Earth and Planetary Science Letters 296 (2010) 103–114

Contents lists available at ScienceDirect

Earth and Planetary Science Letters

journal homepage: www.elsevier.com/locate/epsl

Ontogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($\delta^{18}O$, $\delta^{13}C$)

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 ($\delta^{18}O$ and $\delta^{13}C$) 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. Leiostraca vs. Trachyostraca). We concentrate mainly on $\delta^{18}O$ for temperature results and added $\delta^{13}C$ 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 (*Hypacanthoplite*s, *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 $\delta^{18}O$ 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 $\delta^{18}O$ and $\delta^{13}C$ 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 $\delta^{13}C$ 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.

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 (leiostracans) 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).

0012-821X/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.epsl.2010.04.053

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 ($^{16}O/^{18}O$ and $^{12}C/^{13}C$) 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 ($\delta^{18}O$ and $\delta^{13}C$) 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

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

(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 ($\delta^{18}\mathrm{O}_{\mathrm{water}} = -1.0\text{‰}_{\mathrm{SMOW}}$ 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

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

assuming that the isotope ratio is strongly related to

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

(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

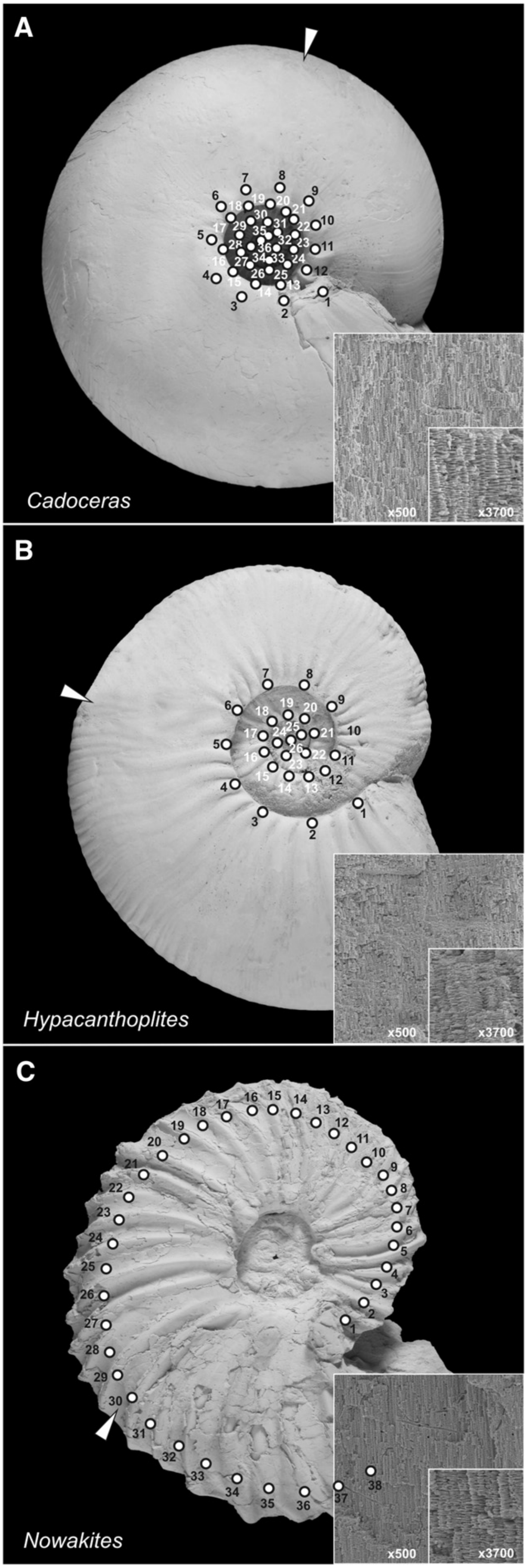

Fig. 1. Lateral view with numbered samples in ontogenetic direction, growth direction with indicated SEM images of aragonitic ultrastructure, ×500 and ×3700, of (A) *Cadoceras*, (B) *Hypacanthoplites* and (C) *Nowakites* shells.