Early Albian marine environments in Madagascar: An integrated approach based on oxygen, carbon and strontium isotopic data

Yuri D. Zakharov [a, *], Kazushige Tanabe [b], Yasunari Shigeta [c], Peter P. Safronov [a], Olga P. Smyshlyaeva [a], Sergei I. Dril [d]

[a] Far Eastern Geological Institute of Russian Academy of Sciences (Far Eastern Branch), Stoletiya Prospect 159, Vladivostok 690022, Russia
[b] The University Museum and the Department of Earth and Planetary Science, The University of Tokyo, Tokyo 113-0033, Japan
[c] National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan
[d] Institute of Geochemistry of Russian Academy of Sciences (Siberian Branch), Favorsky Street 1a, Irkutsk 664033, Russia

ABSTRACT

New palaeotemperature reconstructions have been obtained on the basis of oxygen isotopic analysis of 178 aragonitic shell samples taken from specimens of three ammonoid orders (and some corresponding families): Phylloceratida (Phylloceratidae), Lytoceratida (Tetragonitidae) and Ammonitida (Oppeliidae, Desmoceratidae, Silesitidae, Cleoniceratidae and Douvilleiceratidae). Those obtained from aragonite shells, secreted in the lower epipelagic and in the middle mesopelagic zones during coolest season (winter), range from 15.4 to 16.8 °C, and from 11.8 to 12.0 °C, respectively. Presumed spring/autumn palaeotemperatures obtained from aragonite shells, secreted apparently in the upper and lower epipelagic, upper and middle mesopelagic zones, are somewhat higher. Presumed summer palaeotemperatures, calculated apparently for the upper and lower epipelagic, and upper mesopelagic zones range from 19.4 to 21.7 °C, from 17.7 to 19.4 °C, and from 14.4 to 16.1 °C, respectively. The predominant part of investigated ammonoids from Madagascar inhabited the epipelagic zone, but some phylloceratid, tetragonitid and silesitid ammonoids preferred deeper, cooler conditions (upper-middle mesopelagic zone). The study supports the hypothesis that Madagascar was located in middle latitudes within the tropical-subtropical climatic zone during the early Albian. Available carbon and strontium isotope data allow us to assume a more or less expressed carbon and strontium isotope stratification of the water column in this region in the early Albian. On the basis of the stable isotope data, following partly Lukeneder (2015), two large ethological groups can be recognised mainly in mid-aged and adult ammonoids. Some ammonoids (group 1) preferred apparently mesopelagic conditions, and to a lesser degree the epipelagic zone, being mainly cool-requiring animals. However, a significant part of the isotopically investigated ammonoids (group 2) preferred, on the contrary, only epipelagic conditions, being mainly thermophilic dwellers.

1. Introduction

There is a comprehensive literature on Triassic, Jurassic and Cretaceous ammonoids (Cephalopoda) from Madagascar (e.g., Collignon, 1932, 1933–1934, 1949, 1950a, 1950b). However, since only the aragonite preserved in Jurassic and Cretaceous cephalopods can be used for isotopic investigations, there are still few works on this respect about Madagascar faunas. Among Late Jurassic (Oxfordian) molluscs from the region only the ammonoid *Perisphinctites* and the bivalve *Astarte* from southwestern Madagascar (Morondava Basin) have been investigated isotopically by Lécuyer and Bucher (2006), who documented that δ^{18}O values in most well preserved aragonitic ammonoid shells and calcitic bivalve shells fluctuate from −0.85 to −1.11‰ and from −2.57 to −1.79‰, respectively. However, the first data on oxygen isotope values, obtained from some cephalopod shells from the lower Albian Ambarrimaninga Formation of northwestern Madagascar (Mahajanga Province), show that they are noticeably higher (Zakharov, Shigeta, Nagendra, et al., 2011), which illustrates that early Albian climate in Madagascar was cooler compared to the Oxfordian in the same region.

In this work, we focus on seasonal palaeotemperature fluctuations in Madagascar during the early Albian (*Cleoniceras besairiei* and possibly *Douvilleiceras inaequinodum* zones), using the most representative original data on stable isotope composition of aragonitic cephalopod shells from the Mahajanga Province.

2. Geographical and geological setting

The ammonoid locality in the Mahajanga Province, northwestern Madagascar is situated in a long quarry near the top of an escarpment, 3 km to the west of the village of Ambatolafia (coordinates: Lat. 16°33′23.6″ S, Long. 46°12′10.2′ E) (Fig. 1). All investigated cephalopod fossils occur most likely in the 15—20-cm-thick hard, basal glauconitic sandstone layer, (Ambarrimaninga Formation, Ambatolafia locality), where local villagers have collected ammonoid shells for sale during many years; above the ammonoid-bearing bed follows a nearly 15 cm thick layer of dark grey, glauconitic siltstone ("microfossil bed") (Kiel, 2006).

Based on assemblages recovered mainly from Ambarimaninga, Ambatolafia, Bafamonto and Diégo Suarez areas, the Albian of Madagascar is represented by the following 10 ammonoid zones in descending orders (Collignon, 1963; corresponding zones and subzones in the European faunal province are given in parentheses according to Hart, Amédro, & Owen, 1996; and Owen, 1999): (1) *Pseudosonneraila sakalava* Zone (the *Leymeriella acuticostata* Subzone of the lower Albian *Leymeriella tardefurcata* Zone), (2) *Cleoniceras besairiei* Zone (possibly the lower *Cleoniceras flaridum* Subzone of the *Sonneratia chalenis* Zone), (3) *Douvilleiceras inaequinodum* Zone (possibly the upper *Cleoniceras flaridum* Subzone of the lower Albian *Sonneratia chalenis* Zone), (4) *Lemuroceras spathi—Brancoceras besairiei* Zone (possibly the lower Albian *Otohoplites auritiformis* Zone), (5) *Lyelliceras lyelli* Zone (the same name subzone of the middle Albian *Hiplites dentatus* Zone), (6) *Oxytropidoceras acutocarinatum—"Manuaniceras"* [= *Oxytropidoceras*; Wright, Callomon, & Howarth, 1996] *jacobi* Zone (possibly middle Albian *Euhoplites loricatus* Zone), (7) *Diploceras cristatum* Zone (the same name subzone of the upper Albian *Mortoniceras* (*Mortoniceras*) *inflatum* Zone), (8) *Hysteroceras binum* Zone (possibly the upper part of the upper Albian *Mortoniceras* (*Mortoniceras*) *inflatum* Zone), (9) *"Pervinquieria"*[= *Mortoniceras*; Wright et al. 1996] *inflata* Zone (possibly the *Mortoniceras rostratum* and *Mortoniceras*

(*Durnovarites*) *parinflatum* subzones of the upper Albian *Stoiczkaia dispar* Zone), and (10) *Neophlycticeras madagascariense* Zone (possibly the *Pleurohoplites* (*Arrhaphoceras*) *briacensis* Subzone of the upper Albian *Stoiczkaia dispar* Zone).

Stratigraphically the ammonoid fauna from the Ambatolafia locality belongs to the *Cleoniceras besairiei* (Kiel, 2006) and possibly *Douvilleiceras inaequinodum* zones of the middle part of the lower Albian. In a sequence stratigraphic content, the glauconitic sandstones, which occur commonly in the Albian of Madagascar (Luger et al., 1994), are frequently associated with condensed sections and transgressive-systems-tracts (e.g., Harding et al., 2014; Webby & Van Den Houvel, 1965). Judging from a plate tectonic reconstruction (e.g., Stampfli & Borel, 2002), the area was located at palaeolatitudes of 40—45°S in late Early Cretaceous times.

3. Material and methods

Isotopically investigated early Albian ammonoids from the Mahajanga Province consist of nine species of the following genera: *Phylloceras, Eotetragonites, Aconeceras, Puzosia, Beudanticeras, Neosilesites, Desmoceras, Cleoniceras* and *Douvilleicera*s. Specimens were selected from the collections in the National Museum of Nature and Science, Tsukuba and the University Museum, the University of Tokyo.

In addition, well-preserved ammonoid shells of *Leymeriella schrammeni* (Jacob) from the lower Albian of the Lower Saxony Basin, Germany (K. Tanabe's coll.) were analized for comparison.

The following criteria were used to determine diagenetic alteration: (1) hand-sample visual indications (Fig. 2 and Fig. S1), (2) percentage of aragonite in cephalopod shells, which were originally represented by 100% aragonite, (3) presence or lack of diagenetic admixture, determined by X-ray diffraction analysis, (4) the degree of integrity of shell microstructure, determined under a scanning electron microscope (SEM) (Figs. 3—4).

We have usually recognized four stages in diagenetic alteration of aragonitic cephalopod shells: 1st stage, where secondary calcite is absent (100% aragonite) or presented by a small portion, not more than 1—5%; 2nd stage characterised by appearance of a larger portion (5—30%) of secondary calcite; 3rd stage, where shell material consists of approximately 30—50% secondary calcite; 4th stage characterised by presence of more than 50% secondary calcite with very pronounced change in isotopic composition (Zakharov, Naidin, & Teiss, 1975, 2006c, 2013a).

Polished sections (Fig. S1) of selected cephalopod shell samples were investigated with a SEM (EVO50 XVP), after etching with 1.0% HCl with frequent interruptions for visual control − total treatment duration was about 3—6 min, as recommended by Sælen (1989), Podlaha, Mutterlose, and Veizer (1998) and Voigt, Wilmsen, Mortimore, and Voigt (2003), in order to obtain textural information and ascertain the degree of diagenetic alteration.

X-ray powder analyses were carried out at the Analytical Centre (FEGI) in Vladivostok using a desktop X-ray diffractometer MiniFlex II (Rigaku Firm).

SEM and X-ray studies of lower Albian cephalopods from the Madagascar area suggest that all of them, apparently, retain their original shell microstructure, and C, O stable isotope and Sr isotope compositions. The X-ray diffraction analysis particularly shows the lack of secondary admixtures, including α-SiO_2, in the investigated samples from this area and the almost 100% aragonitic composition of most analysed cephalopod shells.

Samples for our stable isotope analyses were carefully removed from the investigated shells using a special method (Zakharov et al., 2005): material was taken by a scalpel mainly from narrow, small areas along growth striations on the external surface of ammonoid shells, which enabled shell material secreted apparently during

Fig. 1. The lower Albian fossil locality in the Mahajanga Basin, northeastern Madagascar (based on Kiel, 2006).
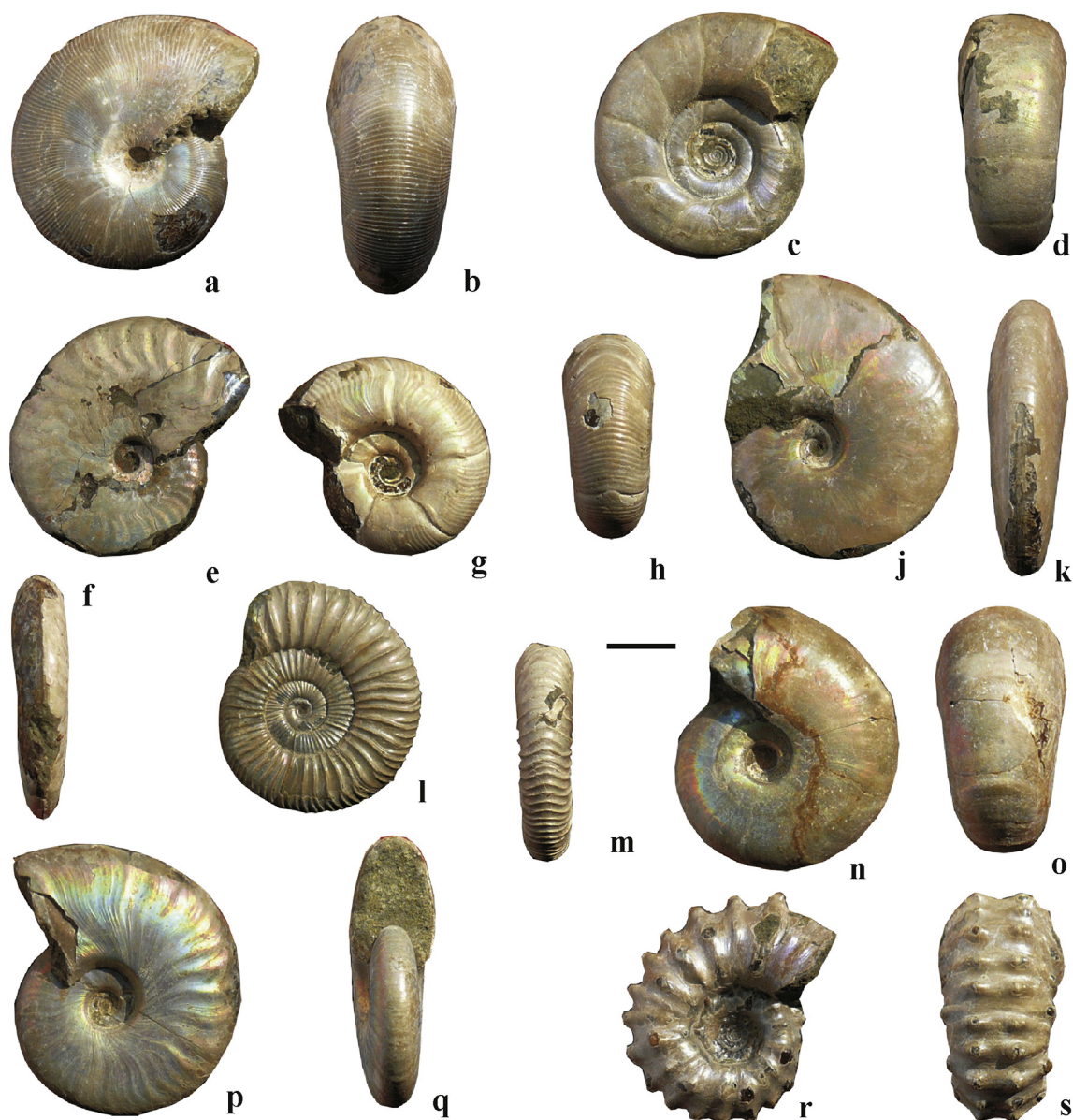
Fig. 2. Investigated ammonoid shells from the lower Albian of the Mahajanga Basin (specimens selected from the collection in the National Museum of Nature and Science, Tsukuba). a—b — *Phylloceras* sp. (specimen M—73); c—d — *Eotetragonites umbilicostriatus* Collignon (specimen M—85); e—f — *Aconeceras* sp. (specimen M—77); g—h — *Puzosia* sp. (specimen M—57); j—k — *Beudanticeras* sp. (specimen M—81); l-m — *Neosilesites* sp. (specimen M—69); n—o — *Desmoceras* sp. .(specimen M—89); p—q — *Cleoniceras* sp. (specimen M—65); r—s — *Douvilleiceras* sp. (specimen M—61). Scale bar = 10 mm.

different seasons of the year to be identified. Apparently the same method has been used earlier by Stevens and Clayton (1971).

In the prominent part of investigated ammonoid shells from the lower Albian of Madagascar, samples for oxygen and carbon isotope investigation were taken in detail from their external whorls. Following the method described in Zakharov (1978), we assume that each whorl of an adult Mesozoic ammonoid shell was secreted on an average during 1.3—1.7 year, or somewhat in a shorter time. If our assumption is correct, oxygen isotope profiles obtained for the considerable part of external whorls of the examined ammonoid shells possibly reflect some temperature conditions representative of the all or almost all year's seasons in the latest part of the ammonoid life-cycle.

Oxygen-, carbon- and strontium-isotope measurements were carried out using a Finnigan MAT-252 (FEGI, Analytical Centre, Vladivostok; Institute of Geochemistry of Russian Academy of Sciences, Siberian Branch, Irkutsk). The laboratory gas standard used in the measurements was calibrated relatively to NBS-19 $\delta^{13}C = 1.93‰$ and $\delta^{18}O = -2.20‰$ (Coplen, Kendall, & Hopple, 1983). Reproducibility of replicate standards was always better than 0.1‰.

The following equation was used for palaeotemprature calculation (Grossman & Ku, 1986):

$$T\,(°C) \;=\; 20.6 - 4.34\left(\delta^{18}O_{aragonite} - \delta_w\right)$$

In this equation $T\,(°C)$ is ambient temperature; $\delta^{18}O_{aragonite}$ is the measured oxygen-isotope values of aragonite (versus VPDB), and δ_w (‰) is the ambient water isotope ratio (versus VSMOW). A δ_w of -1.0 ‰ is often assumed to be appropriate for an ice-free world (e.g., Hudson & Anderson, 1989; Huber, Norris, & MacLeod, 2002; Lukeneder, Harzhauser, Müllegger, & Piller, 2010; Price & Hart, 2002; Pirrie & Marshall, 1990; Shackleton and Kennet, 1975).
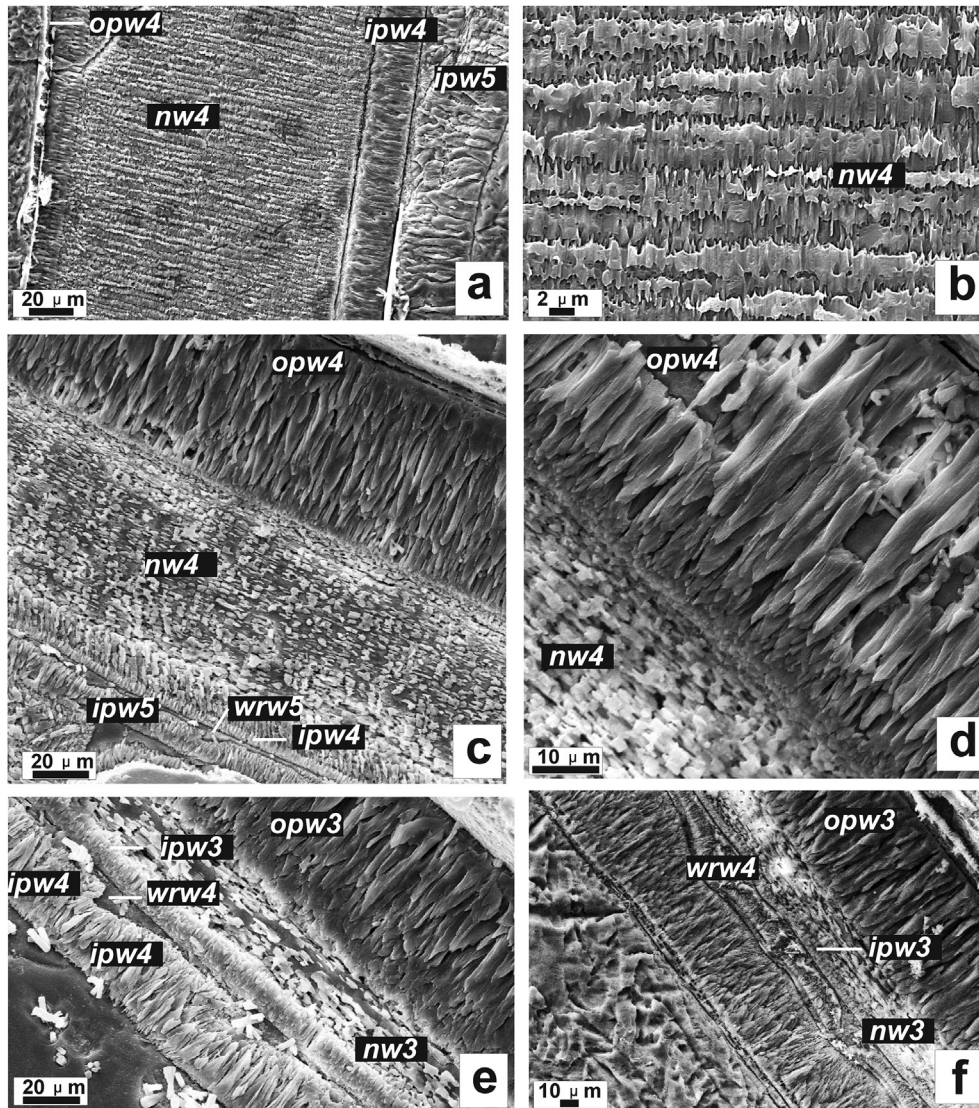
Fig. 3. SEM images of well-preserved ammonoid (*Eotetragonites, Puzosia* and *Beudanticeras*) shell structure: a-b − *Eotetragonites umbilicostriatus* Collignon, specimen M-85: a − median section of the shell wall in the 4th and 5th whorls, b − the detail of a (nacreous layer); c−e *Puzosia* sp., specimen M-69: c − median section of the shell wall in the 4th and 5th whorls, d − the detail of c, e − median section of the shell wall in the 3rd and 4th whorls; f − *Beudanticeras* sp., specimen M−81, median section of the shell wall in the 3rd and 4th whorls. Abbreviations: *opw3, opw4* − outer prismatic layers in the 3rd and 4th whorls, *ipw3, ipw4* and *ipw5* − inner prismatic layers in the 3rd, 4th and 5th whorls, *nw3* and *nw4* − nacreous layers in the 3rd and 4th whorls, *wrw4* and *wrw5* − wrinkle layers in the 4th and 5th whorls.

However, isotopic composition of Cretaceous seawater may have varied considerably due to freshwater input and/or evaporation.

4. X-ray, C, O stable isotope and Sr isotope results

In our second study of isotopic investigation of cephalopod shells from the lower Albian of Madagascar (Mahajanga Province), started after 2011, 178 aragonitic samples have been taken additionally for oxygen and carbon isotope and X-ray analyses from ammonoids *Phylloceras* sp. (Phylloceratidae), *Eotetragonites umbilicostriatus* Collignon (Tetragonitidae), *Aconeceras* sp. (Oppeliidae), *Puzosia* sp., *Beudanticeras* sp. (Desmoceratidae), *Neosilesites* sp. (Silesitidae), *Desmoceras* (*Desmoceras*) sp., *Cleoniceras* sp. (Cleoniceratidae) and *Douvilleiceras* sp. (Douvilleiceratidae) (Fig. 2). All of them are characterised by a 96−100% aragonitic shell-composition (Table 1). This material corresponds only to the 1st stage in diagenetic alteration and therefore is fully suitable for isotopic investigation.

For preliminary Sr-isotope investigation specimens of *Eotetragonites umbilicostriatus* Collignon, *Desmoceras* sp., *Cleoniceras* sp. and *Douvilleiceras* sp. (97.7−100% aragonite) from the lower Albian Ambarrimaninga Formation at the Mahajanga Province (Madagascar) were used.

Main results on the detailed oxygen and carbon isotope investigation of cephalopods from the lower Albian of Madagascar (Fig. 5, Fig. S2−S13) show that most of them are characterised by chiefly negative $\delta^{18}O$ vaues, fluctuating from −1.5 to 0‰. In case of normal salinity these values correspond mainly to palaeotemperatures of 16.4−21.7 °C. However, some contemporaneous ammonoids (representatives of the genera *Phylloceras, Eotetragonites* and *Neosilesites*) show mainly positive $\delta^{18}O$ values, varying between 0 and 0.72‰, which corresponded to lower palaeotemperatures (about 11.8−15.4 °C). We assume that variations in $\delta^{18}O$ value are connected with the shell secretion at different depths within the epipelagic and mesopelagic zones, respectively (Fig. 5).
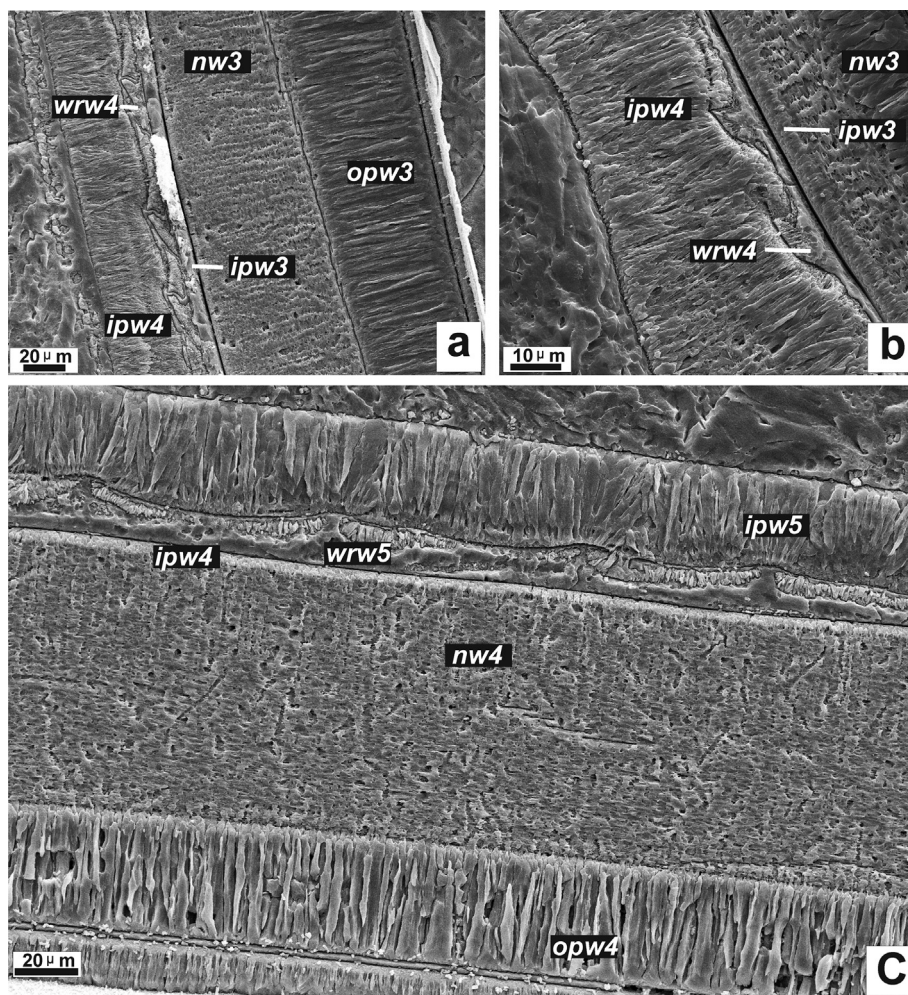
Fig. 4. SEM images of well-preserved ammonoid (*Desmoceras* and *Neosilesites*) shell structure: a—b — *Desmoceras* sp., specimen M-89: median section of the shell wall in the 3rd and 4th whorls, b — the detail of Fig. 4a (wrinkle layer); c — *Neosilesites* sp., specimen M-69: median section of the shell wall in the 4th and 5th whorls. Abbreviations: *opw4* — outer prismatic layers in the 4th whorl, *ipw4* and *ipw5-*— inner prismatic layers in the 4th and 5th whorls, *nw4* — nacreous layers in the 4th whorls, *wrw5* — wrinkle layer in the 5th whorl.

The mixing of investigated early Albian ammonoids from distinct habitats in a single glauconitic sandstone bed of the Mahajanga Province could suggest transportation by marine currents during a transgression (Harding et al., 2014; Webby & Van Den Houvel, 1965). However, it is reasonable to suspect that all investigated ammonoids from the middle part of the lower Albian of the Mahajanga Province existed in the same climate zone. Therefore, analysis of the stable isotope data obtained from numerous ammonoids of this area allow us to reconstruct both their depth distribution and seasonal temperature fluctuations.

Reconstruction of early Albian seasonal temperatures for the presumed epipelagic and mesopelagic zones of the Madagascar marine basin was made on the basis of detailed data on 12 ammonoid shells (Figs. S2—S13). Isotopic palaeotemperatures seem to have been around (1) 16.4—17.2 °C (lower epipelagic zone) and 11.8—12.0 °C (upper mesopelagic zone) for the presumed winter season; (2) 15.5—19.8 (upper epipelagic zone), 16.6—17.7 °C (lower epipelagic zone), 12.4—15.6 (upper mesopelagic zone) and 12.0—13.9 °C (middle mesopelagic zone) for the presumed autumn and spring seasons; (3) and about 19.4—21.7 °C (upper epipelagic zone), 17.7—19.4 °C (lower epipelagic zone), and 14.4—16.4 °C (upper mesopelagic zone) for the presumed summer season (Fig. 6).

The highest δ^{13}C vaues have been discovered in *Desmoceras* (up to 1.2‰) and *Douvilleiceras* (up to 0.9‰), secreted in conditions of

the upper epipelagic zone; in other ammonoids from the lower Albian of Madagascar δ^{13}C values fluctuate mainly from −2.3 to +0.6‰ (Fig. 7).

The lowermost ^{87}Sr/^{86}Sr value (0.707241) has been discovered in the *Eogaudryceras* shell, secreted in cool conditions of the upper mesopelagic zone, and the uppermost values (0.707275, 0.707276 and 0.707296) in the *Cleoniceras*, *Douvilleiceras* and *Desmoceras* shells, secreted in warmer conditions of the lower and upper epipelagic zones (Fig. 7A).

5. Discussion

5.1. Early Albian palaeotemperature conditions

New evidence shows that Albian palaeotemperatures interpreted as summer values for epipelagic waters in Madagascar (20.2—21.7 °C) are similar with those calculated from the isotopic composition of the ammonoids *Otohoplites raulinianus* and *Beudanticeras beudanti* (coll. Y. Shigeta), from the northern middle palaeolatitude area of Normandy (19.3—21.6 °C) (Zakharov, Smyshlyaeva, Popov, & Shigeta, 2006), and of belemnite rostra and the ammonoid *Oxytropidoceras* sp. from Pas de Calais in northern France (10.1—21.2 and 18.0 °C, respectively) (Y.D. Zakharov's coll.; Zakharov, Smyshlyaeva, Shigeta et al., 2006). However, these values are somewhat higher than those calculated

Table 1
Carbon and oxygen isotope analyses of ammonoid shells from the lower Albian Ambarimaninga Formation of Madagascar and lower Albian Schrammen Zone of Vöhrum, Lower Saxony Basin, Germany* (H, whorl height in the ammonoid shell).

Sample	Shell	Species	Location (H in mm)	Diagenetic alterations				$\delta^{13}C$ (VPDB)	$\delta^{18}O$ (VPDB)	T, °C
				Diagenetic Stage	Aragonite, %	Admixture (e.g., α-SiO_2), %	Colour			
M-73-1	M-73	*Phylloceras* sp. (Fig. S2)	H = 23.5	1st	98	No	Cream	−0.69	0.35	12.83
M-73-2	Same shell	Same species	H = 23.0	1st	100	No	Cream	−0.23	0.59	16.90
M-73-3	Same shell	Same species	H = 22.5	1st	100	No	Cream	−0.09	0.66	12.53
M-73-4	Same shell	Same species	H = 22.0	1st	100	No	Cream	−0.10	0.73	12.22
M-73-5	Same shell	Same species	H = 21.7	1st	100	No	Cream	0.38	0.59	12.63
M-73-6	Same shell	Same species	H = 21.5	1st	100	No	Cream	0.26	0.68	12.44
M-73-7	Same shell	Same species	H = 21.0	1st	100	No	Cream	0.35	0.61	12.74
M-73-8	Same shell	Same species	H = 20.5	1st	100	No)	Cream	0.33	0.79	11.96
M-73-9	Same shell	Same species	H = 20.0	1st	100	No	Cream	0.71	0.82	11.83
M-73-10	Same shell	Same species	H = 19.5	1st	−	No	Cream	0.0.72	0.82	11.83
M-73-11	Same shell	same species	H = 19.0	1st	−	No	Cream	0.84	0.84	11.75
M-73-12	Same shell	Same species	H = 18.0	1st	99	No	Cream	0.64	0.70	12.35
M-73-13	Same shell	Same species	H = 17.5	1st	100	No)	Cream	0.42	0.71	12.31
M-73-14	Same shell	Same species	H = 17.0	1st	100	N	Cream	0.63	0.76	12.09
M-73-15	Same shell	Same species	H = 15.5	1st	99	No	Cream	0.28	0.68	12.44
M-73-16	Same shell	Same species	H = 15.0	1st	100	No	Cream	0.42	0.72	12.27
M-73-17	Same shell	Same species	H = 14.0	1st	99	No	Cream	−0.10	0.55	13.01
M-73-18	Same shell	Same species	H = 12.5	1st	100	−	Cream	0.23	0.59	12.83
M-85-1	M-85	*Eotetragonites umbilicostriatus* Collignon (Fig. S3)	H = 16.2	1st	99.0	No	Cream	−5.16	0.53	13.09
M-85-2	Same shell	Same species	H = 13.7	1st	98.9	No	Silvery-cream	−4.84	0.42	13.57
M-85-3	Same shell	Same species	H = 13.2	1st	99.0	No	Silvery	−4.82	0.36	13.83
M-85-4	Same shell	Same species	H = 13.0	−	−	−	Silvery	−4.01	0.26	14.26
M-85-5	Same shell	Same species	H = 12.5	1st	99.6	-o	Silvery	−2.70	0.40	13.66
M-85-6p	Same shell	Same species	H = 12.0	−	−	−	Silvery	−3.69	0.45	13.44
M-85-6	Same shell	Same species	H = 11.5	1st	98.6	−	Silvery	−2.78	0.36	13.83
M-85-7	Same shell	Same species	H = 11.0	−	−	−	Silvery	−2.93	0.23	14.39
M-85-8	Same shell	Same species	H = 10.5	1st	99.0	No	Silvery	−2.34	0.53	13.09
M-85-9	Same shell	Same species	H = 10.0	−	−	−	Silvery	−3.01	0.36	13.83
M-85-10	Same shell	Same species	H = 9,5	1st	99.2	No	Silvery	−2.64	0.69	12.40
M-85-11	Same shell	Same species	H = 9.0	−	−	−	Silvery	−2.56	0.49	13.27
M-85-12	Same shell	Same species	H = 8.5	1st	99.0	No	Silvery	−2.56	0.46	13.40
M-85-13	Same shell	Same species	H = 8.0	1st	99.0	98.9	Silvery	−3.20	0.43	13.53
M-85-14	Same shell	Same species	H = 7.5	−	−	−	Silvery	−3.72	0	15.39
M-85-15	Same shell	Same species	H = 7.2	1st	98.4	No	Silvery	−3.66	0.23	14.39
M-85-16	Same shell	Same species	H = 7.0	−	−	−	Silvery	−4.89	0.16	14.70
M-85-17	Same shell	Same species	H = 6.5	−	−	−	Silvery	−4.26	0.27	14.22
M-85-18	Same shell	Same species	H = 6.0	1st	97.9	$MnCO_3$ (trace)	Silvery	−2.30	−0.12	15.91
M-85-19	Same shell	Same species	H = 5.5	−	−	−	Silvery	−2.60	−0.16	16.09
M-77-1	M-77	*Aconeceras* sp. (Fig. S11)	H = 20.5	1st	100	No	Silvery	−0.24	−0.55	17.78
M-77-2	Same shell	Same species	H = 20.0	1st	100	No	Silvery	−0.10	−0.63	18.13
M-77-3	Same shell	Same species	H = 19.5	1st	100	No	Silvery	−0.31	−0.73	18.56
M-77-4	Same shell	Same species	H = 19.0	1st	100	No	Silvery	−0.90	−0.62	18.08
M-77-5	Same shell	Same species	H = 18.0	1st -	100	No	Silvery	−0.18	−0.54	17.74
M-77-6	Same shell	Same species	H = 16.5	1st	100	No	Silvery	−0.43	−0.76	18.69
M-77-7	Same shell	Same species	H = 15.5	1st	100	No	Silvery	−0.88	−0.76	18.69
M-77-8	Same shell	Same species	H = 15.0	1st	100	No	Silvery	−0.91	−0.78	18.78
M-77-9	Same shell	Same species	H = 14.0	1st	100	No	Silvery	−1.30	−0.78	18.78
M-77-10	Same shell	Same species	H = 13.0	1st	100	No	Silvery	−0.93	−0.78	18.78
M-77-11	Same shell	Same species	H = 11.5	1st	100	No	Silvery	−1.13	−0.83	18.99
M-77-12	Same shell	Same species	H = 10.5	1st	100	No	Silvery	−1.17	−0.81	18.91
M-57-1	M-57	*Puzosia* sp. (Fig. S5)	H = 14.0	1st	100	No	Cream	0.50	−0.17	16.13
M-57-2	Same shell	Same species	H = 13.5	1st	100	No	Cream	0.51	−0.27	16.56
M-57-3	Same shell	Same species	H = 13.0	1st	100	No	Cream	0.39	−0.12	15.91
M-57-4	Same shell	Same species	H = 12.8	1st	100	No	Cream	0.23	−0.04	15.57
M-57-5	Same shell	Same species	H = 12.5	1st	100	No	Cream	0.16	−0.01	15.44
M-57-6	Same shell	Same species	H = 12.3	1st	100	No	Cream	0.51	−0.02	15.31
M-57-7	Same shell	Same species	H = 12.2	1st	100	No	Cream	0.44	−0.02	15.48
M-57-8	Same shell	Same species	H = 12.0	1st	100	No	Cream	−0.05	−0.05	15.61
M-57-9	Same shell	Same species	H = 11.5	1st	100	No	Cream	0.02	−0.22	16.35
M-57-10	Same shell	Same species	H = 11.3	1st	100	No	Cream	−0.10	−0.23	16.39
M-57-11	Same shell	Same species	H = 10.9	1st	100	No	Cream	−0.20	−0.26	16.52
M-57-12	Same shell	Same species	H = 10.5	1st	100	No	Cream	−0.05	−0.22	16.35
M-57-13	Same shell	Same species	H = 10.2	-d	−	−	Cream	−0.13	−0.13	15.96
M-57-14	Same shell	Same species	H = 9.8	−	−	−	Cream	0.16	−0.09	15.78

Table 1 (*continued*)

Sample	Shell	Species	Location (H in mm)	Diagenetic alterations				δ13C (VPDB),	δ18O (VPDB),	T, °C
				Diagenetic Stage	Aragonite, %	Admixture (e.g., α-SiO₂), %	Colour			
M-57-15	Same shell	Same species	H = 9.5	1st	100	No	Cream	0.60	−0.08	15.74
M-57-16	Same shell	Same species	H = 8.8	–	–	–	Cream	0.33	−0.21	16.30
M-57-17	Same shell	Same species	H = 8.0	–	–	–	Cream	−0.11	−0.60	18.00
M-57-18	Same shell	Same species	H = 7.5	–	–	–	Cream	−0.52	−0.80	18.86
M-57-19	Same shell	Same species	H = 7.0	–	–	–	Cream	−0.24	−050	17.56
M-57-20	Same shell	Same species	H = 6.5	–	–	–	Cream	−0.19	−060	18.00
M-81-1	M-81	*Beudanticeras* sp. (Fig. S6)	H = 22.2	1st	98	No	Silvery-cream	0.18	−0.35	16.91
M-81-2	Same shell	Same species	H = 21.8	1st	100	No	Silvery	0.05	−0.53	17.69
M-81-3	Same shell	Same species	H = 21.0	1st	98.1	No	Silvery	−0.43	−0.49	17.52
M-81-4	Same shell	Same species	H = 20.0	1st	98.0	No	Silvery	−0.77	−0.76	18.69
M-81-5	Same shell	Same species	H = 19.0	1st	100	No	Silvery	−0.22	−0.56	17.82
M-81-6	Same shell	Same species	H = 18.5	1st	100	No	Silvery	−0.41	−0.62	18.08
M-81-7	Same shell	Same species	H = 18.0	1st	100	No	Silvery	−0.38	−0.73	18.56
M-81-8	Same shell	Same species	H = 17.5	1st	100	No	silvery	−0.16	−0.79	18.82
M-81-9	Same shell	Same species	H = 16.5	1st	100	No	Silvery	−0.26	−0.71	18.47
M-81-10	Same shell	Same species	H = 15.5	1st	100	No	Silvery	−0.46	−0.67	18.30
M-81-11	Same shell	Same species	H = 14.5	1st	100	No	Silvery	−0.67	−0.91	19.34
M-81-12	Same shell	Same species	H = 13.5	1st	100	No	Silvery	−0.74	−0.94	19.47
M-81-13	Same shell	Same species	H = 12.0	1st	100	No	Silvery	−0.82	−1.20	20.60
M-81-14	Same shell	Same species	H = 11.5	1st	100	No	Silvery	−0.49	−1.14	20.34
M-81-15	Same shell	Same species	H = 9.0	1st	–	–	Silvery	−0.51	−1.17	20.47
M-69-1	M-69	*Neosilesites* sp. (Fig. S9)	H = 11.0	1st	100	SiO₂	Cream	−1.01	0.08	15.04
M-69-2	Same shell	Same species	H = 10.5	1st	100	No	Cream	−1.30	−0.04	15.57
M-69-3	Same shell	Same species	H = 10.0	1st	100	No	Cream	−1.09	−0.03	15.52
M-69-4	Same shell	Same species	H = 9.5	1st	100	No	Cream	−0.38	0.16	14.70
M-69-5	Same shell	Same species	H = 9.0	1st	100	No	Cream	−1.33	0.15	14.74
M-69-6	Same shell	Same species	H = 8.6	1st	100	No	Cream	−1.84	0.03	15.26
M-69-7	Same shell	Same species	H = 8.0	–	–	–	Cream	−2.21	−0.04	15.57
M-69-8	Same shell	Same species	H = 7.5	1st	99.2	No	Cream	−0.35	0.03	15.26
M-69-9	Same shell	Same species	H = 7.0	–	–	–	Cream	−1.09	0.01	15.35
M-69-10	Same shell	Same species	H = 6.5	1st	100	No	Cream	−1.35	−0.10	15.83
M-69-11	Same shell	Same species	H = 6.0	–	–	–	Cream	−1.22	−0.08	15.74
M-69-12	Same shell	Same species	H = 5.5	–	–	–	Cream	−1.12	−0.17	16.13
M-89-1	M-89	*Desmoceras* sp. (Fig. S8)	H = 19.8	1st	98.6	MnCO₃ (trace)	Silvery-cream	−0.89	−0.85	19.08
M-89-2	Same shell	Same species	H = 19.5	1st	99.2	No	Silvery-cream	−0.56	−0.76	18.69
M-89-3	Same shell	Same species	H = 19.0	1st	100	No	Silvery-cream	−0.78	−0.77	18.73
M-89-4	Same shell	Same species	H = 18.0	1st	100	No	Silvery-cream	−0.62	−0.72	18.52
M-89-5	Same shell	Same species	H = 17.5	–	–	–	Silvery-cream	−0.59	−0.66	18.26
M-89-6	Same shell	Same species	H = 17.0	1st	100	No	Silvery-cream	−0.76	−0.76	18.69
M-89-7	Same shell	same species	H = 16.5	1st	99.4	No	Silvery-cream	−1.29	−0.99	19.73
M-89-8	Same shell	Same species	H = 16.0	–	–	–	Silvery-cream	−1.05	−0.65	18.21
M-89-9	Same shell	Same species	H = 15.5	1st	100	No	Silvery-cream	−0.10	−0.75	18.65
M-89-10	Same shell	same species	H = 15.0	1st	100	No	Silvery-cream	−0.83	−0.92	19.38
M-89-11	Same shell	Same species	H = 14.5	–	–	–	Silvery-cream	−0.89	−0.86	19.12
M-89-12	Same shell	Same species	H = 14.0	1st	100	No	Silvery-cream	−1.40	−1.02	19.82
M-89-13	Same shell	Same species	H = 13.5	–	–	–	Silvery-cream	−1.75	−1.04	19.91
M-89-14	Same shell	Same species	H = 13.0	1st	100	No	Silvery-cream	−1.38	−1.15	20.38
M-89-15	Same shell	Same species	H = 12.5	–	–	–	Silvery-cream	−1.22	−1.10	20.17
M-89-16	Same shell	Same species	H = 12.0	1st	100	No	Silvery-cream	−1.07	−1.20	20.60
M-89-17	Same shell	Same species	H = 11.5	–	–	–	Silvery-cream	−1.02	−1.13	20.30
M-89-18	Same shell	Same species	H = 11.0	1st	100	No	Silvery-cream	−0.86	−1.16	20.43
M-89-19	Same shell	Same species	H = 10.8	–	–	–	Silvery-cream	−1.16	−1.02	19.82
M-89-20	Same shell	Same species	H = 10.7	1st	100	No	Silvery-cream	−0.85	−1.15	20.38
M-89-21	Same shell	Same species	H = 10.2	1st	99.6	No	Silvery-cream	−1.72	−1.38	20.38
M-89-22	Same shell	Same species	H = 10.0	1st	98.0	No	Silvery-cream	−2.14	−1.46	21.73
M-89-23	Same shell	Same species	H = 9.5	1st	100	No	Silvery-cream	−1.48	−1.35	21.25
M-89-24	Same shell	Same species	H = 9.0	–	–	–	Silvery-cream	−1.69	−1.28	20.95
M-65	M-65	*Cleoniceras* sp. (Fig. S10)	H = 20.0	1st	98.6	No	Silvery-cream	−0.57	−0.52	17.65
M-61	M-61	*Douvilleiceras* sp. (Fig. S12)	H = 16.5	1st	97.7	No	Silvery-cream	−0.70	−1.02	19.82
G-1*	G-1	*Leymeriella (Proleymeriella) schrammeni* (Jacob)	H = 7.0	1st	100	No	Cream	2.34	−0.30	16.69
G-2*	G-2	Same species	H = 6.0	1st	100	No	Cream	2.42	−0.06	15.65

Stable isotope data on *Cymatoceras?* sp. (M1), *Eotetragonites unbilicostriatus* (M2), *Cleoniceras besairei* (M3), *Desmoceras* sp. (M4), *Douvilleiceras* sp. (M5) are given in Zakharov, Shigeta, Nagendra, et al. (2011, Table 3).
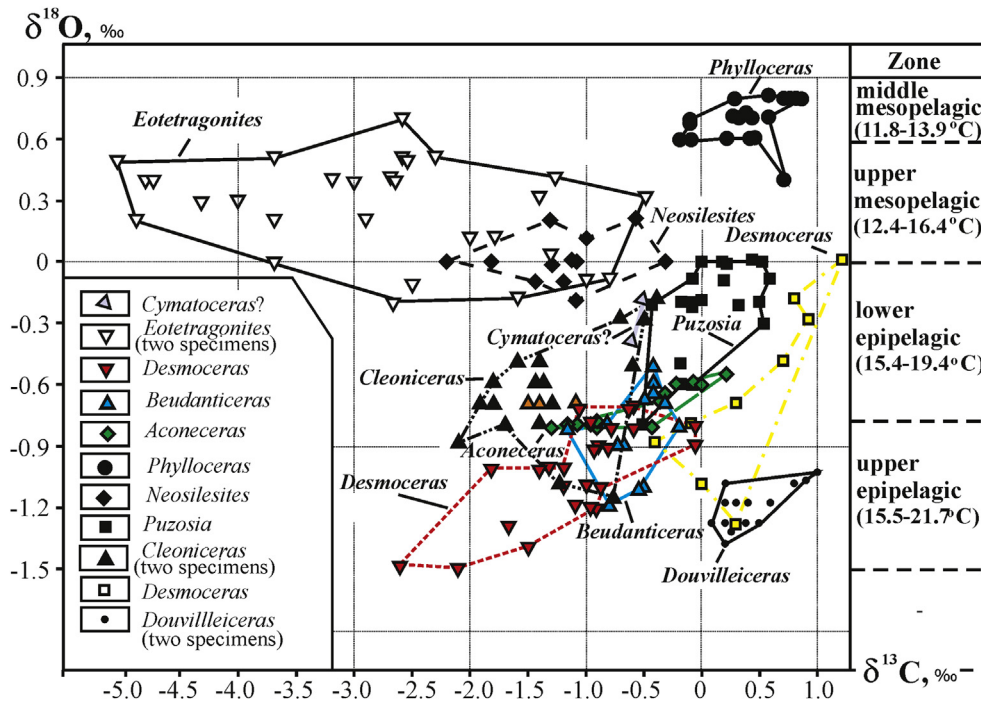
Fig. 5. Scatter plot of δ18O and δ13C values for 11 cephalopod (ammonoid and nautiloid) genera from the lower Albian Ambarimaninga Formation, Madagascar, showing a possible cephalopod habitation within both the mesopelagic and the epipelagic zones.

from the isotopic composition of ammonoid *Leymeriella* (*Proley-meriella*) *schrammeni* (K. Tanabe' coll.) from central Germany (15.6–16.7 °C) (this study, Table 1), and significant higher than corresponding summer values obtained from early Albian belemnite rostra of southern high latitude areas: Argentina (7.7–10.9 °C), Antarctic (6.1–10.7 °C) and western Australia (7.8–11.3 °C) (Pirrie, Marshall, Doyle, & Riccardi, 2004) (Fig. 8).

5.2. Early Albian carbon and strontium isotope stratification

Available carbon and strontium isotope data allow us to assume a more or less pronounced carbon and strontium isotope stratification of the water column in the Madagascar region during the early Albian. No early Albian positive carbon isotope anomalies have been observed there (Table 1). However, the highest δ13C values derived from *Desmoceras* (up to 1.2‰) and *Douvilleiceras* (up to 0.9‰), seem to have been secreted in warmest conditions of the presumed upper epipelagic zone; the lowermost δ13C values (−2.3 to −0.5‰) recognised in fossils were secreted apparently in cooler conditions of the presumed upper mesopelagic zone. Rather low δ13C values in fossils from the early Albian Madagascar marine basin, especially from the mentioned zone, seem to be connected with low phytoplancton productivity in the upper 100 m-deep-water-mass, provoked apparently by a weakening of vertical circulation in this basin (e.g., Bogorov, 1974).

The $^{87}Sr/^{86}Sr$ ratios in early Albian ammonoids from Madagascar range from 0.707241 to 0.707296, and are similar to those in upper Aptian–Albian limestones of Resolution Guyot, Mid-Pacific Mountains (Jenkyns, Paull, Cummins, & Fullagar, 1995; Jones & Jenkyns, 2001). However, the higher and more variable $^{87}Sr/^{86}Sr$ ratios have been recently reported for limestones of the upper Aptian–lower Albian Mural Formation of Sonora, Mexico (0.707479–0.708790; Madhavaraju et al., 2015).

The $^{87}Sr/^{86}Sr$ ratios of recent oceans (0.7092) seem to be mainly a mixture of hydrothermal and continental flux (0.7035 and 0.7120, respectively; Davis, Bickle, & Teagle, 2003; Peterman, Hedge, &

Tourtelot, 1970). In Endmond's (1992) opinion, the riverine mass flux (continental flux) is almost certainly higher today than at any time in the Phanerozoic.

According to Madhavaraju et al. (2015), the relatively high $^{87}Sr/^{86}Sr$ ratios in limestones of the Mural Formation suggest significant weathering of local granitic provenance, which released a significant amount of radiogenic Sr through riverine flux.

On the contrary, the lower $^{87}Sr/^{86}Sr$ ratios, documented in both upper Aptian–Albian limestones from Resolution Guyot (Jones & Jenkyns, 2001) and lower Albian ammonoid shells from Madagascar (this study), might have been related to global environmental changes biased by possible increasing of late Aptian–early Albian hydrothermal activity at ocean ridges. A gradual decrease of Sr-isotope ratio in ammonoid shells, secreted in habitats from shallow to deeper zones of the early Albian Madagascar sea, seems to be in agreement with this assumption.

5.3. Oxygen isotope composition of aragonite preserved ammonoids: environmental and ethological significance

It is known that *Nautilus* and *Allonautilus*, the sole representatives of externally shelled cephalopods have a relatively long life span of more than 20 years in the wild (Cochran, Rye, & Landman, 1981; Saunders, 1983). A depth limit for the living *Nautilus* seems to be 6–700 m (e.g., Hayasaka, Oki, Tanabe, Saisho, & Shinomiya, 1987; Hewitt & Westermann, 1990; Kannie, Fukuda, Akayama, Seki, & Hattori, 1980; Westermann & Ward, 1980; Westermann, 1982;); large daily vertical migration (up to 200 m) is common for it (e.g., Carlson, McKibben, & de Gruy, 1984; Ward, Carlson, Weekly, & Brumbaugh, 1984). Mark-and-recovery and telemetric experiments also demonstrated that living nautiluses exhibit a long-term horizontal migration with speeds as high as 2 km/day (Auclair, Lécuyer, Bucher, & Sheppard, 2004; Saunders and Spinosa, 1979). After hatching, nautiluses live in warm shallow water (25–28 °C), followed by gradual migration to cooler (14–16 °C), deeper water (e.g., Landman, Cochran, Rye, Tanabe, & Arnold, 1994; Oba, Kai, &
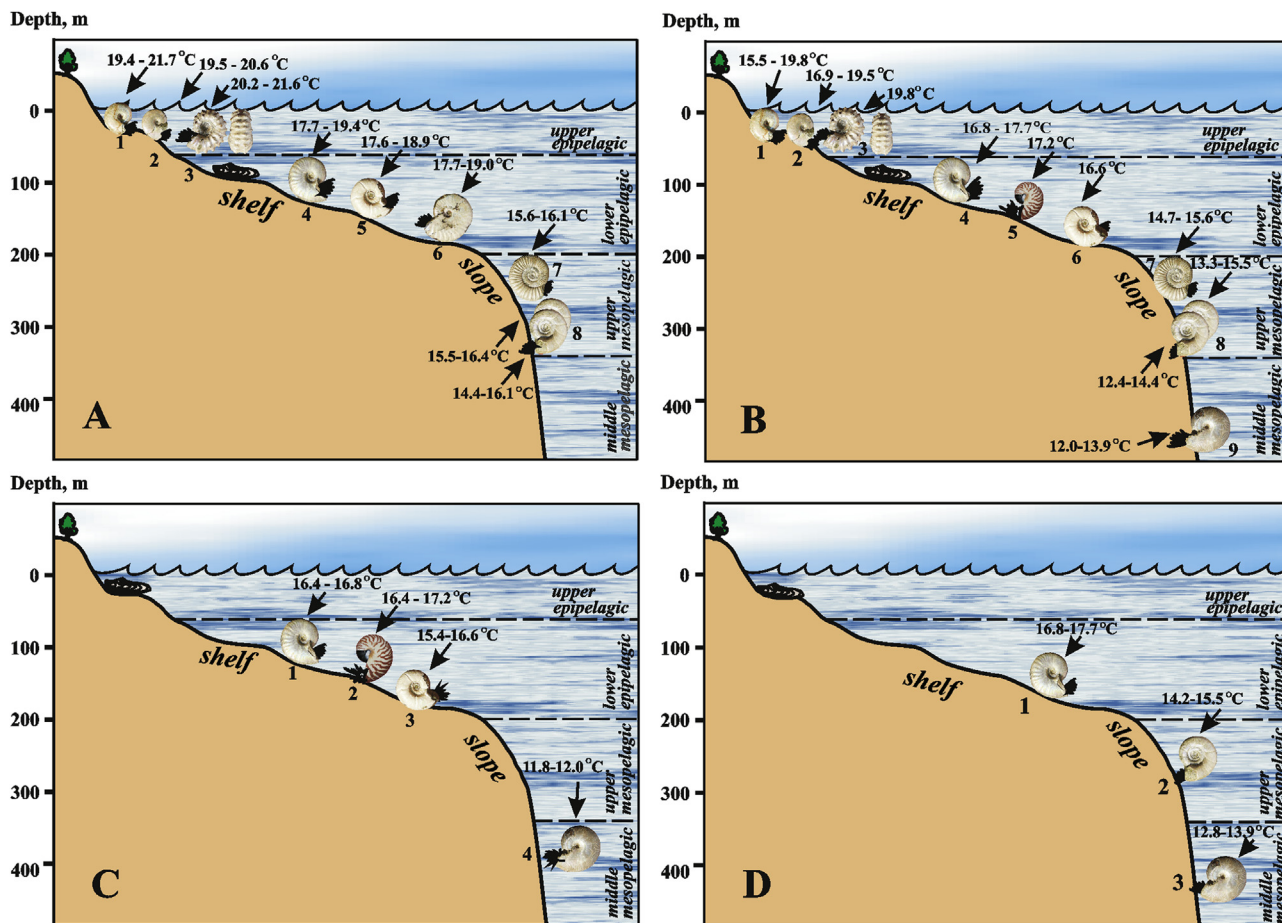
Fig. 6. Assumed natural habitat for early Albian cephalopods of Madagascar (seasonal palaeotemperatures): A — assumed summer palaeotemperatures (ammonoids: 1 — *Desmoceras*, 2 — *Beudanticeras*, 3 — *Douvilleiceras*, 4 — *Cleoniceras* 5 — *Puzosia*, 6 — *Aconeceras*, 7 — *Neosilesites*, 8 — *Eotetragonites*; B — assumed autumn palaeotemperatures (ammonoids: 1 — *Desmoceras*, 2 — *Beudanticeras*, 3 — *Douvilleiceras*, 4 — *Cleoniceras*, 5 — *Cymatoceras*?, 6 — *Puzosia*, 7 — *Neosilesites*, 8 — *Eotetragonites*, 9 — *Phylloceras*; C — assumed winter palaeotemperatures (ammonoids and nautiloids: 1 — *Cleoniceras*, 2 — *Cymatoceras*?, 3 — *Puzosia*, 4 — *Phylloceras*; D — assumed spring palaeotemperatures (ammonoids: 1 — *Cleoniceras*, 2 — *Eotetragonites*, 3 — *Phylloceras*).

Tanabe, 1992). According to Oba et al. (1992), the stepwise increase in $\delta^{18}O$ from septa 7 to 10 may in part reflect post-embryonic migration to deeper waters. Our preliminary stable isotope examination (Zakharov, Shigeta, Smyshlyaeva, et al., 2006) demonstrates a direct relationship between carbon isotope values in septa of the specimen of *Nautilus pompilius* captured alive in late March 1999 from the Bohol Sea, the Philippines, and the corresponded sun activity (at the beginning of cycle 23), which is in agreement with data on contenporaneous brachiopods from the same area.

There is information on stable isotope compositions of aragonite-bearing ammonoid shells from the Upper Carboniferous of the south Urals (Zakharov, Boriskina, Cherbadzhi, & Popov, 1999, 2001), Lower Triassic of Arctic Siberia (Zakharov et al., 1975, 2009; Zakharov, Boriskina, Cherbadzhi, et al., 1999), Middle Triassic of Arctic Siberia (Zakharov, Boriskina, Cherbadzhi et al., 1999, 2009), Upper Triassic (e.g., Fabricius, Friedrichsen, & Jacobshagen, 1970; Kaltenegger, Preisinger, & Rögl, 1971), Jurassic (e.g., Jordan and Stahl, 1970; Lécuyer & Bucher, 2006; Stahl & Jordan, 1969; Zakharov, Smyshlyaeva, Shigeta, Popov, & Zonova, 2006) and the Cretaceous (e.g., Zakharov, Boriskina, Ignatyev, et al., 1999; Zakharov, et al., 2004; Zakharov et al., 2005, Zakharov, Shigeta, Tanabe, et al., 2006, Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov, Smyshlyaeva, Shigeta, et al., 2006; Zakharov, Shigeta, Nagendra, 2011; Zakharov, Shigeta, Smyshlyaeva, et al., 2011;

Zakharov et al., 2012; Zakharov, Baraboshkin, et al., 2013; Zakharov, Haggart, Beard, & Safronov, 2013; Zakharov, Tanabe, Safronov, & Smyshlyaeva, 2014; this study; Cochran, Landman, Turekian, Michard, & Schrag, 2003; Henderson and Price, 2012; Moriya, Nishi, Kawahata, Tanabe, & Takayanagi, 2003; Lukeneder et al., 2010; Lukeneder, 2015; Moriya, 2015; Smyshlyaeva et al., 2002; Stevens, Mutterlose, & Wiedenroth, 2015).

Partly in accordance to Lukeneder (2015), we recognise two large ethological groups (group 1 and group 2) mainly in mid-aged and adult ammonoids on the basis of stable isotope data, which are supported by data from the literature.

The species of the following ammonoid genera from group 1 apparently preferred mesopelagic conditions, and to a lesser degree the epipelagic zone, being mainly cool-requiring animals: middle Gzhelian *Glaphyrites* (only juvenile forms were isotopicaly investigated; Zakharov, Boriskina, & Popov, 2001), late Hauterivian *Simbirskites* (Stevens et al., 2015), early Albian *Phylloceras, Eotetragonites, Grantziceras* and *Neosilesites* (Zakharov, Shigeta, Nagendra, 2011; this study), Turonian *Tragodesmoceroides* (Zakharov, Boriskina, Ignatyev, et al., 1999), Campanian *Tetragonites, Damesites, Eopachydiscus, Canadoceras* and *Menuites*, and early Maastrichtian *Pachydiscus* (Zakharov, Shigeta, Tanabe, et al., 2006; Zakharov, Smyshlyaeva, Popov, et al., 2006). This group seems to be more or less homogeneous, consisting of planispiral ammonoids.
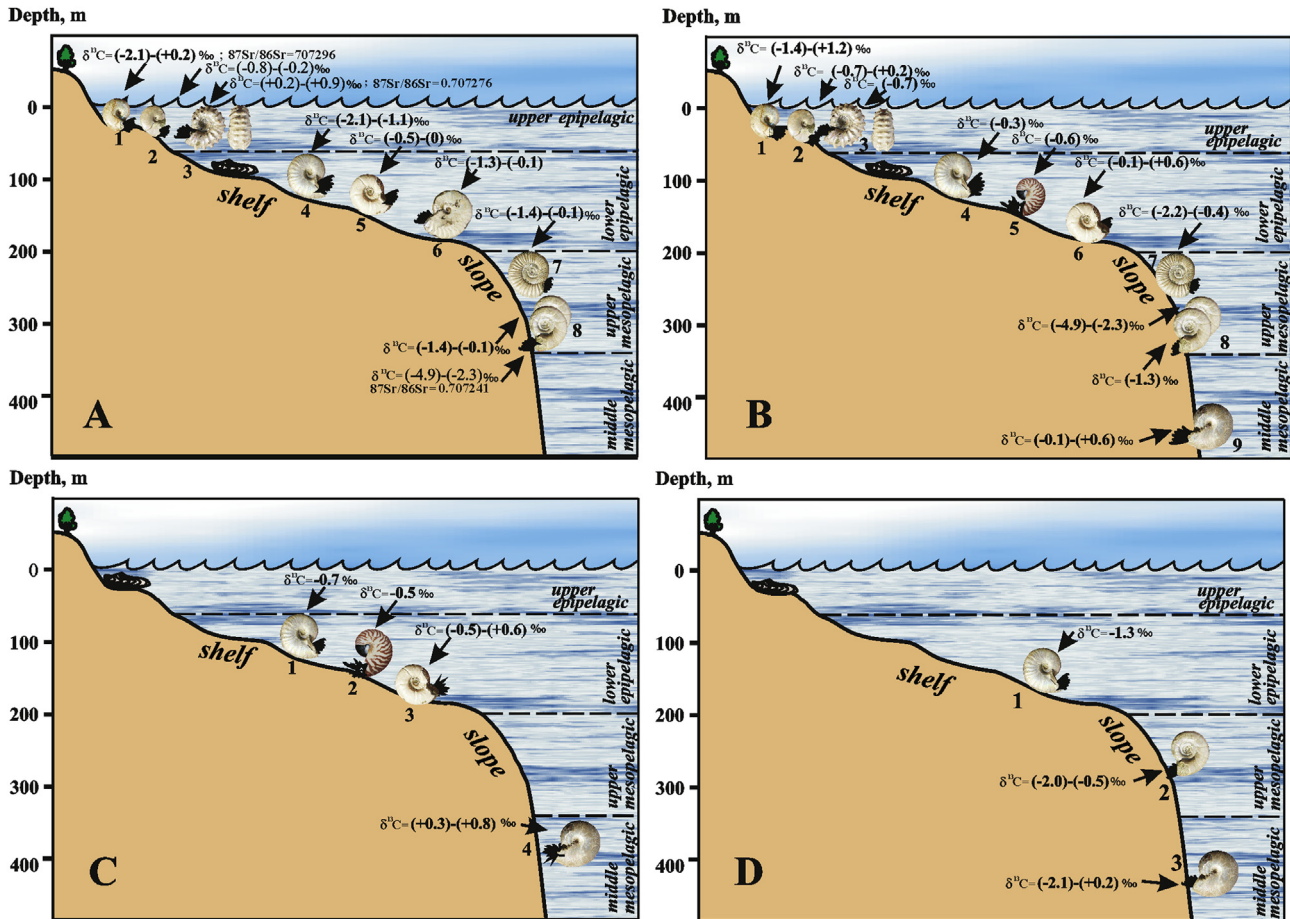
Fig. 7. Assumed natural habitat for early Albian cephalopods of Madagascar (seawater carbon and strontium isotope values): A – assumed summer season (ammonoid genera as in Fig. 6A); B – assumed autumn season (ammonoid genera as in Fig. 6B); C – assumed winter season (ammonoid and nautiloid genera as in Fig. 6C); D – assumed spring season (ammonoid genera as in Fig. 6D).

Some doubts about belonging to this group were cast upon some ammonoids distributed in the regions with stronger seasonal fluctuation. We mean first the early Callovian *Cadoceras* from the Russian Platform (Lukeneder et al., 2010; Lukeneder, 2015; Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov, Smyshlyaeva, Shigeta, et al., 2006) and Campanian-Maastrichtian *Gunnarites* from southern high palaeolatitudes (Pirrie & Marshall, 1990), both showing high $\delta^{18}O$ values in some ontogenetic stages.

We would like to dwell at length on data on the *Cadoceras*, which life strategy is compared by Lukeneder (2015) with those of *Nautilus* and *Sepia*. $\delta^{18}O$ data have been obtained from the three *Cadoceras* species: *Cadoceras emiliantsevi*, *Cadoceras elathmae* and *Cadoceras* sp. (Lukeneder et al., 2010; Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov, Smyshlyaeva, Shigeta, et al., 2006). In *C. emiliantsevi* (100% aragonite) the palaeotemperatures decrease from 21.2 °C for juveniles down to 12.1 °C for mid-aged individuals, and back up 16.9 °C in adults (Lukeneder et al., 2010; Lukeneder, 2015); in adult specimens of *C. elathmae* it fluctuates from 13.3 °C (95% aragonite) to 20.7 °C (100% aragonite) (Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov, Smyshlyaeva, Shigeta, et al., 2006). Investigated *Cadoceras* sp. has been found in association with belemnite rostra and shallow-water brachiopods *Praecyclothyris badensis*. Palaeotemperatures, calculated from the oxygen-isotope compositions of the *Cadoceras* sp. (in its adult stage, 100% aragonite), belemnite rostra and brachiopods are 17.6 °C, 11.9 °C and 9.8–16.7 °C, respectively (Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov, Smyshlyaeva, Shigeta,

et al., 2006). If we consider that palaeotemperatures, obtained from brachiopod shells correspond to seasonal ones at the shelf, stable isotope curves proposed for the *C. emiliantsevi* also reflect in this case mainly seasonal temperature fluctuations, but not a bathymetric range of 50–700 m that was suggested by Lukender (2015). Furthermore, the latter seems to conflict with some palaeogeographic data. Makridin (1964) documented that during the Late Palaeozoic – Early Jurassic, no marine conditions were present in the Russian Platform, with exception of some areas near Caspian Sea and Donetsk, and only shallow-water marine basin existed at the Russian Platform during the Middle and Late Jurassic. There is also evidence that it was likely not deeper than 50–100 m during the Cretaceous (Baraboshkin, Naidin, Benjamovski, Herman, & Akhmetiev, 2007; Zakharov, Baraboshkin et al., 2013).

Our new interpretation on the mode of life of the early Callovian *Cadoceras* from the Russian Platform is based on limited data on isotopic composition of contemporaneous brachiopods, ammonoids and belemnites and palaeogeography, and, as such, remains in the realm of a working hypothesis. However, based on the restricted data on juvenile *Glaphyrites* (Zakharov, Boriskina, Popov, 2001) and mid-aged *Simbirskites* (Stevens et al., 2015), *Phylloceras* and *Eogaudryceras* (this study) we suspect that the ethological type of this group resembles the pattern in living *Nautilus*, whose migrational behaviour is characterised by shallow to significantly deeper environments and back during ontogeny.

Most isotopically investigated ammonoids of group 2 preferred, on the contrary, epipelagic conditions, being mainly thermophilic
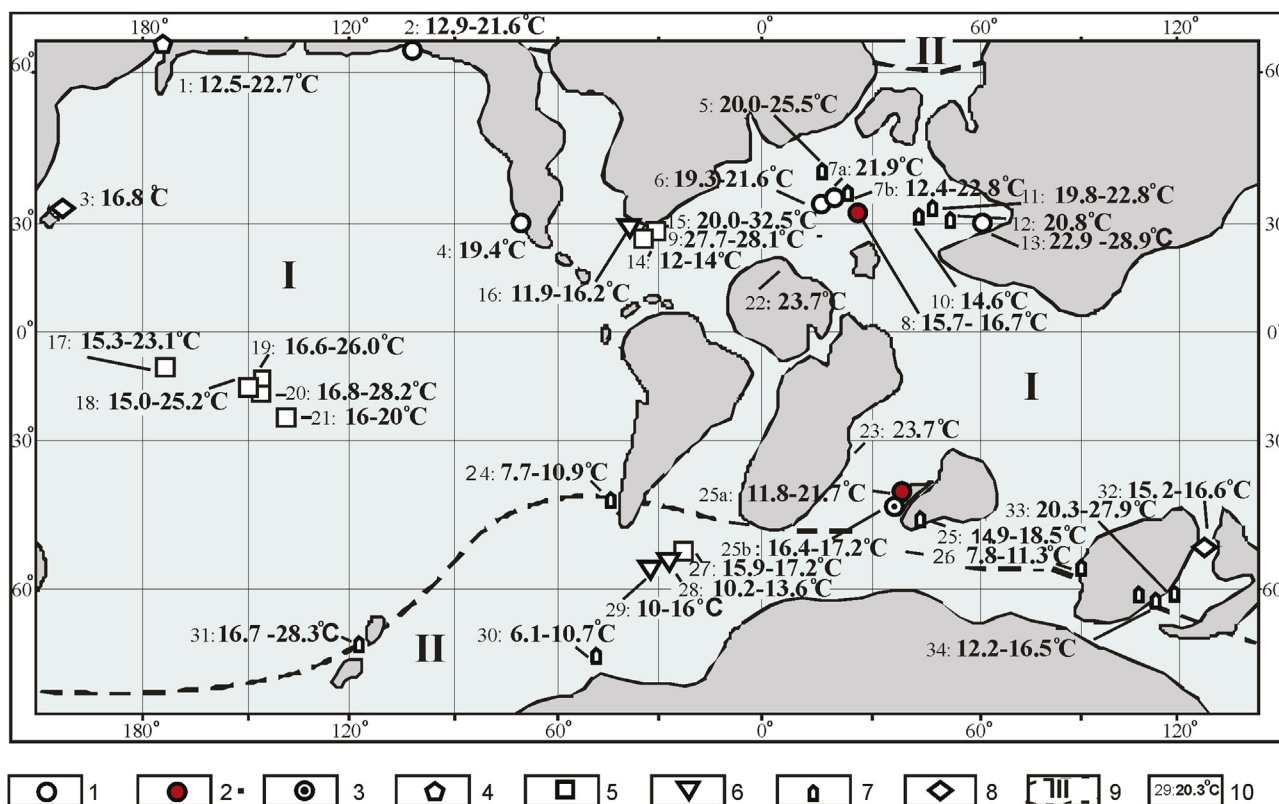
Fig. 8. Map showing isotopic palaeotemperatures for the Albian. 1 and 2 — from ammonoid shells: 1 — original data, 2 — published data, 3 — from nautiloid shells (original data), 4 — from brachiopod shells (published data), 5 — from planktic foraminifera (literary data), 6 — from benthic foraminifera (literary data), 7—8 — from belemnite rostra: 7 — literary data, 8 — original data, 9 — from bivalve shells (literary data), 10 — climatic zones (I — tropical-subtropical, II — warm-temperate), 11 — locality number and palaeotemperature. Localities: 1 — Melkaya River — late Albian (Zakharov, Shigeta, Tanabe et al., 2006), 2 — South Alaska — early Albian (Zakharov et al., 2011), 3 — Horokanai area, Hokkaido — late Albian (Zakharov, Shigeta, Tanabe et al., 2006), 4 — Shaeta county, California — Albian (Lowenstam, Epstein, 1959), 5 — England — Albian (Bowen, 1961), 6 — Northern France, Normandy — early Albian (Zakharov, Shigeta, Tanabe et al., 2006), 7 and 8 — Northern France, Pas de Calais — middle Albian (Zakharov, Shigeta, Tanabe, et al., 2006): 7 — from ammonoid shell, 8 — from belemnite rostra, 9 — Southern France Albian (Bowen, Fontes, 1963), 10 and 11 — Crimea (Teiss, Naidin, 1973): 10 — early Albian, 11 — late Albian, 12 — Kheu River, North Caucasus (Teiss, Naidin, 1973), 13 —Mangyshlak — late early and late Albian ammonoids (Zakharov, Shigeta, Tanabe, et al., 2006, 14—16 — Blake Nose (Erbacher et al., 2001; Norris and Wilson, 1998; Huber et al., 2002).

dwellers. Among them are middle Gzhelian *Aristoceras* (Zakharov et al., 2001); Callovian *Toricellites*? (Zakharov et al., 2001; Zakharov, Smyshlyaeva, Shigeta, et al., 2006); early Aptian *Deshaesites, Sinzovia, Proaustraliceras* and *Volgoceratoides* (Zakharov, Shigeta, Nagendra, 2011); late Aptian *Hypacanthoplites* (Lukeneder et al., 2010); early Albian *Phylloceras, Eotetragonites, Aconeceras, Puzosia, Beudanticeras, Neosilesites, Desmoceras, Cleoniceras, Douvilleiceras* (Zakharov, Baraboshkin, et al., 2013; this study); Santonian *Nowakites* (Lukeneder et al., 2010); early Cenomanian *Acanthoceras* and late Cenomanian *Euomphaloceras* (Henderson & Price, 2012); Coniacian *Kosmaticeras, Scaphites, Yezoites, Pachydesmoceras, Hauriceras* and *Protexanites* (Zakharov et al., 2012) and late Santonian *Pseudoschloenbachia* (Zakharov, Haggart, et al., 2013); early Campanian *Polyptychoceras, Yokayamaoceras, Sumortoniceras*; late Campanian *Baculites* (Zakharov, Smyshlyaeva, Popov, et al., 2006); Maastrichtian *Sphenodiscus, Hoploscaphites* and *Discoscaphites* (Cochran et al., 2003). The early Callovian *Cadoceras* seems to be a representative of this group.

This list demonstrates that group 2 is obviously heterogeneous, because it is represented by two major morphogroups, the planispirals and the heteromorphs (Westermann, 1996). Among typical representatives of planispiral ammonoids of this group can be indicated the *Douvilleiceras* from the lower Albian of Madagascar, a strongly ribbed inhabitant of the upper epipelagic zone. According to stable isotope data, both heteromorphs and planispirals likely preferred very similar near bottom temperature conditions in the shelf, mainly like those of benthic dwellers

(Landman, Cobban, & Larson, 2012; Moriya, 2015; Moriya et al., 2003; Smyshlyaeva et al., 2002; Zakharov et al., 2004; Zakharov et al., 2005; Zakharov, Shigeta, Smyshlyaeva, et al., 2006; Zakharov, Smyshlyaeva, Popov, et al., 2006; Zakharov et al., 2012), but characterised by different modes of life. Some ammonoids from this group were euryhaline (e.g., Cochran et al., 2003; Tsujita & Westermann, 1998; Westermann, 1996; Zakharov et al., 1975; Zakharov, Boriskina, Cherbadzhi, et al., 1999; Zakharov, Shigeta, Tanabe, et al., 2006; Zakharov et al., 2014; Zaborski, 1982), which might have been reflected in their behaviour (e.g., longer horizontal migrations within the epipelagic zone to find food resources).

Judging from information on the ontogenetic history of some of them (e.g., *Hypacanthoplites* (Lukeneder et al., 2010), *Baculites* (Fatherree, Harries, & Quinn, 1998) and *Perispinctes*; Lécuyer & Bucher, 2006), representatives of this group continued to live within the epipelagic zone after hatching at shallower depths of the same zone. Therefore their possible vertical migrations might have been significantly more restricted as compared with those of representatives of group 1, as well as with the living nautilids. Group 2 has not, apparently, the corresponding analogues in modern ectocochleate and endocochleate cephalopods.

6. Conclusions

1. New oxygen isotope data derived from finely preserved early Albian ammonoids confirm our previous suggestion that Madagascar was in middle latitudes during Albian time, within

the tropical-subtropical climatic zone. Albian palae-otemperatures interpreted as summer values for epipelagic waters in Madagascar are similar with those calculated from isotopic composition of early Albian cephalopods from northern middle palaeolatitude areas (Normandy, Pas de Calais and central Germany). Early Albian seasonal temperature variations in the presumed upper epipelagic zone of the Madagascar marine basin were close to the 6.2 °C range, and relatively strong when compared to the 2.1—4.2 °C range calculated for the upper and middle parts of the presumed mesopelagic zone of this basin.

2. New isotopic data suggest a more or less pronounced carbon and strontium isotope stratification of the Madagascar sea during the early Albian. Judging from our data, among the middle mesopelagic, upper mesopelagic, lower epipelagic and upper epipelagic zones, provisionally recognised on the basis of the $\delta^{18}O$ data, the latter is characterised by highest $\delta^{13}C$ values and ^{87}Sr—^{86}Sr ratios (up to 1.2‰ and 0.707296, respectively). However, their values and ratios are much lower in the *Eotetragonites* and some other ammonoid shells (<−0.1‰ and 0.707241, respectively), secreted most likely in the upper mesopelagic zone.

3. Most ammonoids from the Ambarimaninga Formation inhabited apparently the epipelagic zone of the early Albian Madagascar sea (group 1), but some representatives of the families Phylloceratidae (*Phylloceras*), Tetragonitidae (*Eotetragonites*), and Silesitidae (*Neosilesites*) preferred deeper, cooler conditions of the presumed middle and upper mesopelagic zones (group 2).

Acknowledgements

References

Auclair, A.-C., Lécuyer, C., Bucher, H., & Sheppard, S. (2004). Carbon and oxygen isotope composition of *Nautilus macromphalus*: a record of thermocline water off New Caledonia. *Chemical Geology, 207*, 91—100.

Baraboshkin, E. J., Naidin, D. P., Benjamovski, V. N., Herman, A. B., & Akhmetiev, M. A. (2007). *Prolivy severnogo polushariya v melu i paleogene (Northern hemisphere seaways in Cretaceous and Paleogene)*. Moscow: Publishing House of Geological Faculty of Moscow State University, 182 pp. (in Russian).

Bogorov, V. G. (1974). *Plankton Mirovogo okeana (Plankton of the World ocean)*. Moscow: Nauka, 320 pp. (in Russian).

Carlson, B. A., McKibben, J. N., & de Gruy, M. V. (1984). Telemetric investigation of vertical migration of *Nautilus belauensis*. *Pacific Science, 38*, 183—188.

Cochran, J. K., Landman, N. H., Turekian, K. K., Michard, A., & Schrag, D. P. (2003). Paleoceanography of the Late Cretaceous (Maastrichtian) Western Interior Seaway of North America: evidence from Sr and O isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology, 191*, 45—64.

Cochran, J. K., Rye, D. M., & Landman, N. H. (1981). Growth rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. *Paleobiology, 7*, 469—480.

Collignon, M. (1932). Les Ammonites pyriteuses de l'Albien supérieur du Mont Raynaud de Madagascar. *Annales Géologiques du Service des Mines, Madagascar, 2*, 2—36.

Collignon, M. (1933-1934). Paléontologie de Madagascar XX — Les cephalopods du Trias inférieur. *Annales de Paléontologie, 22—23*, 151—180, 1—43.

Collignon, M. (1949). Recherches sur les faunas Albiennes de Madagascar. I. L'Albien d'Ambbarimaninga (Madagascar). *Annales Géologiques du Service des Mines, Madagascar, 16*, 1—28.

Collignon, M. (1950a). Recherches sur les faunas Albiennes de Madagascar. III. L'Albien de Komihevitra (Cercle de Soalala). *Annales Géologiques du Service des Mines, Madagascar, 17*, 19—54.

Collignon, M. (1950b). Recherches sur les faunas Albiennes de Madagascar. IV. L'Albien de Mokaraha (Cercle de Soalala). *Annales Géologiques du Service des Mines, Madagascar, 17*, 55—85.

Collignon, M. (1963). Atlas des fossils caractéristiques de Madagascar (Ammonites), Albian. *Service Géologique Tananariver, 10*, 1—184.

Coplen, T. B., Kendall, C., & Hopple, J. (1983). Comparison of stable isotope reference samples. *Nature, 302*, 236—238.

Davis, A. C., Bickle, M. J., & Teagle, D. A. H. (2003). Imbalance in the oceanic strontium budget. *Earth and Planetary Science Letters, 66*, 191—213.

Endmond, J. M. (1992). Himalayan tectonics, wethering processes, and the strontium isotope record in marine limestones. *Science, 258*, 1594—1597.

Fabricius, F., Friedrichsen, H., & Jacobshagen, V. (1970). Paläotemperaturen und Paläoklima in Obertrias und Lias der Alpen. *Geologische Rundschau, 59*(2), 805—826.

Fatherree, J. W., Harries, P. J., & Quinn, T. M. (1998). Oxygen and carbon isotopic "dissection" of *Baculites comptessus* (Mollusca: Cephalopoda) from Pierre Shale (Upper Campanian) of South Dakota: implications for paleoenvironmental reconstructions. *Palaios, 13*, 376—385.

Grossman, E. L., & Ku, T.-L. (1986). Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effect. *Chemical Geology, 59*, 59—74.

Harding, ShC., Nash, B. P., Petersen, E. U., Ekdale, A. A., Bradbury, ChD., & Dyar, M. (2014). Mineralogy and geochemistry of the Main Glauconite bed in the Middle Eocene of Texas: paleoenvironmental implications for the Verinr facies. *PLOS One, 9*(2). http://dx.doi.org/10.1371/journal.pone.0087656.

Hart, M., Amédro, F., & Owen, H. (1996). The Albian stage and substage boundaries. *Bulletin de l'Institut Royal des Sciences Natutales de Belgique, 6*, 45—56.

Hayasaka, S., Oki, K., Tanabe, K., Saisho, T., & Shinomiya, A. (1987). On the habitat of *Nautilus pompilius* in Tanon Strait (Phillippines) and the Fiji Island. In B. Saunders, & N. H. Landman (Eds.), *Nautilus* (pp. 179—200). New York: Plenum Press.

Henderson, R. A., & Price, G. D. (2012). Paleoenvironment and paleoecology inferred from oxygen and carbone isotopes of subtropical mollusks from the Late Cretaceous (Cenomanian?) of Bathurst Island, Australia. *Palaios, 27*, 617—626.

Hewitt, R. A., & Westermann, G. E. G. (1990). Nautiloid shell strength:variance as an indicator of habitat depth limits. *Neues Jahrbuch für Geologic Paläontologie Abh, 179*, 73—97.

Huber, B. T., Norris, R. D., & MacLeod, K. G. (2002). Deep-sea paleotemperature record of extreme warmth during the Cretaceous. *Geology, 30*, 123—126.

Hudson, J. D., & Anderson, T. F. (1989). Ocean temperatures and isotopic compositions through time. *Transactions of the Royal Society of Edinburgh: Earth Sciences, 80*, 183—192.

Jenkyns, H. C., Paull, C. K., Cummins, D. I., & Fullagar, P. D. (1995). Strontium—isotope stratigraphy of Lower Cretaceous atoll carbonates in the mid-Pacific Mountains. In E. L. Winterer, W. W. Sager, J. V. Firth, & J. M. Sinton (Eds.), *Proceedings of the ocean drilling program, scientific results 143* (pp. 89—97).

Jones, C. E., & Jenkyns, H. C. (2001). Seawater strontium isotopes, oceanic anoxic events, and seafloor hydrothermal activity in the Jurassic and Cretaceous. *American Journal of Science, 301*, 112—149.

Jordan, R., & Stahl, W. N. (1970). Isotopische Paläotemperatur-Bestimmungen an jurassischen Ammoniten und grudsätzliche Voraussetzungen für diese Methode. *Geologisches Jarbuch, 89*, 33—62.

Kaltenegger, W., Preisinger, A., & Rögl, F. (1971). Palaeotemperature determinations of aragonitic mollusks from the Alpine Mesozoic. *Palaeogeogrraphy, Palaeoclimatology, Palaeoecology, 10*, 273—291.

Kannie, Y., Fukuda, Y., Akayama, H., Seki, H., & Hattori, M. (1980). Implosion of living *Nautilus* under increased pressure. *Paleobiology, 6*, 44—47.

Kiel, S. (2006). New and little-known gastropods from the Albian of the Mahajanga Basin, Northwestern Madagascar. *Journal of Paleontology, 80*(3), 455—476.

Landman, N. H., Cobban, W. A., & Larson, N. I. (2012). Mode of life and habitat of scapitid ammonoids. *Geobios, 45*, 87—98.

Landman, N. H., Cochran, J. K., Rye, D. M., Tanabe, K., & Arnold, J. M. (1994). Early life history of *Nautilus*: evidence for isotopic composition of an aquarium-reared specimen. *Paleobiology, 20*, 40—51.

Lécuyer, C., & Bucher, H. (2006). Stable isotope compositions of a Late Jurassic ammonite shell: a record of seasonal surface water temperatures in the southern hemisphere? *Earth, 1*, 1—7.

Luger, P., Gröschke, M., Bussmann, M., Dina, A., Mette, W., Uhmann, A., et al. (1994). Comparison of the Jurassic and Cretaceous sedimentary cycles of Somalia and Madagascar: implications for the Gondwana breakup. *Geologische Rudschau, 83*, 711—727.

Lukeneder, A. (2015). Ammonoid habitats and life history. In C. Klug, D. Korn, K. De Baets, I. Kruta, & R. H. Mapes (Eds.), *Ammonoid paleobiology: From anatomy to ecology. Topics in Geobiology 43* (pp. 697—800). Dordrecht: Springer. http://dx.doi.org/10.1007/978-94-017-9630-9_18. chap. 18.

Lukeneder, A., Harzhauser, M., Müllegger, S., & Piller, W. E. (2010). Ontogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($\delta^{18}O$, $\delta^{13}C$). *Earth and Planetary Science, 296*, 103—114.

Madhavaraju, J., Scott, R. W., Lee, Y. I., Bincy, K. S., González-León, C. M., &

Ramasamy, S. (2015). Facies, biostratigraphy, and depositional environments of Lower Cretaceous strata, Sierra San José section,Sonora (Mexico). *Carnets de Géologie, 15*(10), 103–122.

Makridin, V. P. (1964). *Brachiopody yurskikh otlozhenij Russkoj Platformy i nekotorykh prilegayuschikh k nei oblastei (Brachiopods from Jurassic sediments of the Russian Platform and some adjacent areas)*. Moscow: Izdatel'stvo "Nedra", 396 pp. (in Russian).

Moriya, K. (2015). Isotope signature of ammonoid shells. In C. Klug, D. Korn, K. De Baets, I. Kruta, & R. H. Mapes (Eds.), *Ammonoid paleobiology: From anatomy to ecology. Topics in Geobiology 43* (pp. 801–844). Dordrecht: Springer. http://dx.doi.org/10.1007/978-94-017-9630-9_19. chap. 19.

Moriya, K., Nishi, H., Kawahata, H., Tanabe, K., & Takayanagi, Y. (2003). Demersal habitat of Late Cretaceous ammonoids: evidence from oxygen isotopes for the Campanian (Late Cretaceous) northwestern Pacific thermal structure. *Geology, 31*(2), 167–170.

Oba, I., Kai, M., & Tanabe, K. (1992). Early life history and habitat of *Nautilus pompilius* inferred from oxygen isotope examinations. *Marine Biology, 113*, 211–217.

Owen, H. G. (1999). Correlation of Albian European and Tethyan ammonite zonations and boundaries of the Albian Stage and substages: some comments. *Scripya Geologica, 3*, 129–149. Special Issue.

Peterman, Z. E., Hedge, C. E., & Tourtelot, H. A. (1970). Isotopic composition of strontium in sea water throughout Phanerozoic time. *Geohimica et Cosmochimica Acta, 34*, 105–120.

Pirrie, D., & Marshall, J. D. (1990). High-paleolatitude Late Cretaceous paleotemperatures: new data from James Ross Island. *Antarctic Geology, 18*, 31–34.

Pirrie, D., Marshall, J. D., Doyle, P., & Riccardi, A. C. (2004). Cool early Albian climates; new data from Argentina. *Cretaceous Research, 25*, 27–33.

Podlaha, O. G., Mutterlose, J., & Veizer, J. (1998). Preservation of δ18O and δ13C in belemnite rostra from the Jurassic/Early Cretaceous successions. *American Journal of Science, 298*, 324–347.

Price, G. D., & Hart, M. B. (2002). Isotopic evidence for Early to mid-Cretaceous ocean temperature variability. *Marine Micropaleontology, 46*, 45–58.

Shackleton, N. J., & Kennet, J. P. (1975). Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation. Oxygen and carbon isotope analyses in DSDP Sites 277, 279 and 281. In J. P. Kennett, R. E. Houtz, et al. (Eds.), *Initial reports of the deep sea drilling project 29* (pp. 743–756). Washington: U.S. Government Printing Office.

Smyshlyaeva, O. P., Zakharov, Y. D., Shigeta, Y., Tanabe, K., Ignatiev, A. V., Velivetskaya, T. A., et al. (2002). Optimal temperatures of growth in Campanian ammonoids of Sakhalin (Krilyon) and Hokkaido oxygen and carbon isotope data. In *The IV International Symposium of International Geological Correlation Program Project 434-Cretaceous continental margin of East Asia: Stratigraphy, sedimentation, and tectonics. Program and abstracts, Khabarovsk* (pp. 97–98).

Saunders, W. B., & Spinosa, C. (1979). *Nautilus* movement and distribution in Palau, western Caroline Island. *Science, 204*, 1199–1201.

Saunders, W. B. (1983). Natural rates of growth and longevityof *Nautilus belauensis. Paleobiology, 9*, 280–288.

Stahl, W., & Jordan, R. (1969). General considerations on isotopic paleotemperature determinations and analyses on Jurassic ammonites. *Earth and Planetary Science Letters, 6*, 173–178.

Stampfli, G. M., & Borel, G. D. (2002). A plate tectonic model for the Paleozoic and Mesozoic constrained by dynamic plate boundaries and restored synthetic oceanic isochrones. *Earth and Planetary Science Letters, 186*, 17–33.

Stevens, G. R., & Clayton, R. N. (1971). Oxygen isotope studies on Jurassic and Cretaceous belemnites from New Zealand and their biogeographic significance. *New Zealand Journal of Geology and Geophysics, 14*, 829–897.

Stevens, K., Mutterlose, J., & Wiedenroth, K. (2015). Stable isotope data (δ18O, δ13C) of the ammonite genus *Simbirskites*—implications for habitat reconstructions of extinct cephalopods. *Palaeogeography, Palaeoclimatology, Palaeoecology, 417*, 164–175.

Sælen, G. (1989). Diagenesis and construction of the belemnite rostrum. *Palaeontology, 32*, 765–797.

Tsujita, C. J., & Westermann, G. E. G. (1998). Ammonoid habitats and habits in the Western Interior Seaway: a case study from the Upper Cretaceous Bearpaw Formation of southern Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology, 144*, 135–160.

Voigt, S., Wilmsen, M., Mortimore, R. N., & Voigt, T. (2003). Cenomanian palaeotemperatures derived from the oxygen isotopic composition of brachiopods and belemnites: evaluation of Cretaceous palaeotemperature proxies. *International Journal of Earth Science (Geologische Rundschau), 92*, 285–299.

Ward, P., Carlson, B., Weekly, M., & Brumbaugh, B. (1984). Remote telemetry of daily vertical and horizontal movement of *Nautilus* in Palau. *Nature, 309*, 248–250.

Webby, B. D., & Van Den Houvel, H. B. (1965). Note on glauconitic sandstones in the Wayrara, New Zealand. *New Zealand Journal of Geology and Geophysics, 8*(1), 81–84.

Westermann, G. E. G. (1982). The connecting rings of *Nautilus* and Mesozoic ammonoids: implications for ammonoid bathymetry. *Lethaia, 16*, 373–384.

Westermann, G. E. G. (1996). Ammonoid life and habitat. In N. H. Landman, K. Tanabe, & R. A. Davis (Eds.), *Ammonoid Paleobiology. Topics in Geobiology 13* (pp. 607–707). New York: Plenum Press.

Westermann, G. E. G., & Ward, P. D. (1980). Septum morphology and bathymetry in cephalopods. *Paleobiology, 6*, 48–50.

Wright, C. W., Callomon, J. H., & Howarth, M. K. (1996). *Treatise on invertebrate paleontology. Part L. Mollusca 4, revised* (Vol. 4). The Geological Society of America and the University of Kansas. Cretaceous Ammonoidea 362 pp.

Zaborski, P. M. P. (1982). Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bulletin of the British Museum Natural History (Geology), 36*, 303–332.

Zakharov, Y. D. (1978). *Rannetriasovye ammonoidei vostoka SSSR (Early Triassic ammonoids of the east USSR)*. Moscow: Izdatel'stvo "Nauka", 224 pp. (in Russian).

Zakharov, Y. D., Baraboshkin, E. Y., Weissert, H., Michailova, I. A., Smyshlyaeva, O. P., & Safronov, P. P. (2013). Late Barremian–early Aptian climate of the northern middle latitudes: stable isotope evidence from bivalve and cephalopod molluscs of the Russian Platform. *Cretaceous Research, 44*, 183–201.

Zakharov, Y. D., Boriskina, N. G., Cherbadzhi, A. K., & Popov, A. M. (1999). Main trends in Permo-Triassic shallow-water temperature changes: evidence from oxygen isotope and Ca–Mg ratio data. *Albertiana, 23*, 11–22.

Zakharov, Y. D., Boriskina, N. G., Ignatyev, A. V., Tanabe, K., Shigeta, Y., Popov, A. M., et al. (1999). Palaeotemperature curve for the Late Cretaceous of the northwestern circum-Pacific. *Cretaceous Research, 20*, 685–997.

Zakharov, Y. D., Boriskina, N. G., & Popov, A. M. (2001). *Rekonstruktsiya uslovij morskoj sredy pozdnego paleozoya i mezozoya po izotopnym dannym (na primere severa Evrazii) (The reconstruction of Late Palaeozoic and Mesozoic marine environments from isotopic data: Evidence from north Eurasia)*. Vladivostok: Izdatel'stvo "Dalnauka", 112 pp. (in Russian).

Zakharov, Y. D., Haggart, J. W., Beard, G., & Safronov, P. P. (2013). Late Cretaceous climatic trends and a positive carbon isotope excursion at the Santonian-Campanian boundary in British Columbia. *Sedimentary Geology, 295*, 77–92.

Zakharov, Y. D., Ignatiev, A. V., Velivetskaya, T. A., Smyshlyaeva, O. P., Tanabe, K., Shigeta, Y., et al. (2004). Early-Late Cretaceous climate of the northern high latitudes. *Journal of the Geological Society of Thailand, 1*, 11–34.

Zakharov, Y. D., Naidin, D. P., & Teiss, R. V. (1975). Oxygen isotope composition of Early Triassic cephalopod shells of Arctic Siberia and salinity of the boreal basins at the beginning of Mesozoic. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya, 4*, 101–113 (in Russian).

Zakharov, Y. D., Sha, J., Popov, A. M., Safronov, P. P., Shorochova, S. A., Volynets, E. B., et al. (2009). Permian to earliest cretaceous climatic oscillations in the eastern Asian continental margin (Sikhote-Alin area), as indicated by fossils and isotope data. *GFF, 131*, 25–47.

Zakharov, Y. D., Shigeta, Y., Nagendra, R., Safronov, P. P., Smyshlyaeva, O. P., Popov, A. M., et al. (2011). Cretaceous climate oscillations in the southern palaeolatitudes: new stable isotope evidence from India and Madagascar. *Cretaceous Research, 32*, 623–645.

Zakharov, Y. D., Shigeta, Y., Smyshlyaeva, O. P., Popov, A. M., Velivetskaya, T. A., & Afanasyeva, T. B. (2011). Cretaceous climatic oscillations in the Bering area, Alaska and Koryak Upland: isotope and palaeontological evidences. *Sedimentary Geology, 235*, 122–131.

Zakharov, Y. D., Shigeta, Y., Smyshlyaeva, O. P., Popov, A. M., Velivetskaya, T. A., Popov, A. M., et al. (2006). Relationship between δ13C and δ18O values of the recent Nautilus and brachiopod shells in the wild and problem of reconstruction of fossil cephalopod habitat. *Geosciences Journal, 10*, 325–338.

Zakharov, Y. D., Shigeta, Y., Tanabe, K., Iba, Y., Smyshlyaeva, O. P., Sokolova, E. A., et al. (2006). Campanian climatic change: isotopic evidence from Far East, North America, North Atlantic and western Europe. *Acta Geologica Sinica, 81*(6), 1049–1069.

Zakharov, Y. D., Smyshlyaeva, O. P., Popov, A. M., & Shigeta, Y. (2006). *Izotopnyj sostav pozdnemezozojskikh organogennykh karbonatov Dalnego Vostoka (stabilnye izotopy kisloroda i ugleroda, osnovnye paleoklimaticheskiye sobytiya i ikh globalnaya korrelyatsiya) (Isotopic composition of Late Mesozoic organogenic carbonates of Far East (oxygen and carbon isotopes, palaeoclimatic events and their global correlation))*. Vladivostok: Izdatel'stvo "Dalnauka", 204 pp. (in Russian).

Zakharov, Y. D., Smyshlyaeva, O. P., Popov, A. M., Velivetskaya, T. A., Afanasyeva, T. B., Tanabe, K., et al. (2012). Pole to equator temperature gradient for Coniacian, Late Cretaceous: oxygen and carbon isotope data on the Koryak Upland and Hokkaido. *Journal of Earth Science, 23*(1), 19–32. http://dx.doi.org/10.007/s12583-012-0230-0.

Zakharov, Y. D., Smyshlyaeva, O. P., Shigeta, Y., Popov, A. M., & Zonova, T. D. (2006). New data on isotopic composition of Jurassic – Early Cretaceous cephalopods. *Progress in Natural Science, 16*, 50–67 (Special Issue).

Zakharov, Y. D., Smyshlyaeva, O. P., Tanabe, K., Shigeta, Y., Maeda, H., Ignatiev, A. V., et al. (2005). Seasonal temperature fluctuations in the high northern latitudes during the Cretaceous period: isotopic evidence from Albian and Coniacian shallow-water invertebrates of the Talovka River Basin, Koryak Upland, Russian Far East. *Cretaceous Research, 26*, 113–132.

Zakharov, Y. D., Tanabe, K., Safronov, P. P., & Smyshlyaeva, O. P. (2014). New data on microstructure and isotopic composition of some cephalopods from the Upper Cretaceous of North America and Europe: significance for oxygen isotope palaeotemperature measurements. In B. Berning, & A. Lukeneder (Eds.), *Studies on fossil and recent cephalopods. Denesia 32* (pp. 113–132).

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2015.08.014