

Marine Reptiles and Climates of the Jurassic and Cretaceous of Siberia

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Abstract—All current data on the Jurassic and Cretaceous climates of Siberia based on isotope, paleontological, and lithological proxies are summarized. The late Pliensbachian cooling episode, early Toarcian warming, promptly replaced by long-term Middle Jurassic cooling at the end of the Toarcian, and a long-term warm interval in the Late Jurassic are clearly recorded. From the end of the Ryazanian, a gradual cooling episode began, which apparently continued throughout the Early Cretaceous except for a brief warming episode in the early Aptian. At the beginning of the Late Cretaceous, the climate became warmer; the peak of warming is recorded at the Cenomanian–Turonian boundary. Then, the middle–late Turonian was marked by a relatively cold episode. Later, in the Coniacian–Campanian, the climate warmed again, but at the end of the Campanian another cooling episode occurred. New findings of marine reptiles are described from the Toarcian, Kimmeridgian, Volgian, and Santonian–Campanian deposits of north of Eastern Siberia. All existing records of marine reptiles known from the Jurassic and Cretaceous of Siberia are revised, and all the findings (from 51 localities) are positioned in relation to paleolatitudes. It is established that the majority of occurrences of these fossils were within the polar paleolatitudes (70°–87°). We found no direct correlation between climate fluctuations and the distribution of these organisms. Taking into account the newest data showing that representatives of the majority of Jurassic and Cretaceous large groups of marine reptiles were able to maintain a more or less constant body temperature and were also able to undertake large-scale seasonal migrations, it is reasonable to be cautious in interpreting the presence of remains of these animals as indicators of a warm climate.

Keywords: paleoclimate, Siberia, Jurassic, Cretaceous, marine reptiles, glendonites, *Classopollis*, $\delta^{18}\text{O}$

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INTRODUCTION

Marine reptile remains have been known from the Mesozoic of Siberia for almost 150 years (the first find was made by A.L. Czekanowski's expedition in 1875 (Jakowlew, 1903)); however, they remain insufficiently studied. Most of these finds are mentioned only in various publications on regional geology and stratigraphy, and only a few specimens from the Jurassic of the Lena River basin (Jakowlew, 1903; Menner, 1948) and Lower Cretaceous of the Anabar River (Efimov, 2006; Efimov and Efimov, 2011) and Uyedeniya Island (Ryabinin, 1939) have been described and illustrated. At the same time, in the studies of the Mesozoic climates (primarily high-latitude), the presence of marine reptile remains, as a rule, served as a proxy for warm-water conditions (Hallam, 1985). Data on the fossil remains of these organisms in vari-

ous horizons of the Mesozoic of Siberia were interpreted in the same way (Golbert, 1979, 1983, 1987; Golbert and Polyakova, 1966; Golbert et al., 1968, 1978, 1984; Knyazev et al., 1991; *Paleoklimaty...*, 1977). However, in recent years, newly obtained data have cast doubt on the value of marine reptiles for reconstruction of paleotemperature.

On one hand, various reptile assemblages have been described from high latitudes and, judging by the abundance of glendonite, apparently cold-water upper Aptian deposits of Australia (Kear, 2005, 2006a, 2006b) and Arctic Canada (Vavrek et al., 2014).

On the other hand, it has been shown that at least some representatives of these groups were able to maintain a constant body temperature (Bernard et al., 2010; Fleischle et al., 2018; Harrell et al., 2016; Motani, 2010; Wintrich et al., 2017a, 2017b).

And finally, there is growing evidence that many Jurassic and Cretaceous reptiles had wide (including bipolar) ranges and were likely to have been able to undertake significant seasonal migrations comparable to those of modern cetaceans and some fishes (Zverkov et al., 2015).

Extensive materials on the paleothermometry of the Jurassic and Cretaceous Siberian seas were obtained mainly in the 1960s–1970s, when domestic researchers began studying the oxygen isotope composition of belemnite rostra (Berlin et al., 1967; Naidyn and Teis, 1976; Naidyn et al., 1966; Teis et al., 1968, 1978). In parallel with these works, methods were developed for paleotemperature reconstruction based on the Ca/Mg ratio in mollusk shells (Berlin and Khabakov, 1966; Berlin et al., 1970), while the results of studying the same belemnite samples by both methods showed fairly good convergence (Berlin and Khabakov, 1970).

At the same time, the first attempts were made to clarify changes in the Mesozoic climate of Siberia using paleobotanical data (Golbert and Polyakova, 1966; Iljina, 1969, 1985; Kiritchkova, 1985; Teslenko, 1963, 1964; Vakhrameev, 1964, 1987, 1991), including data on the relative content of *Classopollis* pollen in the spore-pollen assemblages to detect warming and cooling episodes (Vakhrameev, 1978, 1982).

Along with temperature variations, paleobotanical data allowed the degree of climate aridity to be identified.

In the late 1970s, Kaplan (1977, 1978, 1980) summarized the distribution of glendonites (calcite pseudomorphs after the metastable mineral ikaite, indicative of cold-water environments) in the Jurassic and Cretaceous deposits of Siberia, and using this, conclusions were drawn about climate change in the region under consideration. Various data on the climate of Jurassic and Cretaceous Siberia obtained in the 1960s–1980s (primarily, data on flora, facies and paleothermometry) were summarized by Golbert (1987).

Over the next 30 years, despite the appearance of extensive new material, no further such reviews were published, with the exception of small papers by Zakharov (1994, 1997, 2002) and Zakharov et al. (2010).

It should be noted that it is not always possible to directly use data from the 1960s–1980s, either because of changes in the suitability of samples for isotopic studies or because of substantial revision of the age of some stratigraphic intervals in recent years, primarily in the Middle Jurassic.

In recent years, new isotopic data have been obtained, allowing us to refine our understanding of the change in water temperature in the Arctic in the Late Jurassic–Cretaceous (Dzyuba et al., 2013, 2018; Nunn, 2007; Price and Mutterlose, 2004; Žák et al., 2011; Zakharov et al., 2011, 2014; Dzyuba et al., 2013, 2018). However, it should be noted that isotopic paleothermometry data can indicate trends, not specific

temperature values. This is especially significant for high-latitude sections. First, the isotopic composition of oxygen is significantly affected by fluctuations in water salinity, which are very likely in Siberian shallow-water epicontinental basins and include those that cannot be identified by changes in faunas (for example, similar in scale to those established in the Late Jurassic of the Central Russian Sea; see Wierzbowski et al., 2018). Secondly, the annual mean seawater oxygen isotope ratio in high latitudes of the Northern Hemisphere differs substantially from the mean oceanic value, being enriched in the lighter oxygen isotope (LeGrande and Schmidt, 2006). The same patterns of oxygen isotope ratios in the high latitude basins of the Late Mesozoic are established as a result of modeling (Zhou et al., 2008) and are suggested by a study of the oxygen isotope ratios in belemnite rostra and glendonites (Price and Nunn, 2010). For the Late Cretaceous, promising paleoclimatic reconstructions were obtained using data on the morphology of fossil angiosperm leaves (Herman, 2004; Herman and Spicer, 1997; Herman et al., 2002; Spicer and Herman, 2010). Thanks to new findings, it was possible to clarify the characteristics of the stratigraphic and geographical distribution of Jurassic and Cretaceous glendonites in the Arctic (Morales et al., 2017; Rogov and Zakharov, 2010; Rogov et al., 2017; Zakharov et al., 2010). Although some of the factors controlling the glendonite distribution remain a subject of debate (Morales et al., 2017; Qu et al., 2017; Stockmann et al., 2018; Zhou et al., 2015), most authors agree upon their contiguity with cold-water environments, and that the parent mineral for the formation of glendonite is ikaite (Grasby et al., 2017; Rogov et al., 2017; Vickers et al., 2018). In addition to the recent data on paleoclimates, over the past 10 years, M.A. Rogov collected numerous bones of marine reptiles from the Mesozoic deposits of various ages in the north of Eastern Siberia.

Thus, the emergence of new data and the need for a critical review of previously published results determine the main objectives of this study:

- (1) summary of existing data on the Jurassic and Cretaceous climates of Siberia;
- (2) a review of available data on marine reptile occurrences in the Jurassic and Cretaceous deposits of Siberia with a description of new finds¹;
- (3) comparison of the data obtained on the Jurassic and Cretaceous climates with the distributional patterns of marine reptiles.

The age of some stratigraphic intervals, primarily in the Middle Jurassic and Lower Cretaceous, is currently debated owing to the complexity of the Boreal-

¹ The new finds described in this paper are housed in the collections of the Saratov State Technical University (Saratov, specimen numbers begin with “SSTU”), the TsNIGR Museum (St. Petersburg, specimen numbers begin with “TsNIGR”), and the Geological Institute of the Russian Academy of Sciences (Moscow, specimen numbers begin with “GIN”).

Tethyan correlation. For the Jurassic, the boundaries of the substages mainly follow Zakharov and Rogov (2008); only for the Aalenian in this work is a twofold division used, which is traditional for Siberia (Shurygin et al., 2011). The boundary of the lower and upper Bajocian is traditionally drawn at the base of the Borealis Zone. In recent years, speculations have been made about the Early Bajocian age of ammonite zones located below the Arcticus Zone (de Lagausie and Dzyuba, 2017; Meledina, 2014), but because they are based on indirect evidence, they remain, in our view, insufficiently substantiated.

The subdivision of the lower Cretaceous is accepted mainly according to Baraboshkin (2004), taking into account the data for the Subpolar Urals: the Bojarkensis Zone, which has traditionally been considered to be Hauterivian, is assigned to the terminal part of the Valanginian (Nunn et al., 2010), although it cannot be ruled out that its upper part may already be of Hauterivian age. The ammonite-free interval, which in Siberia contains *Buchia sublaevis*, whose Hauterivian age is based on data from California (Zakharov, 2015) and the East European Platform (Zakharov, 1981), is also assigned to the lower Hauterivian. The Upper Cretaceous is subdivided according to the data of Zakharov et al. (2002, 2003).

AN OVERVIEW OF THE JURASSIC AND CRETACEOUS CLIMATES OF SIBERIA

Early Jurassic

According to palynological data, in the north of Eastern Siberia at the beginning of the Jurassic, there was a humid, warm-temperate seasonal climate. The Early Jurassic flora in Western and Eastern Siberia was relatively uniform, dominated by conifers and Ginkgoales with a significant content of Bennettitales (Ilyina, 1969). In the Vilyui River basin, there have been records of representatives of a flora characteristic of the Indo-European region. Spores of sphagnum mosses *Stereisporites* are used as proxies for the Early Jurassic climate. Like other sphagnum mosses, these plants, apparently, needed abundant stagnant moisture and relatively moderate temperatures (Ilyina, 1985). Analysis of the distribution of spores of *Stereisporites* in the Jurassic of Siberia showed that sphagnoid plants during this period were particularly well represented during episodes of a humid warm-temperate climate (Sinemurian–Pliensbachian, Aalenian, Bajocian) and disappeared during periods of sharp warming (early Toarcian) and aridization (Ilyina, 1985). The genus *Steriosorites* was the most common in Siberia in the late Pliensbachian, and it is also found in large numbers in nonmarine sediments of this age, common in the south of Siberia (Ilyina, 1985).

Cooling is registered for the late Pliensbachian. It was accompanied by the disappearance of representatives of Subtethyan and Subboreal genera of bivalves,

foraminifers, and ostracodes from benthic communities (Nikitenko and Shurygin, 1994; Zakharov, 1994; Zakharov et al., 2006). The late Pliensbachian of Eastern Siberia is also characterized by an extremely wide distribution of glendonites, which have been recorded repeatedly both in natural outcrops and in the borehole cores (Rogov, 2015) (Fig. 1). Levels with the upper Pliensbachian glendonites extend for hundreds and thousands of kilometers and were used as marker horizons for geological mapping (Kirina, 1966). In the same stratigraphic interval, dropstones have been recorded (Suan et al., 2011), although some of them are not related to ice rafting (Knyazev et al., 1991).

The extremely low taxonomic diversity of ammonites (which are represented only by amalthoids and sometimes by cosmopolitan phylloceratids) and data indicating a significant late Pliensbachian water temperature decrease in middle and low latitudes of the Northern Hemisphere (Arabas et al., 2017; Dera et al., 2011; Gómez Fernández et al., 2016; Rosales et al., 2004) are in good agreement with the notions of a noticeable cooling of the climate in the late Pliensbachian not only in the Arctic but also in other regions of the Earth.

Information on the isotopic composition of the shells of Hettangian–Pliensbachian mollusks of Eastern Siberia is scarce. The references in the literature to the “Pliensbachian” paleotemperature datings from belemnite rostra (e.g., Berlin et al., 1970) result from erroneous dating and refer to the lower Toarcian. Only Devyatov (1983) provided the paleotemperature for the Vilyui River basin calculated from the isotopic composition of oxygen in late Pliensbachian–Aalenian bivalve shells (Fig. 1). These data also confirm relatively low paleotemperatures for the late Pliensbachian, which rose substantially at the beginning of the Toarcian. Henceforth, the study of bivalves, which are quite often found in the Hettangian–Pliensbachian sections and often have well-preserved shells, is promising for determining the paleotemperatures from the oxygen isotope composition.

Significant warming associated with the onset of the Toarcian is clearly recorded by the changes in the assemblages of both marine organisms and terrestrial vegetation. The appearance of the thermophile *Ptilophyllum* (Bennettitales) (Kiritchkova, 1985; Vakhrameev, 1987) in the Kolyma and Vilyui river basins was confined to the early Toarcian, and at the same time, the amount of pollen of thermophilic conifers sharply increased in the pollen spectra (Ilyina, 1985; Markova and Skuratenko, 1983; Zakharov et al., 2006).

Plants characteristic of the Indo-European region were recorded in the Toarcian of the Kuznetsk, Chulym-Yenisei, Kansk, and Irkutsk basins (Teslenko, 1964). At the same time, judging by the nature of the accumulation of early Jurassic coals, the early Toarcian warming episode was not accompanied by aridization and occurred against a background of a humid

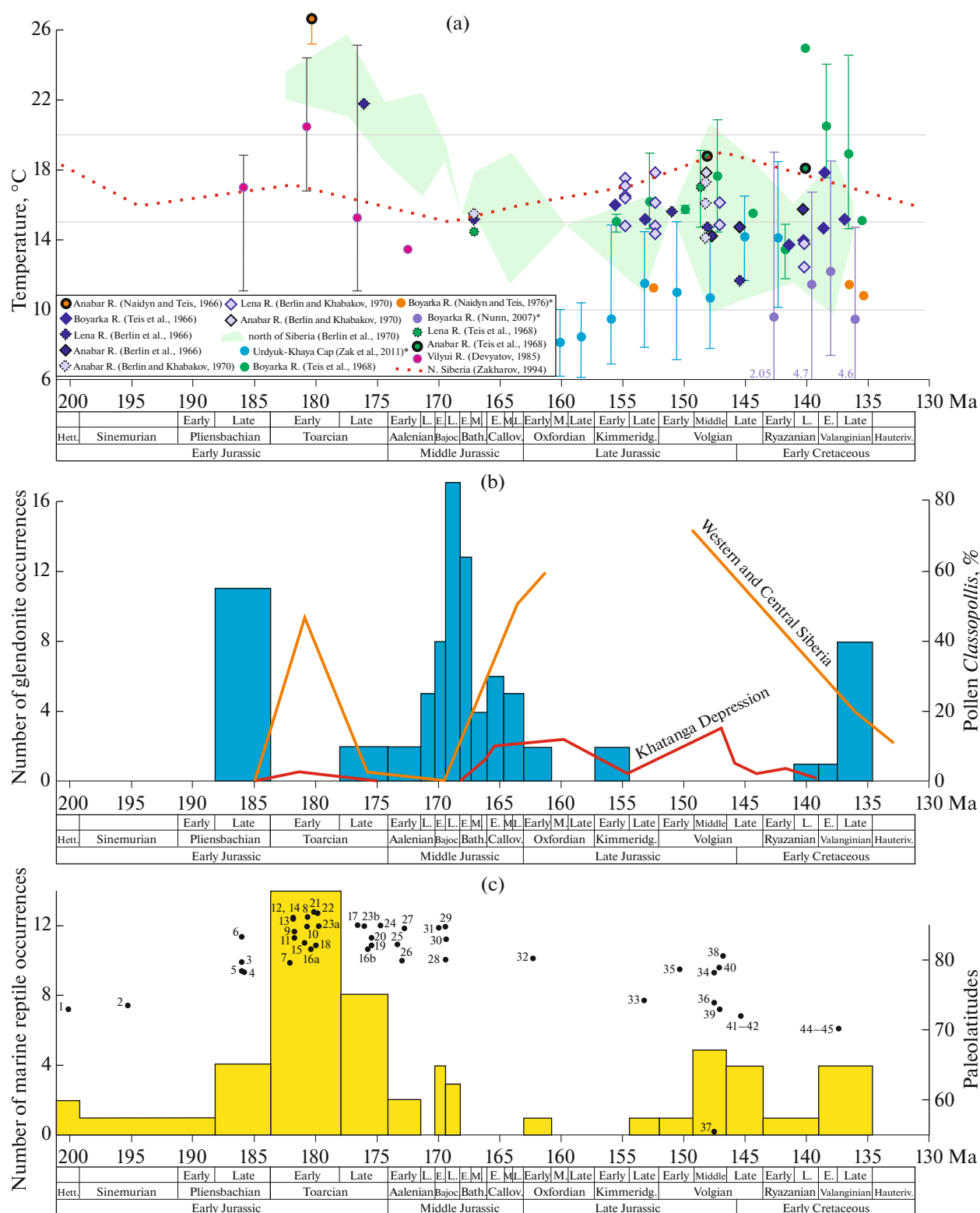


Fig. 1. Jurassic–Early Cretaceous climate indicators for Northern Siberia (a, b) and occurrences of marine reptiles (c). In Fig. 1a, circles show the results of determining the paleotemperature from the oxygen isotopic composition, rhombs are results from the Ca/Mg ratio; asterisks mark studies where initial data on the isotopic composition of belemnite rostra were cited, calculated by the authors using the standard formula for calcite (modification (Anderson and Arthur, 1983), with a mean isotopic composition of water characteristic of the ice-free climate (-1‰), see Table S1). The filled areas show the temperature range in terms of Ca/Mg ratios. The *Classopollis* pollen content is given according to Vakhrameev (1982) with clarifications according to Ilyina (1985), Markova and Skuratenko (1983), and Nikitenko et al. (2015). The paleolatitudes to which the bones of marine reptiles are confined (shown by dots in Fig. 1c, the numbers correspond to the numbers in Fig. 3 and in Table 1) were calculated using the <http://paleolatitude.org> online facilities.

climate. It is significant that, despite the warming, the type of vegetation in Siberia in general remained the same as in earlier Jurassic intervals, and finds of *Ptilophyllum* leaves are absent in coal-bearing sediments with abundant remains of ferns, Czekanowskiales, and Ginkgoales (Vakhrameev, 1987).

At this time in Eastern Siberia, there was a significant northward shift of the ranges of thermophilic taxa of bivalve mollusks, foraminifers, and dinocysts, while Boreal taxa disappeared (Zakharov et al., 2006).

The early Toarcian transgression also led to an expansion of the connection between the basins within the Panboreal Superrealm, so that many immigrant taxa arrived during the warming episode in the Siberian seas. Compared to the late Pliensbachian, the diversity of cephalopods increased, but in bivalves it declined significantly (Meledina et al., 2005), apparently because of the wide development of black shale facies. At this time, various belemnites first appeared in Siberia and immediately became abundant (Meledina et al., 2005). The earliest finds of ammonites in Western Siberia are early Toarcian (Devyatov et al., 2006). Starting from the base of the Toarcian, glendonites and dropstones disappear completely from Siberian sections. Moreover, no lower Toarcian glendonites are known from anywhere in the world. The literature contains a significant number of determinations of the isotopic composition of oxygen in the rostra of Toarcian belemnites from various Siberian regions (Berlin et al., 1970; Golbert, 1987; Golbert et al., 1968; Naidyn and Teis, 1976). However, as noted by the authors of these works, the paleotemperature results obtained (usually above 20°C) seem to be too high, and it seems that at that time the freshening of seawater affected the isotopic composition of oxygen.

The early Toarcian warming in Siberia was short-lived (Ilyina, 1985; Vakhrameev, 1987). Vakhrameev (1987) noted that, in the early Toarcian, thermophilic plants penetrated only into areas along the seacoasts, whereas the warming episode was apparently too brief to change the nature of the flora of areas remote from the coast.

Already in late Toarcian, there are clear signs of cooling in Eastern Siberia. Thermophilic plants disappear from the floral assemblages. Ferns known from the Indo-European Realm are almost absent; the number of conifers producing Pinaceae pollen close in morphology to the extant genera *Picea* and *Pinus* increased (Ilyina, 1969). This cooling episode is also recorded in Western Siberia (Teslenko, 1963). In the north of Eastern Siberia, the diversity of ammonites decreases, and most assemblages are represented only by the genus *Pseudolioceras*. At this time, the endemism of both ammonite and belemnite boreal faunas increased (Meledina et al., 2005). At the top of the Toarcian of Eastern Siberia, relatively few glendonites are recorded (Nikitenko, 2009; this paper). Apparently, the cooling episode that began at the end of the

Toarcian (also recorded in Northwestern Europe), which had a significant impact on the climate of the entire Middle Jurassic of Siberia, was caused primarily by paleogeographic and tectonic events, namely, the almost complete cessation of the connection of the Arctic Basin to Northwestern Europe through the Viking Strait, which led to a change in the direction of currents (Korte et al., 2015).

Middle Jurassic

In the Aalenian, the climatic cooling that began at the end of the Toarcian gradually increased. This is recorded from paleobotanical data obtained from materials from Western and Eastern Siberia (Ilyina, 1968, 1985; Teslenko, 1963), according to paleotemperature determinations made from belemnite rostra, and also from the gradual increase in the number of occurrences of glendonites compared to the Toarcian (Fig. 1). The Aalenian terrestrial flora was impoverished and uniform. It lacked both immigrant species from the southern phytochoremas and Early Jurassic plants that could not adapt to the deterioration of temperature regime and possibly to an increase in the seasonality of the climate (Ilyina, 1985, p. 169). For the first time, the Boreal bivalves *Retroceramus* appeared in the Aalenian in the north of Siberia and later became one of the most characteristic elements of benthic faunas throughout the Middle Jurassic, becoming rare only in the Callovian. Aalenian ammonites of Eastern Siberia were represented by an impoverished assemblage close to the late Toarcian and consisting of *Pseudolioceras* and rare phylloceratids. By the end of the Aalenian, the diversity of belemnites and bivalve mollusks was also significantly reduced (Meledina et al., 2005).

In the second half of the early Bajocian in Siberia, a short-term warming episode is recorded, marked by the occurrence of plants of southern origin. In the north of Eastern Siberia, the presence and higher content of spores characteristic of the Bajocian of Mangyshlak (Ilyina, 1985) are recorded in the palynoflora of this interval. The occurrences of the rare ammonite genera *Normannites* and *Lissoceras* are recorded at the same level (Meledina, 1991). However, this warming is not marked by changes in paleothermometry (Fig. 1), although for the early Bajocian there is an increase in minimum temperatures. At the same time, records of glendonites in the lower Bajocian are fairly widespread. If an early Bajocian warming episode took place, then it was apparently very brief, and from the beginning of the late Bajocian (or rather from the very end of the early Bajocian), there are signs of significant cooling. In the late Bajocian, Central Asian immigrant species disappear from pollen assemblages, the diversity of ferns is reduced, the Lycopodiaceae become widespread, and as in the late Pliensbachian, sphagnoid mosses become abundant (Ilyina, 1985).

The ammonite faunas of the late Bajocian of Eastern Siberia were mainly represented by endemics, sometimes supplemented by immigrant taxa from the North Pacific (Meledina et al., 2005), and *Megaspheeroceras* on Franz Josef Land (Repin, 1999) appeared at this level. In the upper Bajocian deposits of Siberia, glendonites are unusually widespread and are found in the maximum number of Jurassic localities (Fig. 1). At the same time, glendonites are usually abundantly present in sections and are represented by morphologically diverse bodies, although their findings are often confined to several relatively narrow stratigraphic intervals. According to paleothermometry, the trend toward a decrease in the paleotemperatures from the Toarcian to the late Bajocian is clearly recorded (Fig. 1). Bajocian deposits in the Lena River basin often contain dropstones that Tuchkov (1973) interpreted as indicators of ice rafting. We have seen almost unrounded pebbles both in the upper Bajocian and in the lower Bathonian of the middle reaches of the Lena River. Their presence may be due to distribution by seasonal ice. The beginning of the Bathonian, owing to the significant warming of the climate, which was particularly noticeable in the southern regions, was marked by a significant restructuring of Siberian floras. In the south of Siberia, aridization of the climate also began at this time and later continued in the north of Eurasia throughout the Late Jurassic (Abbink et al., 2001; Hu et al., 2017). In the Kansk-Achinsk Basin, palynological records show an increased content of taxa inherent in the Western European and southern palynoflora and the appearance of *Classopollis* pollen. In the north of Eastern Siberia, warming was less significant, but this region is characterized by records of ferns spores *Marattisporites*, *Lophotriletes torosus* Sachs et Iljina, and occasional *Classopollis* (Ilyina, 1985). At the same time, because of the continuing isolation of the Arctic Basin, mollusk assemblages (primarily ammonites) remained relatively poor and were characterized by a high degree of endemism. The number of glendonites in comparison with the Bajocian decreased, and the size of these pseudomorphs in the Bathonian was on average less than in the Bajocian.

From the late Bathonian and especially Callovian, against the background of the boreal transgression, the climate in the south of Siberia became increasingly arid, while in the north of Siberia it remained largely humid and warm-temperate.

In the south of Western and Eastern Siberia, in conditions of a semiarid climate, coniferous trees with *Classopollis* pollen, which later, at the beginning of the Late Jurassic, became dominant in the flora of southern Siberia, became widespread. The increased aridization of the climate is indicated by the cessation of coal accumulation and the sedimentation at first of carbonate rocks and then variegated rocks in the Kansk-Achinsk Basin and in the south of the West Siberian Plain (Ilyina, 1985).

The upper Bathonian in the north of Siberia contains the first records of Subboreal cosmoceratids (Meledina et al., 1991), but the late Bathonian–Callovian was, nevertheless, sharply dominated by boreal cardioceratids. Only in Western Siberia are relatively infrequent finds of cosmoceratids recorded in all Callovian substages, and occasional finds of other Subboreal ammonites (Proplanulitinae) are also known (Alifirov and Meledina, 2010; Alifirov et al., 2016).

In the Callovian, glendonites became increasingly rare, and from the beginning of the Oxfordian, these pseudomorphs disappeared in the sections of Eastern Siberia. Ilyina (1985), who noted some discrepancy between the paleobotanical evidence of noticeable warming in the Callovian in the north of Siberia and the presence of glendonites, suggested that in this case the presence of glendonites may be associated with an increase in the depth of the basin during a transgression.

According to paleothermometry data, however, it is impossible to speak of any significant warming (Fig. 1), since the maximum temperatures increased, but the minimum temperatures became lower. Rather, it can be assumed that, owing to some warming, the seasonality of the climate increased at high latitudes, and because of a rising sea level, the temperature gradient between the near-bottom and near-surface waters could have increased.

Late Jurassic

In the Oxfordian, warming that began in the late Middle Jurassic continued. This time was marked by mass penetration of southern and western European plants into northern Siberia. This was associated with an increase in temperature against a background of aridization, which continued in Eurasia during the Late Jurassic. At the same time, in the east of Siberia, the climate remained humid, as evidenced by the maximum of Late Jurassic coal accumulation recorded at this time in the South Yakutian coal basin (Ilyina, 1985). *Classopollis* pollen (up to 12–20%) is noted in the lower Oxfordian palynological assemblages of the western coast of the Anabar Bay, and its content in the Ust-Yenisei region reaches 31%; the assemblages also contain Gleicheniaceae and Caytoniales (Ilyina, 1985). Thermophilic land palynomorphs are found in large numbers (up to 20% or more) in samples from the upper Oxfordian–Kimmeridgian of the deepest part of the Yenisei-Khatanga Strait (Nordvik Peninsula), and only at the very end of Kimmeridgian and in the Volgian did the amount of these palynomorphs decrease (Nikitenko et al., 2015). The Upper Jurassic deposits as a whole are characterized by a fairly widespread occurrence of glauconite (Kaplan, 1976). While in the Oxfordian Siberian ammonite faunas remained relatively impoverished and were characterized mainly by cardioceratids (and only in the lower reaches of the Lena River did they co-occur with Pacific Phylloceratida), in the Kimmeridgian, Subbo-

real Aulacostephanidae became widespread in the Yenisei-Khatanga Strait, which in shallow coastal facies (Boyarka and Kheta rivers) at some levels composed most of the ammonite assemblages (Mesezhnikov, 1984). North of East Taimyr, Aulacostephanidae were found only at some levels, whereas they were not found in the parts of the basin that were the deepest and most distant to the east toward the paleopole (Nordvik Peninsula). At the same time, uncommon Tethyan aspidoceratids migrated to the Subpolar Urals (Zakharov et al., 2005). The Kimmeridgian of the Nordvik Peninsula contains the northernmost occurrences of Jurassic calcareous nannoplankton (Rogov and Ustinova, 2018). In the early Kimmeridgian of the Nordvik Peninsula, thermophilic foraminifers appeared during a transgressive episode (Nikitenko et al., 2015). Later, during the Volgian, the biogeographic differentiation of marine biota gradually increased. A warming episode that continued in Siberia throughout the Late Jurassic is also supported by isotope data obtained in recent years from belemnite rostra (Dzyuba et al., 2013, 2018; Nunn, 2007; Price and Mutterlose, 2004; Žak et al., 2011; Zakharov et al., 2005, 2014). According to the palynological data from the Subpolar Urals, for the Jurassic-Cretaceous boundary beds, warming is recorded at the very end of the Volgian (Dzyuba et al., 2018). Glendonites are rare in the Upper Jurassic of Siberia; they are known in the lower Oxfordian, and recently unconfirmed glendonites were also found in the Kimmeridgian AH-3 Borehole drilled in eastern Taimyr; there are no glendonites in the Volgian Stage of Siberia. All these data agree well with the hypothesis of a relatively warm climate that prevailed in the Late Jurassic in the north of Siberia, whereas a slight cooling possibly began only at the end of the Volgian (Zakharov and Saks, 1980). It should be noted that the paleothermometry data obtained from the Ca/Mg ratios contradict data on the Late Jurassic climate obtained by other methods and show a long-term cooling from the late Toarcian to the Kimmeridgian (Fig. 1). This is consistent with the hypothesis that the Ca/Mg ratios in the molluscan shells is equivocally correlated with temperature and cannot be used with certainty as an indicator of paleotemperatures (Rosales et al., 2004; Wanamaker et al., 2008). In modern bivalves, the relationships between Ca/Mg and temperature are sensitive to salinity (Wanamaker et al., 2008) and to the season of shell growth and differ in the outer and inner shell layers (Schöne et al., 2013). At the same time, in the Nordvik section, the lowest paleotemperatures are recorded in the Oxfordian and Kimmeridgian. A slight decrease in temperature in the early Kimmeridgian, followed by a warming episode at the boundary of the early and late Kimmeridgian, which primarily led to an increase in temperature in the lower part of the water column against a background of almost unchanged mean temperatures (Colombié et al., 2018), is also recorded in Europe. At the same time, in different parts of the Arctic Basin,

warming and cooling episodes during the Kimmeridgian did not always coincide, which may be due to the circulation of water masses. Thus, on Spitsbergen, two episodes of warming can be identified in the early Kimmeridgian, as recorded by the strong prevalence of aulacostephanids in ammonite assemblages. At the boundary of the early and late Kimmeridgian, a cooling episode is recorded, suggested by the presence of glendonites and a sharp change in ammonite assemblages, completely lacking Subboreal Aulacostephanidae.

Early Cretaceous

At the beginning of the Cretaceous in Siberia, the climate gradually cooled, although in general it remained rather warm and humid. In the Subpolar Urals during the Ryazanian and Valanginian, the flora developed in a warm and humid climate, enabling the preservation of relict forms and promoting the profuse development of tropical ferns and thermophilic conifers (Golbert et al., 1972). At the beginning of the Early Cretaceous, the diversity of cycads and Bennettitales increased in the Lena River basin (Kiritchkova, 1985), and these groups remained abundant until the Aptian. The climate here changed gradually, which, according to Vakhrameev (1991), is supported by the wide distribution of coal. Ryazanian and Valanginian marine biota of Siberia was strongly dominated by taxa of Arctic origin, but some levels contained taxa close to or identical to those of Pacific origin. The rare records of the ammonite genus *Sachsia* (Himalayitidae) in the lower part of the Ryazanian on the Kheta River, as well as the Pacific species of heteromorph *Bochianites* in the Ryazanian and Valanginian of Northern Siberia (Rogov and Igolnikov, 2009; Shulgina, 1985; Zakharov et al., 2014), should be noted. Paleothermometry data confirm the decrease in seawater temperature at the beginning of the Cretaceous, both in the north of Eastern Siberia, which is in good agreement with the data on the distribution of glendonites, and to the west in the Subpolar Urals. The first, still rare glendonites appear at the top of the Ryazanian of Northern Siberia, becoming abundant at the end of the Valanginian (Rogov et al., 2017). During the Early Cretaceous in Siberia, the content of *Classopollis* pollen gradually decreased. In general, from the beginning of the Ryazanian to the Hauterivian, there is a gradual cooling with minimum temperatures at the Valanginian–Hauterivian boundary. This time interval was characterized by a decrease in the diversity of mollusks; benthonic faunas of the Hauterivian were dominated by the typical Boreal bivalves of the genus *Buchia*. In the Hauterivian–Barremian palynological assemblage of Western Siberia, the amount of *Classopollis* pollen becomes even more reduced compared with earlier assemblages, and in the Barremian, this pollen becomes very rare (Chlonova et al., 1990).

By the end of the Hauterivian, marine sediments are preserved only in Western Siberia, and the sea left

the region in the Barremian. During the Early Cretaceous Epoch, a gradual cooling was observed, which was apparently interrupted by minor early Aptian and early Albanian warming episodes, of which the first is recorded by flora, and the second by appearance of the ammonites *Archthoplites* (*Subarchthoplites*) and *Pseudopulchellia* and bivalves *Inoceramus anglicus* Woods in Western Siberia (Zakharov et al., 2000). Apparently, in the late Albian–early Cenomanian, the cooling reached a minimum (Vakhrameev, 1978). The appearance of redbeds in the upper Aptian lake sediments of the southwestern, southern, and southeastern parts of Western Siberia indicates aridity of the climate. The northern boundary of the arid zone in Western Siberia at this time shifted to the south compared with the early epochs of the Cretaceous period, and a relatively uniform humid regime was established in this region. The apparent zonality of the precipitation distribution, which is fixed from the late Valanginian to the early Aptian, was smoothed out in the late Aptian (Golbert, 1987). Information about the Albian climate is inconsistent. According to Golbert (1987), geological indicators clearly show that a very warm humid climate (close to the modern tropical) at the end of the Early Cretaceous was characteristic of almost the whole of Western Siberia up to the present Arctic Circle, which is confirmed by the greatest development of bauxite formation in the Meso-Cenozoic history of Siberia marked in this interval. The early–middle Albian flora is distinguished by the highest species diversity for the Cretaceous (about 100 species) (Golovneva, 2005). At the same time, the late Albian flora of the territory of Siberia is known only in the West Siberian region. In Eastern Siberia, most of the late Albian has a gap in sedimentation (Golovneva, 2005). The fossil flora of this age is known from adjacent regions, such as Kotelnii Island (Herman and Spicer, 2010; Kuzmichev et al., 2009, 2018). On the other hand, the cooling in the late Aptian–early Albian is confirmed by the wide distribution of glendonites in sediments of this age (including in the Northeast of Russia; see Rogov et al., 2017), in some cases encountered together with dropstones, interpreted as indicators of ice rafting (upper Aptian–lower Albian of Spitsbergen; see Dalland, 1977). Cretaceous glendonites are not found higher than the lower Albian, reappearing in the geological record only at the end of the Paleogene. The isotopic paleotemperature data for the Aptian–Albian Arctic are scarce. Several data points obtained from aragonite of ammonite shells have been published only for North Alaska and the Koryak Highlands (Zakharov et al., 2011) (Fig. 2).

Late Cretaceous

In Siberia, the climate during the transition from Early to Late Cretaceous changed insignificantly; only in Western Siberia in the Cenomanian there is a sharp shift of the areas of bauxite formation to the south,

which according to Golbert (1987) indicates some cooling and humidification of climate.

At the same time, massive coal accumulation, an increased carbonate content of siliciclastic rocks, and the formation of deposits of oolitic iron ores, as well as the widespread occurrence of kaolinite, indicate that a rather warm climate remained. Slightly south of the region under consideration (in Kazakhstan), gradual warming is recorded in the interval from the Albian to the Cenomanian according to the distribution of *Classopollis* pollen and analysis of angiosperm leaves by the CLAMP method (Herman, 2004; Herman et al., 2002; Vakhrameev, 1982). Cenomanian floras of Western Siberia are very close to late Albian in composition and ecological appearance, while the large thin leaves of most plants indicate significant humidity. In general, the climate of the southern part of Western Siberia in the Cenomanian can be considered as humid (Golovneva, 2005).² The Cenomanian floral assemblages of northern Eastern Siberia are markedly different from those described above: they are represented by plants of the Early Cretaceous type with an abundance of ferns, an almost complete absence of flowering plants, and the presence of cycadophytes, ancient ginkgoales, and conifers. At that time, the climate of southern Eastern Siberia remained warm and humid, as indicated by high species diversity, the prevalence of taxa with large leaves among flowering tree plants, and the presence of taxa with smooth-edged leaves (Golovneva, 2005). The Cenomanian marine deposits in the Ust-Yenisei Depression show the presence of the cosmopolitan species *Inoceramus pictus* Sow., as well as *Inoceramus* of Pacific origin. At the same time the ammonites *Placenticeras* and *Borissiakoceras* appeared in the West Siberian Basin (Zakharov et al., 2003). In the Turonian of Western Siberia, the number of plants with smooth-edged leaves decreased, and species with large leaves with a serrated edge prevailed; most taxa were deciduous, indicating a climate cooling. Among the Taxodiaceae, evergreen representatives of the genus *Sequoia* were replaced with shoot-shedding representatives of the genus *Taxodium* (Golovneva, 2005). Similar changes in the flora are also recorded in Eastern Siberia. In the north of Siberia (Kheta River basin), conifers were highly diverse and abundant, whereas flowering plants here were relatively rare. The dominance of Platanaeae and the morphology of leaves of flowering plants indicate a predominance of deciduous vegetation and a warm temperate humid climate (Golovneva, 2005). Even closer to the estimated paleopole, on New Siberia Island, according to CLAMP analysis of the Turonian flora, the climate was close to warm-temperate,

² The age of the Late Cretaceous floras of Western Siberia is debatable. According to Shchepetov (2018), flora which, according to Golovneva (2005), corresponds to the interval from the Albian to Maastrichtian belongs to the substantially narrower Albian–Cenomanian (? Turonian) stratigraphic interval.

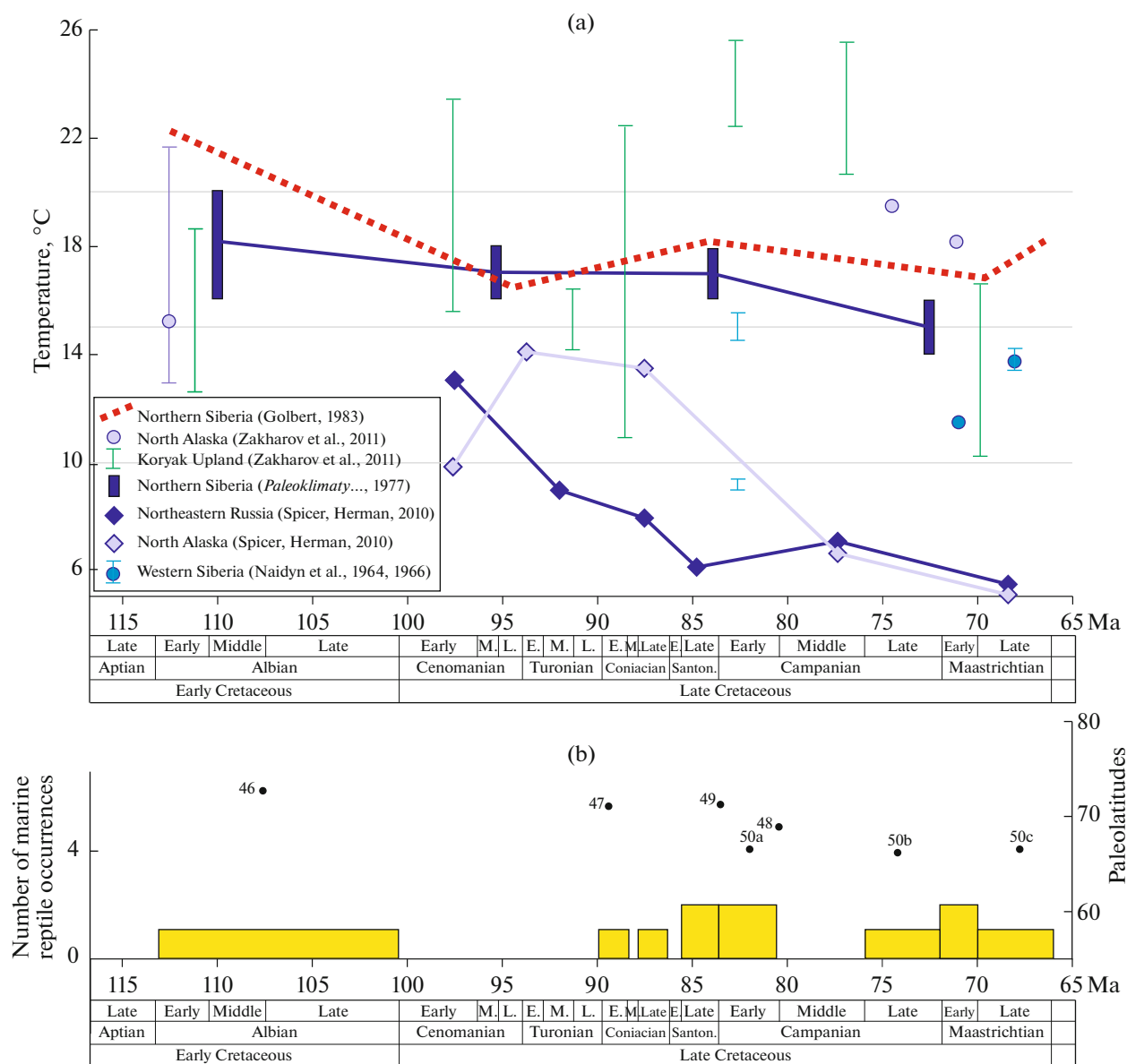


Fig. 2. Climate indicators of the second half of the Early Cretaceous and Late Cretaceous of Northern Siberia (a) and occurrences of marine reptiles (b).

with mean annual temperatures of $+9.2... \pm 2.2^{\circ}\text{C}$ (Herman and Spicer, 2010).

Vakhrameev (1978) attributed the Turonian cooling episode recorded in the flora of Western Siberia to the influence of a large transgression that involved the entire West Siberian lowland. In the Turonian marine biota, a number of events mainly related to the appearance of cosmopolitan taxa in Western Siberia among bivalves and foraminifers are established. At the same time, the Cenomanian–Turonian boundary interval coinciding with the maximum warming was followed by a relative cooling during the middle to late Turonian (Zakharov et al., 2003). The oxygen isotope composition in the molluscan shells of the Turonian of

Ust-Yenisei Depression was extensively studied, but any conclusions about the paleotemperature of water based on these measurements have not been made, and low $\delta^{18}\text{O}$ values were interpreted as a result of the salinity decrease (Naidyn et al., 1978; Teis et al., 1978).

The results obtained later in separate analysis of calcite and aragonite parts of belemnite rostra (Naidyn et al., 1978) also show $\delta^{18}\text{O}$ values corresponding to clearly elevated temperatures (Table S1³), which may be due to both the effect of salinity decrease and the

³ Additional materials for the Russian-language online version of the article are available at <https://journals.eco-vector.com/0869-592X>, and for the English version at <https://link.springer.com/journal/volumesAndIssues/11506>.

water isotopic composition in the West Siberian basin. The Turonian cooling episode is also established by analyzing the floras of Northeast Asia, and it is especially pronounced in a decrease in the mean annual temperature and temperature of the coldest month (Herman, 2004; Spicer and Herman, 2010). In the Coniacian–Campanian, climatic conditions in general remained close to those of the Cenomanian–Turonian, but in some places, signs of some decrease in humidity are recorded. Short-term relatively warm intervals in the Coniacian–Campanian time can be assumed from the occurrences of thermophilic bivalve mollusks *Pycnodonte* and *Lopha* on the Usa River in the upper parts of the Coniacian and in the terminal Santonian (Marinov et al., 2002). The Campanian flora of Western Siberia is characterized by small leaf sizes, which correspond to a certain aridization of the climate observed during the Santonian–Campanian in most of North Asia. However, the warming of the climate that occurred at that time on Sakhalin and in the Anadyr–Koryak region and was generally recorded in the Campanian (Vakhrameev, 1978) did not manifest itself in this region (Golovneva, 2005). Small leaves, associated with an increase in aridity of climate, are recorded in the Santonian–Campanian flora of the Vilyui Depression. In northern Siberia, the Santonian–Campanian boundary beds are mainly dominated by platanaceous genus *Arthollia* and species of the genus *Trochodendroides* and *Sequoia* (Taxodiaceae) (Golovneva, 2005). The abundance of large leaves of *Pseudoprotophyllum*, represented by the same species as in the Turonian of the Khatanga Depression, indicates the preservation of a humid warm-temperate climate in the north of Siberia in the late Santonian–early Campanian (Golovneva, 2012). In the Coniacian–Campanian, warming recorded in the northeast of Western Siberia (Marinov et al., 2008) was replaced by a brief cooling in the late Campanian (Zakharov et al., 2003). For this matter, paleotemperature determinations obtained from belemnites from the “Pterium beds” in the basal Campanian from the Synya River seem to be interesting (Naidyn et al., 1966). The paleotemperatures are determined at 9.1–9.3°C (for the rostra of *Paractinocamax*) and 14.4–15.6°C (for the rostra of the small *Actinocamax*), which is probably due to differences in the lifestyle of these belemnites (Naidyn et al., 1966; Teis and Naidyn, 1973). A late Campanian (?) cooling episode is also recorded in Arctic Canada (Super et al., 2018).

The Campanian–Maastrichtian boundary in northern Western Siberia lies in a uniform siliciclastic sandy-silt series. The Maastrichtian succession of the Tanama River shows no signs of carbonate deposition. The northernmost sections, containing carbonate rocks of this age, were opened by boreholes in the latitudinal reaches of the Ob River, related to the influence of warm water input through the Turgai Strait, which opened up during the Maastrichtian. A warming episode in the early Maastrichtian of Western

Siberia was reported by Marinov et al. (2008). For the southern part of Western Siberia (Ayat River), there are several determinations of the oxygen isotopic composition from belemnite rostra. The values of 11.6°C were obtained for the early Maastrichtian and 13.5–15.2°C for the late Maastrichtian (Naidyn et al., 1964).

OVERVIEW OF THE OCCURRENCES OF MARINE REPTILES IN THE JURASSIC AND CRETACEOUS OF SIBERIA

Remains of marine reptiles have been reported regularly from the Mesozoic of Siberia: during geological surveys, prospecting, and other works, researchers often found remains of “saurs” and “gigantic saurians,” while indicating finds of both isolated bones and skeletons. Unfortunately, only a few of these reported finds were collected and transferred to museums, most of them remained at the place of detection, and only records in field diaries and cursory references in the literature have remained (Fig. 3; Table 1).

Table 1 and Fig. 3 summarize all available information on the findings of marine reptiles in the Jurassic and Cretaceous of Siberia. Most finds come from the Pliensbachian–Bajocian interval; information about them was obtained mainly through the works of Mener (1948) and, to a greater extent, Kirina (1966, 1976), as well as the observations of V.G. Knyazev and V.P. Devyatov (Knyazev, pers. comm.; Knyazev et al., 1991, 2003). Isolated occurrences are recorded by Bidzhiev and Minaeva (1961), Tuchkov (1973), and Melendina et al. (1978). There are no data on marine reptile finds from the Bathonian–Callovian of Siberia.

Marine reptiles reappear in the fossil record of Siberia in the Late Jurassic. At the same time, only single occurrences are recorded in the Oxfordian and Kimmeridgian (Table 1). Several finds are known from the Volgian, the first of which (plesiosaur vertebra and coracoid) was described at the beginning of the last century (Jakowlew, 1903). Later, in 1961, an ichthyosaur vertebra was found by Zakharov in the middle Volgian succession on the Dyabaka-Tara River (Taimyr). Subsequent discoveries of remains of ichthyosaurs and plesiosaurs were made only recently by Rogov (Table 1). It is important to note a few finds from the base of the Lower Cretaceous. For example, Ryabinin (1939) mentioned a skeleton of a plesiosaur from the “Valanginian” (that is, in the modern sense, either Ryazanian or Valanginian) of the Polar Urals. Efimov (2006) mentioned the discovery of ichthyosaur remains on the Anabar River; Sachs et al. (1963) also recorded vertebrae of marine reptiles in the Valanginian of the Anabar basin.

In younger Cretaceous deposits, finds of marine reptiles are distributed sporadically. There is one discovery from the Albion of Uyedineniya Island (Ryabinin, 1939), two vertebrae from the lower Coniacian of the Yangoda River (Zakharov et al., 1989), bones from

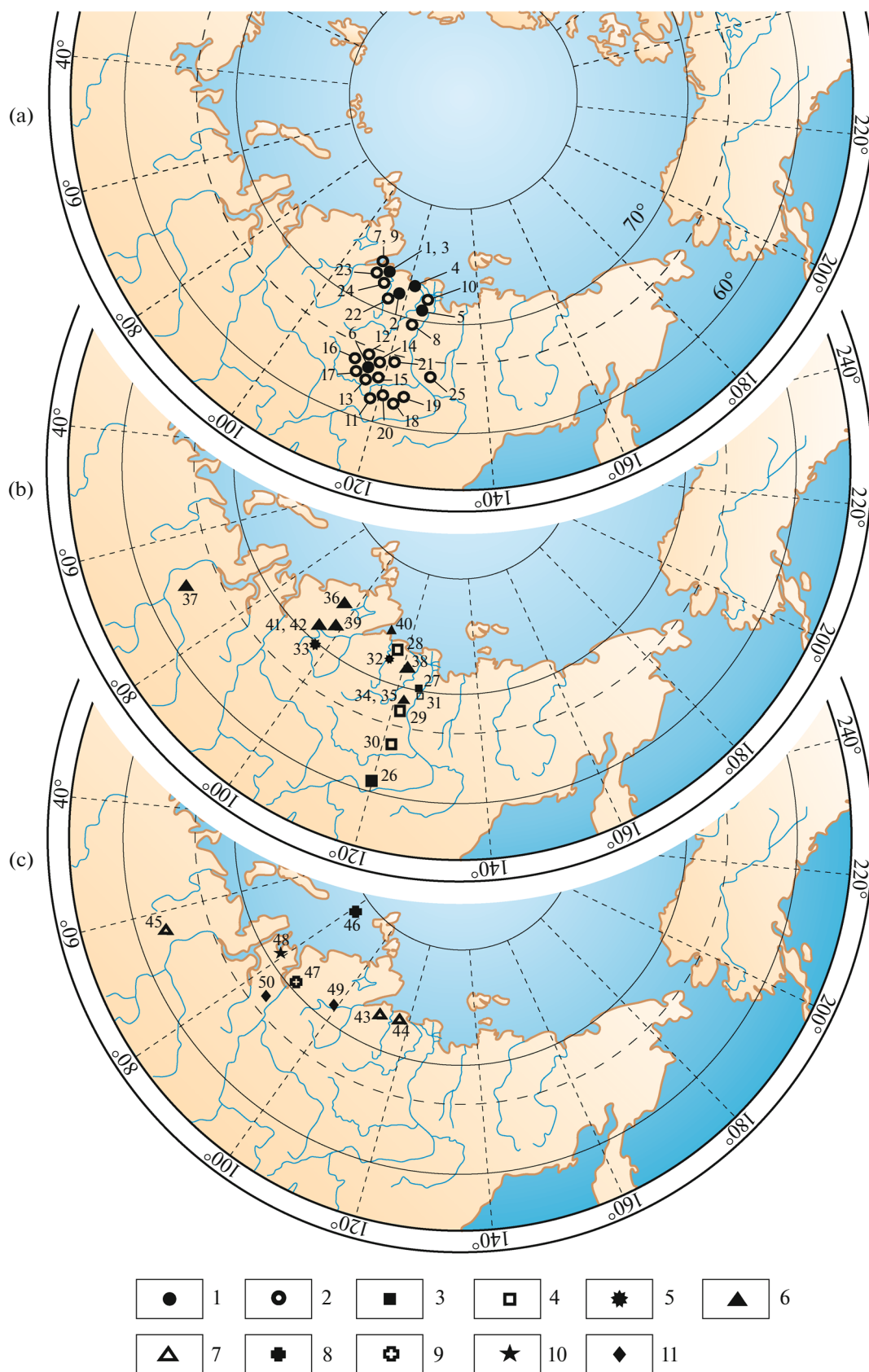


Fig. 3. Localities of marine reptiles in the Early Jurassic (a), Middle–Late Jurassic (b), and Cretaceous (c). Legend: (1) Hettangian–Pliensbachian, (2) Toarcian, (3) Aalenian, (4) Bajocian, (5) Oxfordian–Kimmeridgian, (6) Volgian, (7) Ryazanian–Valanginian, (8) Albian, (9) Coniacian, (10) Turonian–?Maastrichtian, (11) Santonian–Maastrichtian.

Table 1. Finds of remains of marine reptiles in the Jurassic and Cretaceous of Siberia

Locality no.	Age	Geographic location	Modern coordinates	Paleolatitude (N)*	Herpetofauna		References; repository and specimen number if available
					Original identification	Emended identification	
1	Hettangian—lower part of upper Pliensbachian (Zimnyaya Formation)	Anabar Bay (Outcrop 5, Beds 18, 20, 29, 54)	73.31487 N 113.16558 E	73.4	Bones and vertebrae of reptiles	Reptilia indet.	Knyazev et al., 1991; Knyazev, pers. comm.
2	Hettangian, lower substage	Olenek River basin, Kyra-Khos-Teryuttek River	71.7793 N 120.8922 E	73.6	Bones and vertebrae of reptiles; ichthyosaur vertebrae (identifications by S.M. Kurzanov)	Ichthyosauria indet.	Knyazev, pers. comm.; Devyatov, 1985
3	Pliensbachian, upper substage	Anabar River	73.08663 N 112.9614 E	79.8	Bones and vertebrae of reptiles	Reptilia indet.	Knyazev, pers. comm.
4	Pliensbachian, upper substage	Olenek River basin, Kelinyar River (loc. 7)	72.5545 N 122.4756 E	78.1	Vertebrae of reptiles	Reptilia indet.	Knyazev, pers. comm.
5	Pliensbachian, upper substage	Left bank of the Lena River between the villages of Dzhardan and Govorovo	70.2446 N 125.2661 E	78.2	Plesiosaur vertebrae	Plesiosauria indet.	Bidzhiev and Minaeva, 1961
6	Pliensbachian, upper substage (“Domerian clay member”)	Vilyui River basin, Tenkensakaya Nyuchuku River, Outcrop 12	61.9545 N 116.6268 E	83.6	Ichthyosaurs and plesiosaurs	Ichthyosauria indet., Plesiosauria indet.	Kirina, 1966
7	Toarcian, lower substage	Nordvik Peninsula (Yuryung-Tumus)	73.89811 N 110.52246 E	79.5	Dorsal vertebra similar to <i>Plesiosaurus robustus</i>	Plesiosauria indet.	Ryabinin, 1939; <i>Stratigrafiya...</i> , 1972
8	Toarcian	Molodo River, 2.5 km downstream of the mouth of the Muogdan River	69.68264 N 123.55466 E	86.1	Marine reptile vertebrae	Reptilia indet.	Devyatov, 1983
9	Toarcian, lower substage	Yuryung-Tumus Peninsula	73.89811 N 110.52246 E	84.3	Remains of plesiosaurs, a rib of Plesiosauridae	Plesiosauria indet.	Kalinko, 1953
10	Toarcian	Left bank of the Kelimyar River, 3.5 km south of the mouth of the Hotugu-Muyokanda-Yurege River	71.35149 N, 125.75580 E	84.9	Ichthyosaur vertebrae	Ichthyosauria indet.	Meledina et al., 1978

Table 1. (Contd.)

Locality no.	Age	Geographic location	Modern coordinates	Paleolatitude (N)*	Herpetofauna		References; repository and specimen number if available
					Original identification	Emended identification	
11	Toarcian, lower substage	Right bank of the Vilyui River, at the mouth of the Iligira (Ulgir) River, 30 km upstream of the village of Suntar	61.91617 N 117.24150 E	83.5	Isolated fragments of <i>Eretmosaurus rzasnickii</i> Menner, <i>Eretmosaurus (?) jakowlewi</i> Menner	Plesiosauria indet.	Menner, 1948; Kirina, 1966
12	Toarcian, ? lower substage	Mouth of the Couture-Yuryah River, Markha Gorge (Outcrop 9)	64.26977 N 116.39572 E	85.9	Isolated fragments of <i>Eretmosaurus rzasnickii</i> Menner	Plesiosauria indet.	Menner, 1948
13	Toarcian, lower substage	Markha River, 7 km downstream of the village of Ulahan-Kyuel (Outcrop 16–19)	63.84607 N 116.52285 E	85.5	Limb bones of large plesiosaurs	Plesiosauria indet.	Kirina, 1966
14	Toarcian, lower substage	Markha River, downstream of the mouth of Sobo Creek (Outcrop 9)	64.26977 N 116.39572 E	85.9	Reptiles bone	Reptilia indet.	Kirina, 1966
15	Toarcian, lower substage	Namana River	61.50634 N 120.38496 E	82.7	Fragment of a plesiosaur propodium	Plesiosauria indet.	Menner, 1948
16	Toarcian, lower substage (16a), upper substage(16b)	Basin of the Vilyui River, Markha River	63.6 N 116.5 E	81.9	Remains of plesiosaurs and ichthyosaurs	Plesiosauria indet., Ichthyosauria indet.	Kirina, 1966; Nesov et al., 1988
17	Toarcian, upper substage	Basin of the Vilyui River, Ygyatta River	63.38410 N 115.73305 E	85.1	Remains of plesiosaurs and ichthyosaurs	Plesiosauria indet., Ichthyosauria indet.	Kirina, 1966; Nesov et al., 1988
18	Toarcian, lower substage	Sinyaya River, Outcrop 53	62.00305 N 124.28066 E	82.4	Plesiosaur bones	Plesiosauria indet.	Kirina, 1966
19	Toarcian, upper substage	Sinyaya River	62.00305 N 124.28066 E	82.4	Plesiosaurs	Plesiosauria indet.	Kirina, 1966
20	Toarcian, upper substage	Vilyui River	61.9 N 117.37 E	83.5	Plesiosaurs and ichthyosaurs	Plesiosauria indet., Ichthyosauria indet.	Kirina, 1966
21	Toarcian, lower substage	Vilyui River basin, Tyung River, Outcrops 26, 28, 29, 31	65.59725 N 119.28390 E	86.6	Plesiosaur remains	Plesiosauria indet.	Kirina, 1966; Nesov et al., 1988
22	Toarcian, lower substage	Anabar River	72.05531 N 113.93715 E	86.2	Ichthyosaur teeth, sea turtle bones <i>Chelonia</i> sp. (identifications by S.M. Kurzanov)	Ichthyosauria indet. ?Testudinata indet.	Knязев et al., 1991

Table 1. (Contd.)

Locality no.	Age	Geographic location	Modern coordinates	Paleolatitude (N)*	Herpetofauna		References; repository and specimen number if available
					Original identification	Emended identification	
23	Toarcian, lower substage (23a), upper substage (23b)	Anabar Bay	73.44531 N 113.17315 E	84.8	Giant reptile bones	Reptilia indet.	Knyazev et al., 2003; V.G. Knyazev, pers. comm.
24	Toarcian, upper substage	Anabar Bay	73.31487 N 113.16558 E	84.9		Cervical vertebra of a plesiosaur, Plesiosauria indet.	Collected by M.A. Rogov, 2008 (SGTU MEZ, no. 4/121 ¹)
25	Toarcian—Aalenian (?)	To the north of the Baybykan River, on the Dorukchan River	64.21892 N 130.34969 E	82.3	Bones and skeletons of plesiosaurs and ichthyosaurs	Plesiosauria indet., Ichthyosauria indet.	Kirina, 1976
26	Aalenian Stage, ? lower substage	Right bank of the Vilyui River downstream of the mouth of the Ilgir River	61.91617 N 117.24150 E	80.2	Fragments of vertebral columns of <i>Eretmosaurus</i> sp.	Plesiosauria indet.,	Kirina, 1966
27	Aalenian Stage, lower substage	Left bank of the Molodo River, 5 km downstream of the mouth of the Syugyude River	69.22141 N 123.03859 E	84.6	Fragment of vertebral column of a plesiosaur; vertebra of large plesiosaurs and ichthyosaurs	Plesiosauria indet., Ichthyosauria indet.	Bidzhiev and Minaeva 1961; <i>Stratigrafiya</i> ..., 1976
28	Bajocian Stage	Anabar Bay, Bus-Khaya	73.17590 N 113.68652 E	80.3	<i>Plesiosaurus</i> sp., reptile bones	Plesiosauria indet.	Yemelyantsev, 1954; V.G. Knyazev, pers. comm.
29	Bajocian Stage	Zhigansk area	66.77459 N 123.32153 E	84.8	Reptile bones	Reptilia indet.	Tuchkov, 1973
30	Bajocian Stage	Vilyui River basin, mouth of the Tyung River	63.77012 N 121.54607 E	82.8	Ichthyosaur bones	Ichthyosauria indet.	Nesov et al., 1988; age emended according to (<i>Stratigrafiya</i> ..., 1976)
31	Bajocian Stage, lower substage	Molodo River basin	69.22141 N 123.03859 E	84.6	Saurian bones	Reptilia indet.	<i>Stratigrafiya</i> ..., 1976
32	Oxfordian Stage, lower substage	Anabar River basin, Polovinnaya River	72.53473 N 114.29077 E	80.5	Fragments of a plesiosaur skeleton	Plesiosauria indet.	M.A. Alekseeva, V.G. Knyazev, pers. comm.

Table 1. (Contd.)

Locality no.	Age	Geographic location	Modern coordinates	Paleolatitude (N)*	Herpetofauna		References; repository and specimen number if available
					Original identification	Emended identification	
33	Kimmeridgian Stage	Levaya Boyarka River (Outcrop 23)	70.3419 N 97.1829 E	74.8		Ichthyosaur vertebra Ophthalmosauridae indet.	Collected by M.A. Rogov, 2014 (SGTU MEZ, no. 4/122)
34	Volgian Stage, ? middle substage	north of Zhigansk, Tungus-Apata River, near the Khoronko Station	67.77603 N 122.56348 E	78.3	Vertebra and coracoid of a plesiosaur	Plesiosauria indet.	Jakowlew, 1903; Nesov et al., 1988
35	Volgian Stage, lower substage	Cis-Verkhoyansk Trough, Sogoruu-Sasarangnaan and Ogonn-yor-Yurege rivers	68.43151 N 123.17871 E	78.9	Pliosaur vertebrae	Pliosauridae indet.	Bidzhiev and Mikhailov, 1966
36	Volgian Stage, middle substage	Byrranga Mountains, Dyabaka-Tari River	74.10932 N 97.56308 E	74.4	Ichthyosaur vertebra	Ichthyosauria indet.	Zakharov, 1981; collected by V.A. Zakharov
37	Volgian Stage, middle substage	Aprelevskaya-10 Borehole	62.5 N 69.0 E	55			Collected by I.V. Panchenko
38	Volgian Stage	Olenek River Basin	72.10094 N 123.17871 E	80.7	Remains of marine reptiles	Reptilia indet.	<i>Stratigrافيya...</i> , 1972
39	Volgian Stage, middle and upper substages	Levaya Boyarka River (Outcrop 23)	70.570 N 97.306 E	72.7		Part of the spinal column of Ichthyosauria indet.	Collected by M.A. Rogov, 2014 (SGTU MEZ, no. 4/125)
40	Volgian Stage, middle and upper substages (?)	Urdyuk-Khaya Cape	73.87060 N 113.16783 E	78.4	Ichthyosaurs, plesiosaurs	Ichthyosauria indet., Plesiosauria indet.	Zakharov, 1981; Iljina, 1985; A.S. Alifirov, pers. comm.
41	Volgian Stage, upper substage	Kheta River, Outcrops 18–19 (after Sachs et al., 1969)	70.54938 N 95.3228 E	72.1		Incomplete ichthyosaur skeleton, family Ophthalmosauridae	Collected by M.A. Rogov, 2015
42	Volgian Stage, upper substage	Kheta River, 4 km from Outcrop 18–19	70.53750 N 95.42722 E	72.1		Tooth crown of Thalassophonea indet.	Collected by M.A. Rogov, 2015 (TsNIGRI/13307)
43	Valanginian Stage, lower substage	Anabar River, mouth of the Kharabyl River	72.82344 N 113.14541 E	70.0	Saurian vertebrae	Reptilia indet.	Saks et al., 1963

Table 1. (Contd.)

Locality no.	Age	Geographic location	Modern coordinates	Paleolatitude (N)*	Herpetofauna		References; repository and specimen number if available
					Original identification	Emended identification	
44	Valanginian Stage	Anabar River, village of Yuryung-Khaya	72.8108 N 113.2321 E	70.0	Fragments of a skull of the ichthyosaur <i>Yasykovia</i> sp.	Ichthyosauria indet.	Efimov, 2006; Efimov and Efimov, 2011 (?UPM no. 1351)
45	Valanginian or Ryazanian (?) Stage	Syortynya River, Subpolar Urals	64.15895 N 60.64398 E	51 ²	Fragments of a plesiosaur skeleton	Plesiosauria indet.	Ryabinin, 1939
46	Albian Stage	Uyedineniya Island	77.49461 N 82.46338 E	72.4	Remains of <i>Plesiosaurus latispinus</i> Owen	Elasmosauridae indet.	Ryabinin, 1939; Saks, Ronkina, 1957; age emended according to Samoilovitch et al., 1981 (TsNIGRI/5926)
47	Coniacian Stage, lower substage	Yangoda River (Dzhagoda), right tributary of the Agapa River, basin of the Pyasina River	70.87972 N 88.41973 E	70.8	Vertebra of plesiosaurs of the families Elasmosauridae and Polycotylidae	Elasmosauridae indet., Polycotylidae indet.	Zakharov et al., 1989
48	Turonian – Maastrichtian stages	Tanama River, left tributary of the Yenisei River, Sigirte-Nago Gorge (Outcrop 7)	70.38951 N 80.38766 E	68.4	Remains of mosasaurs and ichthyosaurs	Mosasauridae indet.	Zakharov et al., 1986; Zakharov et al., 2003
49	Upper Santonian – lower Campanian	Kheta River, scree in the type section of the Mutino Formation	71.678758 N, 100.246350 E	70.9		Plesiosauria indet., proximal fragment of the femur, pectoral vertebra and other bone fragments	Collected by M.A. Rogov, 2015 (SGTU MEZ, no. 4/123, no. 4/124); age after Khomentovsky et al., 1999
50a, b, c	Campanian (a, b), Maastrichtian (c)	Bolshaya Laida River	68.82806 N 84.77202 E	66.3	Remains of large reptiles	Reptilia indet.	Marinov and Sobolev, 2006

* Paleolatitudes are from paleolatitude.org (van Hinsbergen et al., 2015).

¹ Material from this work is housed in the collection of the Saratov State Technical University.² Not shown in Fig. 3.



Fig. 4. Photographs of the marine reptile remains at their localities (collected by M.A. Rogov). (a) Plesiosaur cervical vertebra, Anabar Bay, Eren Formation, upper Toarcian; (b) pliosaur tooth in a concretion, Kheta River, Outcrop 23, upper Volgian, Oken-sis Zone; (c) part of the vertebral column and ribs of an ichthyosaur in a concretion, Levaya Boyarka River, middle-upper Vol-gian, scree; (d) ichthyosaur vertebrae and rib in a concretion, Kheta River, Outcrops 18–19, upper Volgian, Okensis Zone.

the Turonian–Maastrichtian deposits on the Tanama River (Zakharov and Khomentovsky, 1989; Zakharov et al., 1989), bones from the Campanian–Maastrich-tian deposits of the Bolshaya Laida River (Marinov and Sobolev, 2006), and fragments of plesiosaur bones from the Santonian–Campanian Mutino Formation on the Kheta River (this paper).

DESCRIPTION OF SOME NEW FINDS OF MARINE REPTILES FROM THE JURASSIC AND CRETACEOUS OF SIBERIA

During the field work in the Anabar Bay in the summer of 2008 in the Eren Formation (Toarcian), M.A. Rogov found an isolated cervical vertebra of a plesiosaur (Fig. 4a). The vertebral centrum has a cylindrical shape; articular surfaces are circular in outline, with width exceeding height (ratio of 0.8). The length of the centrum is comparable to its height (Figs. 5a–5c). Bipartite facets for the ribs are present. The neural arch is fused to the centrum without a visible suture; however, a distinct lateral ridge can be observed in the place

of their supposed articulation (Fig. 5b). This vertebra can be identified as Plesiosauria indet.

An isolated vertebra from a caudal region of a medium-sized ichthyosaur was found by M.A. Rogov in 2014 on the Levaya Boyarka River (Outcrop 23 (Sachs et al., 1969)) in a loose concretion of Kimmeridgian age, although an early Volgian age cannot be excluded. This vertebra is significantly shortened and is characterized by rounded outlines of articular surfaces, tapering in the upper part, giving it a slightly pear-shaped outline (Fig. 5d), which is observed in Ophthal-mosauridae (McGowan and Motani, 2003; Moon and Kirton, 2016). Similar vertebrae were described by Ryabinin (1912) from the Kimmeridgian of the Pechora region. The Volgian deposits of the Levaya Boyarka River (Outcrop 23) contained a nodule fragment with a partly preserved vertebral column and ribs of a small ichthyosaur (Fig. 4c). This finding cannot be identified more precisely than Ichthyosauria indet.

In 2015, M.A. Rogov found remains of marine reptiles in the Upper Volgian deposits on the Kheta

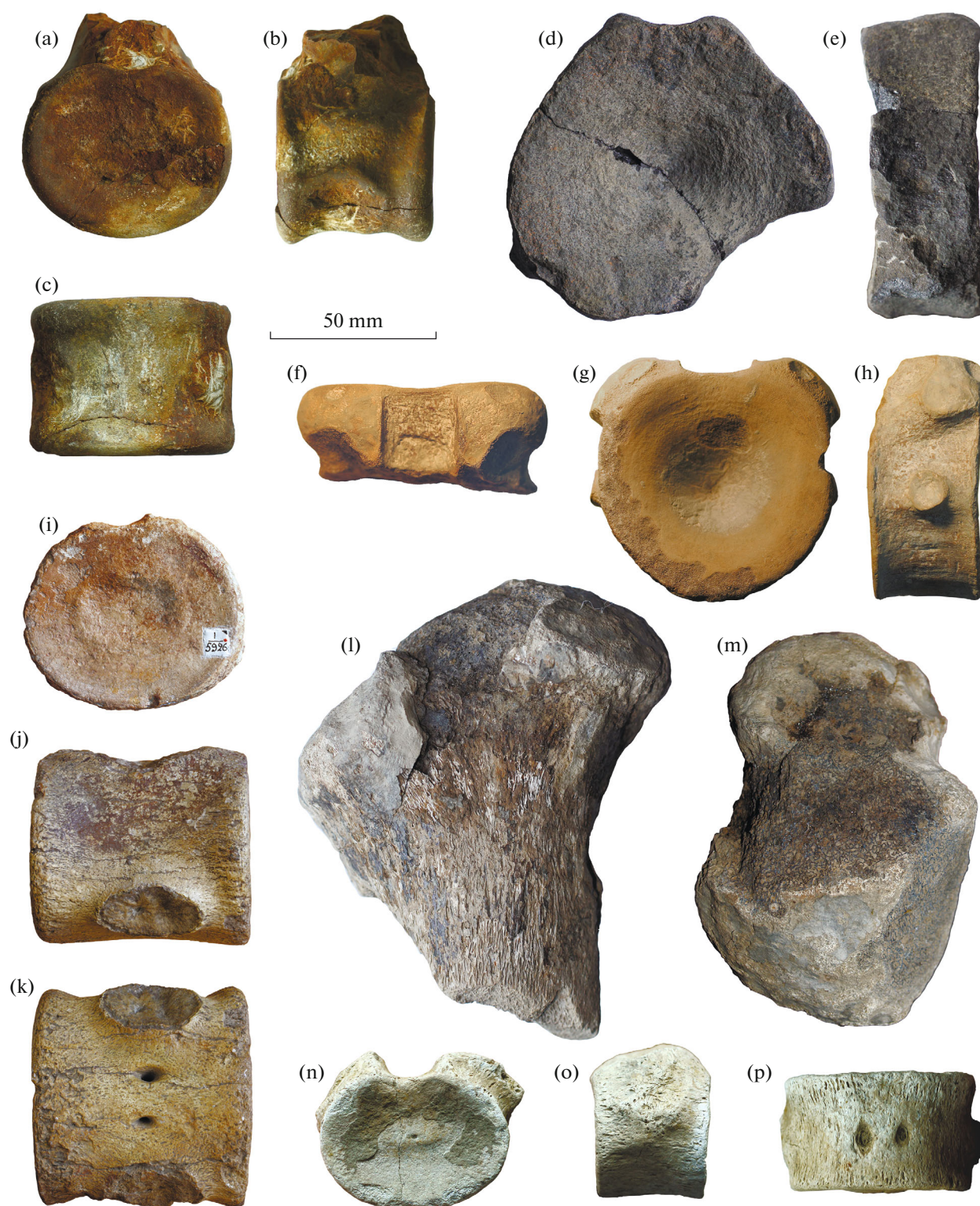


Fig. 5. Remains of marine reptiles. (a–c) Plesiosauria indet., cervical vertebra of a medium-sized plesiosaur, SSTU MEZ, no. 4/121, Anabar Bay, Eren Formation, upper Toarcian, collected by M.A. Rogov (see also Fig. 4a); (d, e) Ichthyosauria indet., caudal vertebra, SSTU MEZ, no. 4/122, Levaya Boyarka River, Outcrop 23, Kimmeridgian, collected by M.A. Rogov; (f–h) Ichthyosauria indet., anterior presacral vertebral centrum, Dyabaka-Tara River, middle Volgian, collected by V.A. Zakharov; (i–k) cervical vertebra of the plesiosaur Elasmosauridae indet., CNIGR 1/5926, Uyedineniya Island, Albian (see Ryabinin, 1939); (l, m) the proximal part of the femur of a large plesiosaur, specimen MSTU MEZ 4/124, Kheta River, scree in the stratotype of the Mutino Formation, Santonian–Campanian, collected by M.A. Rogov; (n, p) pectoral vertebra of a small-sized plesiosaur Elasmosauridae indet., specimen SSTU MEZ, no. 4/123, Kheta River, scree in the stratotype of the Mutino Formation, Santonian–Campanian, collected by M.A. Rogov.

River: a tooth of the pliosaurid *Thalassophonea* indet. (Fig. 4b; Zverkov et al., 2018) and ichthyosaur bones (Fig. 4d), enclosed in massive concretions. Their description will be published elsewhere after preparation and detailed study.

An isolated ichthyosaur vertebral centrum was found by V.A. Zakharov in 1961 on the Dyabaka-Tara River in the middle Volgian deposits (Dorsoplanites maximus–Taimyrosphinctes excentricus ammonite zones; *Buchia taimyrensis* Zone; see Zakharov, 1981). This centrum (Figs. 5f–5h) belongs to the anterior part of the vertebral column, as evidenced by the characteristic position of the rib facets: the diapophyses are merged with the facets of the neural arches and the anterior edge of the vertebra; the parapophyses are separated and located in the middle of the height of the vertebra (Fig. 5h). This vertebra is very similar in shape to those of *Arthropterygius* sp. (Zverkov et al., 2015, figs. 5e, 5f); however, this form of the anterior presacral vertebrae is characteristic of most of the Middle to Late Jurassic and some Early Jurassic ichthyosaurs; therefore, the finding cannot be determined more accurately than *Ichthyosauria* indet.

M.A. Rogov found fragments of plesiosaur bones in the scree of the type section of the Mutino Formation (Santonian–Campanian). The proximal part of the femur of a relatively large plesiosaur is fairly well preserved (Figs. 5f–5h). The head of the bone is rounded and convex, which indicates a mature animal. The dorsal tuberosity is rather well developed and also has rounded outlines; however, it is not completely detached from the head by the zone of the cortical bone. This bone could equally belong to *Elasmosauridae* or *Polycotylidae* widely distributed in the Late Cretaceous; similar characteristics are also observed in some more primitive plesiosaurs; for this reason, we identify the specimen as *Plesiosauria* indet. A pectoral vertebra of a small plesiosaur (Figs. 5i–5k) was also found in this locality. It is characterized by a proportionally small length and flat articular faces (platyclous type). At the same time, the width of the articular surface exceeds its height, giving it an oval shape (ratio of 0.73). Such proportions are characteristic of *Elasmosauridae*, which allows this vertebra to be identified as *Elasmosauridae* indet. This vertebra is of special interest, indicating the presence of small-sized and presumably young plesiosaurs along with large individuals at high latitudes during the Campanian–Maastrichtian (see the discussion below).

MARINE REPTILES AS CLIMATE INDICATORS

In the past two decades, a lot of new data on Mesozoic marine reptiles have been published, which made it possible to substantially change the views not only on their evolution but also on many aspects of their biology. The most important discoveries include evidence supporting high metabolic rates in the majority

of advanced representatives of the main groups of marine reptiles (ichthyosaurs, plesiosaurs, and mosasaurs) (Bernard et al., 2010; Harrell et al. 2016; Motani, 2010).

The first hypotheses about high metabolic rates in Mesozoic marine reptiles were made in the last century (Buffrénil and Mazin, 1990), but only recently the convincing evidence supporting earlier suggestion was obtained. For example, an analysis of the stable isotope $\delta^{18}\text{O}$ in the teeth of ichthyosaurs and plesiosaurs showed that the calculated temperature of their bodies could have ranged from 35 ± 2 to $39 \pm 2^\circ\text{C}$, which coincides with the temperature of modern cetaceans (Bernard et al., 2010). Similar calculations for mosasaurs demonstrated that the mean temperature of various members of this group ranged from 33.1 to 36.3°C , which did not depend on the estimated body mass of the animals. The latter suggests that these reptiles were endothermic, rather than gigantothermic as was previously thought (Bernard et al., 2010; Harrell et al., 2016; Motani, 2010).

The histology of the fossil bones of marine reptiles also supports their active metabolic rate. According to the highly vascularized fibrolamellar bone and the widely spaced cyclical growth marks, juvenile plesiosaur individuals had high growth rates at which a significant increase in the size of the animal occurred during the first year of life (Wintrich et al., 2017a); furthermore, the calculations of the resting metabolic rate of plesiosaurs demonstrates values in the range of birds (Fleischle et al., 2018). Additionally, recently studied patterns of blood circulation can support hypotheses of rapid growth and active metabolism of plesiosaurs (Wintrich et al., 2017b). Similar data on rapid growth rates based on well vascularized fibrolamellar bone structure were obtained for ichthyosaurs (Houssaye, 2013; Houssaye et al., 2014).

Although for ichthyosaurs viviparity was established more than a century ago, for plesiosaurs and mosasaurs, evidence for giving birth to live young was obtained only relatively recently, whereas for all these groups a transition to viviparity is supposed to take place from the early stages of adaptation to life in water. It has also been suggested that viviparity could have developed as a preadaptation in the terrestrial ancestors of some marine reptiles (Field et al., 2015; O’Keefe and Chiappe, 2011; Motani et al., 2014). It is still unclear whether the marine reptiles migrated to give birth to live young in any breeding ground. The assumption that some plesiosaurs were born in high-latitude seas is confirmed by the findings of remains of very small and supposedly young plesiosaurs in high-latitude localities (Campbell et al., 2013; Kear, 2007; Martin, 2002; Martin et al., 2007; Vavrek et al., 2014). This is also supported by our data (specimen SGTU MEZ 4/124). Given the rapid growth in the early ontogenetic stages established for plesiosaurs (Wintrich et al., 2017a), it is more likely that these reptiles could have been born in

high latitudes, rather than young individuals traveling there at an early age from low-latitude regions. Marine reptile assemblages have also been described from high-latitude and, judging by the abundance of glendonites, apparently cold-water Upper Aptian deposits of Australia (Kear, 2006a, 2006b) and Arctic Canada (Vavrek et al., 2014). It remains unclear whether they lived permanently in cold waters of high latitudes or made seasonal migrations like cetaceans (Mate et al., 2015; Rasmussen et al., 2007; Stevick et al., 2010). Nevertheless, for some marine reptiles, there is evidence on wide ranges covering both low and high paleolatitudes. In a number of recent studies, pathways were proposed for the distribution of some marine reptile taxa in the Late Jurassic (Fernández and, Maxwell, 2012; Gasparin and Fernández, 2005; Zverkov et al., 2015) and in the Late Cretaceous (Grigoriev et al., 2015).

Thus, at present, marine reptiles are perceived as highly specialized active predators which completely lost the link to land in the early stages of their evolutionary history and relatively quickly adapted to the pelagic lifestyle. Viviparity, high metabolic rate, and rapid growth allowed them to occupy the tops of food chains in marine ecosystems during the Mesozoic. All this casts doubt on the assumption that a cold climate could have somehow limited their ranges.

CONCLUSIONS

We analyzed all the available data on the Jurassic and Cretaceous climates of Siberia and on the distribution of marine reptiles in this region. Most of the localities for Siberian marine reptiles are in high paleolatitudes (70°–87° N). At the same time, no direct connection was found between climate fluctuations and the distribution of marine reptiles. Although the highest number of their occurrences corresponds to the warmest epochs (early Toarcian and Volgian), they were also relatively common during cooler episodes (late Pliensbachian, Aalenian–Bajocian), but are unknown in some certainly warmer water intervals (Callovian). Cretaceous records of marine reptiles are very scarce in Siberia, while they are known from the relatively “cold” Valanginian; their remains have not yet been reported from the Ryazanian. In the Albian–Late Cretaceous time interval, the remains of marine reptiles are relatively rare and remain poorly known. The modern understanding of the biology of marine reptiles differs significantly from the views of the past century; in recent works, it has been shown that a number of advanced Jurassic and Cretaceous marine reptiles had a high level of metabolism and were homoeothermic. In view of the foregoing, it can be concluded that finds of marine reptiles cannot be used as indicators of a warm climate.

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