



## *Aturia* from the Miocene Paratethys: An exceptional window on nautilid habitat and lifestyle

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### ABSTRACT

Many examples of drifted *Aturia* shells in shallow littoral deposits have been reported worldwide, suggesting that the paleobiogeographic distribution of this Cenozoic nautilid could be a mere *post-mortem* artifact. An exceptional Lower Miocene deposit from the Central Paratethys yields abundant (about 500 specimens) and very well-preserved newly hatched as well as adult shells, associated with upper and lower jaws, representing the first unequivocal case of autochthonous *Aturia* and one of the most exceptional nautilid deposits reported so far. Oxygen isotope ratios show that *Aturia* lived like *Nautilus*, being nektonic at all stages of its development. But unlike *Nautilus*, both newly hatched and adult *Aturia* lived at the same water depth and temperature (about 240–330 m and 13–17.6 °C) in which the eggs were laid. The dysoxic paleoenvironmental setting in which *Aturia* occurs in abundance may be interpreted in light of both the capacity of *Nautilus* to exploit/tolerate oxygen-depleted waters, and the molecular phylogenetic tree of cephalopods, suggesting plesiomorphic physiological traits associated with hypoxia tolerance. Since the last common ancestor of *Aturia* and *Nautilus* may be traced back at least into the Jurassic, this sheds new light onto the relative scarcity of Mesozoic and Cenozoic nautilids in well-oxygenated, epicontinental shelf deposits.

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### 1. Introduction

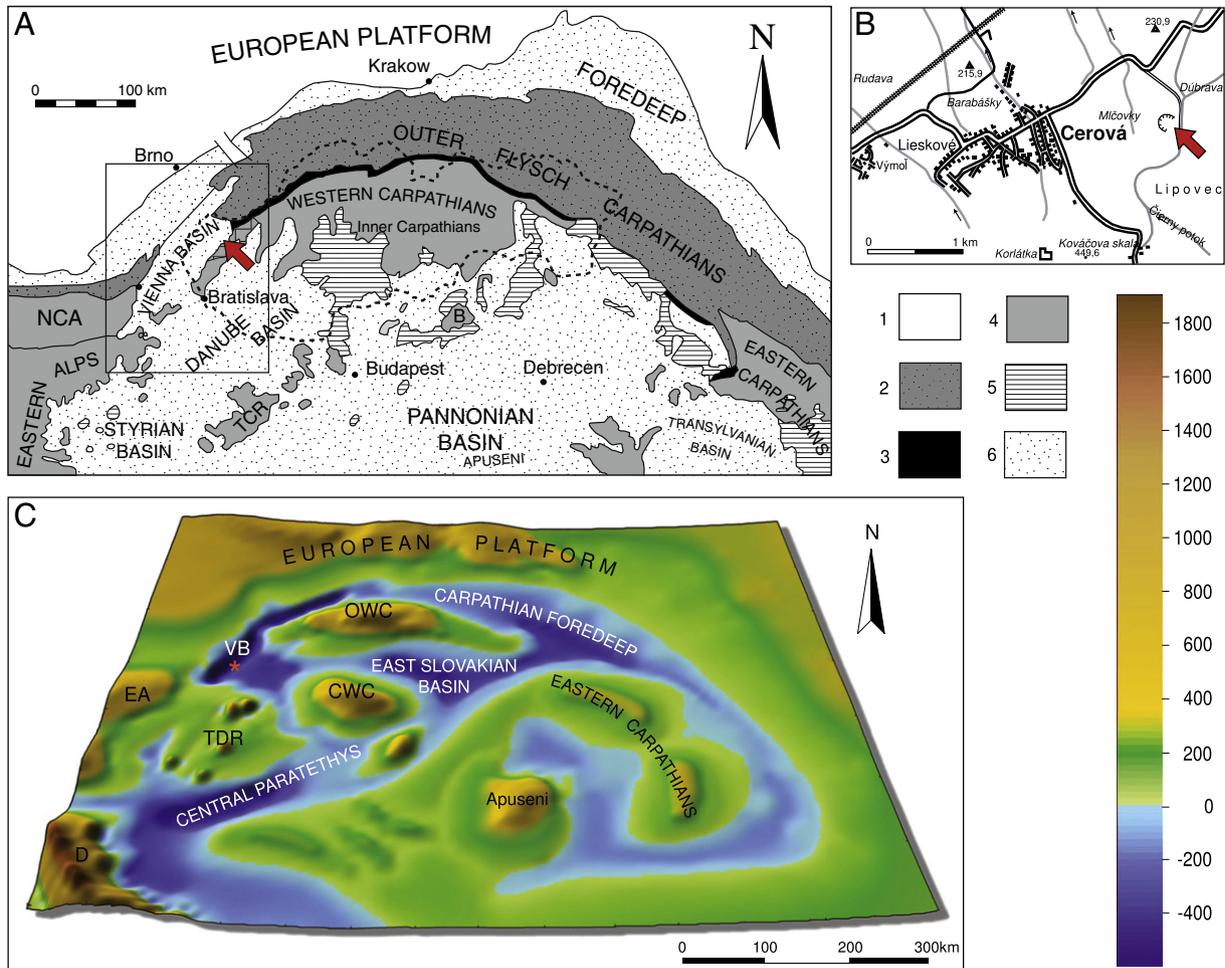
Drifted *Nautilus* shells are found on beaches sometimes thousands of kilometers outside distribution areas of living animals (House, 1987). This *post-mortem* drift constitutes a potential caveat for the interpretation of the paleobiology and paleoecology of chambered cephalopods and the extent to which this process biases their paleobiogeographic distribution remains difficult to evaluate. The nautilid genus *Aturia* (Paleocene–Miocene) constitutes a flagrant illustration of this bias. The unusually high number of reported cases of drifted shells in shallow littoral deposits worldwide (e.g., Stenzel, 1935; Kobayashi, 1954; Beu, 1973; Zinsmeister, 1987; Tomida et al., 2002; Mapes et al., 2010a) casts serious doubts on the real nature of the worldwide distribution of this genus that could be a mere *post-mortem* artifact (Chirat, 2000). Westermann (1999) already suggested a bathyal or mesopelagic habitat for *Aturia*, based on septa and neptal neck configurations. However no example of unequivocal autochthonous *Aturia* has been reported to date and where this genus actually lived still remains a conundrum.

In this paper, we report the discovery of an exceptional Miocene deposit from the Paratethys that provides the first unequivocal case of autochthonous *Aturia*. The habitat and lifestyle of this fossil nautilid are clarified using foraminiferal diversity and stable oxygen isotope analyses performed on shells of *Aturia* and other associated mollusks and foraminifera.

### 2. Material

The material studied here was collected in a 13.6 m thick section close to Cerová-Lieskové village (Fig. 1), at the foothills of the Malé Karpaty Mountains (N–E Vienna Basin). During the Miocene, this NNE–SSW sedimentary basin was part of the Central Paratethys. Marine sedimentation took place from the Early Burdigalian to Late Serravallian. Uppermost Burdigalian (equivalent of Karpatian in the Paratethyan stratigraphic chart, Harzhauser and Piller, 2007) deposits are characterized by offshore marine calcareous clay of the Lakšárska Nová Ves Formation (Špička and Zapletalová, 1964), generally massive, with thin silty lenses, thin tempestites with plant debris (up to 10 mm thick) and several intercalated thin sandstone layers in the uppermost part of the section (Fig. 2). The relief of the Vienna Basin during the Karpatian is difficult to reconstruct because of the later tectonic reconfiguration of the whole Carpathian area. Based on

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**Fig. 1.** A. Position of the Vienna Basin in the Carpathian-Pannonian system, locality marked by arrow. B. Location of the Cerová-Lieskové clay pit, indicated by arrow. C. Paleogeographic scheme of the Central Paratethys and adjacent areas during the Karpatian. Locality is marked by asterisk (modified from Kvaček et al., 2006). 1. European platform units. 2. Carpathian-Alpine externides. 3. Pieniny Klippen Belt. 4. Alpine-Carpathian-Dinaride and Pannonian internides. 5. Neogene volcanics. 6. Neogene basins. B – Bükk, CWC – Central Western Carpathians, D – Dinarides, EA – Eastern Alps, NCA – Northern Calcareous Alps, TCR, TDR – Transdanubian Central Range, VB – Vienna Basin.

recent studies, it appears however that the sea floor of the basin was very irregular, with several submarine elevations (ridges), representing tilted blocks of underlying Alpine and Western Carpathian units (Fodor, 1995), which probably started to uplift at that time. The Cerová-Lieskové locality was situated on the slope of such a submarine elevation (uplifting Male Karpaty Mts).

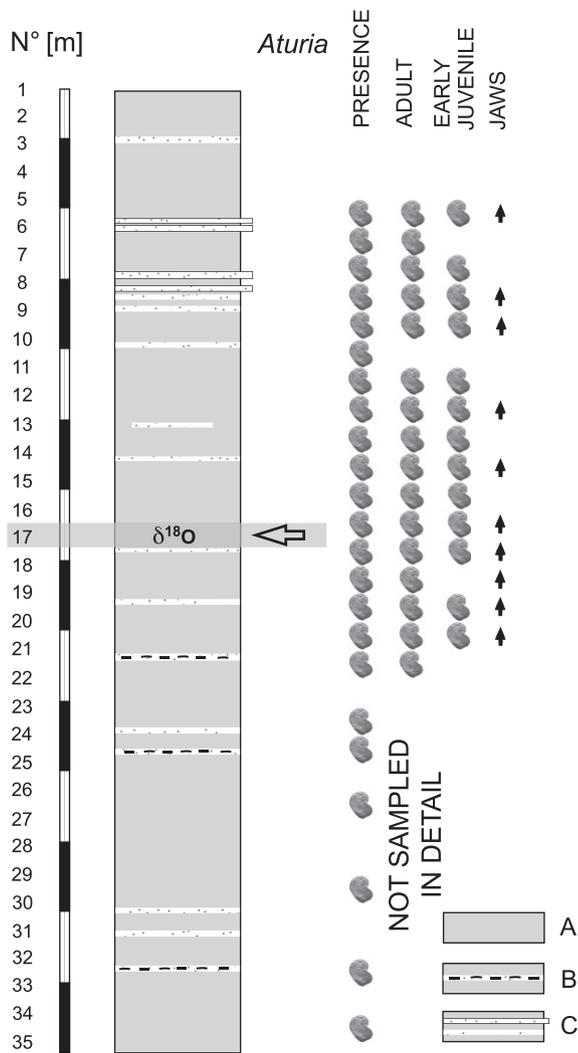
Thirty five samples were collected from the section with a sampling spacing of ~40 cm for benthic and planktonic foraminiferal analyses. Associated microfossils including radiolarians, ostracods, fish otoliths, coleoid statoliths, bathyal shark teeth and diatoms were also found in the samples. Macrofossils include vertebrates (fishes) and invertebrates (small sized bivalves and gastropods, scaphopods (Harzhauser et al., 2011), nautilids, coleoids, regular and irregular echinoids, brittle stars, siliceous sponges and crustaceans (Hyžný and Schlögl, 2011). *Aturia* is distributed through the entire section in which about 500 specimens have been collected (Figs. 2, 3A–B). *Aturia* assemblages comprise adult (as indicated by approximation of last septa, black band along the shell edge, thickened peristome (Fig. 3E) and crowded growth lines on the body chamber) as well as juvenile and newly hatched specimens (Fig. 3B–D), associated in the deposits with their jaws (Fig. 3G–H). The phragmocones are empty, and more compressed than the body chambers which are filled with sediment. Although shells are exceptionally well preserved (Fig. 3F), their compression prevents a detailed taxonomic identification.

### 3. Methods

#### 3.1. Foraminiferal diversity analyses

The 35 samples dedicated to the study of foraminiferal assemblages were wet sieved over 200 µm, 125 µm and 71 µm screens. Foraminifera (benthic and planktonic) were first picked and identified for biostratigraphic analysis. In addition, about 200–300 benthic foraminiferal specimens by sample were randomly picked, identified and counted. The raw data were transformed into percentages over the total abundance and percent abundance curves were plotted (Fig. 4). Species with similar environmental significance were grouped in order to better interpret their distribution patterns. Paleoeological parameters were evaluated for the 2.20 m thick part of the section (Fig. 2; 7 samples in total, labeled 14 to 20), which encompasses the level that was studied by means of oxygen isotopes (sample 17). Paleodepths and bottom oxygenation were determined from the presence and dominance of taxa that exhibit special environmental significance.

Paleodepths were estimated following the two step depth-equations developed by Hohenegger (2005) (Fig. 5A). Taxon-related depth ranges (Fig. 4) are based on previously published data (e.g., Sgarrella and Moncharmont-Zei, 1993; Meric et al., 2004; Spezzaferri et al., 2004; Hohenegger, 2005; Rasmussen et al., 2005). The effect of



**Fig. 2.** Simplified section through the Cerová-Lieskové clay pit. A. Massive calcareous clay. B. Thin tempestite layers with plant debris. C. Thin siltstone/sandstone layers or silt lenses.

potential *post-mortem* mixing of taxa caused by transport, reworking and sediment mixing was eliminated by removing the taxa that lived in a water depth-range which is inconsistent with the assemblage (Hohenegger, 2005). For comparison, we also use summarizing plots of Murray (1973, 2006) based on test wall structure and species diversity (Fig. 5B, C).

Finally, benthic foraminiferal oxygen indices (BFOI) were calculated using the method of Kaiho (1994, 1999). The equation  $BFOI = \{[S/(S+D) - 1] \times 50\}$  was used for assemblages lacking oxic species and  $BFOI = \{[O/(O+D)] \times 100\}$  was applied when oxic species occurred. *O*, *S* and *D* are numbers of specimens of oxic, suboxic and dysoxic indicators, respectively. In our study, paleoecological interpretations follow Kaiho (1999) who correlated the BFOI index to the absolute dissolved oxygen (in ml/l) (Fig. 5A).

### 3.2. Oxygen isotope analyses

For oxygen isotopes, we focused on a 40 cm thick interval (below and above sample 17, Fig. 2) which yielded a particularly abundant assemblage of *Aturia* (238 specimens), and a rich and well-preserved associated micro- and macrofauna. Redeposited microfossils from shallow water habitat (mainly foraminifers) are rare in this interval (Fig. 5A). *Aturia* is represented by newly hatched to adult shells and

their jaws. Shell microstructure has been analysed under scanning electron microscopy (SEM) (Fig. 3F). Prior to isotope analyses, the crystallographic nature of shell carbonate was analysed using Raman spectroscopy (Jobin Yvon, HR800). Maxima at  $702\text{ cm}^{-1}$  and  $706\text{ cm}^{-1}$  characteristic of aragonite are found for all bivalve, gastropod, scaphopod and *Aturia* specimens. Planktonic foraminifers exhibit a maximum at  $713\text{ cm}^{-1}$  characteristic of calcite. Therefore, the fossil shells of the studied interval are exceptionally well-preserved. Oxygen isotope analyses were performed on *Aturia* with only the outer shell wall (not septa) being sampled at all accessible ontogenic stages. Sampling density was dependent on outer shell accessibility and shell preservation. For several specimens, a part of the last whorl was removed to reach the preceding whorl. Oxygen isotope compositions were measured on six *Aturia* specimens among which 1 specimen in embryonic stage only, 3 specimens with embryonic and early post-hatching stages and 2 adult or almost adult specimens. In all, 18 embryonic and 19 post-hatching samples of *Aturia* were measured. Co-occurring shells of gastropods (*Nassarius janschoegli*, *Cylichna cf. salbriacensis*), scaphopods (*Gadila gracilina*) and bivalves (*Parvamusium felsineum*, *Yoldia nitida*) were also analysed. To avoid the contribution of planktonic larval stages on the oxygen isotope ratio of studied bivalves, sampling started at about 1.5 mm distance from the umbo. A similar bias of planktonic stages has been avoided while sampling gastropods shells. Samples were taken parallel to growth lines. Stable isotope compositions of monospecific samples of planktonic foraminifera were also measured. Selected specimens exhibited a glassy appearance with neither carbonate infillings nor visible dissolution documenting a good preservation. Oxygen isotopes were measured on the symbiotic surface-dweller *Cassigerinella* sp. and the non-symbiotic, deeper dwellers *Globigerina praebulloides/bulloides* and *Globigerina ottnangiensis* (Keller, 1985). The number of analysed specimens ranged from 50 (for *Globigerina*) to 200 (for *Cassigerinella*) individuals.

All carbonate powders were reacted with 100% phosphoric acid at  $75\text{ }^{\circ}\text{C}$  using a Kiel III online carbonate preparation line connected to a ThermoFisher 252 mass spectrometer. All values are reported in per mil relative to V-PDB by assigning a  $\delta^{18}\text{O}$  value of  $-2.20\text{‰}$  to NBS (National Bureau of Standards) 19. Reproducibility was monitored by replicate analyses of NBS 19 and was better than  $\pm 0.07\text{‰}$  ( $1\sigma$ ). Paleotemperatures are calculated using the equations given by Grossman and Ku (1986) and Erez and Luz (1983) for aragonite and calcite, respectively, and a seawater  $\delta^{18}\text{O}$  value ( $\delta^{18}\text{O}_{\text{sw}}$ ) ranging from  $-0.5\text{‰}$  (Miller et al., 1987) to  $-0.8\text{‰}$  (Lear et al., 2000) which is characteristic for the Miocene of Paratethys.

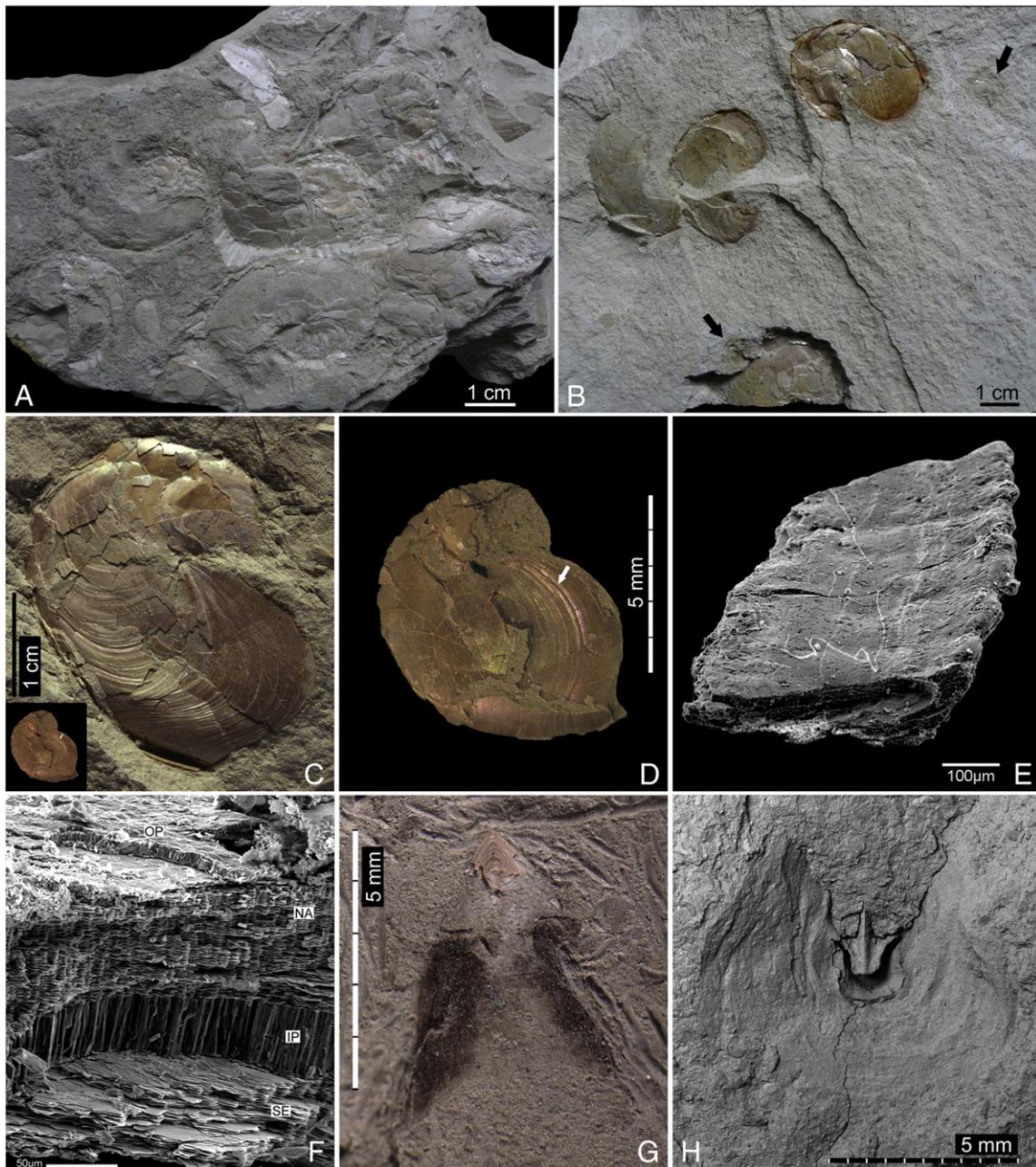
## 4. Results

### 4.1. Biostratigraphy

A late Karpatian age of the deposits is determined based on the co-occurrence of the foraminiferal taxa *Uvigerina graciliformis* and *Globigerinoides bisphericus*, and the absence of *Praeorbulina*. The Lowest Occurrence (LO) of *U. graciliformis* delineates the base of the Karpatian stage, the LO of *G. bisphericus* occurs within Zone M4b of Berggren et al. (1995) and correlates with the late Karpatian, and the LO of *Praeorbulina* occurs at the base of the Badenian stage (Cicha and Rögl, 2003). The Karpatian is consistently considered to be time-equivalent to the latest Burdigalian.

### 4.2. Foraminiferal diversity analyses

Benthic foraminiferal assemblages are dominated by infauna to deep infauna. *Bolivina fastigia*, *Bolivina hebes*, *Bulimina marginata*, *Bulimina elongata* and *Uvigerina* spp. represent dysoxic–suboxic index



**Fig. 3.** *Aturia* sp. from the Cerová–Lieskové locality. A. Accumulation of adult shells. B. Three adults associated with two newly hatched specimens (arrows). C. Comparison of adult and newly hatched specimens. D. Detail view of the newly hatched specimen (nepionic constriction arrowed). E. Thickened peristome. F. Shell microstructure, OP – outer prismatic layer, NA – nacreous layer, IP – inner prismatic layer, SE – septum. G. Upper jaw with rhyncholite partly preserved in place. H. Upper jaw with in situ rhyncholite partly covered by sediment.

species. Only three samples (14, 19, 20) contain the oxiphylic genera *Cibicides* and *Cibicoides*. Analysed samples yield BFOI index values ranging from –30 to –20 when oxidic indicators are absent, and from 2.2 to 4.2 when oxidic indicators are present (Fig. 5A). According to Kaiho (1999), BFOI values comprised between 0 and –40 correspond to dissolved oxygen concentrations (DO) ranging from 0.3 to 1.2 ml/l, and likely refer to dysoxic conditions (Bernhard and Sen Gupta, 2002). BFOI index values between 0 and 15 correspond to DO ranging from 1.2 to 2 ml/l, and are classically seen as dysoxic or low oxidic conditions (e.g., Tyson and Pearson, 1991).

Paleodepth analyses allow us to estimate water depths of 240–330 m with extreme values ranging from 149 m to 498 m. The shallowest paleodepth of 238 m is estimated for the assemblage found in sample 16. The deepest paleodepth of 330 m was calculated for sample 15 (Fig. 5A). Based on the methods of Murray (1973, 1991),

most of the shelf and deep sea assemblages have Fisher  $\alpha$  diversity values ranging from 5 to 15, and Shannon H values from 1.5 to 3.5. Evaluated samples show Fisher  $\alpha$  values ranging from 5.5 to 8 and Shannon H values from 1.9 to 2.6 (Fig. 5B). Our ternary plot for representation of wall type structures confirms that the assemblages characterize shelf (samples 14, 15, 16, 17 and 18) and deep marine environments (19, 20) (Fig. 5C). To sum up these data, dysoxic to low oxygen bottom water conditions and absolute paleodepths of 240 to 330 m are indicated for the 2.20 m thick studied interval.

#### 4.3. Oxygen isotopes

Oxygen isotope values of all ontogenic stages of *Aturia* shells range from 0.21‰ to 0.92‰ with a mean value of  $0.60 \pm 0.20\%$  ( $n = 37$ ),

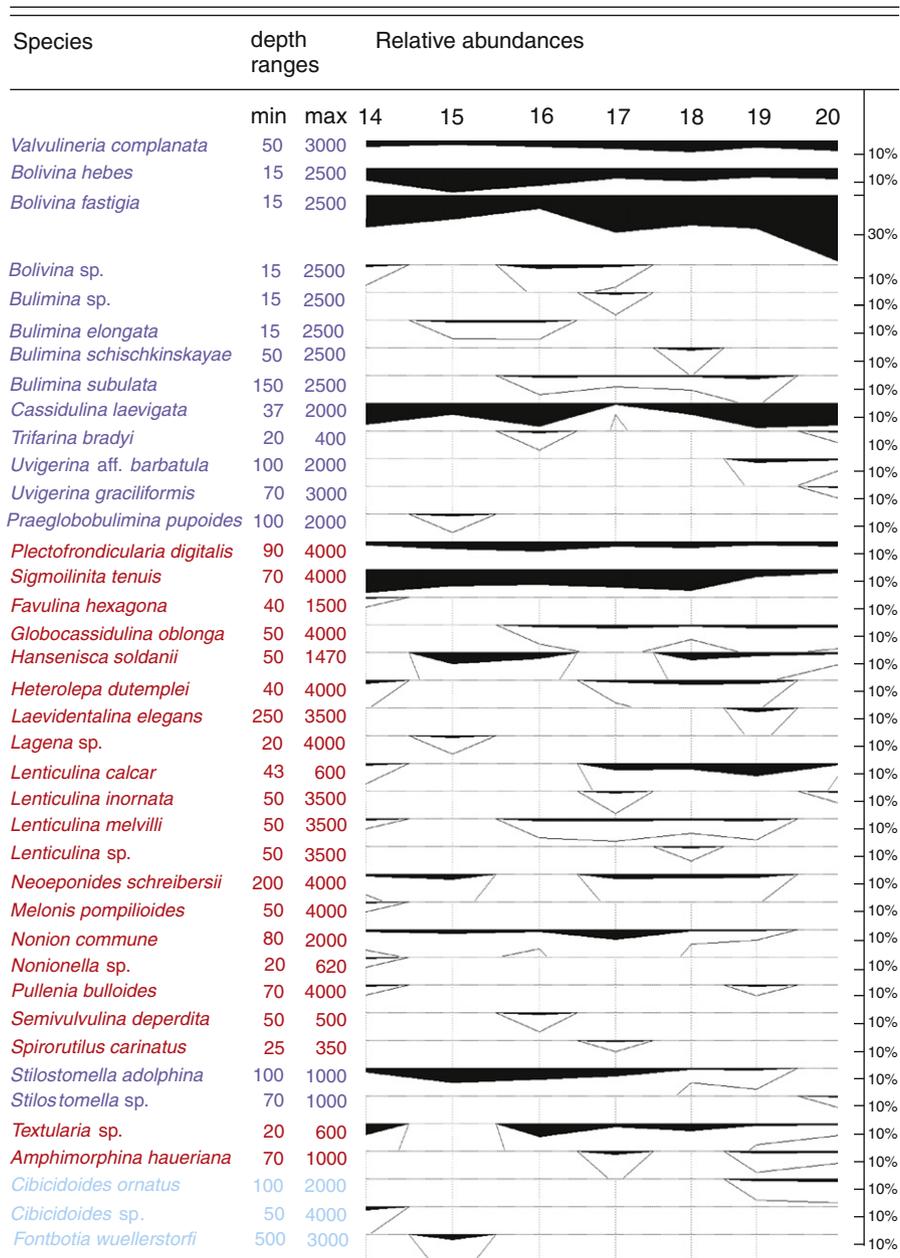


Fig. 4. Depth ranges of benthic foraminiferal taxa with their dominance and distribution in the 220 cm thick part of section, including the interval studied for stable isotopes. Deep blue, red and light blue mark dysoxic, stressed suboxic, and oxic taxa, respectively.

suggesting that shells were precipitated at temperatures ranging from about 13 °C to 16.2 °C, or 14.3 °C to 17.6 °C respectively, depending on the value of  $\delta^{18}\text{O}_{\text{sw}}$  (Fig. 6A).  $\delta^{18}\text{O}$  values of bivalves ( $0.42 \pm 0.02\%$ ,  $n=7$ ), gastropods ( $0.60 \pm 0.02\%$ ;  $n=8$ ) and scaphopods ( $0.32 \pm 0.01\%$ ,  $n=2$ ) are similar to those measured on *Aturia*, suggesting temperatures of 13.3 to 16.4 °C or 14.8 to 17.9 °C respectively. Planktonic foraminifera (*Globigerina* sp. and *Cassigerinella* sp.) are depleted in  $^{18}\text{O}$  with a mean  $\delta^{18}\text{O}$  value of  $-1.09 \pm 0.02\%$  ( $n=6$ ).

Oxygen isotope compositions of the planktonic foraminifera *Globigerina* sp., interpreted to have preferentially mineralized at intermediate depths of the mixed layer (>50 m), suggest temperatures ranging from about 17.2 to 18.7 °C or 18.6 to 20.2 °C respectively (Fig. 6A). Calculated sea surface temperatures of 20.6 or 22.1 °C respectively and 22.1 °C are estimated based on analyses of the shallower-dweller *Cassigerinella* sp.

## 5. Discussion

### 5.1. Shell preservation and autochthony

Most drifted *Nautilus* shells found on beaches have partially or totally destroyed body chambers. For example, Hamada (1964) reported that 80% of *Nautilus* shells stranded on beaches in Thailand had lost their body chamber, and 50% display breakage of the last septum. This state of preservation characterizes the great majority of *Aturia* shells, found mostly drifted in shallow littoral deposits (Chirat, 2000). This is in contrast with the exceptional preservation of our specimens, which mostly display their complete body chamber and preserve the very thin peristome. All specimens are free of epifaunal encrustations, which mainly occur in drifted shells (Landman et al., 1987) but also in autochthonous/paraautochthonous shells in environments that exhibit

low sedimentation rates (Roux et al., 1991; Mapes et al., 2010a, Mapes et al., 2010b). However this was not the case of the here studied deposits.

Stenzel (1957, p. 893) stressed that “... in an average Tertiary deposit one finds that there are in excess of 1000 other mollusk

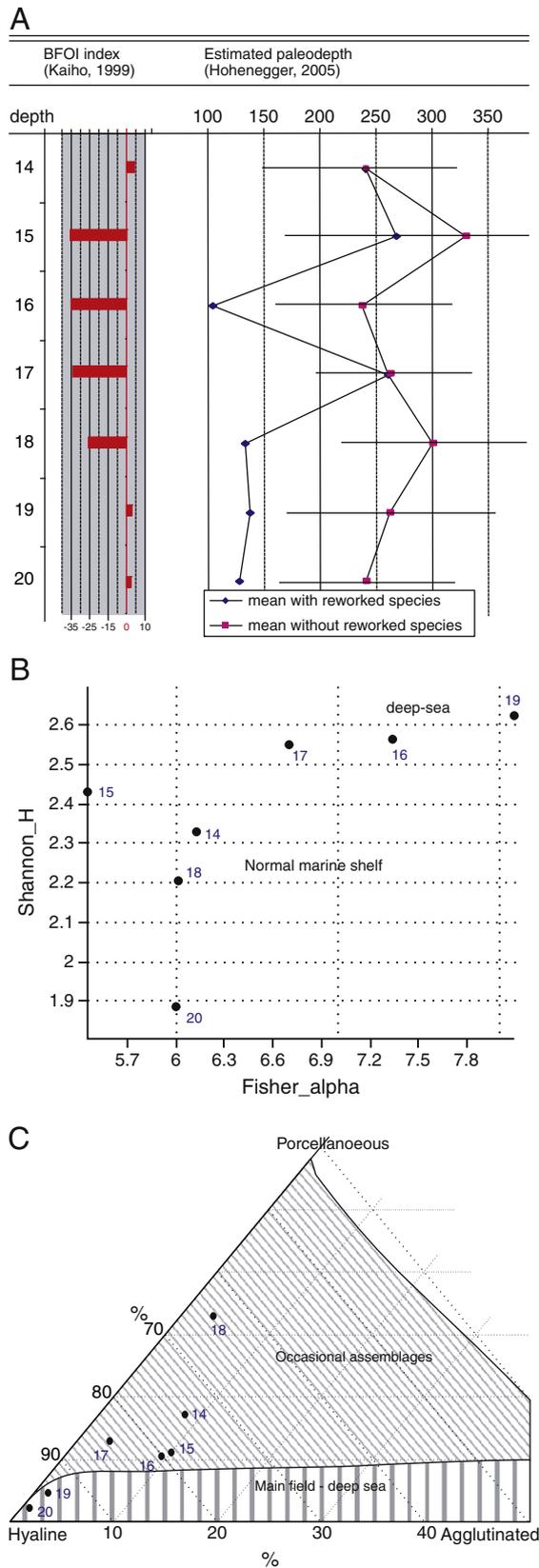
specimens to 1 nautiloid shell. The proportion may even surpass 10000 to 1. Such scarce material does not invite ecological interpretation.” This scarcity is obvious for *Aturia*. Most published studies are based on very few (<10) or isolated specimens found in shallow littoral deposits. The finding of 25 phragmocones in a Upper Eocene beach deposit of the Seymour Island, Antarctica (Zinsmeister, 1987) as well as the numerous *Aturia* specimens (180) found in the Lower Miocene Lincoln Creek Formation, Washington state (Moore, 1984), constitute the only exceptions reported so far. Apart from the latter example, discussed below, the number of shells usually discovered in Cenozoic deposits is by no means comparable to the abundance reported in this study (about 500 specimens) which supports the inference of autochthony herein.

Chamberlain et al. (1981) provided an insightful study of the *post-mortem* physical behavior of *Nautilus* shells. The *post-mortem* ascent of a shell is due to the rapid buoyancy gain resulting from the removal of the body from the shell by predators or scavengers, or by deterioration of the muscle-shell attachment (that may take place in 12 h). The critical (initial) depth of ascent below which the shell does not reach the surface and drift, depends upon the relative magnitudes of the shell ascent rate and the rate of hydrostatic pressure induced seawater influx into the phragmocone through the siphuncle. If the flooding is sufficiently rapid relative to the ascent rate, the shell becomes negatively buoyant and sinks to the sea floor in the area inhabited by the living animal. The critical depth is positively correlated with shell size, small shells reaching the surface only if they begin to rise from very shallow depths (see also Wani et al., 2005). An estimated critical depth of about 50 m for a *Nautilus* shell of 50 mm in diameter with only 20% flooded siphuncle (Fig. 6 in Chamberlain et al., 1981) undoubtedly represents an underestimation of the critical depth of comparably sized *Aturia* shells. Indeed the long impermeable septal necks and reduced surface of permeable siphuncular connecting ring of this genus decreased the phragmocone flooding rate and increased the critical depth as compared to that of *Nautilus*. In addition to the estimated water depth of about 240–330 m, the measured diameters of studied *Aturia* shells ranging from 7 and 38 mm argue for their autochthony.

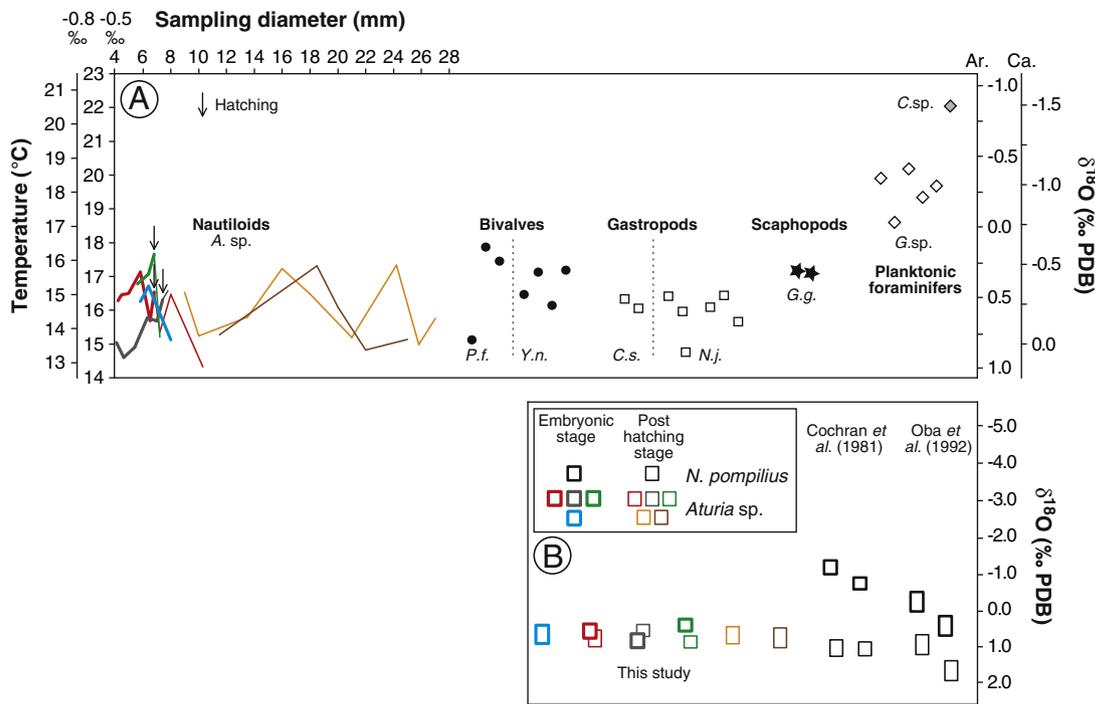
Upper and lower jaws with both their anterior calcitic parts (rhyncholites and conchorhynch), and posterior chitinous portion occur in association with *Aturia* (Fig. 3G–H). Elements of nautilid upper or lower jaws are most commonly found isolated in Mesozoic and Cenozoic deposits, and very rarely in the living chamber (Saunders et al., 1978; Klug 2001; see also Wani, 2007 for the experimental taphonomy on *Nautilus* shells) due to the early *post-mortem* separation of the body from the shell. The facts that *Aturia* is the only nautilid genus found in the deposits, that the vertical distribution of shells and jaws closely match each other (Fig. 2) and that the size of these nautilid jaws falls within the range expected from the size range of *Aturia* shells, suggest that the jaws belong to the same species, further supporting autochthony.

### 5.2. *Aturia* habitat and lifestyle

Bottom water temperature estimates based on bivalve, gastropod and scaphopod  $\delta^{18}\text{O}$  values are in the range of those calculated from



**Fig. 5.** A: Water depth estimates following Hohenegger (2005). Estimated depths with minimum and maximum deviations in the right side of the picture. Red squares show mean of the estimated depths after elimination of reworked species. Deep blue diamonds show mean of depth interval estimated with shallowest species, documenting transport from shallower environment. B: Species diversity plot (Fisher  $\alpha$  diversity vs. Shannon H) with applying depth interpretation of Murray (1973, 2006). C: Ternary diagram plots proportional representation of wall types (triangle corners represent 100% of the labeled components). Hatched area represents fields of typical deep marine assemblages. Main field of the deep sea assemblages are plotted along the hyaline–agglutinated axis, generally with less than 10% of porcellanaceous walls (original fields defined by Murray 1973, 2006).



**Fig. 6.** A. Paleotemperatures ( $^{\circ}\text{C}$ ) calculated from oxygen isotopes of calcitic (foraminifers) and aragonitic (cephalopods, bivalves, gastropods and scaphopods) shells. Ar and Ca represent  $\delta^{18}\text{O}$  scale for aragonite and calcite. Paleotemperatures calculated assuming  $\delta^{18}\text{O}_{\text{sw}}$  of  $-0.5$  and  $-0.8$ ‰ (Miller et al., 1987; Lear et al., 2000). Intra-specimen variation in  $\delta^{18}\text{O}$  of six *Aturia* specimens represented by colored lines with embryonic stage highlighted by bold line, nepionic constriction by vertical arrow, and post-hatching stage by thin line. Abbreviations as follow: *A.sp.*, *Aturia sp.*; *P.f.*, *Parvamusium felsineum*; *Y.n.*, *Yoldia nitida*; *C.s.*, *Cylichna cf. salbriacensis*; *N.j.*, *Nassarius janschoegli*; *G.g.*, *Gadila gracilina*; *G.sp.*, *Globigerina sp.*; *C.sp.*, *Cassigerinella sp.* B. Compilation of oxygen isotope values for *Aturia* and living *Nautilus* which exhibit an embryonic/post hatching sequence. The embryonic and post-hatching stages are represented by bold and thin boxes, respectively.

coeval *Turritella* shells (13 to 26  $^{\circ}\text{C}$ ) from the Northern Korneuburg Basin (Central Paratethys), which has been interpreted to have been under estuarine influences during the Karpatian (Latal et al., 2006). Calculated temperatures for *Aturia* are comparable to bottom water temperatures given by benthic mollusks (Fig. 6A), suggesting that *Aturia*, like *Nautilus*, had a nektobenthic lifestyle at all stages of its development. *Nautilus* is known to swim close to the bottom, from about 100 m (exceptionally near the surface) to 600 m depths along fore-reef slopes in the Indo-Pacific (e.g., Ward et al., 1984). However, the preferred depth range of *Nautilus* is restricted to 150–300 m in Palau or to 150–500 m in the Tañon Strait, these depths corresponding to temperatures of 17 to 9  $^{\circ}\text{C}$  and 20 to 17  $^{\circ}\text{C}$ , respectively (Hayasaka et al., 1987; Saunders and Ward, 1987). The upper limit of this depth range is controlled by predation and temperature, with temperatures exceeding 25  $^{\circ}\text{C}$  being lethal (Saunders and Ward, 1987). *Nautilus* undertakes extensive vertical migrations, rising along reef slopes to shallow waters at night and retreating to cooler, deeper waters during daytime (Carlson et al., 1984; Ward et al., 1984; O'Dor et al., 1993). A similar behavior has often been assumed for fossil species, notably for *Aturia*, in the light of its peculiar siphuncular morphology and structure, similar to that of the current vertically migrant sepioid genus *Spirula* (Ward, 1987). A daily vertical migration of *Aturia* does not become evident based on measured oxygen isotope ratios and potentially could only be resolved using a high-resolution sampling strategy.

### 5.3. A complete “family picture”

*Nautilus* egg capsules have never been discovered in their natural habitat. However, in aquaria, eggs require warm waters (22 to 25  $^{\circ}\text{C}$ ) over a long incubation period (7.5 to 14 months) to hatch (Carlson et al., 1992; Uchiyama and Tanabe, 1999). Hatching is recorded on the

shell by the nepionic constriction at diameters ranging from 22 to 32 mm. Oxygen isotope data reveal that the embryonic development of *Nautilus* occurs in the wild in warm waters (22–24  $^{\circ}\text{C}$ ) corresponding to depths of 100 to 200 m depending on localities, and that newly hatched individuals further migrate to deeper and colder waters (Cochran et al., 1981; Oba et al., 1992; Landman et al., 1994) (Fig. 6B). In fossil nautilids previously reported hatching sizes range from 9 to 57 mm (Chirat, 2001). The nepionic constriction in *Aturia* occurs between 7 and 8 mm in shell diameter. The presence of well preserved newly hatched individuals (in the range of 7–15 mm) suggests close proximity of spawning grounds. However, contrary to *Nautilus*, no clear shift in  $\delta^{18}\text{O}$  occurs between embryonic and post-embryonic shells.  $\delta^{18}\text{O}$  values measured on *Aturia* suggest that the incubation temperature for the eggs was about 13  $^{\circ}\text{C}$  to 17.6  $^{\circ}\text{C}$ , depending on the value of  $\delta^{18}\text{O}_{\text{sw}}$ , implying that newly hatched individuals and adults lived in water depths where the eggs were laid.

### 5.4. Life in low oxygenated waters

*Nautilus* is a slow-moving, low-metabolic-rate animal that is able to cope with low oxygen levels in deep waters in which it episodically descends and scavenges food on the ocean floor, escaping from its hypoxia-sensitive predators and exploiting ecological niches unavailable to most other competitors (Wells et al., 1992; Boutilier et al., 2000). Although many current coleoids are active predators in well oxygenated waters, some species are hypoxia tolerant, most notably the vampire squid, *Vampyroteuthis infernalis*, that is thought to live its entire life cycle directly in the core of the oxygen minimum layer (Seibel et al., 1999). Like *Nautilus*, *Vampyroteuthis* is deep rooted in the molecular phylogenetic tree of cephalopods (Yokobori et al., 2007) suggesting that the capacity of *Nautilus* to exploit zones of low oxygen concentration is likely to be associated with an ancestral physiological

trait. This interpretation is consistent with the dysoxic paleoenvironmental setting in which *Aturia* occurs in both absolute and relative abundance (*Aturia* is at least 10 times more abundant than any other associated mollusk species in the Cerová-Lieskové locality). As noted before, the only exception to the rarity of Cenozoic nautilids reported so far is the occurrence of *Aturia* in the Lower Miocene Lincoln Creek Formation in Knappton, Washington state. According to Moore (1984), 180 juvenile and adult specimens, ranging from 30 to 180 mm in diameter, with large portions of the body chamber preserved, have been found in sediments with estimated depositional depths ranging from 100 to 350 m (continental slope or marginal basin). Interestingly, Moore (1984) noted that *Aturia* is 20 times as abundant as any other mollusk in these low oxygenated deposits. This example is in many ways similar to our case study (except of the fact that no jaw elements are reported) and might as well constitute an autochthonous occurrence of *Aturia*. If this proves to be the case, it would confirm that this Cenozoic nautilid was a main component of the fauna of relatively deep and low oxygenated waters. Since the last common ancestor of *Aturia* and *Nautilus* may be traced back at least into the Jurassic, this could shed new light onto the relative scarcity of Mesozoic and Cenozoic nautilids in well-oxygenated, epicontinental shelf deposits.

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