

## RESEARCH/REVIEW ARTICLE

# *Trochammina* as opportunist foraminifera in the Lower Jurassic from north Siberia

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r-strategists; colonization; anoxic event; ecostratigraphy; black shale.

**Correspondence**Matías Reolid, Departamento de Geología, Universidad de Jaén, Campus Las Lagunillas sn, ES-23009 Jaén, Spain.  
E-mail: mreolid@ujaen.es**Abstract**

The ecostratigraphic analysis of foraminiferal assemblages from Upper Pliensbachian to Lower Toarcian (Lower Jurassic) mudstones, siltstones and black shales from northern Siberia allows for a better understanding of the response to the benthic biotic crisis related to the Toarcian Oceanic Anoxic Event in a high latitude context. The assemblages were dominated by agglutinated taxa with extremely low diversity values and dominance of *Trochammina*. These features suggest that the foraminiferal assemblages were adapted to restricted conditions, where the main limiting factors were salinity and oxygen degree. The opportunist behaviour of *Trochammina* enabled this genus to survive and adapt to unfavourable conditions. *Trochammina* proliferated in relation to the sea-level fall and probable changes in salinity in the Arctic palaeobasin during the Margaritatus Chron and at the beginning of the Viligaensis Chron (Late Pliensbachian). Another *Trochammina* proliferation is associated with the initial development of the restricted oxygen conditions related to the Toarcian Oceanic Anoxic Event.

Benthic foraminifera are direct bioindicators of physico-chemical parameters at the sea bottom and indirectly of the water column features (Loubere 1996). Fluctuations in oceanic productivity may enhance the accumulation of organic matter at the sea bottom and affect oxygen demand, exercising a direct influence on the features of the benthic foraminiferal assemblage (diversity, shell composition, morphotypes, etc.). Thus, fluctuations in salinity, nutrient availability and oxygenation rate are controlling parameters for the composition and relative abundance of foraminiferal assemblages (e.g., Sjoerdsma & Van der Zwaan 1992; Jorissen et al. 1995; Van der Zwaan et al. 1999). The depth in the sediment where the foraminifera live is predominantly determined by oxygen and nutrient availability (e.g., Tyszka 1994; Jorissen et al. 1995; Van der Zwaan et al. 1999; Ernst & Van der Zwaan 2004; Reolid, Nagy et al. 2008; Reolid, Rodríguez-Tovar et al. 2008). The epifaunal microhabitat is advantageous in environments with nutrient and/or oxygen limitations, whereas infaunal taxa proliferate if nutrients

and oxygen are available. In addition, the opportunist/specialist behaviour of foraminifera and the diversity of the assemblages are related to nutrient input; a nutrient increase favours the proliferation of opportunist taxa (r-type strategy) and produces the diminution of foraminiferal diversity (Sjoerdsma & Van der Zwaan 1992). For this reason, foraminifera provide insights as to the controlling factors behind Jurassic and Cretaceous oceanic anoxic events and the response of microfaunal assemblages before and after an event (e.g., Bartolini et al. 1992; Hylton & Hart 2000; Coccioni & Luciani 2004; Gebhardt et al. 2004; Friedrich et al. 2009; Mailliot et al. 2009; Nikitenko 2009; Souza et al. 2011; Reolid, Rodríguez-Tovar & Nagy 2012; Reolid, Sebane et al. 2012). The r-strategist genera have an important role in such biotic crises, as subsequent survivors or colonizers (e.g., Rey et al. 1994; Tyszka 1994; Reolid et al. 2010; Reolid, Rodríguez-Tovar, Marok et al. 2012; Reolid, Sebane et al. 2012). In nutrient-rich environments (eutrophic waters), r-strategists (opportunists)

proliferate, the rapid increase of their population densities characterized by faster reproduction and generally smaller size (e.g., MacArthur & Wilson 1967; Valentine 1973; Hallock 1985). In low-nutrient environments (oligotrophic waters), K-strategists (specialists) dominate, in turn characterized by long individual life spans, a low reproductive rate and larger shell size (e.g., MacArthur & Wilson 1967; Valentine 1973; Hallock et al. 1991). Generally, the trophic conditions are also related to oxygen availability, with restricted oxygenation in eutrophic waters and abundant oxygenation in oligotrophic waters.

In the case of the Early Toarcian Oceanic Anoxic Event (T-OAE), a foremost environmental change during the Mesozoic resulted in a mass extinction of benthic groups in marine ecosystems (Wignall et al. 2005). In general, the T-OAE is characterized by a record of organic-rich sediments associated with a negative excursion in  $\delta^{13}\text{C}$  (e.g., Jenkyns & Clayton 1997; Röhl et al. 2001; Hesselbo et al. 2007; Hermoso et al. 2009; Suan et al. 2011), in a context of exceptionally warm conditions (e.g., McArthur et al. 2000; Svensen et al. 2007; Gómez & Goy 2011; Suan et al. 2011) and sea-level rise (e.g., Haq et al. 1987; Hallam 2001; Nikitenko 2008, 2009). For the T-OAE, the genera of calcitic and aragonitic foraminifera identified as opportunists (r-strategists) in the Tethys Realm would include *Lenticulina*, *Eoguttulina* and *Reinholdella* (Nocchi & Bartolini 1994; Boutakiout & Elmi 1996; Reolid, Sebane et al. 2012). However, ecostratigraphic analyses of T-OAE-related foraminiferal assemblages in the Boreal Domain, where agglutinated forms dominate, are scarce (Nagy & Johansen 1991; Nagy 1992; Nikitenko & Mickey 2004; Nikitenko 2008). The present contribution is an ecostratigraphic analysis of the foraminiferal assemblages during the T-OAE, with identification of the r-strategist genera at high latitudes.

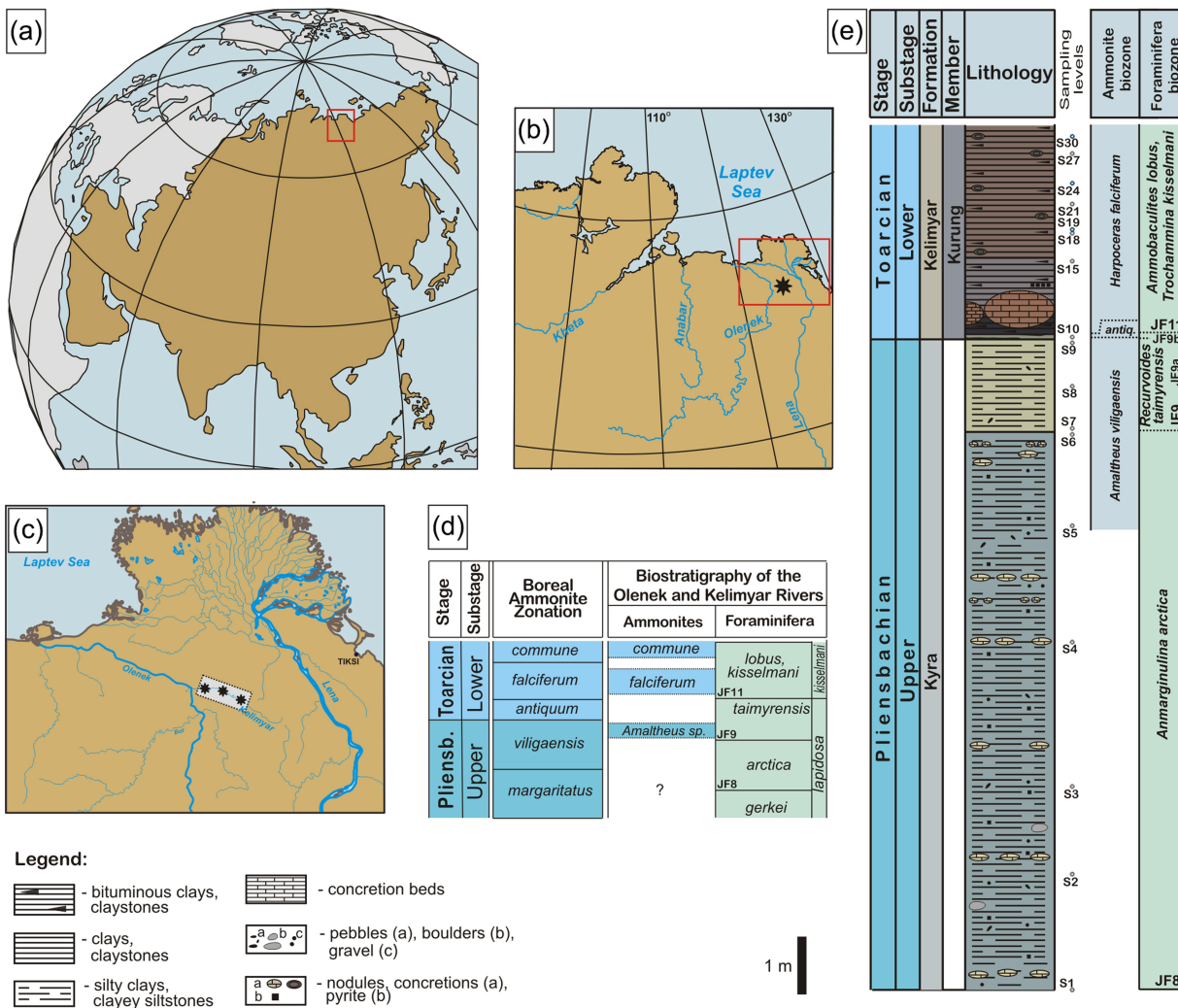
## Geological setting

The Kelimyar River section is located in north-eastern Siberia (Fig. 1), close to the Laptev Sea in the Arctic Ocean. This section exposes an Upper Pliensbachian to Lower Toarcian marine succession made up of sandy siltstones, siltstones and shale clay. These sediments were deposited in a continental shelf environment (Nikitenko 2008, 2009), in the upper sublittoral zone during the Latest Pliensbachian and the middle sublittoral zone during the Early Toarcian (Fig. 2). According to plate tectonic reconstructions, the Kelimyar River district was located several kilometres south-west from the Early Jurassic magnetic North Pole, which was in the delta area of the Lena River (Golonka & Scotese 1995; Ford &

Golonka 2003; Golonka et al. 2003; Golonka 2007, 2011; Scotese 2011; Torsvik et al. 2012; Fig. 2). These data agree with biogeographic and palaeogeographic reconstructions (Nikitenko 2008). The 14.6 m-thick interval studied in this work takes in the Margaritatus Zone to the top of Falciferum Zone. The Upper Pliensbachian corresponds to the Kyra Formation and the Toarcian part of the section corresponds to the Kelimyar Formation (Fig. 1e). A condensed Antiquum Zone of a few centimetres characterizes the succession. The Falciferum Zone is represented by the Kurung Member, with finely laminated black shales, high values of total organic carbon (TOC, 6 wt.%) and a negative carbon isotopic excursion (Suan et al. 2011).

## Material and methods

Analysis of foraminiferal assemblages was undertaken from 17 sampling levels (Fig. 1e). Each sample (200 g) was soaked in tap water for a few days and later disintegrated in boiled water and rinsed through a 56- $\mu\text{m}$  sieve mesh. The residue of each sample was totally retrieved with a very variable amount of picked individuals per sample (Table 1). There were very low numbers of specimens in some samples (S10, S24, S27 and S30; see Table 1). A total of more than 2900 foraminifera were analysed. Foraminiferal analysis was focused mainly on proportions (%) and abundance of foraminifera (specimen/100 g) with different life-styles (epifaunal, shallow infaunal and potentially deep infaunal) based on the morphogroup interpretations of Nikitenko et al. (2013). The characterization of benthic foraminiferal morphogroups in view of palaeoenvironmental assessments has sparked great interest over the last two decades (e.g., Nagy 1992; Tyszka 1994; Reolid, Rodríguez-Tovar et al. 2008; Nagy et al. 2009; Reolid et al. 2010; Murray et al. 2011; Reolid, Sebane et al. 2012; Setoyama et al. 2013). Studies of modern and ancient foraminiferal assemblages demonstrate that the morphology of the foraminiferal shell (general shell morphology, aperture position, mode of coiling and number of chambers) can be directly related to different life-styles and feeding strategies (e.g., Jones & Charnock 1985; Corliss & Chen 1988; Corliss 1991; Nagy 1992; Tyszka 1994; Setoyama et al. 2013). In addition,  $\alpha$ -diversity based on genera (Fisher et al. 1943) was included in the analysis of foraminiferal assemblages. Diversity analysis was based on genera because the taxonomy of some species varies considerably in different publications, whereas the nomenclature of genera is more stable. The samples are housed in the Micropalaeontology Laboratory of the Institute of Petroleum Geology and



**Fig. 1** (a, b, c) Geographic location of Kelimyar River section (e) with location of the sampling levels and (d) and foraminiferal and ammonite biostratigraphy of the Olenek–Kelimyar rivers area (based on Nikitenko 2009) compared to equivalent Boreal and north-west European ammonite zones. Colours in the lithological column correspond to field outcrop appearance.

Geophysics, of the Siberian Branch of the Russian Academy of Sciences (Nikitenko, personal collection).

**Foraminiferal assemblages: results**

The studied foraminiferal assemblages consist of benthic forms belonging to the suborders Textulariina, Lagenina and Robertinina. Agglutinated taxa are dominant (18 genera) and taxa with calcareous-perforated shell forms are secondary (11 calcitic hyaline and 1 aragonitic hyaline). Among the agglutinated forms, *Trochammina lapidosa* is dominant in the Upper Pliensbachian and *Trochammina kisselmani* is dominant in the Lower Toarcian samples (Fig. 3). These assemblages often comprise well-preserved tests and carapaces without any trace of grading

or transportation. Calcareous foraminifera in the latest Pliensbachian and earliest Toarcian were rare. This is not a taphonomic effect, however, because they did not dissolve in the water column of the Anabar–Lena palaeosea. The lysocline level is located at a depth of 1–4 km in modern cold seas, while in Jurassic warm seas, this level should be at a greater depth (e.g., Butler 1982; Thurman & Trujillo 2004). The study area (Kelimyar River district) was located in a mid-shelf environment, in the photic zone of the Anabar–Lena palaeosea, and therefore the depth of this area does not exceed 80–100 m (Nikitenko 2008). Foraminifera with aragonite walls should begin to dissolve at a much shallower depth, but they are present in the section (Pliensbachian). In the Toarcian samples common ostracods are recorded,

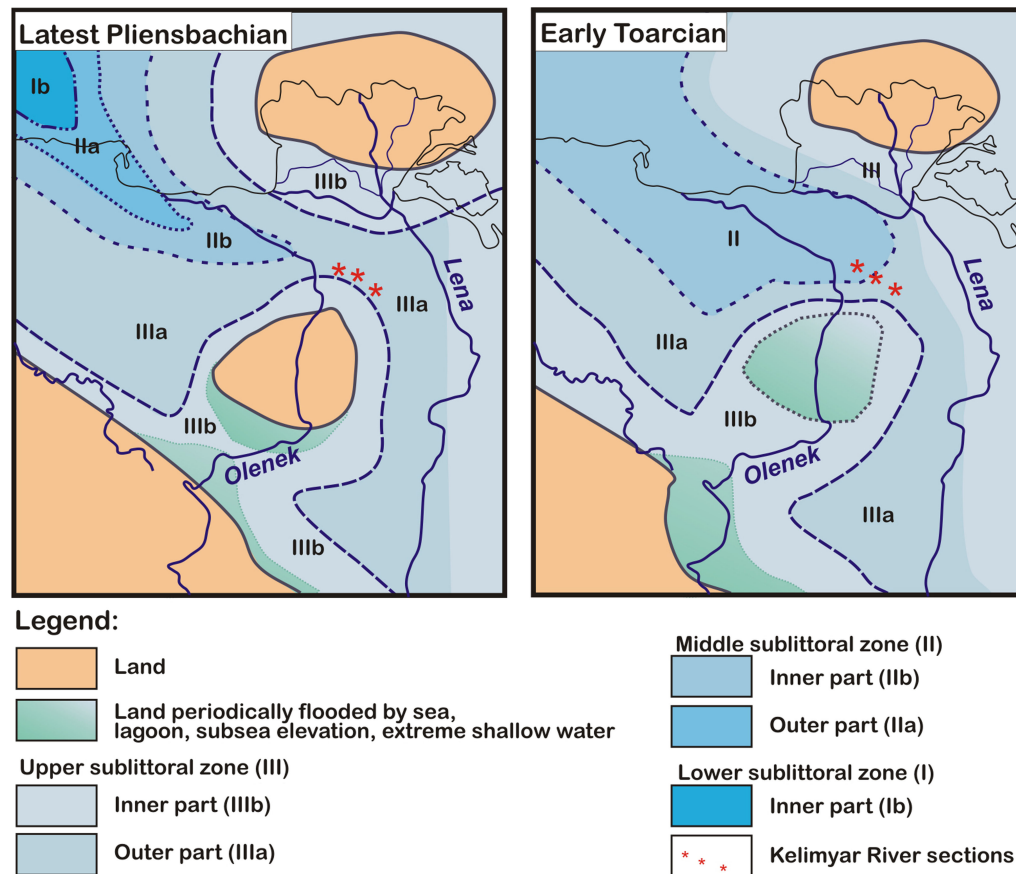


Fig. 2 Palaeogeography of the Anabar–Lena Sea in Late Pliensbachian and Early Toarcian.

having well-preserved sculptured carapaces with thin spikes and no evidence of dissolution (Nikitenko 2008, 2009). In addition, the shells of ammonites, belemnites and bivalves do not bear traces of dissolution either. For these reasons, the composition of foraminiferal assemblages is not severely affected by taphonomic processes.

*Trochammina*, the dominant foraminifera in the studied section, is a globular and plano-convex low trochospiral foraminifera interpreted as epifaunal, with a feeding strategy of detritivore or bacterivore and probably active herbivore, including phytodetritus corresponding to the morphogroup D1 of Reolid et al. (2010) and morphogroup D of Nikitenko et al. (2013).

The base of the Upper Pliensbachian is characterized by the dominance of epifauna (Fig. 4) represented mainly by *Trochammina* and, secondarily, *Conorboides*, *Ammodiscus*, *Hyperammina*, *Glomospirella* and *Lagenina* (sample 1). Aragonitic and calcitic foraminifera are present (24 and 15%, respectively) but with decreasing trends from sample 1 to 3, and eventually they disappear (sample 4). The abundance of foraminifera is relatively high (ca. 60

specimens/100 g) at the base of the section (sample 1). Most of the Kyra Member (Upper Pliensbachian) is characterized by dominance of *Trochammina* (>50% of the assemblage; Fig. 4), increasing values of *Ammodiscus* and *Hyperammina*, and reduced numbers of *Glomospira*, *Reophax*, *Kutsevella*, and *Recurvoides*. However, the last 1.5 m of the Upper Pliensbachian shows an abrupt decrease of *Trochammina* mainly compensated by increasing proportions of *Recurvoides* (Fig. 5). Throughout the Kyra Member infaunal forms decrease (Fig. 4). The analysis of the genus *Trochammina* from the Upper Pliensbachian of Kelimyar section and other outcrops of Siberia evidences that the species determined earlier as *Trochammina lapidosa*, *Trochammina ex gr. inflata*, *Trochammina inflataeformis* and *Trochammina sablei*, should in fact be attributed to one species, *T. lapidosa* (Nikitenko 2009). At the base of the studied section the diversity of foraminifera is higher; diversity then decreases with the increasing abundance of foraminifera, mainly corresponding to *Trochammina*, except for an abrupt decrease in the topmost Pliensbachian. If we consider the abundance of *Trochammina* in light of the abundance of the rest

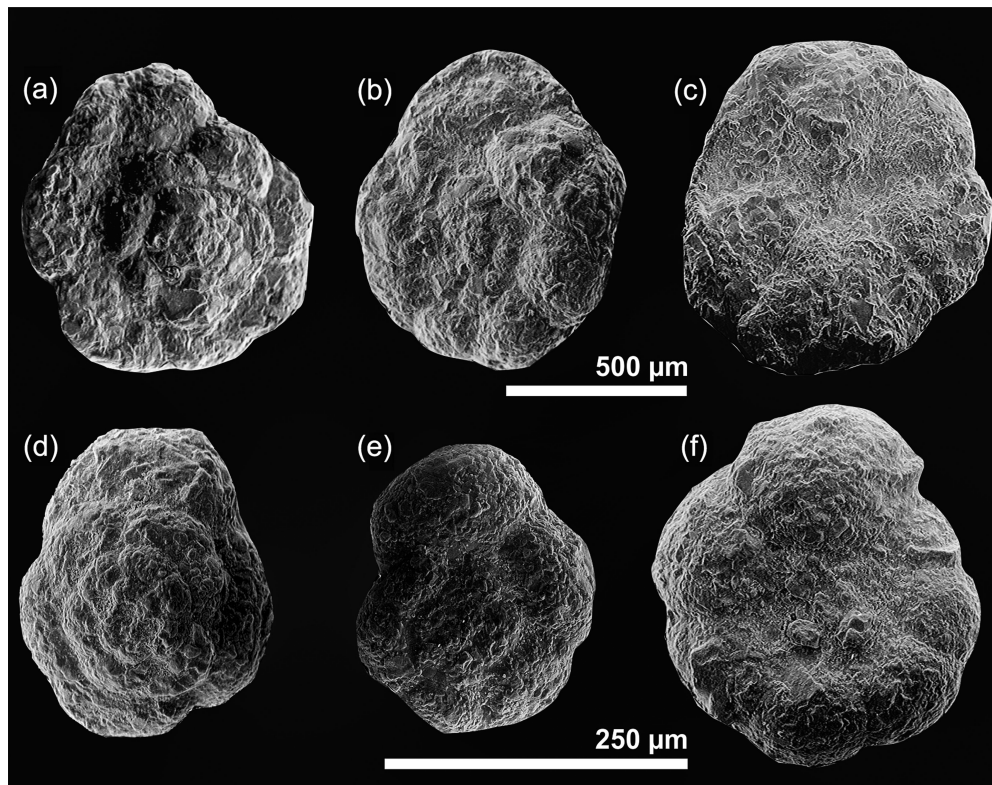
**Table 1** Original count of foraminifera retrieved from 200 g of dried samples from the Kelimyar River section.

Sample	Stage																
	Pliensbachian									Toarcian							
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S15	S18	S19	S21	S24	S27	S30
<i>Ammobaculites</i>	1	0	0	0	0	1	2	2	1	1	2	0	0	0	0	0	
<i>Ammodiscus</i>	10	4	13	5	60	34	55	15	32	0	0	0	0	0	0	2	
<i>Anmarginulina</i>	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
<i>Astacolus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Bulbobaculites</i>	0	0	0	0	0	0	0	0	0	0	2	12	7	10	4	0	
<i>Conorboides</i>	27	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Dentalina</i>	9	6	2	0	0	0	0	0	0	0	0	6	0	0	0	0	
<i>Eoguttulina</i>	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	
<i>Evolutinella</i>	0	0	0	0	0	0	0	0	0	0	10	25	20	0	11	0	
<i>Globulina</i>	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	
<i>Glomospira</i>	3	0	0	7	12	1	10	4	17	10	2	2	0	0	1	0	
<i>Glomospirella</i>	10	0	5	7	0	0	0	0	2	0	0	0	0	0	0	0	
<i>Hyperammina</i>	10	21	50	9	70	36	50	20	15	1	1	12	1	70	2	0	
<i>Ichthyolaria</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Jaculella</i>	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Kutsevella</i>	0	0	2	0	6	6	10	7	3	0	0	0	0	0	0	0	
<i>Lagenammina</i>	0	0	0	0	0	0	0	0	0	0	0	6	4	0	0	0	
<i>Lenticulina</i>	2	2	2	0	0	0	0	0	0	0	0	2	0	0	0	0	
<i>Marginulina</i>	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Nodosaria</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Palmula</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	
<i>Pyrulinoides</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Recurvoides</i>	0	0	0	5	0	0	80	70	80	1	3	0	3	5	0	0	
<i>Reophax</i>	1	0	0	1	0	3	7	10	0	0	7	6	12	0	3	0	
<i>Saccammina</i>	0	0	0	0	0	0	0	0	0	1	0	4	0	8	0	0	
<i>Spiroplectammina</i>	0	0	0	0	0	0	0	0	0	4	5	0	5	0	0	0	
<i>Tolypammina</i>	0	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	
<i>Trochammina</i>	32	115	60	45	180	124	20	40	30	10	85	500	150	120	30	35	
<i>Verneuilinoides</i>	2	1	0	0	4	0	0	0	0	0	2	0	1	0	0	0	

of foraminifera (Figs. 6, 7), it is clear that only *Trochammina* dramatically decrease while the other foraminifera maintain the values of abundance or increase (mainly *Recurvoides* and *Ammodiscus*). Considering percentages, in the topmost Pliensbachian the proportions of *Recurvoides taimyrensis* abruptly increase (44%), whereas proportions of the genera *Trochammina lapidosa* decrease (<24%; Fig. 5). In this uppermost part of the Pliensbachian, infaunal forms experiment a brief increase (Fig. 4). The  $\alpha$ -diversity index and the number of genera drop during the Late Pliensbachian ( $\alpha$ -diversity index from 5 to values usually <2; Fig. 7).

The lowermost part of the Lower Toarcian in this section (more precisely, the Antiquum–Falciferum biozone boundary) is characterized by an abrupt increase of TOC (maximum 6 wt.%; Fig. 7) and a negative carbon isotopic excursion of 6‰ ( $\delta^{13}\text{C}_{\text{TOC}}$  of  $-32\text{‰}$ , Suan et al. 2011; Fig. 7). These values persist 1.8 m over the Pliensbachian–Toarcian boundary. The foraminifera present an abrupt decline in abundance here (Figs. 6, 7),

with the transition to black shales (12 specimens/100 g), and the disappearance of *Ammodiscus* and *Kutsevella*. At this boundary the assemblage is dominated by *Trochammina* (42%) and *Glomospira* (42%); meanwhile, *Recurvoides taimyrensis* dramatically decreases (Fig. 5). In the Lower Toarcian *Trochammina* is represented by *T. kisselmani*. During the stratigraphic interval (1.8 m) with the highest TOC values and the negative excursion of  $\delta^{13}\text{C}_{\text{TOC}}$ , the proportion of *Trochammina* increases rapidly (Fig. 5). Taking into account the abundance of foraminifera, only *Trochammina* increases in the black shales (from sample 10 to 15; Fig. 6). Just at the top of this stratigraphic interval (1.8 m, sample 18), an abrupt recovery is recorded (274 specimens/100 g) led by *Trochammina* (91% of the assemblage) and some infaunal forms (Figs. 4–6), though characterized by low  $\alpha$ -diversity values. The recovery of other foraminifera (sample 21) is delayed with respect to the acme of *Trochammina* (sample 18, Figs. 5, 6). The diameters of both megalosphaeric and microsphaeric generations



**Fig. 3** Scanning electron images of (a, b, c) *Trochammina lapidosa*, Upper Pliensbachian, microsphaeric form, (a) dorsal view, (b, c) megalosphaeric form, (b) dorsal view, (c) ventral view and (d, e, f) *Trochammina kisselmani*, Lower Toarcian, (d, f) microsphaeric form, (d) dorsal view, (f) ventral view, megalosphaeric form, (e) dorsal view.

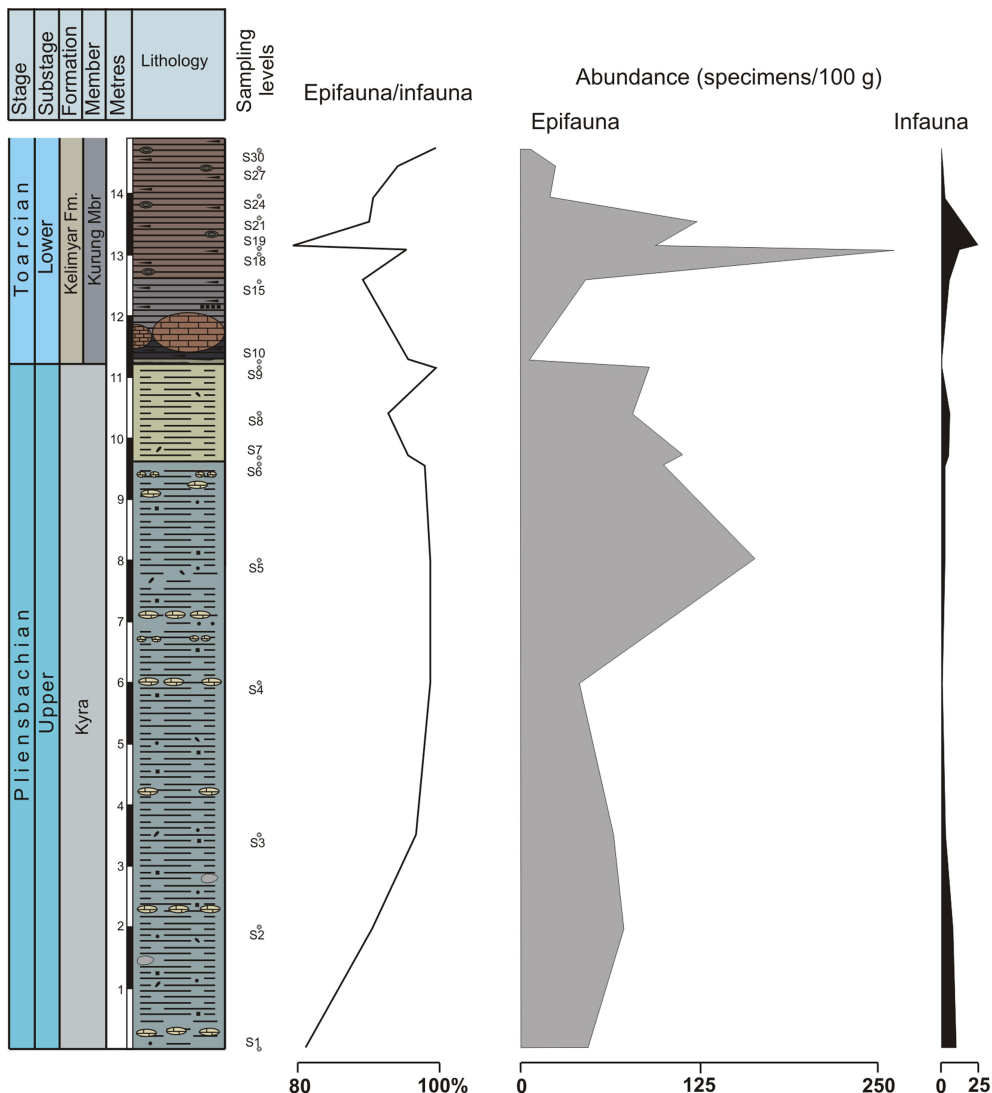
of *T. kisselmani* are about two to three times shorter than *T. lapidosa* (Table 2). In general, after the biotic crisis at the beginning of the Early Toarcian, the size of foraminifera (all taxa) in the assemblages is two to three times lower than in the Late Pliensbachian.

### **Trochammina and palaeoenvironmental fluctuations**

Benthic habitat fluctuations in salinity, nutrient availability and oxygenation rate are limiting palaeoenvironmental parameters, exerting considerable control upon the composition and relative abundance of foraminiferal assemblages from the studied section.

The Upper Pliensbachian is represented by a foraminiferal assemblage dominated by epifauna, with a high proportion of *Trochammina lapidosa*, yet a progressive decline in the diversity and number of genera. This suggests an unfavourable microhabitat for infaunal forms (e.g., *Ammobaculites*, *Dentalina*, *Lenticulina*, *Nodosaria*, *Pyrulinooides*, *Reophax*, *Verneuilinooides*), probably involving salinity fluctuations. *Trochammina* has been proposed as

an opportunist epifaunal taxon tolerating salinity fluctuations (Nagy & Berge 2008; Nagy et al. 2010). Low diversity assemblages of agglutinated foraminifera dominated by *Trochammina* appear to have been widespread in Late Triassic to Middle Jurassic restricted environments along the north-western and western European margins (Golebiowski 1990; Kuerschner et al. 2007; Clémence et al. 2010; Nagy et al. 2010). The decreasing proportions of aragonitic and calcitic hyaline tests (*Anmarginulina*, *Astacolus*, *Conorboides*, *Dentalina*, *Ichthyolaria*, *Lenticulina*, *Marginulina*, and *Pyrulinooides*) confirm the progressive destabilization of the benthic environment. This interpretation is congruent with the context of relative sea-level fall in the Arctic palaeobasin during the Margaritatus Chron and the early Viligaensis Chron (Nikitenko & Mickey 2004). In conjunction with this eustatic fall, abrupt climatic cooling due to the presence of glendonites (calcite pseudomorph after ikaite) has been evoked for north-eastern Siberia (Kaplan 1976; Suan et al. 2011). A sea-level fall has likewise been interpreted for the Pliensbachian–Toarcian boundary in other regions, as well as a drastic cooling event during the last ammonite



**Fig. 4** Ecostratigraphic distribution of epifauna/inafauna ratio (expressed as%) and abundance (specimen per 100 g) of epifaunal and infaunal foraminifera in the Kelimyar River section.

zone of the Pliensbachian (e.g., Price 1999; Rosales et al. 2004; Van de Schootbrugge et al. 2005; Suan et al. 2010; Dera et al. 2011; Korte & Hesselbo 2011).

The topmost 1.5 m of the Pliensbachian records an improvement of environmental features evidenced by an enhanced abundance of foraminifera excepting opportunist *Trochammina*. The favourable conditions are also compatible with the brief increase of infaunal forms (Fig. 4) such as *Reophax* and *Ammobaculites* (Table 1).

The beginning of the Lower Toarcian (exactly at the Antiquum-FalCIFerum zone boundary) is correlated with the T-OAE (increase of TOC and negative carbon isotopic excursion). This event is marked in the Kelimyar River section by an abrupt reduction in the abundance of

foraminifera (Figs. 6, 7), indicating hypoxic conditions at sea bottom. Totally anoxic conditions apparently did not develop, in view of the record of benthic foraminifera (no benthic barren interval). According to Nikitenko & Mickey (2004), monospecific associations of thin-shelled bivalves and thin-shelled ostracods recorded in this interval would confirm the development of oxygen-restricted biofacies. Among the foraminifera, only r-strategist *Trochammina kisselmani* shows a rapid increase after the debut of the black shales, congruent with the association of this genus with a high TOC and poorly oxygenated sediment water interface. *Trochammina* has been proposed as an opportunist epifaunal taxon that tolerates low oxygenation (Bağ 2000; Jenkins 2000;

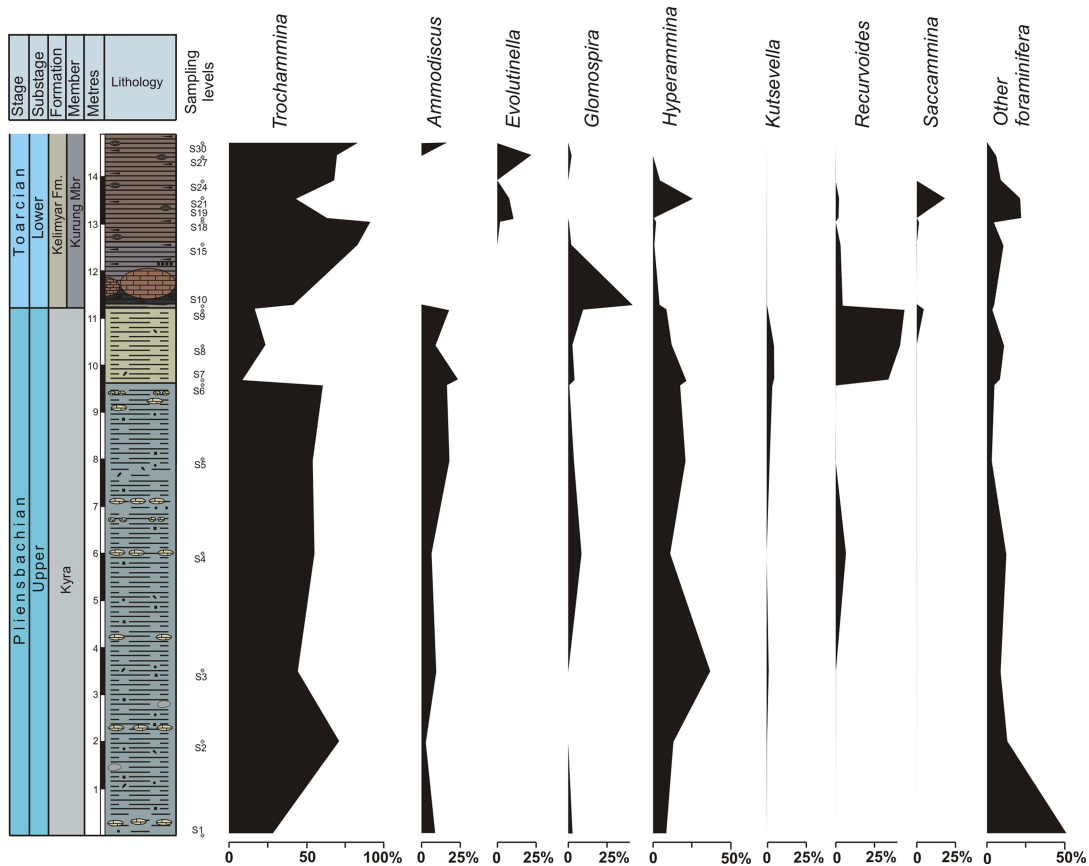


Fig. 5 Ecostratigraphic distribution of proportions of selected epifaunal foraminifera including *Trochammina* in the Kelimyar River section.

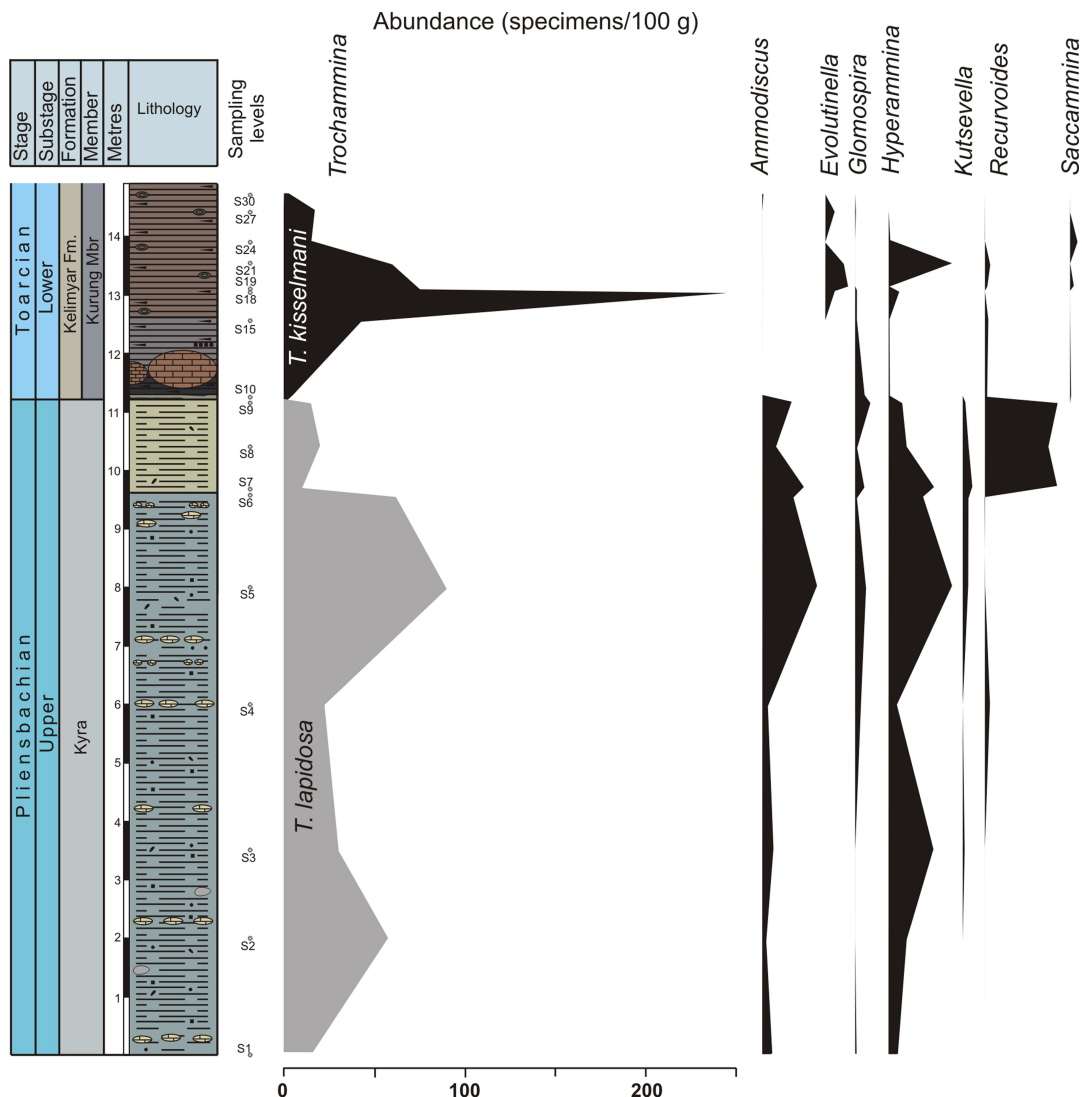
Reolid & Nagy 2008; Reolid et al. 2010), and it has also been registered along with high TOC values after anoxic or suboxic conditions during the Middle Jurassic to Early Cretaceous (e.g., Nyong & Ramanathan 1985; Koutsoukos & Hart 1990; Friedrich et al. 2003; Reolid & Nagy 2008; Reolid, Nagy et al. 2008; Reolid, Rodríguez-Tovar & Nagy 2012). In recent environments *Trochammina* has been seen to increase rapidly in the surficial sediment to consume labile organic matter (Koho et al. 2008), and to survive in environments under hypoxic and eutrophic conditions (Tsumimoto et al. 2006) as well as in marshes with extreme chemical pollution and low pH (McGann & Sloan 1999).

The diameter of foraminifera decreases at the beginning of the Early Toarcian, especially in the case of *Trochammina*. This strategy, enabling them to prosper in more or less confined environments, is known as the Lilliput Effect (Twitchett 2007; Morten & Twitchett 2009; Song et al. 2011) and represents a decrease within the surviving species. This has been described as an adaptative strategy in miliolids and lagenids of the Toarcian from the Middle Atlas of Morocco (Reolid et al. 2013).

Without tough competition, *Trochammina* rapidly reproduced and augmented its population (Figs. 6 and 7). This record is similar to that described in the uppermost Triassic of the Austrian Alps by Clémence et al. (2010), where an event characterized by a negative carbon isotopic excursion, an increase in TOC and a barren foraminiferal interval is followed by an abundance peak of *Trochammina*. These authors use the term “disaster epifaunal agglutinated foraminifera” to describe such *Trochammina* peaks. In this sense, *Trochammina kisselmani* was an effective colonizer of the bottom after hypoxic conditions in the Kelimyar River section, indicating stressful conditions just over the negative carbon isotopic excursion and maximum values of TOC. The advance in the Kurung Member shows a new decrease in abundance and diversity. According to Nikitenko et al. (2013), this new retrocession in the foraminiferal assemblages also affecting *Trochammina* may be related to the persistence of adverse conditions upon foraminiferal assemblages only partially recovered after the debut of the T-OAE.

The stressing environmental conditions related to changes in oxygenation in the sea bottom were driven



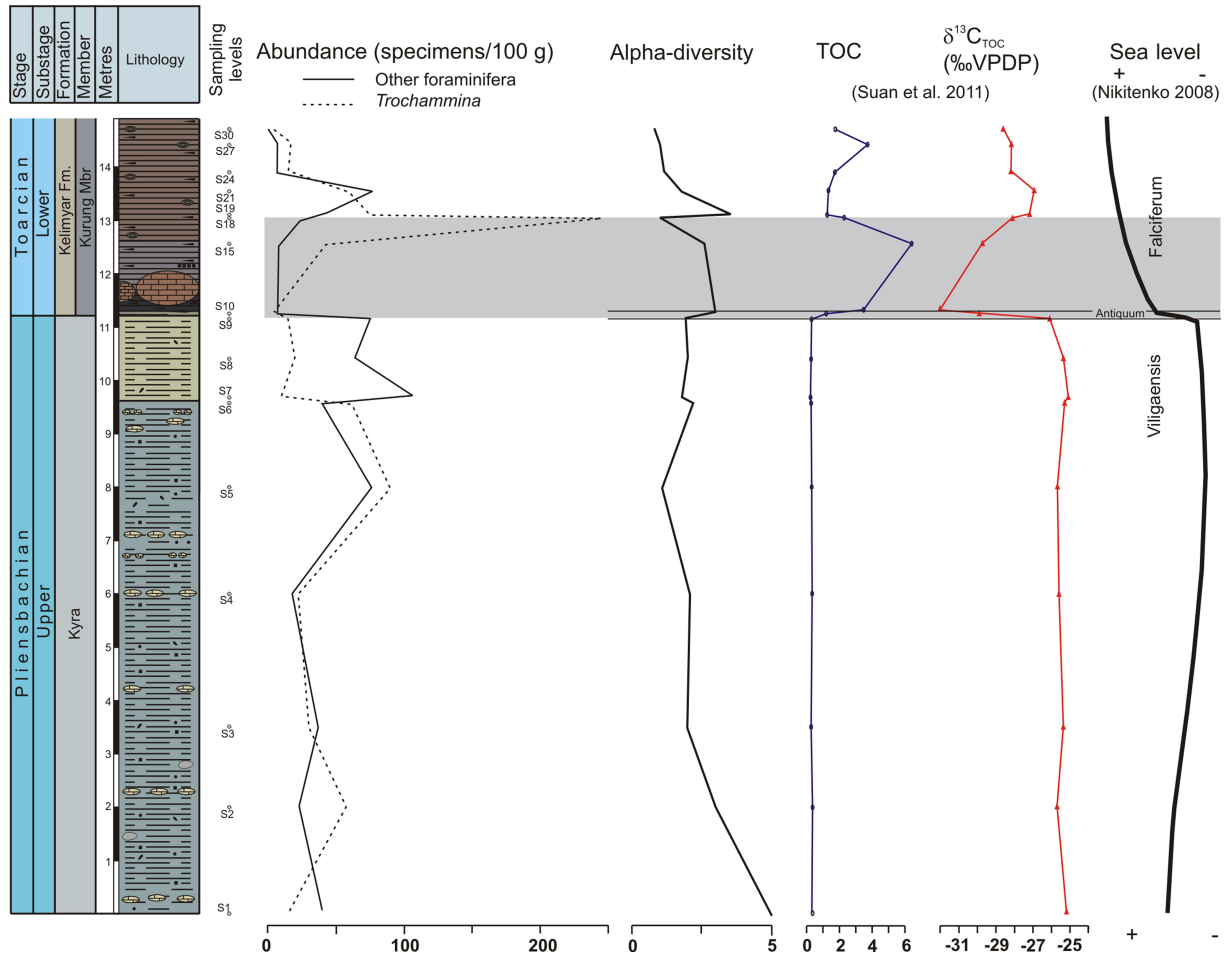


**Fig. 6** Ecostratigraphic distribution of abundance (specimen per 100 g) of selected epifaunal foraminifera including *Trochammina* in the Kelimyar River section.

by climatic changes in the Pliensbachian–Toarcian boundary. According to Nikitenko & Mickey (2004), during the Early Toarcian a climatic warming took place in the Arctic palaeobasins, related to a major eustatic rise. A sea-level rise accompanied by an abrupt warming event has been interpreted for the Early Toarcian in other regions as well (e.g., McArthur et al. 2000; Svensen et al. 2007; Gómez et al. 2008; Suan et al. 2010; Dera et al. 2011; Gómez & Goy 2011; Korte & Hesselbo 2011). The record of ice-rafted boulders and glendonites supports the—at least—intermittent formation of polar sea ice during the Late Pliensbachian in this area (Suan et al. 2011). The subsequent warming during the earliest Toarcian—increasing 6–10°C in some areas (Bailey et al.

2003; Gómez et al. 2008; Suan et al. 2010)—indicates a probable glacially induced sea-level rise due a massive melting of continental ice (Suan et al. 2011). Hallam (1997) interpreted an abrupt sea-level rise about 30–90 m between the uppermost Pliensbachian and the negative  $\delta^{13}\text{C}$  excursion of the Lower Toarcian in European sections. This situation evidently changed the sea-bottom features and produced stressing conditions for benthic foraminifera.

Another essential point collaborating in adverse conditions is that such high palaeolatitudes are always strongly seasonal. This was most likely a main driving force for true opportunists (see the case of *Trochammina hadai*, Kitazato & Matsushita 1996). Tyszka (2009, 2010)



**Fig. 7** Abundance of *Trochammina* vs. rest of foraminifera compared with  $\alpha$ -diversity index, as well as the total organic carbon (TOC) and  $\delta^{13}\text{C}$  from organic matter of Suan et al. (2011), and sea-level fluctuations according to Nikitenko (2008).

proposes the term seasonal opportunists when seasonality is a dominating environmental factor though not usually recognized in average fossil assemblages.

**Conclusions**

The samples of benthic foraminifera analysed correspond to mudstones and siltstones deposited in a middle to upper sublittoral zone. The section is located in northern Siberia and includes the Upper Pliensbachian

and the Lower Toarcian (Lower Jurassic). Salient features of the foraminiferal successions are: the assemblages are dominated by agglutinated taxa; the  $\alpha$ -diversity values are extremely low, and the dominant genus is *Trochammina*.

These characteristics suggest that the foraminiferal assemblages were adapted to restricted conditions, where the main limiting factors were salinity and oxygen degree. However, due the high palaeolatitude, seasonality could be a dominant environmental factor altering tem-

**Table 2** Data on tests of *Trochammina lapidosa* and *Trochammina kisselmani* from 50 individuals.

Generation	Diameter of prolocus (mm)	Diameter (mm)	Height of test (mm)	No. of convolutions
<i>Trochammina lapidosa</i> Gerke et Sossipatrova, 1961				
Megalosphaeric	0.060–0.084	0.42–0.78	0.14–0.27	1.2–2.0
Microsphaeric	0.014–0.028	0.64–0.95	0.27–0.36	2.5–4.0
<i>Trochammina kisselmani</i> Sapjanik et Sokolov, 1991				
Megalosphaeric	0.020–0.070	0.25–0.44	0.098–0.150	1.0–3.0
Microsphaeric	0.012–0.020	0.21–0.31	0.160–0.210	3.0–4.0

perature, nutrients, light, runoff, etc.; the opportunists simply reacted to seasonal food fluxes, explaining why *Trochammina* dominates in nearly all samples.

Episodes featuring a higher proliferation of *Trochammina* may be related to: (a) sea-level fall and consequent changes in salinity in the Arctic Palaeobasin during the Margaritatus Chron and the beginning of the Viligaensis Chron (Late Pliensbachian), and (b) restricted oxygen biofacies (hypoxic conditions) related to the T-OAE.

The opportunist behaviour of *Trochammina*, making possible its survival and adaptation to unfavourable conditions, led this genus to be the main colonizer of the sea bottom after the biotic crisis related to the T-OAE in this section.

### Acknowledgements

The research activity of MR was supported by projects RYC-2009-04316 (Ramón y Cajal Programme), P11-RNM-7408 (Junta de Andalucía) and UJA2011/12/17 (Universidad de Jaén-Caja Rural de Jaén). For their research support, BLN and LG gratefully acknowledge the Arctica and Biosphere scientific programmes of the Russian Academy of Sciences. The authors thank two anonymous reviewers for their valuable comments serving to improve the manuscript. We thank Jean Sanders for reviewing the grammar.

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