



Contents lists available at ScienceDirect

Earth and Planetary Science Letters

journal homepage: www.elsevier.com/locate/epslOntogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$)Alexander Lukeneder^{a,*}, Mathias Harzhauser^a, Stefan Müllegger^b, Werner E. Piller^b^a Department for Geology and Paleontology, Museum of Natural History Vienna, Burgring 7, 1010 Vienna, Austria^b Department for Earth Sciences, Karl-Franzens University, Heinrichstrasse 26, 8010 Graz, Austria

ARTICLE INFO

Article history:

Received 5 October 2009

Received in revised form 27 April 2010

Accepted 29 April 2010

Editor: T.M. Harrison

Keywords:

stable isotopes

ammonoids

paleotemperature

paleoecology

ontogeny

ABSTRACT

Stable isotope ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) ratios were measured in successive aragonitic shell sequences of ammonoids (class Cephalopoda) to determine whether their depth distributions changed within ontogeny and whether stable isotope values differ in various morphological groups (e.g. Leiostroaca vs. Trachyostraca). We concentrate mainly on $\delta^{18}\text{O}$ for temperature results and added $\delta^{13}\text{C}$ data to obtain information on the ontogenetic history, for which full spiral measurements were undertaken for the first time. To obtain valid stable isotope data from ammonoid shells, we measured ontogenetic sequences (full shell) within different genera. Data sets from the Jurassic (*Cadoceras*) and Cretaceous (*Hypacanthoplites*, *Nowakites*) were chosen due to the pure primary aragonitic shell preservation. The study was designed to extract better information on the habitat and life cycle of fossil cephalopods (e.g. ammonoids) in comparison with recent cephalopods (e.g. *Nautilus*, *Spirula*, *Sepia*) possessing equivalent or comparable hard parts. The data from three genera suggest different modes of life in at least two morphological groups.

We detected and established two main groups with different ontogenetic strategies based on the $\delta^{18}\text{O}$ data. The *wcw*-type (warm–cool–warm type) of *Cadoceras* resembles strategies in *Nautilus* and *Sepia*, which migrate from shallow into deeper environments and back in ontogeny (*wc*-type, warm–cool-type), and the *cw*-type (cool–warm type) of *Hypacanthoplites* resembling the first two migration phases of *Spirula* (*cwc*-type), which migrates from deeper into shallower and back again into deeper habitats. The main (three) phases revealed by both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ data sets most probably reflect diet changes in juvenile to mid-aged individuals, followed by a habitat change for spawning adults. In *Cadoceras* the temperatures range from 21.2 °C for juveniles down to 12.1 °C for mid-aged individuals and back up 16.9 °C in adults. The *cw*-type strategy of *Hypacanthoplites* involves a temperature range of 22.8 °C to 28.9 °C. The respective mean values are 24.2 °C (juveniles), 25.8 °C (middle phase) and 27.8 °C (adults).

The $\delta^{13}\text{C}$ values also revealed three ontogenetic stages in *Cadoceras* and *Hypacanthoplites*, including two major shifts from positive to negative and from negative to positive values, which probably correspond to sexual maturation, the initiation of reproduction, and concomitant changes in diet. The presented data, combined with previous ontogenetic studies (e.g. stable isotopes) on *Spirula*, *Nautilus* and *Sepia* can be used as proxies to directly correlate the habitats and ontogeny of recent and fossil cephalopods.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Ammonoids are an extinct group of cephalopods with an external, primary aragonitic shell. Various morphologies exist, ranging from planispiral to heteromorphic shells, from smooth (leiostroacans) to strongly ribbed (trachyostracans) with tubercles or even long spines (Westermann, 1990; 1996). Knowledge of the life cycles, ecology and ontogeny of fossil cephalopods and especially of ammonoids is still poor. While ammonoids are frequently found in Paleozoic and Mesozoic marine sediments worldwide from the tropic–subtropic

via boreal to antarctic–arctic zones, information on their habitat and ecology is scarce and imprecise. Their habitat is suggested to be the epi- and meso pelagic zones (Westermann, 1990; 1996). The epipelagic or sunlight zone is the uppermost part of the water column from 0–200 m depth, whilst the mesopelagic or twilight zone ranges from 200 to 1000 m (Ott, 1996). Ammonoids are considered to have been nektonic or demersal animals. Nektonic organisms live actively swimming in the pelagic zone, whilst demersal or nekto-benthic organisms live actively swimming near or close to the sea bottom (Lincoln et al., 1998). They probably spawned in benthic or even mid-water habitats in the neritic to oceanic zone above the shelf areas and upper slopes within water layers ≤ 1000 m (Westermann, 1996). Females are thought to have laid 100–1000 eggs on the sea-floor (r-strategy), which after hatching as larvae became part of the

* Corresponding author.

E-mail address: alexander.lukeneder@nhm-wien.ac.at (A. Lukeneder).

plankton (e.g. Landman et al., 1983; epiplankton after Westermann, 1996). This strategy is comparable to most other cephalopods, except for the K-strategist *Nautilus*. Ammonoids most probably undertook vertical diel migrations, as is characteristic for many planktonic ocean dwellers such as *Spirula spirula* (Clarke, 1969; Lukeneder et al., 2008).

The aragonitic composition of the external shells in ammonoids makes them suitable for isotopic measurements. Shells of the herein studied genera *Cadoceras*, *Hypacanthoplites* and *Nowakites* (Fig. 1) consist entirely of pristine aragonite. The planispirally coiled shells were formed gradually during ontogeny and therefore are considered to mirror the paleotemperature of the surrounding seawater (Fig. 2). Thus, the exquisitely preserved shells may provide a reliable geochemical archive that reflects the life-span migration cycle of the ammonoids.

Fractionation and isotopic composition in oxygen and carbon isotopes ($^{16}\text{O}/^{18}\text{O}$ and $^{12}\text{C}/^{13}\text{C}$) refers to a change in stable isotope ratios, reflecting chemical and/or physical processes (Hoefs, 2004). Early studies of mollusc shells in respect to stable isotope composition ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) already demonstrated that the isotope composition of carbonate shells is a function of seawater-temperature (Urey et al., 1951). Since then, an enormous body of literature has used stable isotopes of bivalve and gastropod shells as environmental proxies (Bandel and Hoefs, 1975; Wefer, 1985). As noted by Rexfort and Mutterlose (2006), isotope thermometry obtained by analyzing hard parts of cephalopods offers valuable information about paleo- and recent seawater temperatures as well. According to the formula

$$T(^{\circ}\text{C}) = 20.6 - 4.34 \left(\delta^{18}\text{O}_{\text{aragonite}} - \left[\delta^{18}\text{O}_{\text{water}} - 0.2 \right] \right)$$

(Grossman and Ku 1986; McConnaughey et al., 1997; Goodwin et al., 2003), a shift of one per mil in the oxygen isotope ratio corresponds to a temperature change of 4.34°C ($\delta^{18}\text{O}_{\text{water}} = -1.0\text{‰}$ SMOW for the mean isotopic composition in a nonglacial world in Jurassic to Cretaceous times). The latter equation was extrapolated by Lécuyer et al. (2004) to a more appropriate formula for equatorial or tropical molluscs in marine waters by

$$T(^{\circ}\text{C}) = 21.8 - 4.69 \left(\delta^{18}\text{O}_{\text{aragonite}} - \left[\delta^{18}\text{O}_{\text{water}} \right] \right)$$

assuming that the isotope ratio is strongly related to

$$\delta^{18}\text{O}_{\text{water}} = -9.986 + 0.3 * S$$

(GEOSECS Executive Committee, 1987) when S is the salinity with about 35‰ at a depth of around 300–500 m according to data by Auclair et al. (2004) and Watanabe et al. (2003). Subsequently, the heavy/light oxygen ratio can be used to define the relationship between oxygen isotopes and water temperature manifested in aragonitic shells such as those of Recent (*Spirula*, *Sepia*, *Nautilus*) and ancient cephalopods (ammonoids, nautiloids belemnoids). Caution must be exercised because nacreous layers in molluscs are ^{18}O depleted compared to calcite (prismatic layers in cephalopods), which is enriched in ^{18}O (Tarutani et al., 1969; Grossman and Ku, 1986).

Numerous authors have investigated isotope records from Recent cephalopod hard parts. Sclerochronologic isotope data for *Nautilus pompilius*, *N. belauensis*, *Nautilus macromphalus* and *Nautilus* sp. were provided by Eichler and Ristedt (1966a,b), Cochran et al. (1981), Taylor and Ward (1983), Wefer (1985), Landman et al. (1983, 1994) and Auclair et al. (2004). Other research groups focused on isotopic

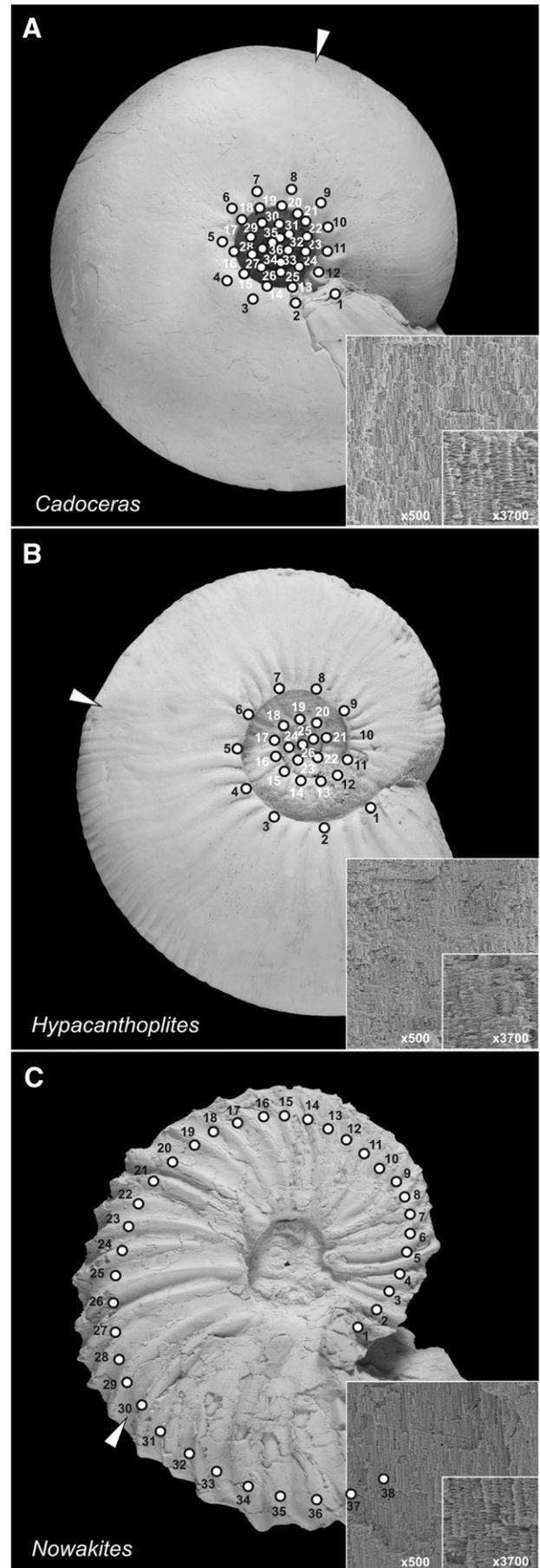


Fig. 1. Lateral view with numbered samples in ontogenetic direction, growth direction with indicated SEM images of aragonitic ultrastructure, $\times 500$ and $\times 3700$, of (A) *Cadoceras*, (B) *Hypacanthoplites* and (C) *Nowakites* shells.

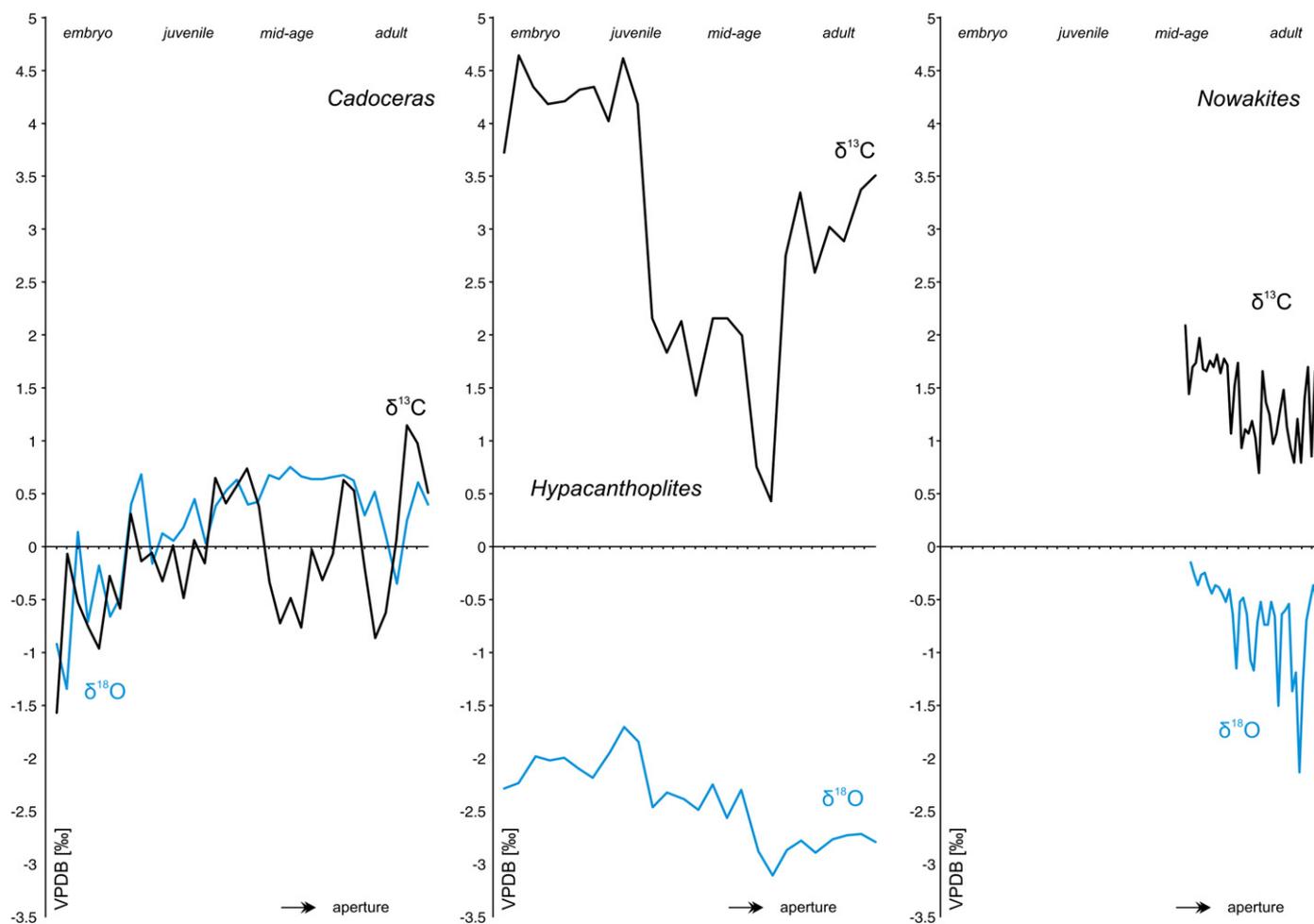


Fig. 2. Stable isotope curves ($\delta^{18}\text{O}$ in blue and $\delta^{13}\text{C}$ in black) for the ammonoids *Cadoceras*, *Hypacanthoplites* and *Nowakites*.

records of sepiids such as *Sepia officinalis* (Longinelli, 1966; Longinelli and Nuti, 1973; Hewitt and Stait, 1988; Bettencourt and Guerra, 1999; Rexfort and Mutterlose, 2006; Cherel et al., 2009). The stable isotope composition of the deep-water squid *S. spirula* was investigated by Lukeneder et al. (2008) and Price et al. (2009).

Stable oxygen isotopes of ectocochleate fossil cephalopods (ammonoids, nautiloids) have been measured to gain insights on ancient ocean water temperatures at different Mesozoic ages by Kaltenecker (1967), Stahl and Jordan (1969), Tourtelot and Rye (1969), Jordan and Stahl (1970), Fabricius et al. (1970), Kaltenecker et al. (1971), Jeletzky and Zapfe (1976), Forester et al. (1977), Marshall (1981), Landman et al. (1983, 1988), Whittaker et al. (1987), Fotherree et al. (1998), Cochran et al. (2003), Moriya et al. (2003) and He et al. (2005). For comparable aims, endocochleate fossil cephalopods (belemnoids) have been analysed by Lowenstein and Epstein (1954), Spaeth et al. (1971), Ditchfield (1997), Podlaha et al. (1998), Price et al. (2000), Schootbrugge et al. (2000), Niebuhr and Jochimski (2002), McArthur et al. (2004), Price and Mutterlose (2004), Wierzbowski and Jochimski (2007, 2009) and Wierzbowski et al. (2009).

The comparison of Recent *Spirula*, *Sepia*, and *Nautilus* allows quite different modes of life to be deciphered based on stable isotope signatures (Fig. 3). Applying these methods to Mesozoic ammonoids might shed light on the strategies and environmental requirements of fossil cephalopods. Due to its unusual morphology, *Spirula* is used as a key genus in paleontological papers that attempt to interpret the mode of life of Mesozoic ammonoids (Lukeneder et al., 2008; Price et al., 2009). The life and habitat during full ontogeny have not yet

been reconstructed for any ammonoid. Past investigations have examined only parts of shells or used only single-point measurements (one-measurement-per-shell) to calculate paleotemperatures for whole oceans. In contrast, we measured entire ammonoid specimens in spiral direction (from embryonic stages to adult aperture) to gain additional information of the ecology and habitat preferences of various ammonoids. One of the main objectives of the present study is to determine possible ontogenetic migrations in the water column in fossil cephalopod groups based on a comparison with stable isotope data from Recent cephalopods. We concentrated mainly on the $\delta^{18}\text{O}$ stable isotope data to detect ontogenetic stages, including shifts in isotope values, corresponding with maturation and concomitant changes in ancient habitats (e.g. water depth).

2. Modern and ancient cephalopods: ontogeny and isotopes

2.1. Recent cephalopods: *Spirula*, *Sepia* and *Nautilus*

2.1.1. *Spirula*

The $\delta^{18}\text{O}$ stable isotope data reported by Lukeneder et al. (2008) for the deep-water squid *S. spirula* display a steady decrease from +3.45 to +3.00‰ to +1.96 to +2.04‰ in juvenile stages and an increase to +2.17 to +2.64‰ in adults (Fig. 3). $\delta^{13}\text{C}$ data also revealed three ontogenetic stages, including a major shift from positive to negative values which corresponds to sexual maturation, the initiation of reproduction, and concomitant changes in diet. A rarely preserved embryonic stage was accompanied by markedly less positive $\delta^{13}\text{C}$ values in the first few chambers. These data are related

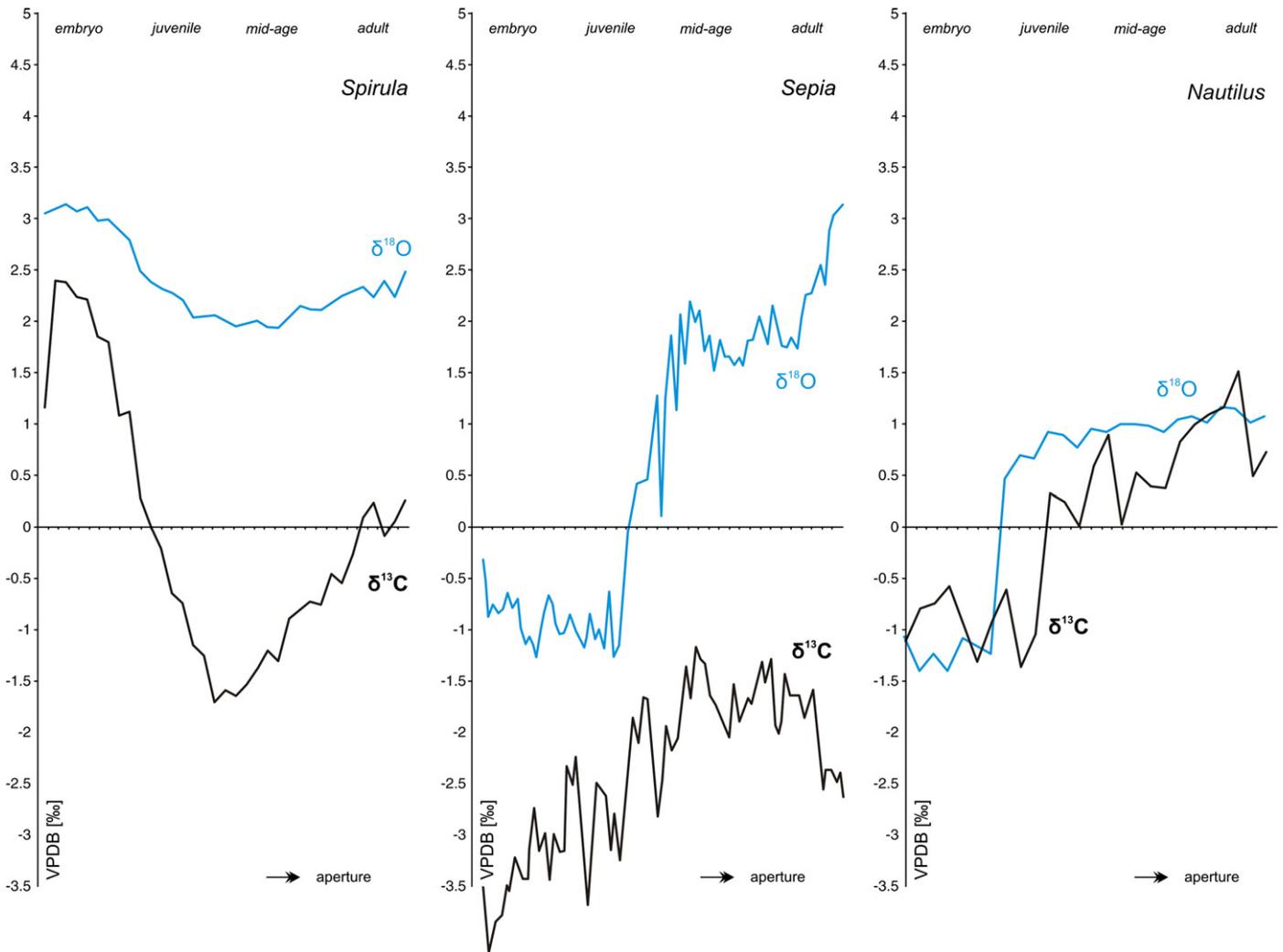


Fig. 3. Stable isotope curves ($\delta^{18}\text{O}$ in blue and $\delta^{13}\text{C}$ in black) for the recent cephalopods *Spirula*, *Sepia* and *Nautilus* (Cochran et al., 1981; Landman et al., 1994; Lukeneder et al., 2008; Rexfort and Mutterlose, 2006).

to habitat changes during ontogeny: after hatching at depths >1000 m at approx. 4–6 °C (Young et al., 1998; Lukeneder et al., 2008; Price et al., 2009), the squid migrates into shallower, warmer waters at depths of 400–600 m (12–14 °C). Subsequently, the animals migrate back into somewhat cooler, deeper habitats.

2.1.2. *Sepia*

S. officinalis hatches in warm waters (above 20 °C) at depths of about 1–20 m (Rexfort and Mutterlose, 2006) and descends to greater depths in accordance with a change in life style. Wild-caught specimens displayed $\delta^{18}\text{O}$ values from -1.28 to +2.98 ‰ during ontogeny, pointing to an experienced temperature of 21 °C in subadult to 5 °C in adult specimens (Fig. 3). This ontogenetic trend of *Sepia* from warm water into deeper and cooler waters was also documented by other isotope studies such as Longinelli and Nuti (1973) and Bettencourt and Guerra (1999). The main difference between *Sepia* and ammonoids is the maximum life-span (see discussion). *Sepia* apparently attains an age of c. 200 days (Rexfort and Mutterlose, 2006), whereas ammonoids might have ranged from 5 to 15 years (Bucher et al., 1996) or even 50–100 years in giant lycoceratids (Westermann, 1996).

2.1.3. *Nautilus* and fossil allies

Various species of *Nautilus* were measured by Eichler and Ristedt (1966a, b), Cochran et al. (1981), Taylor and Ward (1983), Landman

et al. (1983, 1994) and Auclair et al. (2004). *N. macromphalus* needs 5–6 years to reach sexual maturity, with a growth rate of 1 growth line deposited in 2 days and an averaged value of 0.25 mm/day in reared specimens (Martin et al., 1978). Depending on the species, embryonic development takes place at 22–30 °C in a depth of 100–200 m. Typical embryonic $\delta^{18}\text{O}$ values range roughly around -1.07 to -3.00‰. After c. 269 to 362 days (Uchiyama and Tanabe, 1999) hatching takes place and a migration into cooler, deeper waters (150–400 m; 14–16 °C) starts. This is documented by increasing $\delta^{18}\text{O}$ values of +0.40 to +1.21‰ (Fig. 3). The main $\delta^{18}\text{O}$ shift corresponds with the formation of the 7th to 8th septum, reflecting the hatching after the embryonic stage. Consequently, Taylor and Ward (1983) defined 2 different ontogenetic stages by using isotope data: the embryonic and the free-swimming stage. The embryonic stage with $\delta^{18}\text{O}$ values below approx. -1.00‰ (>20 °C) and the free-swimming stage showing $\delta^{18}\text{O}$ values above -1.00‰ (<20 °C).

This behaviour seems to be characteristic for *nautilids* at least since Cretaceous times because similar patterns (from lighter to heavier $\delta^{18}\text{O}$ values after hatching) are observed in fossil *Eutrephoceras* (Landman et al., 1983, Landman, 1988). In *Eutrephoceras*, $\delta^{18}\text{O}$ shifts occur between septa 2 and 4, with a magnitude of 1.60–2.90‰. Earliest stages point to paleo-seawater temperatures of 22–23 °C in the egg and to 14–20 °C after hatching. Afterwards, the nautilid descended into deeper, cooler water of around 14 °C (Landman et al., 1983).

The $\delta^{13}\text{C}$ variations of -1.35 to $+1.52\%$ are correlated with changes from the embryonic to juvenile–adult stages and the change in habitat. Hence the $\delta^{13}\text{C}$ values reveal different stages in early ontogeny of *Nautilus*, the embryonic followed by the free-swimming stage which correspond to early sexual maturation and concomitant changes in diet and water chemistry due to the “habitat change”. A change of habitat defines in the latter case the pre-hatching and the post-hatching cycles in *Nautilus*. Hatching from egg-capsule appears after approx. one year.

2.2. Fossil cephalopods: ammonoids

2.2.1. Ammonoids

Stable isotope analyses ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) on ammonoids are numerous but contribute little to reconstructing ontogeny. Typically, data were obtained as single-point measurements and lumped with other taxa of coeval strata. These investigations were typically designed to reveal ocean water temperatures at distinct time slices, neglecting the enormous effect on the isotope composition due to migration and habitat change. As $\delta^{18}\text{O}$ data of single cephalopod shells can range around 2.00% , spanning almost 8 – 10 °C, these “one-measurement-per-shell-data” are inappropriate for paleotemperature estimations. These ranges are ontogenetically induced and single point measurements will snap-shot ocean water temperatures at a very specific point of development only.

Data exist for the Triassic genera *Arcestes*, *Austroteuthis*, *Carnites*, *Rhacophyllites* and *Sagenites*, the Jurassic genera *Amaltheus*, *Leioceras*, *Parkinsonia*, *Perisphinctes*, *Phlyseogrammoceras*, *Quenstedtoceras* and *Staufenia* and the Cretaceous genera *Acanthoscaphites*, *Baculites*, *Demesites*, *Didymoceras*, *Discoscaphites*, *Eupachydiscus*, *Exiteloceras*, *Gaudryceras*, *Hauericeras*, *Hypophylloceras*, *Menuites*, *Phyllophyceras*, *Polyptychoceras*, *Scaphites*, *Sphenodiscus*, *Tetragonites* and *Yokoyamaoceras* (references below).

Stable isotope data ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of Triassic and Jurassic ammonoid shells from the Northern Calcareous Alps have been studied in order to calculate paleotemperatures for these periods (Kaltenegger, 1967; Fabricius et al., 1970; Kaltenegger et al., 1971; Jeletzky and Zapfe, 1976). Cochran et al. (2003) measured different Maastrichtian ammonoids from the Western Interior Sea (North America) to define various depositional settings, paleoenvironments and the corresponding salinity. The Jurassic *Leioceras*, *Staufenia* and *Quenstedtoceras* were studied to estimate the growth rate of ammonoids (Stahl and Jordan; 1969; Jordan and Stahl, 1970). Seasonal variation of about 8 – 9 °C in the late Middle Jurassic (Callovian) was proposed by these authors for *Quenstedtoceras* and *Staufenia*. Similarly, Lécuycy and Bucher (2006) analysed Late Jurassic *Perisphinctes* from Madagascar (Fig. 4) to obtain seasonal surface water temperatures of the southern hemisphere. Taxa, such as *Phlyseogrammoceras*, display minor variations of 3 – 4 °C (Jordan and Stahl, 1970) indicating considerable differences in the life styles. Several “ranges”, however, are attributed to variations in calcite–aragonite ratios and thus reflect mere diagenetic effects (e.g. *Amaltheus* in Jordan and Stahl, 1970). Only baculitids have repeatedly been used to decipher ontogenetic changes of these Late Cretaceous heteromorphs (Tourtelot and Rye, 1969; Forester et al., 1977; Whittaker et al., 1987; Fatherree et al., 1998) (Fig. 4).

In addition, the Late Cretaceous heteromorph *Polyptychoceras pseudogaltinum* from Hokkaido was analysed by Okamoto and Shibata (1997), who concluded either a demersal mode of life almost touching the sea bottom (= nekto-benthic) or a nekto-planktic mode in the water column. A corresponding life style was proposed by Moriya et al. (2003) for several taxa from the Late Cretaceous of the North Pacific. The relatively short shell-sections utilized for that study, however, exclude a full record of the ontogenetic shifts and potential migrations.

3. Material and methods

A total of three shells – one each of the ammonoid genera *Cadoceras* (Callovian, Jurassic; Gorki, Russia), *Hypacanthoplites* (Aptian, Lower Cretaceous; Vöhrum, Germany) and *Nowakites* (Santonian, Upper Cretaceous; Edelbachgraben, Austria) – were analysed for their stable isotope composition ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) (Figs. 1 and 2). Additional material from the same localities is stored at the Natural History Museum Vienna, Austria. The analysed shells ranged from 90 to 130 mm in maximum diameter and represented fully grown adult specimens. Morphology varies in the analysed specimens from smooth (e.g. *Cadoceras*), over weakly ribbed (e.g. *Hypacanthoplites*) to strongly ribbed forms (e.g. *Nowakites*). The sex of the specimens is unknown. The isotope measurements were conducted in growth direction and targeted ontogenetic variations in the life cycle of the animals.

To take into account possible within-shell variation in isotopic composition (cf. *N. macromphalus*; Auclair et al., 2004), the within-shell variation of *Cadoceras emiliantsevi* was measured. Sub-samples were taken from the septa, siphon, and three areas of the chamber wall: near the siphon, marginally, and opposite the siphon. After drilling samples 1–13, the last whorl had to be removed to gain access to inner whorls (Fig. 1). For samples 17–36, a needle was used to remove shell material. Sampling such a specimen with an open umbilicus near the seam has one main advantage – the problem of sampling two whorls at once (external shell of one whorl and internal shell of the next whorl) can be ruled out. No contamination (e.g. organic or inorganic particles) was observed using light microscope and SEM. The standard deviation was $<0.08\%$ for $\delta^{18}\text{O}$ and 0.04% for $\delta^{13}\text{C}$ based on repeated measurements (5 replicates) of international standards NBS18 and NBS19.

Hypacanthoplites elegans was sampled in opposite ontogenetic growth direction near the seam (Fig. 1). Special attention was given not to sample the sediment filling of the shells. *Nowakites savini* was sampled in ontogenetic growth direction (last whorl); only the external part of the shell was used to gain higher resolution (Fig. 1) because early ontogenetic stages are not preserved in this specimen. All three shells showed no alterations (see supplementary information) or dissolution, and primary iridescence was still present in *C. emiliantsevi* and *H. elegans*.

Isotopic analysis was performed in the Stable Isotope Laboratory at the Institute of Earth Sciences, Karl-Franzens University Graz, using an automatic Kiel II preparation line and a Finnigan MAT Delta Plus mass spectrometer. Samples for the investigation of isotopic composition were drilled with a 0.3 mm-diameter dental drill. Samples were dried and reacted with 100% phosphoric acid at 70 °C. International standard NBS-18 and an internal laboratory standard were analysed continuously for accuracy control. Standard deviation was less than 0.08% for $\delta^{18}\text{O}$ and 0.04% for $\delta^{13}\text{C}$. Isotopic data are reported in conventional δ notation relative to the Vienna Pee Dee belemnite (V-PDB) standard in ‰ units and calculating with SMOW (standard mean ocean water). Paleotemperatures were calculated using the equation of Grossman and Ku (1986); Goodwin et al., 2003) according to

$$T(^{\circ}\text{C}) = 20.6 - 4.34 \left(\delta^{18}\text{O}_{\text{aragonite}} - \left[\delta^{18}\text{O}_{\text{water}} - 0.2 \right] \right).$$

An aragonite formation in isotopic equilibrium with the Mesozoic seawater is assumed. Ocean water is assumed to be -1.0% (relative to SMOW; standard mean ocean water) for a nonglacial world (Shackleton and Kennett, 1975). Primary aragonite was detected by dry chemical powder measurements with a Siemens D5000 θ – θ powder X-ray diffractometer at 25 °C (radiation was $\text{Cu-K}\alpha$, 2.0 s, 0.01° intervals). About 100 mg of powdered sample was loaded into a flat bed sample holder. Scan range was 2θ of 2 – 65° , voltage 45 V, and current 25 mA. Position, height, and distance of the diffractometer

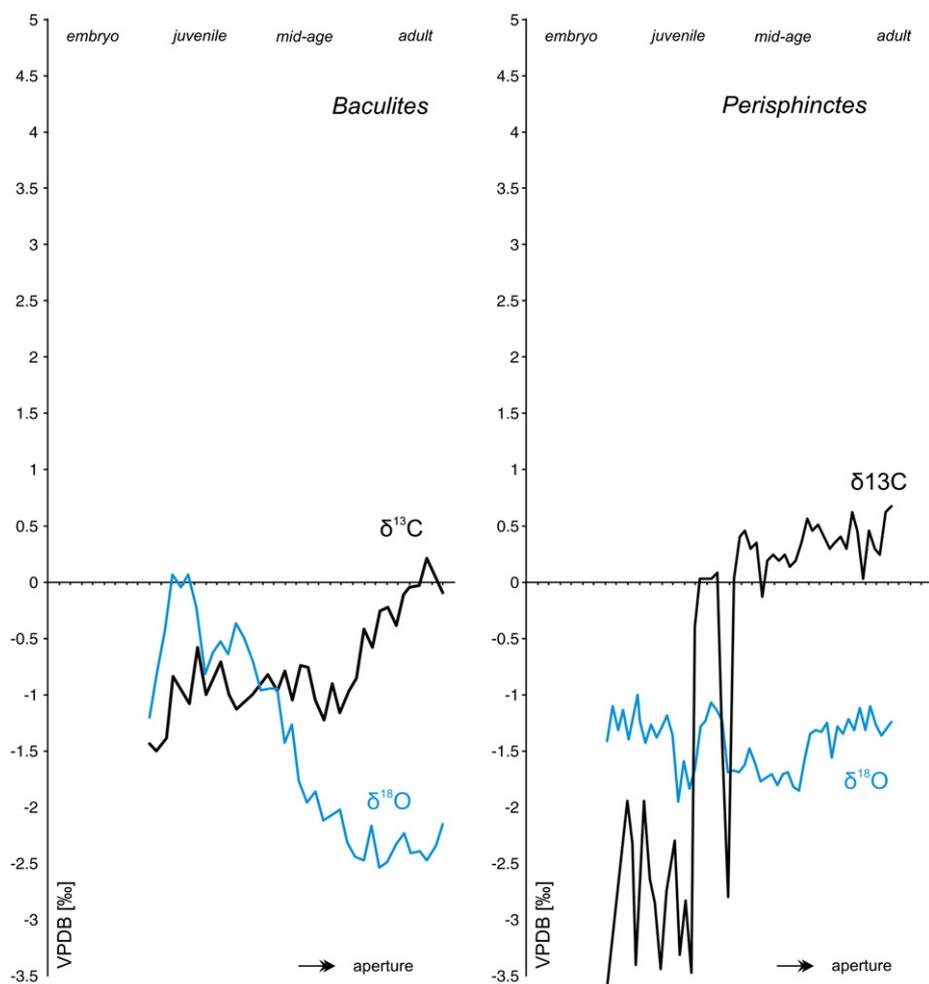


Fig. 4. Stable isotope curves ($\delta^{18}\text{O}$ in blue and $\delta^{13}\text{C}$ in black) for the ammonoids *Perisphinctes* and *Baculites* (Fatherree et al., 1998; Lécuyer and Bucher, 2006).

curve-peaks fit perfectly with pristine and primary aragonite. Pristine aragonite was additionally detected by geochemical analysis as EDX and SEM (Fig. 1). Quantitative chemical analyses were carried out on a JEOL JSM-6400 scanning electron microscope (operation conditions 15 kV acceleration voltage, ~1–2 nA sample current). Standardless chemical analyses (normalized to total sum = 100 %) were performed using the energy-dispersive system KEVEX Si(Li) detector linked to a VANTAGE EDS system. Ammonoid shells were additionally studied by means of cathodoluminescence. Well preserved microstructure of nacreous layers show primary aragonite tablets (>99% aragonite; supplementary data B). Cathodoluminescence was performed on a TESCAN (Vega TC; Wide Field Optics), voltage 10 kV, at 17 mm distance, at scan rate 7 $\mu\text{s}/\text{pixel}$.

No secondary mineral phase was present. The state of preservation is ideal for a precise geochemical analysis in order to reconstruct past seawater temperatures.

4. Results

4.1. Ammonoid data

4.1.1. *Cadoceras emiliantsevi*

36 samples (Fig. 1, see Table 1 in supplementary data); $\delta^{18}\text{O}$ values range from -1.35‰ to $+0.75\text{‰}$ suggesting an overall temperature change from 21.2 °C to 12.1 °C . The juvenile shell points to a mean temperature of 18.0 °C , which is followed by a middle phase of c. 13.4 °C and a final stage of c. 14.3 °C . $\delta^{18}\text{O}$ values of the juvenile shell (samples 1–7) were inconstant but steadily increase from -1.35 to

$+0.14\text{‰}$ up to a middle phase of -0.16 to $+0.75\text{‰}$ and then slightly decrease down to an also unstable phase from -0.36 to $+0.60\text{‰}$ in the adult stage. The $\delta^{13}\text{C}$ values of *Cadoceras* increase inconstantly during ontogeny and range from -1.57‰ to $+1.14\text{‰}$. The $\delta^{13}\text{C}$ values of the juvenile shell (samples 1–7) jump markedly from -1.57 to $+0.07\text{‰}$ up to a middle phase of -0.76 to $+0.73\text{‰}$ and then slightly increase to an unstable phase from -0.87 to $+1.14\text{‰}$ (mean $+0.14$) in adults (Fig. 2). Thus, after hatching at depths of probably less than 100 m at temperatures of 18 °C , *Cadoceras* migrated into deeper, cooler waters of c. 13 °C at depths of 200–400 m. Subsequently, the decreasing $\delta^{18}\text{O}$ values suggest a migration back into somewhat warmer, shallower habitats at 200 m with approx. 14 °C . Near the aperture (samples 33–36), values increase, indicating a temperature rise of about $4\text{--}5\text{ °C}$ during mature age. This may be linked to spawning cycles in adults (Fig. 5).

4.1.2. *Hypacanthoplites elegans*

26 samples (Fig. 1, see Table 1 in supplementary data); $\delta^{18}\text{O}$ values were generally negative and range from -3.11‰ to -1.71‰ suggesting that *Hypacanthoplites* was a warm water dweller living in waters between 23 and 29 °C . $\delta^{18}\text{O}$ values of the juvenile shell (samples 1–10) steadily increase from -2.29 to -1.71‰ , followed by a middle phase of -2.57 to -2.26‰ and then a further decrease down to a third phase ranging from -3.11 to -2.73‰ in adults. Three main phases can also be detected in the $\delta^{13}\text{C}$ values of *Hypacanthoplites*. After hatching at depths of probably less than 100 m at temperatures of c. 24 °C , *Hypacanthoplites* migrated into even shallower and warmer waters of c. 26 °C at depths of c. 50 m.

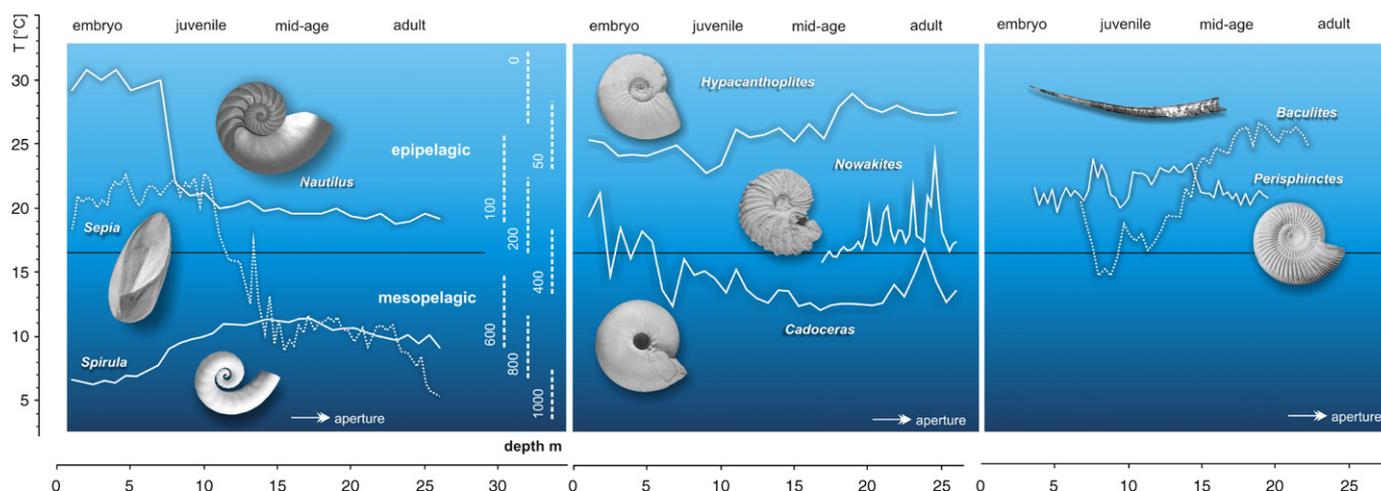


Fig. 5. Ontogeny in recent shelled cephalopods *Spirula*, *Sepia* and *Nautilus* (left) (Cochran et al., 1981; Landman et al., 1994; Lukeneder et al., 2008; Rexfort and Mutterlose, 2006), ancient ammonoids *Cadoceras*, *Hypacanthoplites* and *Nowakites* (middle), and ammonoids *Baculites* and *Perisphinctes* (right) (Fatherree et al., 1998; Lécuyer and Bucher, 2006). $\delta^{18}\text{O}$ curves in growth direction indicating calculated water temperatures and depth distribution of the cephalopods investigated compared with additional recent *Sepia*, *Spirula*, *Nautilus*, and fossil *Perisphinctes* and *Baculites* (all literature data). Clear separation of the juvenile, mid-age and adult phase is evident.

Subsequently, the decreasing $\delta^{18}\text{O}$ values suggest a second shift into even warmer habitats within the uppermost epipelagic zone with a water temperature of c. 27 °C (Fig. 5). $\delta^{13}\text{C}$ values start relatively high during early ontogeny, ranging from +3.73‰ to +4.62‰. A middle phase comprises values between +2.15‰ and +0.41‰ (mean +1.66), during its adult stage, the values increase again, ranging from +2.59‰ to +3.49‰ (mean +3.06) (Fig. 2). The first major decrease seems to mirror a change in habitat and probably also diet as suggested by the oxygen values. The subsequent jump to high values might reflect sexual maturity and mating as documented for *Spirula* (Lukeneder et al., 2008).

4.1.3. *Nowakites savini*

38 samples (Fig. 1, body whorl only, see Table 1 in supplementary data); $\delta^{18}\text{O}$ values range from −2.04‰ to −0.10‰ and display an overall negative trend. The values of the early last whorl (samples 1–12) steadily decrease from −0.09‰ to −0.47 (mean −0.30). This was followed by an unstable phase, jumping between −0.42‰ and −2.04 (mean −0.83) and then an increase to less negative values in a last phase from −0.64 to −0.30‰ (mean −0.46) in adults. $\delta^{13}\text{C}$ values on the last whorl of *Nowakites* are inconstant. In agreement with the phases detected in $\delta^{18}\text{O}$, $\delta^{13}\text{C}$ values start relatively high in early stages of the last whorl and range from +2.07‰ to +1.76‰; thereafter, an irregular phase starts, with rapid shifts between +1.73‰ and +0.71‰ (Fig. 2).

5. Discussion

Our stable isotope data point to various ontogenetically controlled types within the ammonoids. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values mark two to three phases, corresponding to different temperature and habitat levels as observed in modern counterparts. Comparing these fossil patterns with modern analogues requires a short overview of the modern examples *Spirula*, *Sepia* and *Nautilus*. Moreover, own data are compared with the often very spotty data (e.g. one measurement per specimen) on fossil cephalopods. A list of the taxa with isotope data is given in Table 1 (supplementary data).

5.1. Fossil cephalopods: isotopes and ontogeny

5.1.1. *Cadoceras* – a *Nautilus*–*Sepia* equivalent

The observed $\delta^{18}\text{O}$ values of *Cadoceras*, ranging from −1.35‰ to +0.75‰, suggest an overall temperature change from 21.2 °C to

12.1 °C. After hatching at depths of probably less than 100 m at temperatures of 18 °C, *Cadoceras* migrated into deeper, cooler waters of c. 13 °C at depths of 200–400 m. Subsequently, the decreasing $\delta^{18}\text{O}$ values suggest a migration back into somewhat warmer, shallower habitats at 200 m with approx. 14 °C (*wcw*-type, warm–cool–warm type). Near the aperture (samples 33–36), values increase, indicating a temperature rise of about 4–5 °C during mature age. This may be linked to spawning cycles in adults (Fig. 5). This $\delta^{18}\text{O}$ data pattern is reminiscent of that of *Nautilus* (Eichler and Ristedt, 1966a,b; Taylor and Ward, 1983) and *Sepia* (Bettencourt and Guerra, 1999; Rexfort and Mutterlose, 2006). Especially the pattern of *Sepia* is very similar and suggests a start in the epipelagic zone and a main phase in the mesopelagic zone. The tendency of *Cadoceras* to re-appear in the epipelagic zone during latest stages of ontogeny, however, is unparalleled by *Sepia* and *Nautilus* (both *wc*-type; warm–cool-type).

5.1.2. *Hypacanthoplites* and *Baculites* – inhabitants of the epipelagic zone

Throughout its life, *Hypacanthoplites* was a warm water dweller living in waters between 23 and 29 °C. Nevertheless, slight ontogenetic differences are evident. After hatching at depths of probably less than 100 m at temperatures of c. 24 °C, *Hypacanthoplites* migrated into even shallower and warmer waters of c. 26–29 °C in the upper epipelagic zone (*cw*-type, cool–warm type; Fig. 5). $\delta^{13}\text{C}$ values start relatively high in early ontogeny, jump markedly to +4.62‰, go down to a mean of +1.66‰ during a mid-aged phase and increase again to a mean of +3.06‰ in the adult stage. The first major decrease seems to mirror a change in habitat and probably also diet as suggested by the oxygen values.

No direct parallel trend can be observed in the modern cephalopods listed above. Only the recent deep-water squid *Spirula* displays minor similarities as it also starts in deeper habitats and then migrates into shallower areas (Lukeneder et al., 2008). The starting points, however, are completely different because *Spirula* hatches at depths of more than 1000 m at low temperatures of 4–6 °C (Fig. 5). Moreover, the last phase is different in *Spirula* and *Hypacanthoplites*. Mature *Spirula* migrates back into deep and cool habitats, whereas *Hypacanthoplites* apparently stays in surface waters. The general trend to inhabit shallower environments after hatching, however, is common to both taxa. In contrast, the three-phased $\delta^{13}\text{C}$ patterns of *Spirula* and *Hypacanthoplites* are strikingly similar. This suggests a strong change in diet at the transition from the juvenile to the mid-aged animal.

Stable isotope data of *Baculites* were provided by [Fatherree et al. \(1998\)](#) from the Western Interior Seaway (Late Campanian). The oxygen data ([Fig. 4](#)) suggest a seawater-temperature variation of about 10.0 °C, from 19.7 °C to 29.7 °C. Although the data set is incomplete, it appears that the investigated specimen changed into shallower waters after reaching maturity ([Fatherree et al., 1998](#)). In contrast to the pure surface water dweller *Hypacanthoplites*, it thus did change its depth preference and seems to have started as a juvenile in the lower epipelagic zone ([Fig. 5](#)).

5.1.3. *Nowakites* – a migrant between epi- and mesopelagic zones

The $\delta^{18}\text{O}$ values (−2.04‰ to −0.10‰) suggest an overall temperature range from 24.2 to 15.8 °C. The trend within the last whorl of *Nowakites* indicates a general migration history from cooler and deeper waters of 15.8 °C at depths of 200–300 m into somewhat warmer, shallower habitats with approx. 19 °C ([Fig. 5](#)). Close to the aperture (samples 32–38), oxygen values increase by about 1.5‰, pointing to a distinct temperature decrease that might reflect a retreat to the mesopelagic zone in latest ontogenetic stages. This general trend is accompanied by a very rapid fluctuation causing a serrated pattern of the oxygen isotope curve. This regular serration could indicate frequent migration from the deeper and cooler mesopelagic zone into the shallow and warm epipelagic zone. The serration of the $\delta^{13}\text{C}$ curve supports this interpretation.

5.1.4. *Perisphinctes* – same habitat but different prey

Data on *Perisphinctes* have been provided by [Lécuyer and Bucher \(2006\)](#), although they did not cover the earliest ontogenetic stages. A threefold post-embryonic development is signaled by the oxygen values, which point to a shallow and warm late juvenile to mid-aged phase with c. 23–24 °C opposing slightly cooler and deeper juvenile and adult stages with 20–21 °C ([Fig. 5](#)). This pattern is somewhat similar to that of *Spirula* although the deep mesopelagic environment of *Spirula* ([Lukeneder et al., 2008](#); [Price et al., 2009](#)) clearly differs from the epipelagic environment of *Perisphinctes*. The carbon pattern of the latter, however, has little in common with the former but is strongly reminiscent of that of *Nautilus* (very low embryonic and early juvenile values and a considerable shift towards positive values thereafter). As this shift is not reflected in the $\delta^{18}\text{O}$ values, it is likely that a major change in diet or the onset of sexual maturity caused the $\delta^{13}\text{C}$ shift without a marked change in habitat. The animals probably changed their prey preference after attaining a certain size.

5.2. Mode of life

The main difference between ammonoids and Recent cephalopods such as *Spirula* and *Sepia* is the maximum life-span. *Sepia* apparently attains an age of c. 200 days ([Rexfort and Mutterlose, 2006](#)), *Spirula* with lives approx. 2 years ([Lukeneder et al., 2008](#)) whereas ammonoids might have lived 5–100 years ([Bucher et al., 1996](#); [Westermann, 1996](#)). Most estimates are based on proxy data derived from epifauna such as serpulids and bivalves ([Seilacher, 1960](#); [Meischner, 1968](#)) and range between 1 and 15 years. Similar ages are suggested based on growth rate estimates based on growth line counting ([Bucher et al., 1996](#)). Calculations, based on growth rate comparisons with *Nautilus* achieved similar results with individual ages of 1–2 years for small, shallow water ammonites and 5–10 years for most pelagic taxa, comparable to those studied herein. Exceptions are the giant lycoceratids which seem to have grown 50 to 100 years ([Westermann, 1996](#)). Different growth rates in shallow water and deeper basinal environments, however, may complicate the calculations ([Elmi and Benschili, 1987](#)). Due to these uncertainties, we will not discuss the individual ages of the studied ammonites but focus on the clear ontogenetic trends.

Most ammonoids are supposed to have lived in the epipelagic and mesopelagic zones ([Westermann, 1990](#); [1996](#)). An epicontinental

ocean with deeper immersed basins, with epi- and mesopelagic depth areas, is also assumed for deposition for all investigated specimens. In our reconstruction of depth, we use a model of an epicontinental ocean comparable to a gently sloping continental shelf with a steep continental slope. Different morphologies in ammonite shells (planispiral to heteromorphic) and the variety of shell coiling (cadicone, ancylocone etc.) were discussed as a reflection of differences in the mode of life ([Cecca, 1997](#)). Based on shell shape, septal, siphuncle and suture morphology, accompanied by investigations of co-occurring biofacies, [Westermann \(1990; 1996\)](#) proposed different life styles of certain ammonoids: juveniles of several pelagic ammonoids in the open ocean seem to have lived in deeper zones than the adults (e.g.: scaphitids or ancyloceratids). Nevertheless, [Westermann \(1996\)](#) suggested that about 50% of the pelagic ammonoids did not migrate within the water column. The pelagic type was opposed by taxa which seem to have changed from nektonic to a demersal life style (e.g.: cadicone *Fagesia*, heteromorph *Baculites*). A nekto-benthic mode of life for several taxa was also proposed by [Wiedmann \(1973\)](#), [Vašiček and Wiedmann \(1994\)](#) and [Lukeneder \(2003; 2005\)](#). [Ebel \(1992\)](#) suggested also a benthic, more gastropod like, life style for heteromorphs.

Further proxies for the mode of life are shell strength and morphology such as ribbing and whorl cross-section reflected in groups such as the Leiostraca (smooth shells, in deeper water) and the Trachyostraca (sculptured with ribbing, in shallow water) ([Westermann, 1996](#)). The stable isotope data, now, confirm this scenario. Hence, the $\delta^{18}\text{O}$ values of the trachyostracian representatives such as *Hypacanthoplites*, *Nowakites* and *Perisphinctes* reveal them as inhabitants of the epipelagic zone. *Hypacanthoplites* (Deshayesitidae, with moderately coarse ribbing, discocone) is interpreted to be an inhabitant of the photic zone of the uppermost 100 to 50 m in the water column with a planktic to nektonic, mobile life style. *Nowakites* (Pachydiscidae with strong ribbing, platycone–discocone) seem to have preferred the transition from the epipelagic to mesopelagic zone, with a mobile to sluggish mode of life and strong vertical migrations. Heteromorphs, at least *Baculites*, apparently preferred a similar water depth. In contrast, the much more positive $\delta^{18}\text{O}$ values of the leiostracian *Cadoceras* indicate the cooler and deeper mesopelagic zone as the preferred environment. Based on this still low number of species, the general rule of thumb that Trachyostraca dominated in the neritic epipelagic zone <100 m water depth, whereas Leiostraca dominated in the deeper oceanic mesopelagic zone, seems to be valid.

A major difference in the modes of life of many ammonites compared to the modern cephalopods *Spirula*, *Sepia* and *Nautilus* is observed in their latest adult stage of ontogeny. All extant examples tend to retreat into the deepest environments as mature adult animals (*Spirula*, *Sepia*) or at least to remain there throughout their post-juvenile phase (*Nautilus*). In contrast, all measured ammonites except for *Perisphinctes* display a clear tendency to migrate into shallower environments in their latest ontogenetic stage ([Fig. 5](#)).

5.3. Cretaceous seawater temperatures: proxies from *Hypacanthoplites*

Maximum $\delta^{18}\text{O}$ values in *Hypacanthoplites* are −3.11‰ and correspond to temperatures of at least 28.9 °C. This paleotemperature corresponds with Mid-Cretaceous sea-surface temperature estimates of about 30–34 °C ([Mutterlose and Immenhauser, 2007](#)). Similar values of 35 °C in the tropical zone and high-latitude temperatures of c. 20 °C have been proposed by [Bornemann et al. \(2008\)](#) for the Late Cretaceous. Stable isotope data on Atlantic sediments suggest a synchronous shift of $\delta^{18}\text{O}$ values in surface and deep ocean waters during the Middle and Late Cretaceous ([Frakes, 1999](#); [Fassel and Bralower, 1999](#); [Bornemann et al., 2008](#)) caused by an extreme greenhouse climate (supergreenhouse in [Bornemann et al., 2008](#)). Numerous papers discuss atmospheric conditions and ocean-atmosphere coupling during this Mid-Cretaceous climate-optimum ([Caldeira and Rampino, 1991](#); [Wilson and Norris, 2001](#); [Donnadieu et al., 2006](#); [Wagner et al., 2008](#)). The unstratified

Jurassic and Cretaceous oceans allowed a warming of bathyal waters of up to 20 °C during the Cenomanian (Huber et al., 2002) and caused a strong heat flux from the tropic zone into high latitudes (Hay and DeConto, 1999; Mutterlose and Immenhauser, 2007). This explains the high paleotemperatures in the “boreal realm”, as indicated by *Hypacanthoplites* from northern Germany. Moreover, the compilation of $\delta^{18}\text{O}$ literature data (Figs. 6 and 7) reveals an excellent fit of our Aptian *Hypacanthoplites* and Santonian *Nowakites* with expected greenhouse climate values. A comparable “hot” period was detected only during the Triassic (Figs. 6 and 7). Therefore, the estimated narrow migratory range of these taxa as reflected by oxygen values might be distinctly underestimated due to the buffering effect of an insignificant thermocline (Barrera and Johnson, 1999).

6. Conclusions

Both stable isotope records suggest separated main phases which correspond to ontogenetically controlled vertical migrations within the water column. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values mark three to four phases in ontogeny: embryonic, juvenile, mid-aged, and adult. The data demonstrate that the ammonoids started their life cycles in different environments (e.g. depth). This difference in strategies is detected in both stable isotope signatures ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$), reflecting changes in diet, sexual maturity and mating to spawning phase.

The ontogenetic series of stable isotope records of the different ammonoid groups (*Cadoceratidae*, *Deshayesitidae*, *Pachydiscidae*) displayed highly divergent oxygen and carbon curves. This indicates

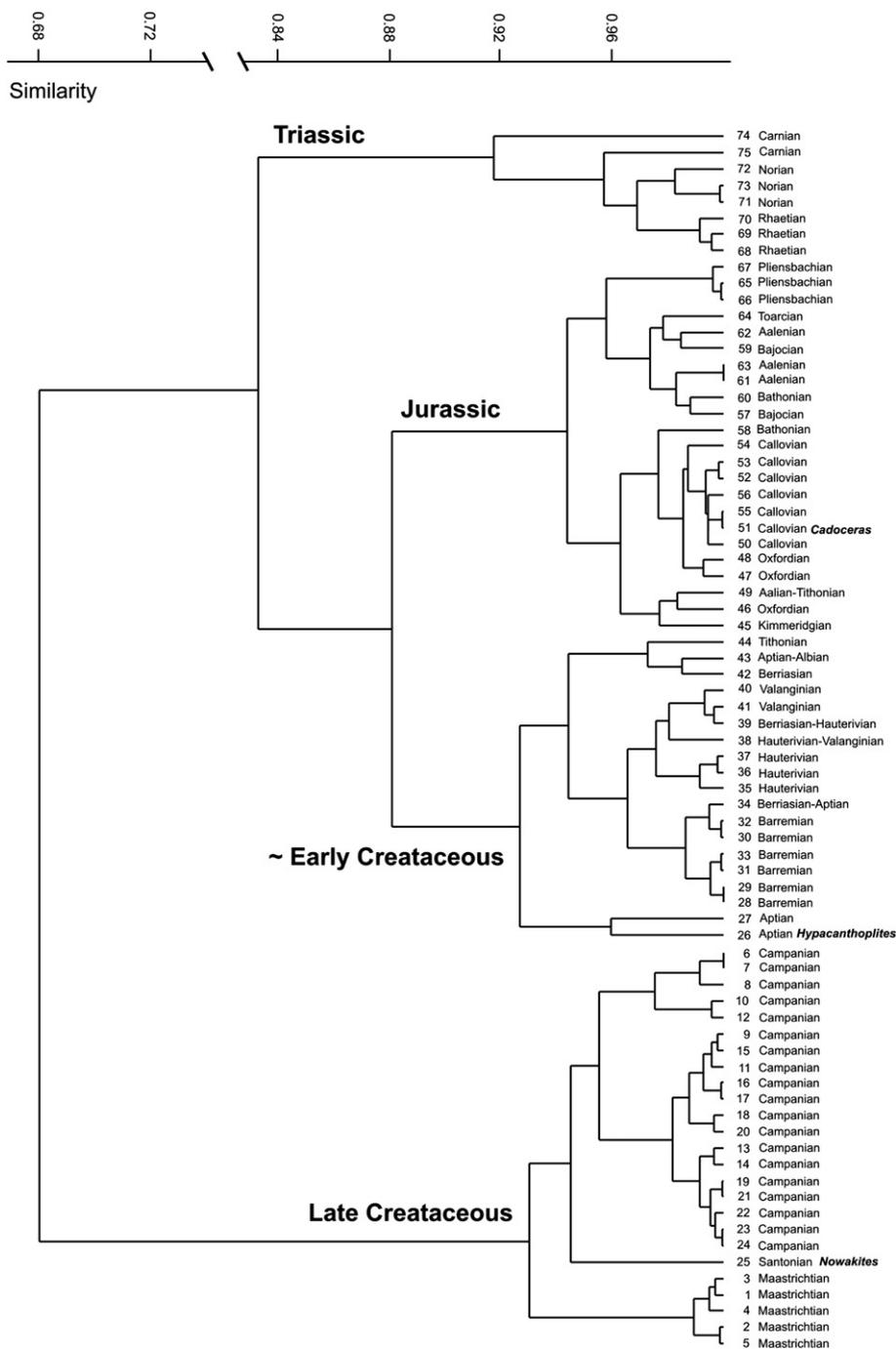


Fig. 6. Cluster analysis after Bray–Curtis of the estimated temperature data set obtained by stable isotope data ($\delta^{18}\text{O}$). Calculated temperatures for *Cadoceras*, *Hypacanthoplites* and *Nowakites* perfectly cluster in the groups of same age estimated from literature data.

- Cecca, F., 1997. Late Jurassic and Early Cretaceous uncoiled ammonites: trophism-related evolutionary processes. *Comptes Rendus de l'Academie des Sciences Series II, Earth Planet. Sci.* 325, 629–634.
- Cherel, Y., Ridoux, V., Spitz, J., Richard, P., 2009. Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopod and giant squid. *Biol. Lett.* 5, 364–367.
- Clarke, M.R., 1969. Cephalopoda collected on the SOND cruise. *J. Mar. Biol. Ass. UK* 49, 961–976.
- Cochran, J.K., Rye, D.M., Landman, N.H., 1981. Growth rate and habitat of *Nautilus pompilius* inferred from radioactive and stable isotope studies. *Paleobiol.* 7, 469–480.
- Cochran, J.K., Landman, N.H., Turekian, K.K., Michard, A., Schrag, D.P., 2003. Paleocyanography of the Late Cretaceous (Maastrichtian) Western Interior Seaway of North America: evidence from Sr and O isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 191, 45–64.
- Ditchfield, P.W., 1997. High Northern palaeolatitude Jurassic–Cretaceous palaeotemperature variation: new data from Kong Karls Land. *Svalbard. Palaeogeogr. Palaeoclimatol. Palaeoecol.* 61, 237–254.
- Donnadieu, Y., Pierrehumbert, R., Jacob, R., Fluteau, F., 2006. Cretaceous climate decoupled from CO₂ evolution? *Earth Planet. Sci. Lett.* 248 (1–2), 426–437.
- Ebel, K., 1992. Mode of life and soft body shape of heteromorph ammonites. *Lethaia* 25, 179–193.
- Eichler, R., Ristedt, H., 1966a. Isotopic evidence on the Earth Life History of *Nautilus pompilius* (Linné). *Science* 153, 734–736.
- Eichler, R., Ristedt, H., 1966b. Untersuchungen zur Frühontogenie von *Nautilus pompilius* (Linné). *Paläont. Z.* 40, 173–191.
- Elmi, S., Benschli, K., 1987. Relations entre la structuration tectonique, la composition des peuplements et l'évolution; exemple du Toarcien du Moyen-Atlas meridional (Maroc). *Boll. Soc. Paleont. Ital.* 26, 47–62.
- Fabricius, F., Friedrichsen, H., Jacobshagen, V., 1970. Paläotemperaturen und Paläoklima in Obetrias und Lias der Alpen. *Int. J. Earth Sci.* 59, 805–826.
- Fassel, M.L., Bralower, T.J., Barrera, E., Johnson, C.C., 1999. Warm, equable mid-Cretaceous: stable isotope evidence. *Evolution of the Cretaceous Ocean–Climate system. Spec. paper 332, Geol. Surv. Am., Boulder*, pp. 121–142.
- Fatherree, J.W., Harries, P.J., Quinn, T.M., 1998. Oxygen and carbon isotopic “dissection” of *Baculites compressus* (Mollusca: Cephalopoda) from Pierre Shale (Upper Campanian) of South Dakota: implications for paleoenvironmental reconstructions. *Palaios* 13, 376–385.
- Forester, R.W., Caldwell, W.G.E., Oro, F.H., 1977. Oxygen and carbon isotopic study of ammonites from Late Cretaceous Bearpaw Formation in southwestern Saskatchewan. *Can. J. Earth Sci.* 14, 2086–2110.
- Frakes, A.L., 1999. Estimating the global thermal state from Cretaceous sea surface and continental temperature data. In: Barrera, E., Johnson, C.C. (Eds.), *Evolution of the Cretaceous Ocean–Climate system. Spec. paper 332, Geol. Surv. Am., Boulder*, pp. 49–57.
- GEOSecs ATLANTIC, PACIFIC and INDIAN OCEAN Expeditions 1987. Shore-based data and graphics GEOSecs Executive Committee IDOE National Science Foundation 7.
- Goodwin, D.H., Schöne, B.R., Dettman, D.L., 2003. Resolution and fidelity of oxygen isotopes as palaeotemperature proxies in bivalve mollusc shell: models and observations. *Palaios* 18, 110–125.
- Grossman, E.L., Ku, T., 1986. Oxygen and carbon isotope fractionation in biogenic aragonite: temperature effects. *Chem. Geol.* 59, 59–74.
- Hay, W.W., DeConto, R.M., 1999. Comparison of modern and Late Cretaceous meridional energy transport and oceanology. In: Barrera, E., Johnson, C.C. (Eds.), *Evolution of the Cretaceous Ocean–Climate system. Spec. paper 332, Geol. Surv. Am., Boulder*, pp. 283–300.
- He, S., Kyser, T.K., Caldwell, G.E., 2005. Paleoenvironment of the Western Interior Seaway inferred from $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of molluscs from Cretaceous Bearpaw marine cyclothem. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 217, 67–85.
- Hewitt, R.A., Stait, B., 1988. Seasonal variations in septal spacing of *Sepia officinalis* and some Ordovician actinocerid nautiloids. *Lethaia* 21, 283–394.
- Hoefs, J., 2004. *Stable Isotope Geochemistry*, fifth ed. Springer Verlag, Berlin-Heidelberg-New York.
- Huber, B.T., Norris, R.D., MacLeod, K.G., 2002. Deep-sea palaeotemperature record of extreme warmth during the Cretaceous. *Geology* 30, 123–126.
- Jelitzky, J.A., Zapfe, H., 1976. Coleoid and Orthocerid Cephalopods of the Rhaetian Zlambach Marl from the Fischerwiese near Aussee, Styria (Austria). *Ann. Naturhist. Mus. Wien* 71, 69–106.
- Jordan, R., Stahl, W., 1970. Isotopische Paläotemperatur-Bestimmungen an jurassischen Ammoniten und grundsätzliche Voraussetzungen für diese Methode. *Geol. Jb* 89, 33–62.
- Kaltenegger, W., 1967. Paläotemperaturbestimmungen an aragonitischen Dibranchiastenrosten der Trias. *Naturwissenschaften* 54, 515.
- Kaltenegger, W., Preisinger, A., Rögl, F., 1971. Palaeotemperature determinations of aragonitic mollusks from the Alpine Mesozoic. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 10, 273–285.
- Landman, N.H., 1988. Early ontogeny of Mesozoic ammonites and nautilids. In: Wiedmann, J., Kulmann, J. (Eds.), *Cephalopods—Present and Past*. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 215–228.
- Landman, N.H., Rye, D.M., Shelton, K.L., 1983. Early ontogeny of *Eutrephoceras* compared to Recent *Nautilus* and Mesozoic ammonites: evidence from shell morphology and light stable isotopes. *Paleobiol.* 9, 269–279.
- Landman, N.H., Cochran, J.K., Rye, D.M., Tanabe, K., Arnold, J.M., 1994. Early life history of *Nautilus*: evidence from isotopic analysis of aquarium reared specimens. *Paleobiol.* 20, 40–51.
- Lécuyer, C., Bucher, H., 2006. Stable isotope composition of late Jurassic ammonite shell: a record of seasonal surface water temperatures in the southern hemisphere? *eEarth Discuss.* 1, 1–7.
- Lécuyer, C., Reynard, B., Martineau, F., 2004. Stable isotope fractionation between mollusc shells and marine waters from Martinique Island. *Chem. Geol.* 213, 293–305.
- LEVITUS 94, 1994. *World Ocean Atlas*, <http://ingrid.ideo.columbia.edu/SOURCES/LEVITUS94/>.
- Lincoln, R., Boxshall, G., Clark, P., 1998. *A Dictionary of Ecology, Evolution and Systematics*. Cambridge University Press, Cambridge, pp. 1–361.
- Longinelli, A., 1966. Ratios of oxygen-18:oxygen-16 in phosphate and carbonate from living and fossil marine organisms. *Nature* 211, 923–927.
- Longinelli, A., Nuti, S., 1973. Revised phosphate–water isotopic temperature scale. *Earth Planet. Sci. Lett.* 19, 373–376.
- Lowenstein, H.A., Epstein, S., 1954. Paleotemperatures of the post-Albian Cretaceous as determined by the oxygen isotope method. *J. Geol.* 62, 207–248.
- Lukeneder, A., 2003. The *Karsteniceras* Level: dysoxic ammonoid beds within the Early Cretaceous (Barremian, Northern Calcareous Alps, Austria). *Facies* 49, 87–100.
- Lukeneder, A., 2005. An equivalent of the *Karsteniceras* Level within the Vienna Woods (Sparbach section, Lunz Nappe, Northern Calcareous Alps, Lower Austria). *Geol. Carpath.* 56, 307–315.
- Lukeneder, A., Harzhauser, M., Müllegger, S., Piller, W., 2008. Stable isotopes ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) in *Spirula spirula* shells from three major oceans indicate developmental changes paralleling depth distributions. *Mar. Biol.* 154, 175–182.
- Marshall, J.D., 1981. Zoned calcites in Jurassic ammonite chambers: trace elements, isotopes and neomorphic origin. *Sedimentology* 28, 867–887.
- Martin, A.W., Catala-Stucki, I., Ward, D.P., 1978. The growth rate and reproductive behaviour of *Nautilus macromphalus*. *N. Jb. Geol. Paläont. Abh.* 156, 207–225.
- McArthur, J.M., Mutterlose, J., Price, G.D., Rawson, P.F., Ruffell, A., Thirlwall, M.F., 2004. Belemnites of Valanginian, Hauterivian and Barremian age: Sr-isotope stratigraphy, composition ($^{87}\text{Sr}/^{86}\text{Sr}$, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, Na, Sr, Mg), and palaeo-oceanography. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 202, 253–272.
- McConnaughey, T.A., Burdett, J., Whelan, J.F., Paul, C.K., 1997. Carbon isotopes in biological carbonates: respiration and photosynthesis. *Geochim. Cosmochim. Acta* 61, 611–622.
- Meischner, D., 1968. Pernicöse Epökie von *Placunopsis* auf *Ceratites*. *Lethaia* 1, 156–174.
- 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, 167–170.
- Mutterlose, J., Immenhauser, A., 2007. Klimawandel in der Erdgeschichte. *Kreidezeit war Treibhauswelt*. *Geowiss. Rubin. Geol.* 2007, 6–12.
- Niebuhr, S., Jochimski, M.M., 2002. Stable isotope and trace element geochemistry of Upper Cretaceous carbonates and belemnite rostra (Middle Campanian, North Germany). *Geobios* 35, 51–64.
- Okamoto, T., Shibata, M., 1997. A cyclic mode of shell growth and its implications in a Late Cretaceous heteromorph ammonite *Polyptychoceras pseudogaultinum* (Yokoyama). *Palaeontol. Res.* 1, 29–46.
- Ott, J., 1996. *Meereskunde. Einführung in die Geographie und Biologie der Ozeane*. UTB Ulmer Verlag, Stuttgart, pp. 1–424.
- Podlaha, O.G., Mutterlose, J., Veizer, J., 1998. Preservation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in belemnite rostra from the Jurassic/Early Cretaceous successions. *Am. J. Sci.* 298, 324–347.
- Price, G.D., Mutterlose, J., 2004. Isotopic signals from late Jurassic–early Cretaceous (Volgian–Valanginian) sub-Arctic belemnites, Yatra River, Western Siberia. *J. Geol. Soc. London* 161, 959–968.
- Price, G.D., Ruffell, A.H., Jones, C.E., Kalin, R.M., Mutterlose, J., 2000. Isotopic evidence for temperature variation during the early Cretaceous (late Ryazanian–mid Hauterivian). *J. Geol. Soc. Lond.* 157, 335–343.
- Price, G.D., Twitchett, R.J., Smale, Ch., Marks, V., 2009. Isotopic analysis of the life history of the enigmatic squid *Spirula spirula*, with implications for studies of fossil cephalopods. *Palaios* 24, 273–279.
- Rexfort, A., Mutterlose, J., 2006. Stable isotope records from *Sepia officinalis* – a key to understand the ecology of belemnites? *Earth Planet. Sci. Lett.* 247, 212–221.
- Uchiyama, K., Tanabe, K., 1999. Hatching of *Nautilus macromphalus* in the Toba aquarium, Japan. In: Olóriz, F., Rodríguez-Tovar, F.J. (Eds.), *Advancing Research on Living and Fossil Cephalopods*. Kluwer Academic/Plenum Publishers, New York, pp. 13–16.
- Schootbrugge, B., Föllmi, K.B., Bulot, L.G., Burns, S.T., 2000. Paleocyanographic changes during the early Cretaceous (Valanginian–Hauterivian): evidence from oxygen and carbon stable isotopes. *Earth Planet. Sci. Lett.* 181, 15–31.
- Seilacher, A., 1960. Epizoans as a key to ammonoid ecology. *J. Paleont.* 34, 189–193.
- Shackleton, N.J., Kennett, J.P., 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotopic analysis in DSDP sites 277, 279 and 281. In: Kennett, J.P., Houtz, R.E., et al. (Eds.), *Initial Reports of the Deep Sea Drilling Project*, vol. 29. U.S. Government Printing Office, Washington, D.C., pp. 743–755.
- Spaeth, C., Hoefs, J., Vetter, U., 1971. Some aspects of isotope composition of belemnites and related paleotemperature. *Geol. Soc. Amer. Bull.* 82, 3139–3150.
- Stahl, W., Jordan, R., 1969. General considerations on isotopic paleotemperature determinations and analysis on Jurassic ammonites. *Earth Planet. Sci. Lett.* 6, 173–178.
- Tarutani, T., Clayton, R.N., Mayeda, T.K., 1969. The effects of polymorphism and magnesium substitution on oxygen isotope fractionation between calcium carbonate and water. *Geochim. Cosmochim. Acta* 33, 987–996.
- Taylor, B.E., Ward, P.D., 1983. Isotopic studies of *Nautilus macromphalus* Sowerby (New Caledonia) and *Nautilus pompilius* L. (Fiji). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 41, 1–16.
- Tourtelot, H.A., Rye, R.O., 1969. Distribution of oxygen and carbon isotopes in the fossil of Late Cretaceous age, Western Interior region of North America. *Geol. Soc. Am. Bull.* 80, 1903–1922.
- Urey, H.C., Lowenstein, H.A., Epstein, S., McKinney, C.R., 1951. Measurements of paleotemperatures and temperatures of the Upper Cretaceous, Denmark, and southeastern United States. *Geol. Soc. Am. Bull.* 62, 399–416.

- Vašiček, Z., Wiedmann, J., 1994. The Leptoceratoidinae: small heteromorph ammonites from the Barremian. *Palaeontology* 37, 203–239.
- Wagner, T., Herrle, J.O., Sinninghe Damsté, J.S., Schouten, S., Stüsser, I., Hofmann, P., 2008. Rapid warming and salinity changes of Cretaceous surface waters in the subtropical North Atlantic. *Geology* 36 (3), 203–206.
- Watanabe, T., Gagan, M.K., Corregge, T., Scott-gagan, H., Cowley, J., Hantoro, W.S., 2003. Oxygen isotope systematics in *Diploastrea heliopora*: new coral archive of tropical paleoclimate. *Geochim. Cosmochim. Acta* 67, 1349–1358.
- Wefer, G., 1985. Die Verteilung stabiler Isotope in Kalkschalen mariner Organismen. *Geol. Jb* 82, 3–111.
- Westermann, G.E.G., 1990. New developments in the ecology of Jurassic–Cretaceous ammonoids. In: Pallini, G., Cecca, F., Cresta, S., Santantonio, M. (Eds.), *Fossili. Evoluzione, Ambiente. Atti II Conv. Int. Pergola. Tecnostampa, Ostra Vetere*, pp. 459–478.
- Westermann, G.E.G., 1996. Ammonoid life and habitat. In: Landman, N.H., Tanabe, K., Davis, R.A. (Eds.), *Ammonoid Paleobiology. Topics in Geobiology* 13. Plenum Press, New York, pp. 607–707.
- Whittaker, S.G., Kyser, T.K., Caldwell, G.E., 1987. Paleoenvironmental geochemistry of the Claggett marine Cyclothem in south-central Saskatchewan. *Can. J. Earth Sci.* 24, 967–984.
- Wiedmann, J., 1973. Upper Triassic heteromorph ammonites. In: Hallam, A. (Ed.), *Atlas of Palaeobiogeography*. Elsevier Scientific Publication Company, pp. 235–249.
- Wierzbowski, H., Joachimski, M.M., 2007. Reconstruction of Late Bajocian–Bathonian marine palaeoenvironments using carbon and oxygen isotope ratios of calcareous fossils from the Polish Jura Chain (central Poland). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 254, 523–540.
- Wierzbowski, H., Joachimski, M.M., 2009. Stable isotopes, elemental distribution, and growth rings of belemnite rostra: proxies for belemnite life habitat. *Palaios* 24, 377–386.
- Wierzbowski, H., Dembicz, K., Praszkiel, T., 2009. Oxygen and carbon isotope composition of Callovian–Lower Oxfordian (Middle–Upper Jurassic) belemnite rostra from central Poland: a record of a Late Callovian global sea-level rise? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 283, 182–194.
- Wilson, P.A., Norris, R.D., 2001. Warm tropical ocean surface and global anoxia during the mid-Cretaceous period. *Nature* 412, 425–429.
- Young, R.E., Vecchione, M., Donovan, D., 1998. The evolution of coleoid cephalopods and their present biodiversity and ecology. *S. Afr. J. Mar. Sci.* 20, 393–420.