (Washington, USA), Maria Rose Petrizzo (Milano, Italy), and three anonymous reviewers. Chief-editor Daniel Marty provided valuable and much appreciated editorial support. A. Waskowska acknowledges AGH SD funds no. 11.11. 140.005.

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