

Relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the Recent *Nautilus* and brachiopod shells in the wild and the problem of reconstruction of fossil cephalopod habitat

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ABSTRACT: Ontogenetic change in $\delta^{18}\text{O}$ values of the investigated *Nautilus pompilius* Linne shell in the Philippines (Tagnan, Panglao Islands, Bohol Island area) confirms data, in which *Nautilus* in the wild shows a marked increase in oxygen isotopic composition between embryonic and post-embryonic stages. The increase in $\delta^{18}\text{O}$ in post-embryonic septa reflects a migration into colder, deeper (about 300 m) waters. Judging from the isotopic composition of aboral and adoral parts of the last septum, the amplitude of the short term vertical migration for the investigated sample seems to be about 70 m. Relative fluctuation in $\delta^{13}\text{C}$ values for the living *Nautilus*, as well as living brachiopods, might be connected with annual cycles of the phytoplankton development. The negative $\delta^{13}\text{C}$ excursion (-2.5%) fixed in the septa 9 of the investigated *Nautilus pompilius* shell seems to be connected with a weakening of phytoplankton bioproductivity related to low solar activity. It is suggested that ammonoids, like living *Nautilus* spent the most part of their lives near the sea-floor but unlike *Nautilus* and late Cretaceous belemnites they did not experience, apparently, significant short-term vertical migration.

Key words: *Nautilus*, ammonoids, oxygen isotopic composition, vertical migration

1. INTRODUCTION

Nautilus is a living cephalopod, which has been used by a lot of workers to provide clues into the life habit of extinct groups such as the ammonoids (Landman et al., 1989a,b). But cladistic analyses (Berthold and Engeser, 1987; Engeser, 1990; 1996) and some paleontological data (Schindewolf, 1933; Flower, 1961; Erben, 1966; Zeiss, 1969; House, 1981; Jacobs and Landman, 1993) both indicate that ammonoids are more closely related to modern coleoids than to *Nautilus*, which was partly reflected, in their mode of life. Analysis of the chamber formation process in living *Nautilus* has been approached through a study of aquarium-reared specimens and the wild ones (Denton and Gilpin-Brown 1966; Martin et al., 1978; Collins et al., 1980; Ward and Martin,

1980; Ward et al., 1981; Westermann and Ward, 1980; Westermann 1982; Hewitt and Westermann, 1988; Oba et al., 1992; O'Dor et al., 1993).

Data on the oxygen-isotopic composition of *Nautilus* shells are present only in relatively few publications (e.g., Eichler and Ristedt, 1966; Cochran et al., 1981 Oba and Tanabe, 1983; Taylor and Ward, 1983; Spaeth and Hoefs, 1986; Ward, 1987; Oba and Kai, 1986; Oba et al., 1992; Landman et al., 1994), most of which do not look into the carbon isotopic composition.

All carbon isotope investigations of living *Nautilus* were made, using aquarium-reared specimens (Spaeth and Hoefs, 1986; Landman et al., 1994) and therefore the $\delta^{13}\text{C}$ data for the investigated specimens are difficult to explain. Spaeth and Hoefs (1986) obtained unusually low $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for investigated *Nautilus* because they were kept in sea water artificially prepared from dry salt dissolved in tap water with a $\delta^{18}\text{O}$ value of -8.2% . The complexities involved in carbon isotope composition were explained by multiple sources for carbon in the carbonate material secreted (air CO_2 pumped through the aquarium, dissolved bicarbonate in the tap water, carbonate in the salt used for the artificial sea water, calcium carbonate in the filter material, carbon from varying food sources). Landman et al. (1994) analyzed the carbon and oxygen isotopic composition of *Nautilus* raised in aquariums filled with natural sea-water ($\delta^{18}\text{O} = -0.20\%$). In this case, the $\delta^{13}\text{C}$ data are also difficult to explain because of multiple sources of carbon in aquarium conditions (Landman et al., 1994).

The primary purpose of this contribution is to show the relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of invertebrates in the wild and an attempt to reconstruct the mode of life of some fossil cephalopods (belemnites and ammonites).

2. MATERIAL AND METHODS

The specimen of *Nautilus pompilius* Linne shell, 101.2

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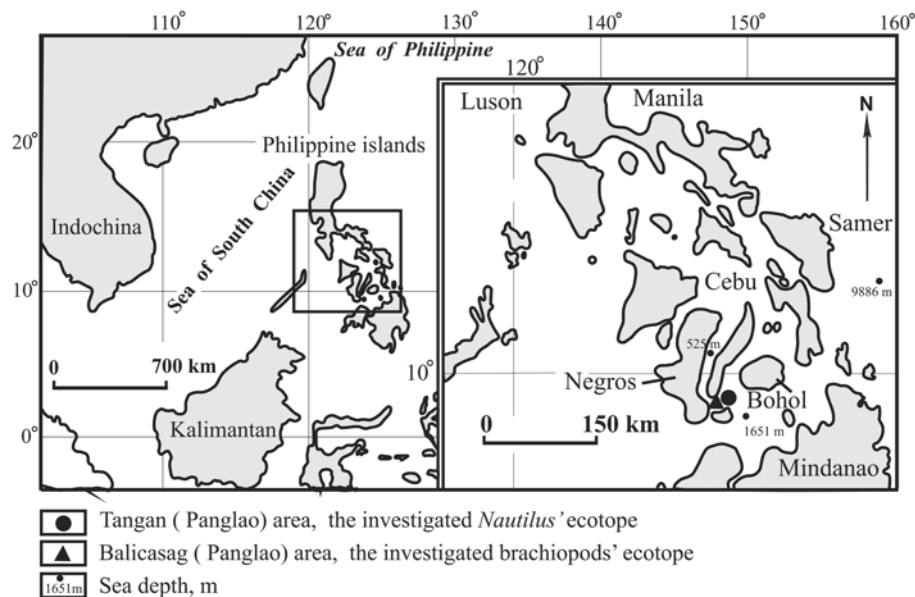


Fig. 1. Location of the Tagnan and Balicasag (Panglao, Philippine) areas.

mm in diameter, and three brachiopod shells were used in this study. *Nautilus pompilius* was obtained from the Philippines (Tagnan, Panglao Islands, Bohol Island area, south of Cebu; 9°37'N, 123°45'E) (Fig. 1) during Prof. Y. Saito and Y. Shigeta's expedition in March 26, 1999. It was captured at depths of 160–230 m characterized by temperatures of about 15–18°C. Additionally they collected brachiopods in the Balicasag (Panglao) area. Belemnite and ammonoid samples for isotope analysis in this study were mainly collected in the Ablain of France (Y.D. Zakharov's and Y. Shigeta's collections).

In the laboratory, the shell of *Nautilus pompilius* was cut along the median plane, and some amounts of powdered aragonite were sampled mainly from the septa (sample from each septum, with the exception of the 27th septum, where two samples were taken only from its aboral and adoral parts)(Fig. 2). Some amounts of calcite were sampled only from the secondary layers of pedicle and brachial valves and the ascending and descending parts of lophophore supports in living brachiopod shells.

Carbon and oxygen isotope measurements were made at the Analytical Center of the Far Eastern Geological Institute (FEGI), Vladivostok, using Finnigan MAT-252 mass spectrometer. The laboratory gas standard used in the measurements was calibrated relative to calcite NBS (National Bureau of Standards) 19 and equals $1.8 \pm 0.10\%$ for oxygen relative to VPDB (Vienna Pee Dee belemnite) and $-0.9 \pm 0.10\%$ for carbon. Reproducibility of replicate standards was always better than 0.10%.

Grossman and Ku's (1986) and Anderson and Arthur (1983) scales were used for temperature calculation. We utilize the biogenic aragonite equation (Grossman and Ku, 1986; Kobashi and Grossman, 2003; Kobashi et al., 2004) to convert the oxygen isotope composition of the investi-

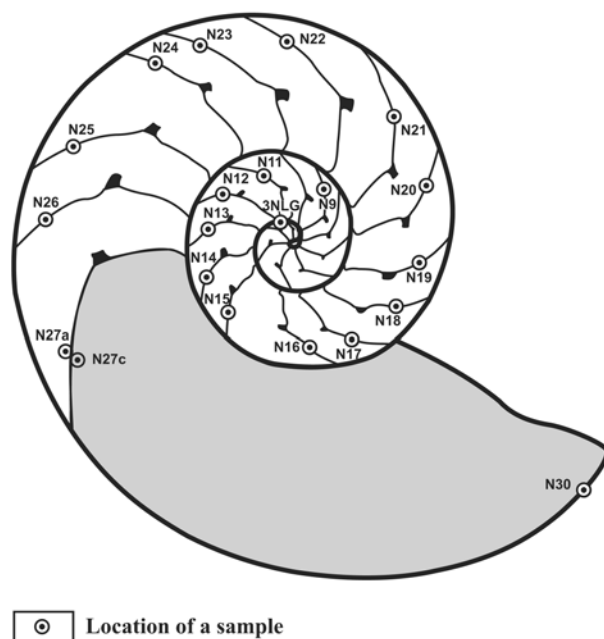


Fig. 2. Investigated *Nautilus pompilius* Linne shell from the Tagnan area and sample location.

gated *Nautilus pompilius* and Cretaceous ammonoid shells to temperature.

The equation is:

$$T (^{\circ}\text{C}) = 20.6 - 4.34 (\delta^{18}\text{O}_{\text{aragonite}} - \delta_w) \quad (1)$$

where $T (^{\circ}\text{C})$ is the ambient temperature, $\delta^{18}\text{O}_{\text{aragonite}} (\text{‰})$ is the oxygen isotope ratio of the aragonite (versus VPDB), and $\delta_w (\text{‰})$ is the $\delta^{18}\text{O}$ of the ambient water versus "average marine water" (Epstein et al., 1953). If δ_w are standardized to the Standard Mean Ocean Water (SMOW), the equation becomes:

$$T (^{\circ}\text{C}) = 19.7 - 4.34 (\delta^{18}\text{O}_{\text{aragonite}} - \delta_w) \quad (2)$$

To convert the oxygen isotope composition to living brachiopod shells and Cretaceous belemnite rostra to temperature the biogenic calcite equation of Anderson and Arthur (1983) was used:

$$T (^{\circ}\text{C}) = 16.0 - 4.14 (\delta^{18}\text{O}_{\text{aragonite}} - \delta_w) + 0.13 (\delta^{18}\text{O}_{\text{calcite}} - \delta_w)^2 \quad (3)$$

where $T (^{\circ}\text{C})$ is the ambient temperature, $\delta^{18}\text{O}_{\text{calcite}} (\text{‰})$ is the oxygen isotope ratio of the calcite (versus VPDB), and $\delta_w (\text{‰})$ is the $\delta^{18}\text{O}$ of the ambient water.

The depth profile of water temperatures for the Panglao area, Philippines, was obtained using the Oceanic Atlas published by Gorshokov (1974) (the δ_w for the sites, in which *Nautilus pompilius* and brachiopods lived, was estimated using the salinity - δ_w for Pacific waters (Craig and Gordon, 1965)):

Depth (m)	T ($^{\circ}\text{C}$)	Salinity (‰)	$\delta_w (\text{‰})$ (standardized to the VSMOW scale)
0	28.3	34.2	0.00
100	21.2	34.9	0.33
200	16.3	34.8	0.31
300	13.7	34.7	0.23
400	11.1	34.7	0.23
500	8.0	34.6	0.20

In calculating the temperatures from the isotopic composition of Cretaceous fossils, since icecaps were not present during most of the Cretaceous Period, a δ_w of -1.2‰ VPDB (equivalent to -1.0‰ VSMOW) was thought to be appropriate.

Microstructures of fossil cephalopods from Koryak Upland (Kamchatka area) and North France were investigated using the SEM (JSM-6300) of Nanjing Institute of Geology and Paleontology. X-ray analyses were carried out using a DRON-3 diffractometer.

3. STABLE ISOTOPE RESULTS

3.1. Carbon-isotope Composition

$\delta^{13}\text{C}$ values in the investigated *Nautilus pompilius* shell fluctuate from -2.5 to 1.5‰ (Table 1; Figs. 3 and 4). Most of the investigated septa is characterized by positive $\delta^{13}\text{C}$ values. Two negative $\delta^{13}\text{C}$ excursions are recognized: first one, most marked (-2.5‰), falls on the ninth septum, the second one (-0.4‰) on the 21st septum. The highest $\delta^{13}\text{C}$ value (1.5‰) has been determined in the wall of the near the aperture of the living chamber. The inner part of the shell wall between second and third septa which formed during the embryonic stage is characterized by negative $\delta^{13}\text{C}$ value (-0.9‰). For comparison carbon isotope values, recent living brachiopod shells have also been analyzed. Their $\delta^{13}\text{C}$ values vary from 0.2 to 0.8‰ (Table 2). Some

Table 1. Oxygen and carbon isotope analyses of the aragonite from a shell of the Recent *Nautilus pompilius* Linne (Philippines, near Bohol Island) and calculated temperatures.

Sample number	Location	$\delta^{13}\text{C}$ (VPDB) (‰)	$\delta^{18}\text{O}$ (VPDB) (‰)	T, $^{\circ}\text{C}$
3N LG	Inner prismatic layer of the lateral wall (between the 2 nd and 3 rd septa)	-0.9	-0.6	23.7
9N	9 th septum	-2.5	1.0	16.8
11N	11 th septum	-1.3	1.3	15.5
12N	12 th septum	-0.1	1.5	14.6
13N	13 th septum	0.0	1.3	15.5
14N	14 th septum	0.3	1.4	15.0
15N	15 th septum	0.2	1.6	14.2
16N	16 th septum	0.4	1.6	14.2
17N	17 th septum	0.4	1.5	14.6
18N	18 th septum	0.3	1.6	14.2
19N	19 th septum	0.5	1.5	14.6
20N	20 th septum	0.5	1.4	15.0
21N	21 st septum	-0.4	1.4	15.0
22N	22 nd septum	0.5	1.5	14.6
23N	23 rd septum	0.6	1.6	14.2
24N	24 th septum	1.0	1.6	14.2
25N	25 th septum	0.6	1.5	14.6
26N	26 th septum	1.0	1.7	13.7
27aN	27 th septum (aboral part represented by the nacreous layer)	1.0	1.2	15.9
27cN	27 th septum (adoral part represented by the inner prismatic layer)	1.3	1.6	14.1
30N	Living chamber wall (apertura)	1.5	1.0	16.8

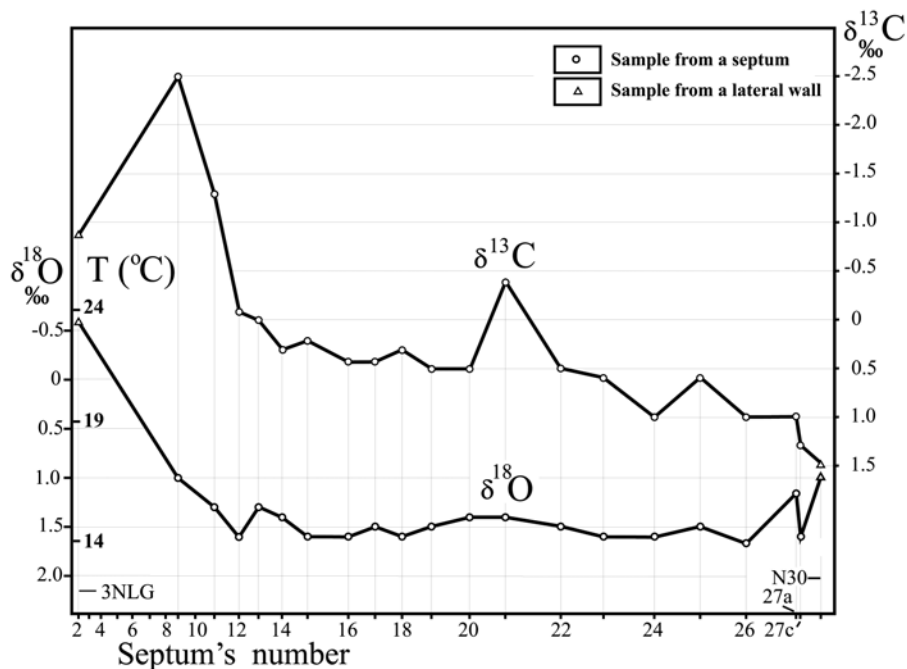


Fig. 3. Diagram showing distribution of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values obtained from aragonite samples of the *Nautilus pompilius* Linne shell from the Tanga area.

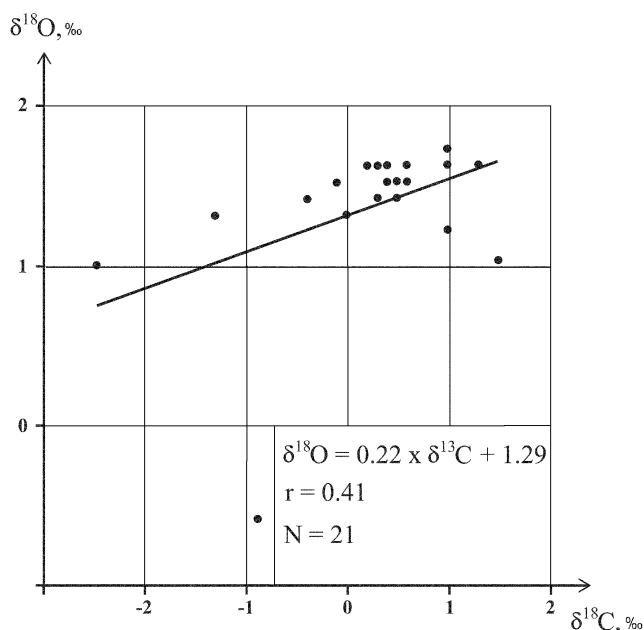


Fig. 4. Scatter plot and regression line for the *Nautilus pompilius* Linne shell from the Tanga area. r – correlation factor (coefficient), N – sample quantity.

results on carbon-isotopic composition of fossil cephalopods (Albain belemnites and ammonoids) are given in Tables 3 and 4 for comparative purposes.

3.2. Oxygen Isotope Composition

We have found that the $\delta^{18}\text{O}$ values of *N. pompilius*

embryonic shell between the 2nd and 3rd septa is negative (-0.6‰). In contrast, all of the 18 postembryonic septa and the distal portion of the living chamber are characterized by positive $\delta^{18}\text{O}$ values, between 1.0 and 1.7‰ (Fig. 3). The 27th septum (last septum) was investigated in detail: its aboral and adoral parts are characterized by different $\delta^{18}\text{O}$ values (1.2 and 1.6, respectively). $\delta^{13}\text{C}$ values in the living brachiopod shells from Balicaag Island area fluctuate between 0.3 to 1.0‰ (Table 2). The results of the oxygen-isotope analysis on some fossil cephalopod shells are given in Tables 3 and 4.

4. DISCUSSION

4.1. Isotopic Evidence on Vertical Migration

Laboratory data show that small and densely septate *Nautilus* specimens can grow from hatching to maturity in only three years, although wild specimens live for 10–15 and even 20 years (Hewitt and Westermann, 1988). The rate at which a *Nautilus* can make new chambers has been widely debated, but the maximum periodicity in chamber formation is determined by some authors differently: 1) 13–14 years on the average (Denton and Gilpin-Brown, 1966), 2) 30-day interval (29.4-day lunar month) (Kahn and Pomea, 1978) or much longer (48–72 days) (Martin et al., 1978; Collins et al., 1980; Ward et al., 1981) in the wild, 3) 50–80 days in an aquarium (Landman et al., 1989b). The first seven septa of wild *Nautilus* were built before hatching (Hewitt and Westermann, 1988), but in an aquarium, nine septa formed during the embryonic stage (Landman et al., 1994).

Table 2. Carbon and oxygen isotope analyses of the Recent brachiopod shells (Philippines, Balicasag Island area) and calculated temperatures

Sample number	Species	Location (L, in mm)	$\delta^{13}\text{C}$ (VPDB)	$\delta^{18}\text{O}$ (VPDB)	T, °C
			(‰)	(‰)	
Br-1-1	Dallinidae	Secondary layer, brachial valve (0.0–8.5)	0.5	0.5	15.3
Br-1-2	- « -	Secondary layer, brachial valve (19.0–22.5)	0.2	0.3	16.1
Br-1-3	- « -	Secondary layer, pedicle valve (34.5–36.1)	0.6	0.7	14.5
Br-1-4	- « -	Secondary layer; ascending branches of brachidium	0.7	0.9	13.7
Br-1-5	- « -	Secondary layer; descending branches of brachidium	0.8	0.9	13.7
Br-2-1	<i>Terebratulina</i> cf. <i>callinome</i> Dall	Primary and secondary layers, brachial valve (23.6–25.6)	0.6	1.0	13.9
Br-3-1	<i>Dallina</i> sp.	Primary and secondary layers, brachial valve (24.0–26.0)	0.8	0.7	14.5

Table 3. Carbon and oxygen isotope analyses of the middle Albian belemnite rostra calcite from the Saint-P Formation (Blanc Nez Cape, Boulonnais, France)

Sample number	Location (D, in mm)	Diagenetic alterations			$\delta^{13}\text{C}$ (VPDB), ‰	$\delta^{18}\text{O}$ (VPDB), ‰	T, °C
		Original calcite, %	Admixture	Colour			
LAM-2-2 (1 st rostrum)	External surface of the rostrum (5.0–5.5)	100	0	Colourless	1.3	-1.7	19.0
LAM-2-3 (same rostrum)	External surface of the rostrum (5–5.0.0)	100	0	Colourless	1.0	-1.0	16.0
LAM-2-4 (same rostrum)	External surface of the rostrum (4.5–5.0)	100	0	Colourless	1.5	-0.9	15.6
LAM-2-5 (2 nd rostrum)	External surface of the rostrum (3.5–4.0)	100	0	Colourless	1.8	-0.9	15.6
LAM-2-6 (same rostrum)	External surface of the rostrum (3.0–3.5)	100	0	Colourless	1.9	-0.8	15.2
LAM-2-7 (same rostrum)	External surface of the rostrum (2.5–3.0)	100	0	Colourless	1.8	-0.8	15.2
LAM-2-8 (3 rd rostrum)	External surface of the rostrum (1.7–2.5)	100	0	Colourless	1.4	-0.9	15.6
LAM-2-9 (same rostrum)	External surface of the rostrum 0.0–1.7	100	0	Colourless	1.3	-1.1	16.4
LAM-2-10	Surface of the rostrum alveolus (7.7–7.9)	100	α -SiO ₂ (trace)	Light-cream	2.1	-2.2	21.2
LAM-2-11 (same rostrum)	External surface of the rostrum (9.5)	100	α -SiO ₂ (trace)	Light-cream	2.2	-2.2	21.2
LAM-2-13	Surface of the rostrum alveolus (16.0)	100	0	White	1.5	-0.7	14.7
LAM-2-14 (4 th rostrum)	Surface of the rostrum alveolus (16.9)	100	0	Colourless	1.0	0.4	10.6
LAM-2-15 (5 th rostrum)	Surface of the rostrum alveolus (7.0)	100	0	White	1.1	-1.2	16.7
LAM-2-16 (same rostrum)	External surface of the rostrum (15.0)	100	0	Colourless	1.5	0.5	10.1
LAM-2-17 (chalk)	From the alveolus of the 4 th rostrum	-	0	White	2.0	-1.2	-
LAM-2-21 (6 th rostrum)	External surface of the rostrum (6.1–6.6)	100	0	Colourless	1.8	-0.8	15.2
LAM-2-22 (same rostrum)	5.8–6.1	100	0	Colourless	2.6	-0.2	12.8
LAM-2-23 (same rostrum)	External surface of the rostrum (5.2–5.8)	100	0	Colourless	2.6	-0.3	13.2
LAM-2-24 (same rostrum)	External surface of the rostrum (4.8–5.2)	100	0	Colourless	2.7	-0.3	13.2
LAM-2-25 (same rostrum)	External surface of the rostrum (4.2–4.8)	100	0	Colourless	2.6	-0.1	12.4
LAM-2-26 (same rostrum)	External surface of the rostrum (3.6–4.2)	100	0	Colourless	2.3	-0.2	12.8
LAM-2-27 (7 th rostrum)	External surface of the rostrum (3.0–3.6)	100	0	Colourless	2.0	-0.3	13.2
LAM-2-28 (8 th rostrum)	External surface of the rostrum (1.5–3.0)	100	0	Colourless	1.8	-0.2	12.8
LAM-2-29 (9 th rostrum)	External surface of the rostrum (0–1.5)	100	0	Colourless	1.3	-0.6	14.4
LAM-2-30 (10 th rostrum)	External surface of the rostrum (4.0)	100	0	Colourless	0.8	-1.0	16.0
LAM-2-31 (11 th rostrum)	External surface of the rostrum (3.5)	100	0	Colourless	-0.2	-2.1	20.7
LAM-2-32 (12 th rostrum)	External surface of the rostrum (3.7)	100	0	Colourless	0.9	-0.5	14.0
LAM-2-33 (13 rd rostrum)	External surface of the rostrum (3.5)	100	0	Colourless	1.7	-0.6	14.4
LAM-2-10 (14 th rostrum)	External surface of the rostrum, immediately below the thin (0.14 mm thick), white colour, calcitic plate (4.9–5.0)	100	0	Colourless	0.2	-0.7	14.7

Table 4. Carbon and oxygen isotope analyses of the Albian ammonoid shells from North France

Sample number	Species	Formation (member)	Location (H, in mm)	Diagenetic alterations				$\delta^{13}\text{C}$ (VPDB), (‰)	$\delta^{18}\text{O}$ (VPDB), (‰)	T , °C
				Diagenetic stage (Zakharov et al., 1975)	Aragonite (%)	Admixture α -SiO ₂	Colour			
LAM-2-19 (Blanc Nez Cape)	<i>Oxytropidoceras</i> sp.	Saint-Po (middle Albian)	Living chamber, adoral part (13.0)	2 nd	86±5	Trace	Greyish-cream	2.6	-1.5	21.9
FR-1 (Normandy)	<i>Otohoplites raulin-</i> <i>ianus</i> (d'Orbigny)	Middle Albian	Living chamber, adoral part (10.0)	1 st	100	Trace	Beige	1.2	-1.4	21.6
FR-2 (Normandy)	<i>Beudanticeras beu-</i> <i>danti</i> (Brongniart)	Upper Albian	Living chamber, adoral part (25.0)	1 st	100	None	Silvery-cream	-1.1	-0.9	19.3

A depth limit for the living *Nautilus* seems to be 800 m (Ward and Martin, 1980; Westermann and Ward, 1980; Kanie et al., 1980; Westermann 1982). They were usually captured in baited traps at 200 to 400 m depths but they live abundantly at depths of 500–600m (Ward et al., 1981; Hewitt and Westermann 1988; Oba et al., 1992; O'Dor et al., 1993). It is interesting to note that the shells implode when the cage is lowered to 730–900 m (Westermann and Ward, 1980).

Willey (1902) was the first to remark on the surprising ability of *Nautilus* for large daily vertical migration. According to the data of Ward et al. (1984) obtained using ultrasonic transmitters, in the Palau population of *Nautilus*, vertical depth changes of up to 200 m per day are common (the mean day and night depths of investigated individuals fluctuated from 120 to 441 m and from 87 to 321 m, respectively).

Eichler and Ristedt (1966) interpreted the anomalously light $\delta^{18}\text{O}$ values in septa 1 to 3 of the two Philippine *Nautilus pompilius* shells (about -2.2‰) as having originated in egg water. $\delta^{18}\text{O}$ values in 5th and 6th septa are about -2.7 and -1.6‰ , respectively. All later septa are characterized by larger $\delta^{18}\text{O}$ values, fluctuating from -0.1 to 1.2‰ . They proposed that after hatching, the *Nautilus* lived in shallow water, followed by a gradual migration to colder (14 – 16°C), deeper water. This is consistent with what many other investigators agree on now (Oba et al., 1992; Landman et al., 1994).

Cochran et al. (1981) and Taylor and Ward (1983), ascribed light $\delta^{18}\text{O}$ values in the first embryonic septa of *Nautilus pompilius* and *N. macromphalus* to non-equilibration between embryonic fluid and seawater, but they determined that *Nautilus* hatched in the wild after the secretion of the 7th septum. By contrast, Crocker et al. (1985) suggested that carbonates of *Nautilus* shells were precipitated in isotopic equilibrium with egg water before hatching in sea water and after hatching. Therefore, hatching depths of living *Nautilus* are almost equivalent to the preferred depths of the immediate postembryonic representatives.

It must be mentioned that Oba et al. (1992) believe that

anomalously light $\delta^{18}\text{O}$ values described by Eichler and Ristedt (1966) and Taylor and Ward (1983) in the first seven septa appear to be enhanced by propane (C_3H_8) produced and trapped on the lattice of the carbonate minerals during the laboratory roasting process of organic-rich samples. Such values indicating high isotopic temperatures ($>30^\circ\text{C}$) have not yet been detected in any of the non-roasted samples. All of the seven Philippine and Fiji *Nautilus pompilius* shells analyzed by Oba et al. (1992) show distinct change in $\delta^{18}\text{O}$ from light values on the first seven septa (corresponding to temperature of 25 – 28°C) to heavier values in the succeeding septa after hatching. According to Oba et al. (1992), the stepwise increase in $\delta^{18}\text{O}$ from septa 7 to 10 may in part reflect post-embryonic migration to deeper water.

Recently, Landman et al. (1994) confirmed the interpretation of Crocker et al. (1985) and Oba et al. (1992), analyzing the isotopic compositions of the septa of *Nautilus* raised in aquariums under controlled temperature conditions.

We investigated *N. pompilius* which lived during its embryonic stage at a temperature of about 23.7°C (Table 2, Fig. 5). The juvenile form with nine septa sank to a depth of about 200 m with temperature of water somewhat warmer than 16.8°C . After building the 10th and 11th septa, the *Nautilus* continued to sink reaching the water layer with a temperature of about 15.5°C . The next fourteen septa were built at temperatures of 14.2 – 15.5°C . Record in sinking (about 300 m) occurred when the 26th septum was formed (water temperature of 13.7°C). The aboral part of the 27th septum was built at a higher level (around 225 m depth) characterized by a temperature of 15.9°C . But its adoral part was formed in colder condition (14.2°C), where the septum was completed just after sinking an additional 70 meters. The aperture of the living chamber was built at warmer conditions (16.8°C), corresponding to a depth of 200 m. As mentioned above, the investigated *Nautilus* was caught at depths of about 180–250 m (15 – 18°C). All these facts demonstrate short-term vertical migration of investigated *Nautilus pompilius* with amplitude of several tens of meters.

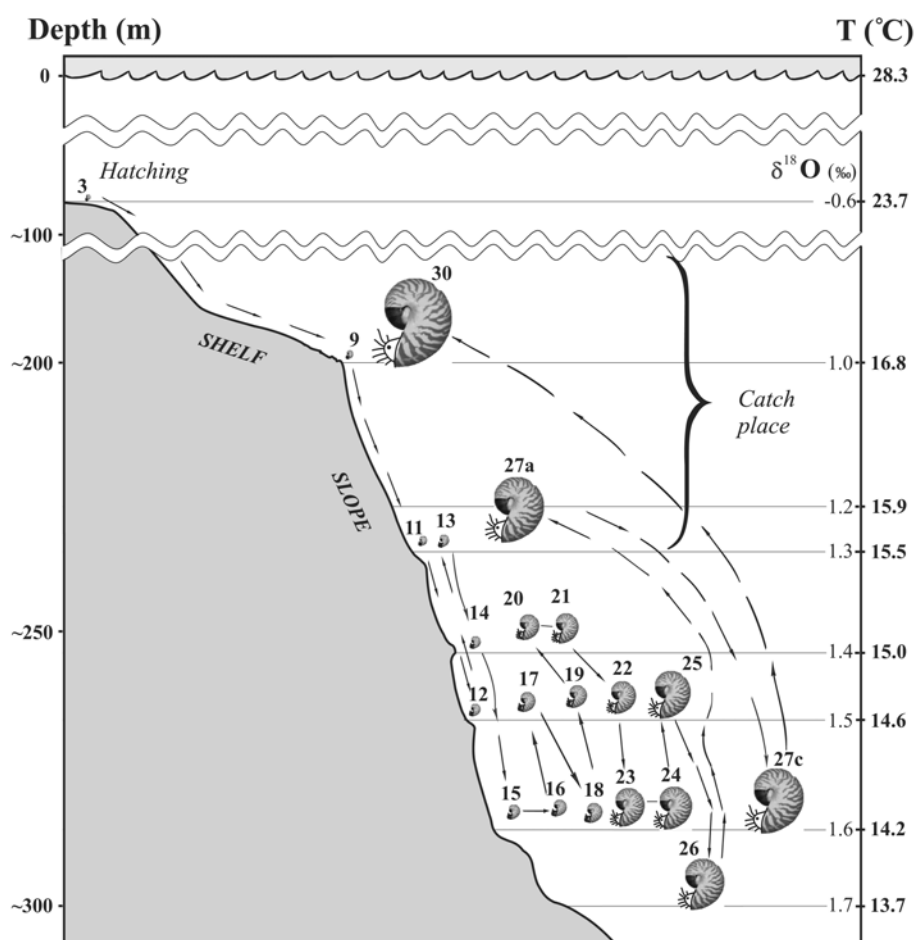


Fig. 5. Interpretation of an ontogenetic vertical migration of *Nautilus pompilius* Linne at the Tangan area from data on isotopic composition of its shell.

4.2 Possible Correlation Between *Nautilus pompilius* and Brachiopod $\delta^{13}\text{C}$ Value Changes and Solar Activity Fluctuations

This paper is the first attempt to show a possible correlation between *Nautilus pompilius* and brachiopod $\delta^{13}\text{C}$ value changes and solar activity. It must be mentioned that there are some deviations from the direct relation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in the investigated *Nautilus pompilius* samples (Figs. 3 and 4) that must be taken into account also in the analysis of fossil cephalopods.

Based on the external and internal morphology, the investigated *Nautilus pompilius* (101.2 mm in diameter) and dallinid and terebratulid brachiopods (25.6–36.1 mm in length) (Table 2) captured at the end of March 1999, seem to be two and a half and about eight years old, respectively.

Information on the sunspot numbers throughout the end of 1996 – beginning of 1999 and carbon isotope values of *Nautilus pompilius* aragonite are plotted in Figures 6 and 7. Our preliminary result indicate a direct relation exists between the sun activity at the beginning of cycle 23 (1996–1999) and carbon isotope values in septa of the investigated *Nau-*

tilus shell occur ($r=0.77$). This is confirmed by the results of living brachiopod analyses.

Relative $\delta^{13}\text{C}$ value fluctuation in the invertebrate shells formed in the Philippine area may be mainly caused by the annual cycles of the phytoplankton development. The most negative $\delta^{13}\text{C}$ excursion in the ninth septum of *Nautilus pompilius* (-2.5‰) seems to be connected with a weakening of phytoplankton bioproductivity provoked by the low solar activity at the end of 1996 (Gnezdilov, 2004) (Figs. 6 and 7). The highest $\delta^{13}\text{C}$ values in the investigated *Nautilus pompilius* (1.5‰) and dallinid brachiopod (0.6–0.8‰) shells were recognized in the portions of their shells built at the beginning of 1999, just before the peak of the solar activity of the 23rd cycle (Fig. 6).

4.3 The Comparative Analysis of Optimal Temperature of Growth for Cretaceous Cephalopods and Living *Nautilus*

Analyses of the isotopic composition of many well-preserved middle and upper Albian belemnite rostra from the Gardis and Saint-Po Formations of Blanc-Nez, France (Plate 1; Table 3) show that $\delta^{18}\text{O}$ values in their adult stage (2.1–

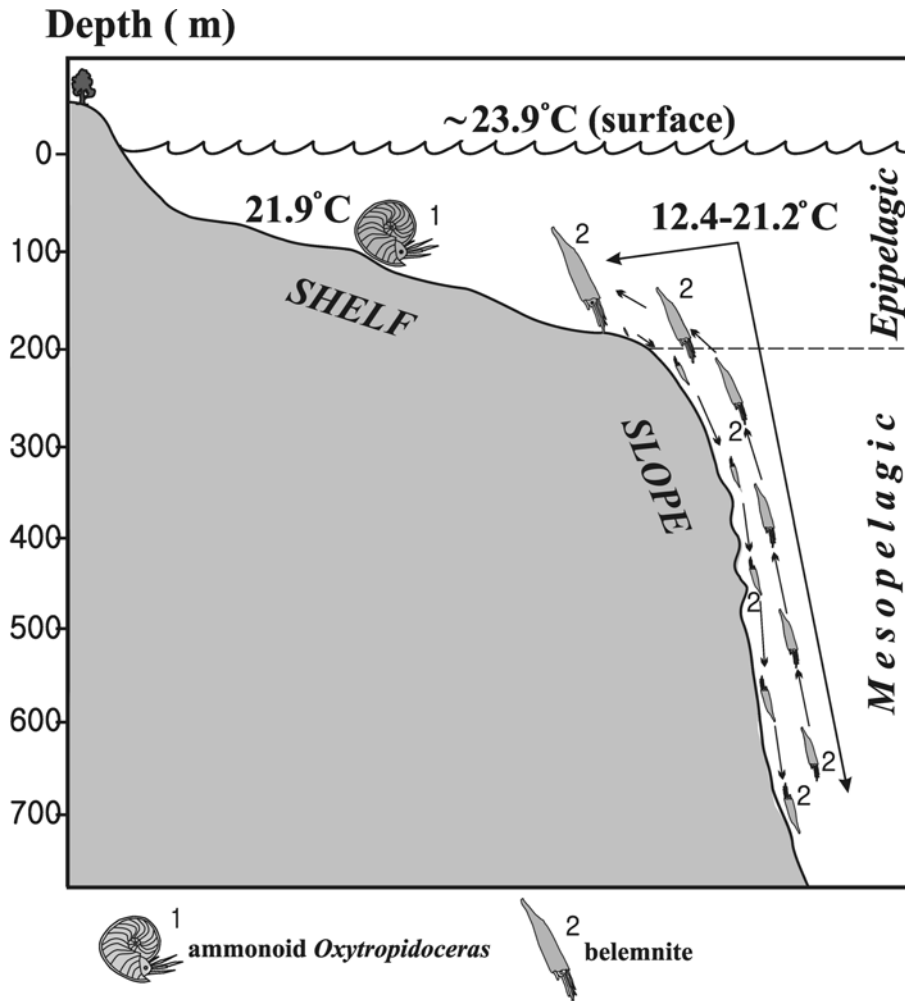


Fig. 6. Interpretation of an ontogenetic vertical migration of middle Albian belemnites of the Blanc-Nez area, France, from data on isotopic composition of their rostra and ammonoid shells.

0.8‰) are frequently lower than those in their juvenile stage (from -0.6 to -0.1 ‰). Such regularity was first pointed out by Teiss and Naidin (1973) in Campanian-Maastrichtian belemnite rostra from the Russian Platform. Temperatures calculated from some adult and juvenile stages of middle-upper Albian belemnite rostra from Blanc-Nez are 15.2 – 20.7° and 12.4 – 14.4°C , respectively. But paleotemperature (21.9°C) (Table 4) calculated from aragonite-preserved *Oxytropidoceras* ammonoid shell, which occur with cited belemnites, is comparable only with higher belemnite temperature level. Similar high paleotemperatures (19.6 – 21.6) were obtained also from well-preserved ammonoid species *Otohoplites raulinianus* (d'Orbigny) and *Beudanticeras beudanti* (Brogniart) from the neighboring region of Normandy, France. It allows us to conclude that belemnites, similar to recent *Nautilus* can reach colder deep-water (bathyal) levels. However, adult belemnites, when they spawn, prefer warmer, shallow-water conditions (Fig. 6). Our interpretation seem to be consistent with Huber and Hodell's (1996) data, in which the $\delta^{18}\text{O}$ paleotemperatures yielded by the Antarctic belemnites are similar to the $\delta^{18}\text{O}$ paleotemperatures derived from the middle to upper bathyal benthic for-

aminifera assemblages for the late Albian-Cenomanian and Santonian-early Campanian ages.

By contrast, recent isotopic analyses of well preserved ammonoid shells from the Campanian of Hokkaido, South Sakhalin (Krilyon Peninsula) (Smyshlyaeva et al., 2002; Moriya et al., 2003; Zakharov et al., 2003; 2004a) and California (Zakharov et al., 2004b), and Maastrichtian of South Sakhalin (Naiba River) (Zakharov et al., 1996, 1999) show that optimal temperatures of their growth are comparable to their co-occurring benthos on the shelf (Fig. 7). None of the early Campanian ammonoids display calcification temperatures equivalent to those of planktonic foraminifera (26°C). Therefore, there is no evidence that the ammonoids underwent a large vertical migration into the surface ocean. Most of the investigated early Campanian ammonoids, inoceramid bivalves and benthic foraminifera of middle latitudes from Far East inhabited temperatures between 17.7 and 24.2°C , 17.5 and 18.0°C , respectively (Zakharov et al., 1999; Smyshlyaeva et al., 2002; Moriya et al., 2003).

A similar picture is apparent from the respective sampling of biogenic carbonates from well-preserved Conia-

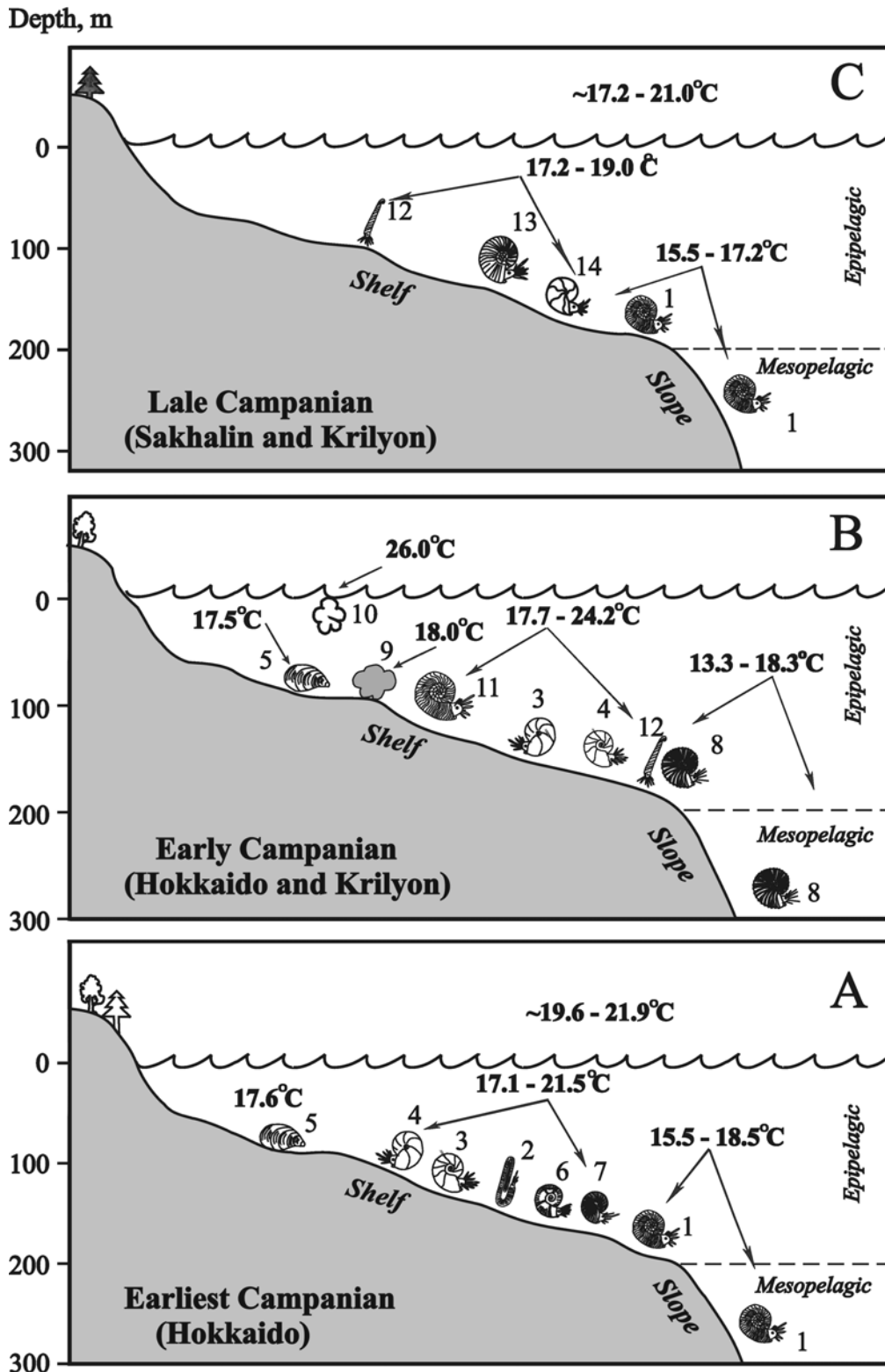


Fig. 7. Ammonoid mode of life reconstruction from data on isotopic composition of Campanian foraminifera, ammonoid and bivalve shells from Hokkaido and Sakhalin. 1 – ammonoid *Menutites*, 2 – ammonoid *Polyptychoceras*, 3 – ammonoid *Damesites*, 4 – ammonoid *Tetragonites*, 5 – inoceramid bivalve, 6 – ammonoid *Yokoyamaoceras*, 7 – ammonoid *Hypophylloceras*, 8 – ammonoid *Eupachydiscus*, 9 – benthic foraminifera (Moriya et al., 2003), 10 – planktic foraminifera (Moriya et al., 2003), 11 – ammonoid *Gaudryceras*, 12 – ammonoid *Baculites*, 13 – ammonoid *Canadoceras*, 14 – ammonoid *Desmophyllites*. A – earliest Campanian, B – early Campanian, C – late Campanian.

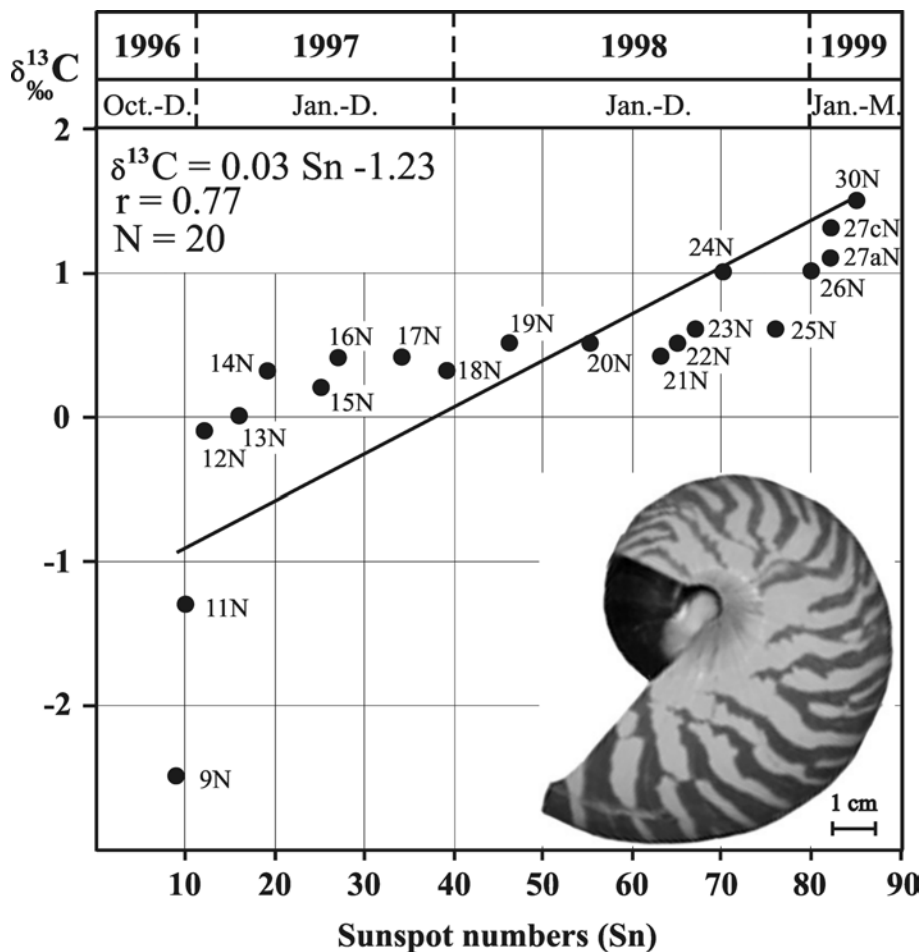


Fig. 8. Correlation between $\delta^{13}\text{C}$ values in living *Nautilus pompilius* Linne shell from Panglao area and sunspot numbers.

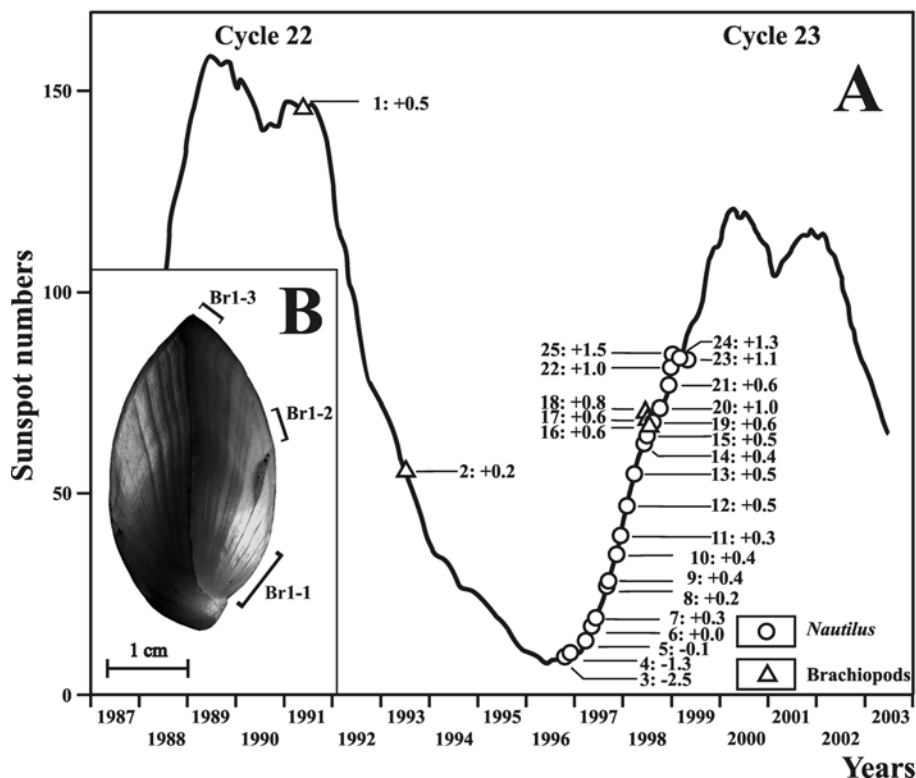


Fig. 9. $\delta^{13}\text{C}$ values in living *Nautilus pompilius* Linne and brachiopod shells from Panglao area and Sun activity during 1991-2003. A – $\delta^{13}\text{C}$ values in *Nautilus* and brachiopod shells; B – brachiopod Dallinidae and *Nautilus* shell samples: 1 – Br1-1, 2 – Br1-2, 3 – N9, 4 – N11, 5 – 12, 6 – N13, 7 – N14, 8 – N15, 9 – N16, 10 – N17, 11 – N18, 12 – N19, 13 – N20, 14 – N21, 15 – N22, 16 – Br1-3, 17 – Br2-1, 18 – Br3-1, 19 – N23, 20 – N24, 21 – N25, 22 – N26, 23 – N27a, 24 – N27c, 25 – N30.

cian ammonoids *Anagaudryceras*, *Gaudryceras*, *Tetragonites*, *Mesopuzosia*, *Kossmaticeras*, *Yokoyamaoceras*, *Scalarites*, *Baculites*, *Yesoites* of Hokkaido (Zakharov et al., 2002b) and Koryak Upland, Kamchatka area (Zakharov et al., 2002a, 2005) (Plate 2), although there are data, which suggest that some differences between bivalve and ammonoid optimal growth temperatures at high latitudes during the Coniacian. The Late Cretaceous ammonoid shells of the circum-Pacific were most likely secreted in near-bottom conditions where the animals spent most of their lives in shallow marine basins. However, judging from our isotopic data (Smyshlyaeva et al., 2002), some large pachydiscid ammonoids (*Canadoceras*, *Menuites*, and *Eupachydiscus*) and possibly some tetragonitid, as well as some desmoceratid ammonoids, were able to migrate to somewhat colder, deeper waters (distal shelf and upper continental slope) during their lives.

Isotopic data in living *Nautilus* and belemnites, on the one side, and ammonoids, on the other side, show some difference in their mode of life: it is suggested that, unlike *Nautilus* and belemnites, ammonoids lived mainly in shallow marine basins and did not undergo significant short-term vertical migrations.

5. CONCLUSIONS

Our results indicate that there are some deviations from the direct relations between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in the investigated *Nautilus pompilius* samples. $\delta^{13}\text{C}$ value fluctuations in living invertebrate shells from the Philippines may be mainly connected with the annual cycles of the phytoplanktonic development; like some fossil cephalopods (belemnites, but not ammonites), living *Nautilus* underwent a large vertical migration in the water column.

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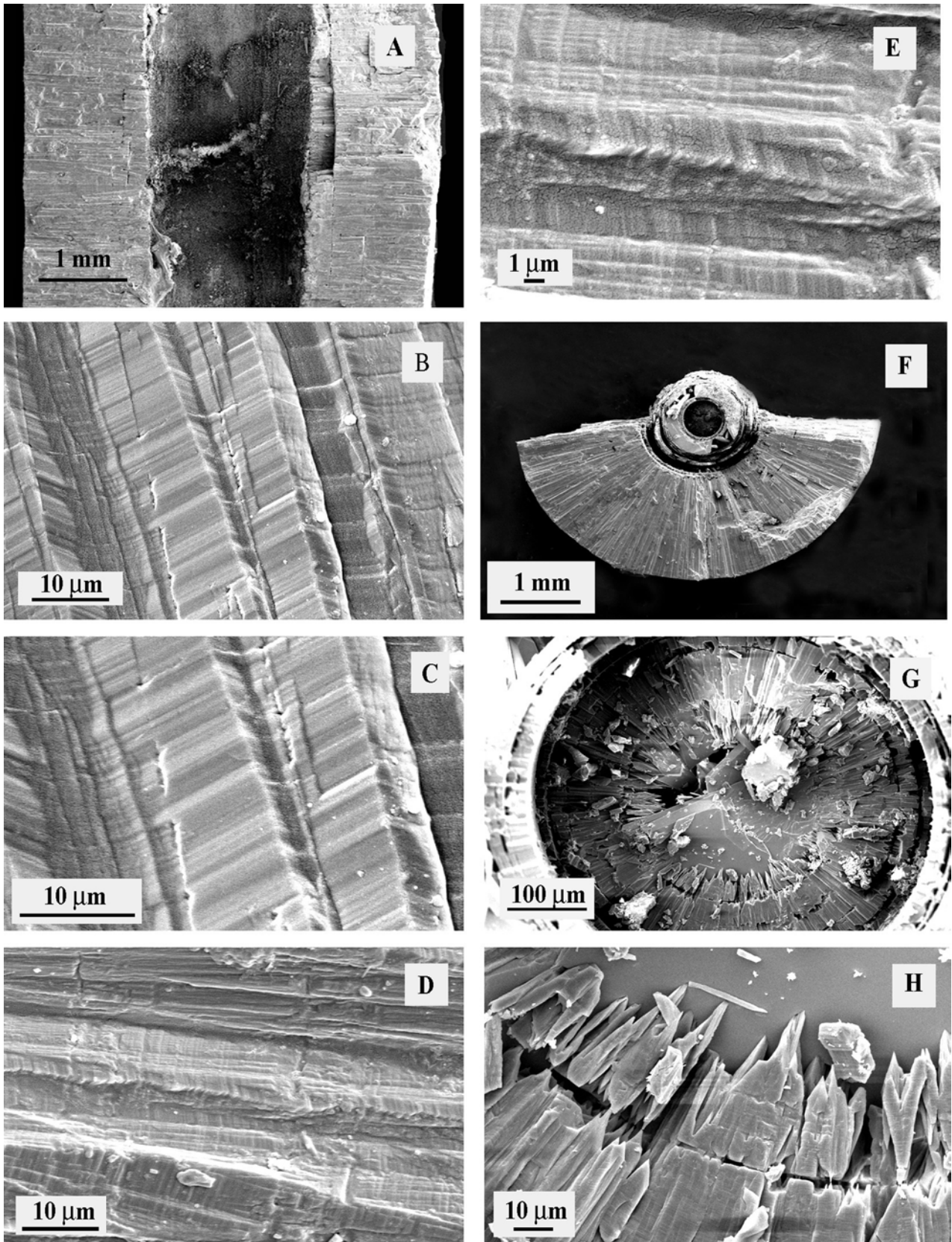


Plate 1. Scanning electron micrographs of the belemnite rostrum LAM-1-9; middle Albian; Blanc-Nez area, France. Fig. A-E, in longitudinal section. Fig. F-H, in cross-section.

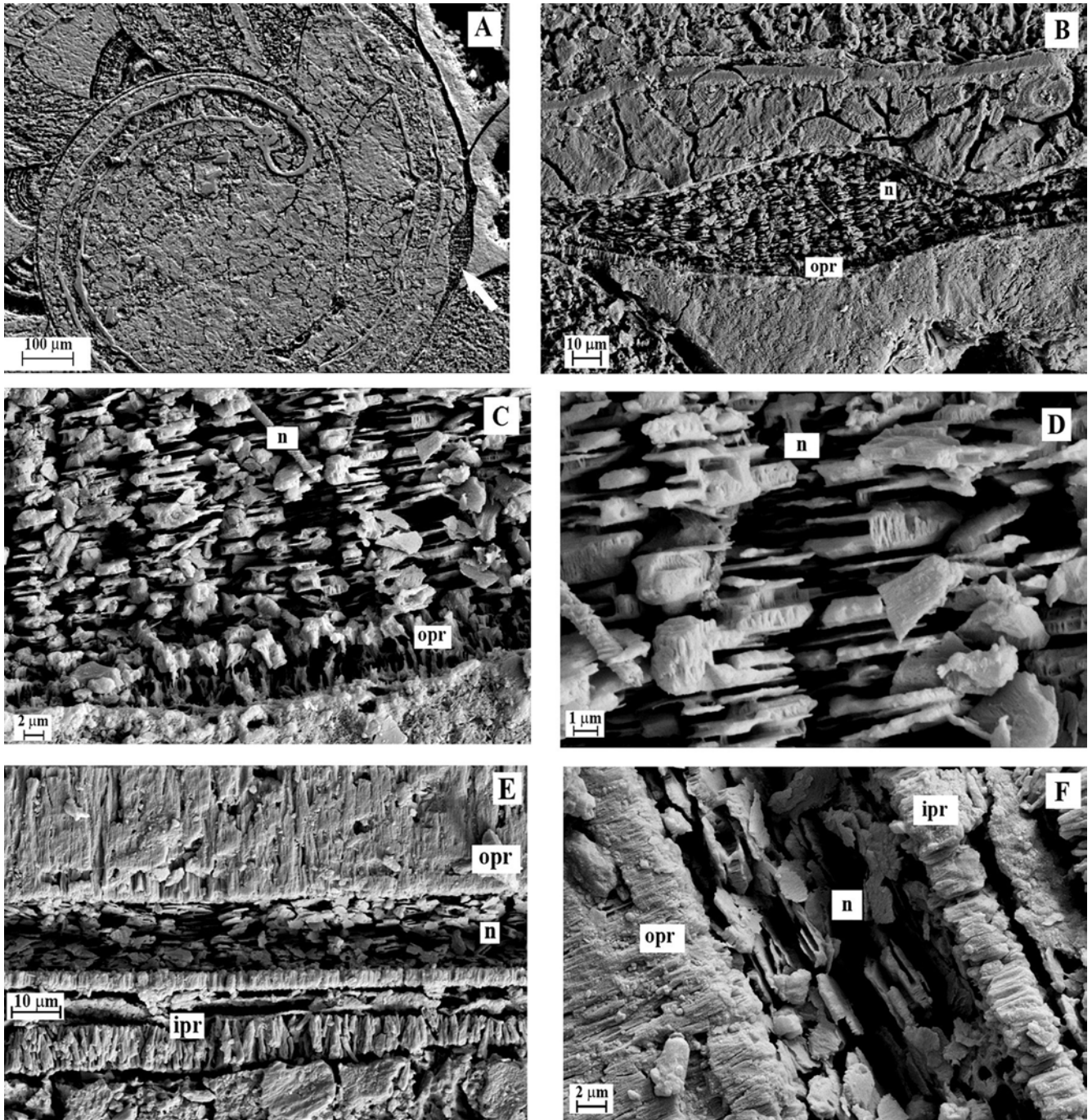


Plate 2. Scanning electron micrographs of the *Kossmaticeras japonicum* Matsumoto shell 715-10-1 in median section; Coniacian; Talovka River, Koryak Upland. Fig. A. – ammonitella, Fig. B-D. Microstructure of the nepionic realm, Fig. E and F. Microstructure of the two areas of the fifth shell whorl (ventral part).