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Article

Preserved colour pattern in *Polititapes tricuspis* (Eichwald, 1829) (Bivalvia: Veneridae) from the Sarmatian holostratotype at Nexing (Lower Austria)

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With 3 figures

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Abstract: A single specimen of the widespread Sarmatian Paratethys bivalve *Polititapes tricuspis* (Eichwald, 1829) with preserved colour pattern is detailed. Despite of an exceptionally comprehensive fossil record, the fossil shell from the Sarmatian holostratotype at Nexing is only the second individual of this species with remnants of colour to be reported. In pure whitish specimens from Nexing, residual colour patterns could be visualised in UV light. The colour pattern closely resembles the colouration of several extant representatives of the Tapetini. The genus *Polititapes* originates from the Early to Middle Miocene of the Mediterranean and Paratethys realms and is today still confined to the Mediterranean and the adjacent Eastern Atlantic.

Key words: Paratethys, palaeobiogeography, Miocene, Tapetini, taxonomy.

Introduction

Colour pattern preservation in Cenozoic mollusks is a relatively common phenomenon and has been reported from a variety of different localities and taxonomic groups (e.g., Hoare 1978; Mapes & Hoare 1987; Kobluk & Mapes 1989; Schneider & Werner 2007; Merle 2008). Nevertheless, the specimen detailed herein is worth to take notice of. The small venerid *Polititapes tricuspis* (Eichwald, 1829) is among the most common and abundant bivalve species of the Sarmatian of the Central Paratethys. First described by Karl Eduard von Eichwald in 1829, thousands of well-preserved shells of *Polititapes tricuspis* from various localities, ranging from Austria to Turkmenistan (Fig. 1) have been collected during the centuries – all of them almost perfectly whitish in colour. At the Sarmatian holostratotype, the "Muschelberg" at Nexing, a polytaxic coquina composed of shells and shell rubble (Harzhauser & Piller 2010) is mined since decades to be used as an additive for chicken food and has yielded countless pure-white shells of *Polititapes tricuspis*. Considering the abundance and geographical distribution of the species, the density of sampled spots, as well as the sampling frequency, it comes as a great surprise that after 180 years of shell collecting and research, only the second specimen with preserved colour pattern was found.

Below, we describe this colour pattern, compare it with similar patterns formed by Recent venerid bi-

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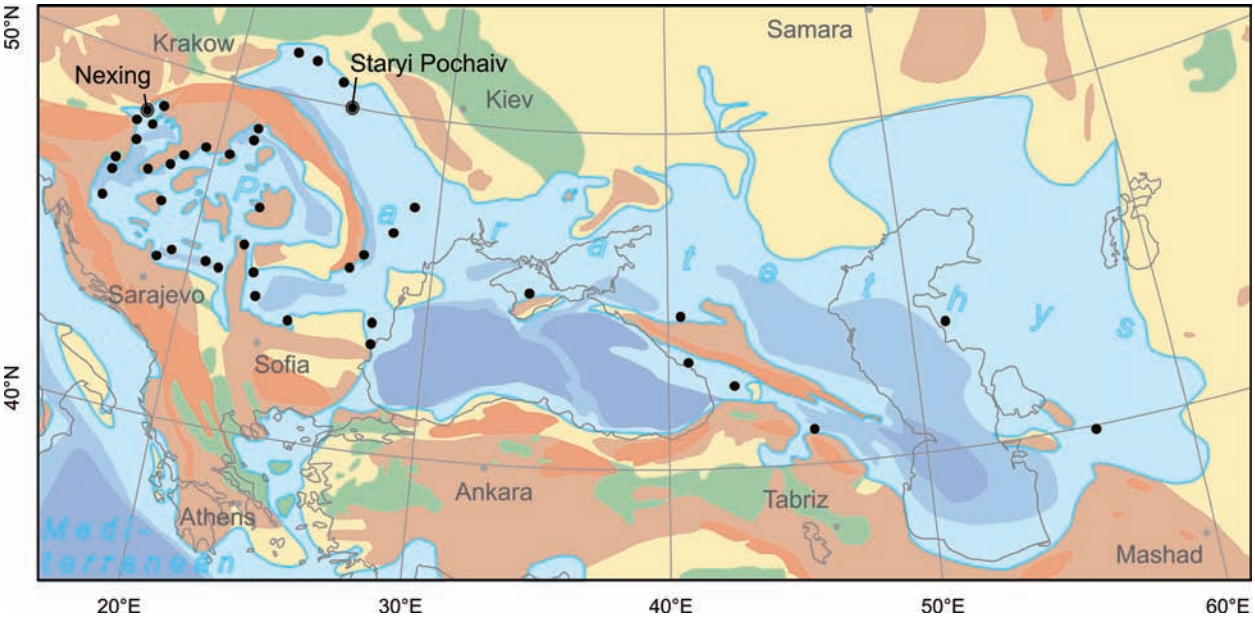

Fig. 1. Sarmatian (Volhynian and Bessarabian) palaeogeography of the Paratethys Sea (modified after Popov et al. (2004), Studencka & Jasionowski (2011), and own results) with occurrences of *Polititapes tricuspis* (Eichwald, 1829) indicated by black dots (based mainly on Schultz (2005) and Nevesskaya et al. (1993)). The positions of Nexing (the sampling locality) and Staryi Pochaiv (the type locality of the investigated species) are marked by an additional ring.

valves, and provide respective illustration. Furthermore, we present residual colour patterns in *Polititapes tricuspis* revealed by ultraviolet light. Moreover, we take these finds as an opportunity to update the taxonomy of this characteristic, stratigraphically and palaeoecologically significant Sarmatian Paratethys bivalve.

Methods

All specimens were first investigated and photographed in daylight. To test for residual colour patterns, five randomly chosen whitish specimens of *Polititapes tricuspis* from Nexing were immersed in concentrated sodium hyplochlorite solution for 24 hours, dried, and photographed under UV light, following the procedure outlined by Merle (2008) and Caze et al. (2010, 2011).

Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Subclass Autobranchia Grobben, 1894
Superorder Heteroconchia Gray, 1854
Clade Heterodonta Neumayr, 1884
Order Venerida Gray, 1854
Family Veneridae Rafinesque, 1815
Tribe Tapetini J. Gray, 1851
Genus *Polititapes* Chiamenti, 1900

Fig. 2. A. *Venerupis geographica* (Gmelin, 1791), Recent, Mediterranean Sea, Malacological Collection of NHMW, Gerstenbrandl Collection, Nr. 5193. B-D. *Polititapes tricuspis* (Eichwald, 1829). B. Left valve with preserved colour pattern; c. 12 Ma, Upper Ervilia Zone (UEZ), Sarmatian, Nexing, Lower Austria (NHMW 2012/0203/0001). C, D. c. 12 Ma, UEZ, Sarmatian, Hölles, Lower Austria. C. Right valve from inside (NHMW 2012/0203/0002). D. Left valve from anterior (D1), inside (D2) and outside (D3) (NHMW 2012/0203/0003). E, F. *Polititapes aureus* (Gmelin, 1791), Recent, Mediterranean Sea, Malacological Collection of NHMW. G. *Polititapes tricuspis* (Eichwald, 1829). Left valve with residual colour pattern revealed by UV light; c. 12 Ma, UEZ, Sarmatian, Nexing, Lower Austria (NHMW 2012/0203/0004). Scale bar = 10 mm.

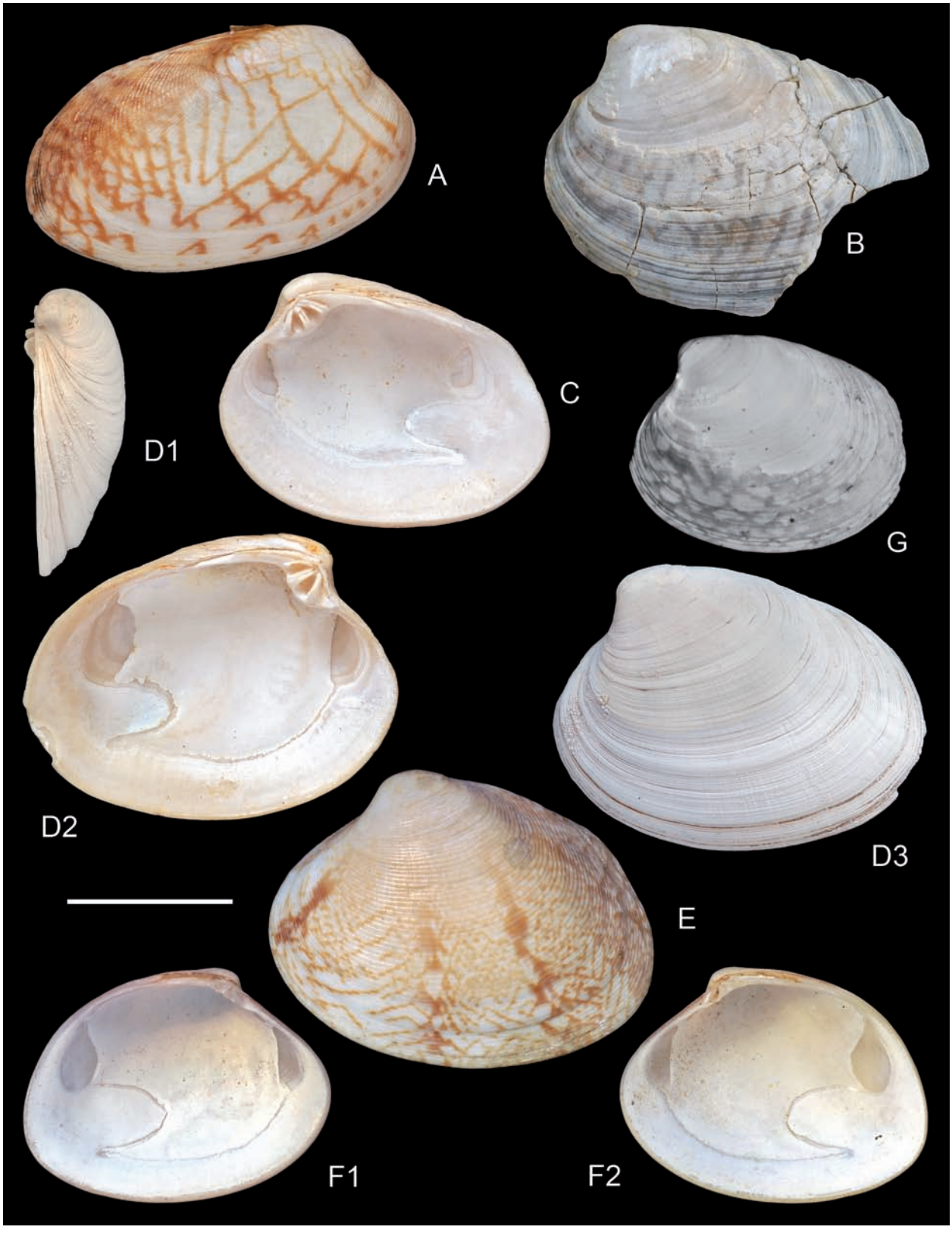

Fig. 2.

Type species: *Venus aurea* Gmelin, 1791 [subsequent designation, Dall 1903].

Polititapes tricuspis (Eichwald, 1829)
Fig. 2A-C

* 1829	*Venus tricuspis*, n. – Eichwald: 282, pl. 4, fig. 15a-c.
1830	*Venus tricuspis*, m. – Eichwald: 205.
1830	*Venus dissita*, m. – Eichwald: 205, nr. 59.
? 1830	*Cytherea nitens* Nobis. – Andrzejowski: 104, pl. 6, fig. 2a-c.
1841	*Venus gregaria* Partsch. – Goldfuss: 247-248, nr. 25, pl. 151, fig. 7a-d.
1844	*Venus Fadiefei* – Orbigny: 484.
1844	*Venus Jacquemarti*, d'Orb., 1844. – Orbigny: 485-486.
1845	*Venus Jacquemarti*, d'Orb. – Orbigny: pl. 5, figs. 18-21.
1845	*Venus Fadiefei*, d'Orb. – Orbigny: pl. 5, figs. 26-29.
1852	*Venus dissita*. – Eichwald: 2, pl. 5, fig. 13a, b.
1852	*Venus tricuspis*. – Eichwald: 2, pl. 5, fig. 15a-c.
1853	*Venus dissita* m. – Eichwald: 105-106, pl. 5, fig. 13a, b.
1853	*Venus tricuspis* m. – Eichwald: 106-107, pl. 5, fig. 15a-c.
1858	*Venus semiplana*, sp. nov. – Baily: 146, pl. 9, fig. 5a, b.
1935	*Tapes tricuspis* Eichw. – Kolesnikov: 72-74, pl. 8, figs 21-24.
1969	*Tapes tricuspis tricuspis* (Eichwald, 1829). – Kojumdgieva: 53, pl. 17, figs. 12-15.
p.p. 2005	*Venerupis* (*Paphirus*) *gregaria* (Partsch in Goldfuss, 1841) ind. ssp. – Schultz: 945-951.
1993	*Venerupis* (*Polititapes*) *tricuspis* (Eichwald, 1829) – Nevesskaja et al.: 188, pl. 47, figs. 1-4.
2005	*Venerupis* (*Paphirus*) *gregaria gregaria* (Partsch in Goldfuss, 1841). – Schultz: 951-953, pl. 142, figs 1-3.
2005	*Venerupis* (*Paphirus*) *gregaria dissita* (Eichwald, 1830). – Schultz: 954-955, pl. 142, figs. 4, 5.

Type locality: "fassilis calcem Poczaiowensem" [sic] (Eichwald 1829), subsequently referred to as "près de Staro Poczacow" (Eichwald 1853), which is an ancient name for Staryi Pochaiv, situated about 55 km NNW of Ternopil, in western Ukraine (Fig. 1).

Material: A single, slightly broken left valve with preserved colour pattern from Nexing (NHMW 2012/0203/0001) (Fig. 1). Numerous additional specimens from Nexing and various other localities of Sarmatian age for comparison.

Description: Shell trigonal-ovate, with strongly projecting, prosogyrous umbo positioned at first third of shell length. Lunule lacking; escutcheon short and narrow. Interior shell surface smooth and shiny. D-shaped anterior and short-ovate posterior adductor muscle scars well demarcated. Pallial line well visible, with distinct but relatively shallow sinus. Hinge of left valve composed of three cardinal teeth; well pronounced and bifid 2a; prominent, massive, bifid 2b; short, narrow but distinct, non-bifid 4b; lateral teeth wanting. Hinge of right valve also composed of three cardinal teeth; prominent, bifid 1; narrow but distinct, non-bifid 3a; strong and pronounced, bifid 3b. Faint elongate swelling or posterior lateral tooth P1 present in some, especially aged specimens right below posterior half of dorsal margin. Outer shell surface ornamented with strong, almost rib-like commarginal growth lines. Very faint radial striae observable only in perfectly preserved specimens.

Specimen with colour pattern visible in daylight: Colour pattern preserved only in ventral half of the shell; outer shell layer in umbonal shell portion eroded. Colour pattern composed of two divaricate sets of almost 0.5 mm wide, slightly blurry, dark-violet stripes. More prominently developed set running in anterior-ventral direction, meeting growth lines at angle of ca 60°; coloured lines regularly flexed with the inflation of the shell. Second set consisting of few short stripes only, running in posterior-ventral direction; meeting growth lines at angle of ca 50°. First and second set of coloured stripes meeting at angle of ca 70°, forming two rows of slightly flexed "y".

Specimens with residual colour patterns visible in UV light: Observed patterns not sharply demarcated. Consisting of two sets of lines, as described above. In places, space between lines filled with colour, forming triangles.

Taxonomic remarks: The genus *Polititapes* Chiamenti, 1900 has been established for Tapetini that are ornamented with "narrow and numerous concentric rugosities" (translation of Chiamenti 1900), i.e. distinct growth lines or commarginal riblets, but (merely) lack radial ornamentation. The type species of the genus, *Polititapes aureus* (Gmelin, 1791) is further characterised by each two bifid cardinal teeth (2a, 2b vs. 1, 3b) and a single non bifid cardinal tooth (4b vs. 3a) in either valve. These hinge characters, as well as the distinct commarginal ornamentation, supplemented by only minute, very faint radial striae, are well-established in the Sarmatian *Venus tricuspis* Eichwald, 1829, which is thus assigned to the genus *Polititapes* Chiamenti, 1900 (Goncharova 1986; Nevesskaya et al. 1993).

Up to the late 1850s, several synonyms of *Polititapes tricuspis* (Eichwald, 1829) were created (see list above). In the 20th century, numerous authors have treated *Venus tricuspis* as a variety or subspecies of *Venus gregaria* Partsch in Goldfuss, 1841 – an obviously invalid combination, since *Venus tricuspis* Eichwald, 1829 has priority. The taxonomic concept applied in the present study has been established by Kojumdgieva (1969) and Nevesskaya et al. (1993) and considers the two aforementioned names as synonyms of a single Sarmatian species. In the Central Paratethys, *Polititapes tricuspis* obviously appeared somewhat earlier (early Sarmatian *Mohrensternia* Zone) than in the Eastern Paratethys (latest Volhynian). In the entire Paratethys Sea, *P. tricuspis* went extinct at the end of the Sarmatian, or mid-Bessarabian, respectively (Papp et al. 1974; Nevesskaya et al. 1993; Schultz 2005).

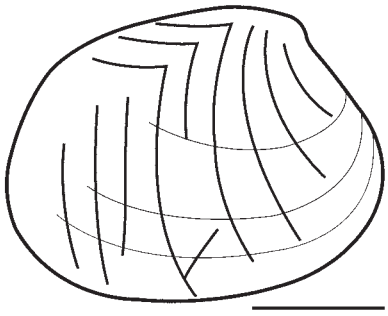

Fig. 3. Schematic drawing of colour pattern in right valve of *Polititapes tricuspis* (Eichwald, 1829) from Voronkivtsi (Ukraine) figured by Kolesnikov (1935). Scale bar = 10 mm.

Polititapes tricuspis (Eichwald, 1829) stands in a row of closely similar species of *Polititapes*, itself originating most likely from *P. vitalianus* (d'Orbigny, 1844), and giving rise to *P. ponderosa* (d'Orbigny, 1844), which appeared in the late Sarmatian *Sarmatimactra* Zone (early Bessarabian) (Papp et al. 1974). The origin of the genus goes back to the Early to Middle Miocene species *P. taurelliptica* (Sacco, 1900) from the northern Mediterranean and *P. merklini* (Goncharova, 1986) from the eastern Paratethys. Except for the Lessepsian emigrants in the Red Sea, *Polititapes* remained restricted to the Mediterranean and Eastern Atlantic realms until today. The Indopacific species classified with *Polititapes* by Goncharova (1986) (e.g., the Australian *Venerupis anomala* (Lamarck, 1818) or *Marcia hiantina* (Lamarck, 1818)) do not belong to this genus.

Discussion

Colour in mollusk shells may be caused by a variety of different chemical substances: carotenoids and indigoids, which usually are subject to rapid decay (Comfort 1950; Hedegaard et al. 2006); melanins, which, in contrast, are highly durable and responsible for the highly resistant colour patterns in fossil and recent neritimorph gastropods at least since the Silurian (Comfort 1950, 1951; Kríz & Lukes 1974; Hedegaard et al. 2006); polyenes, which have been detected in the coloured shell portions of several mollusc species (Hedegaard et al. 2006); and tetrapyroles, especially the cyclic porphyrines, which probably are the most widespread pigments in mollusc shells (Comfort 1950; Hollingworth & Barker 1991). Shell pigments of Tapetini have not yet been analysed, but porphyrines have been detected in the closely related Venerini, i.e. in *Clausinella fasciata* (Da Costa, 1778) (Comfort 1950, 1951). The earliest preserved colour patterns in fossil Veneridae have been documented from Eocene *Callista* and *Costacallista* by Dockery (1980).

The colour pattern observed in *Polititapes tricuspis* basically consists of two sets of oblique coloured lines that meet at an angle of approximately 70°. By omitting parts of these lines, this pattern receives a slightly irregular appearance. In the case of the specimen from Nexing, only one set of lines is truncated, resulting in two adjacent rows of y-shaped elements. The right valve from Voronkivtsi (Ukraine) figured by Kolesnikov (1935) shows two sets of coloured lines that do not cross each other, but diverge from an imaginary line extending from the umbo to the posterior-ventral edge of the shell. Since the illustration in Kolesnikov (1935) is relatively pale and blurry, we provide a schematic drawing of the colour pattern observed in this specimen (Fig. 3). Oblique coloured lines are produced by continuously shifting secretion of colour along the mantle edge of the animal (Oberling 1968; Tichy 1980; Gunji et al. 1999). In *P. tricuspis*, secretion in one set of lines was obviously interrupted at times, causing their truncation. Usually, colour patterns of molluscs are genetically fixed and certain patterns may characterize bivalve or gastropod genera or even families (Hoare & Sturgeon 1978; Tichy 1980; Caze et al. 2010, 2011). The pattern of two sets of narrow, oblique lines is the basic motif of colouration in the Tapetini, found for example in typical specimens of *Venerupis geographica* (Gmelin, 1791) (Fig. 2A), *Tapes literatus* (Linnaeus, 1758) or *T. sericeus* Matsukuma, 1986. All other patterns in this group are merely variations of this motif, resulting from various kinds of truncation of the lines or infill of the regions between them (Fig. 2G).

To date, a particular reason why burrowing bivalves have patterned shells has not been identified, although several scenarios have been proposed (see Schneider & Werner 2007 for discussion). Out of these, only the stabilisation of fragile shells by the incorporation of durable organic compounds (e.g., porphyrines or melanins), as suggested by Kobluk & Mapes (1989), seems convincing – but still has to be proven.

Last not least, the question why exactly the single specimen presented herein – one shell among thousands that have been collected at Nexing – preserves its original colour pattern, remains unanswered. Although we do not believe that this phenomenon is just a freak of nature, there is no reasonable explanation why the diagenetic pathway of this individual should have been different from that of the entire shell bed, where residual colour patterns can be observed in UV light as a rule.

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