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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 nektobenthic 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.

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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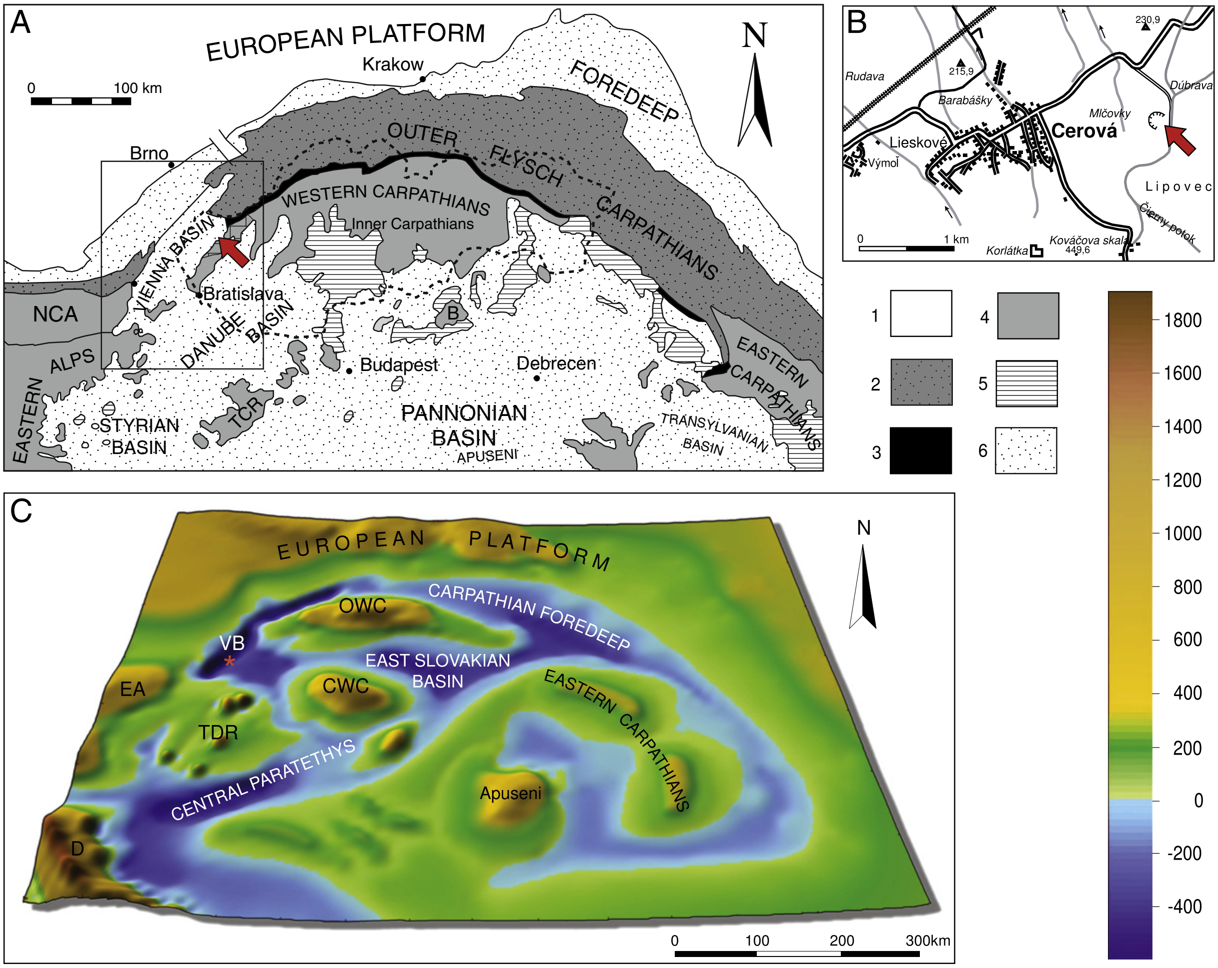

Fig. 1. A. Position of the Vienna Basin in the Carpathian-Pannonian system, locality marked by arrow. B. Location of the Cerová-Lieskové clay pit, indicated by arrow. C. Paleogeographic scheme of the Central Paratethys and adjacent areas during the Karpatian. Locality is marked by asterisk (modified from Kvaček et al., 2006). 1. European platform units. 2. Carpathian-Alpine externides. 3. Pieniny Klippen Belt. 4. Alpine-Carpathian-Dinaride and Pannonian internids. 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. Paleoecological 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