Early ontogeny, paleoecology and intraspecific variability of two *Helminthia* species (Gastropoda: Turritellidae) from the Middle Miocene (Badenian) deposits of the eastern Vienna Basin (Slovakia)

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Abstract: An overview of the Serravallian (Middle Miocene) turritellid gastropod genus *Helminthia* Handmann, 1882 from the Slovak part of the Vienna Basin is presented. New records of *Helminthia* come from the upper Badenian (lower Serravallian) shallow- to deep sublittoral marine facies of the Studienka Formation exposed in the former clay pit and its vicinity located near the Rohožník village. Two species of *Helminthia* have been identified, *Helminthia tricincta* (Borson, 1821) and *Helminthia vermicularis* (Brocchi, 1814). These taxa are briefly discussed, and their stratigraphic and geographic distribution in the Miocene deposits of Slovakia is summarized. Rarely, early whorls including protoconch were recorded in examined specimens, which represent the first protoconch evidence of *Helminthia* from the Central Paratethys. The peculiar intraspecific variability in shells of *H. tricincta* is observed. Prevailing paleoecological conditions in the study area during the upper Badenian are discussed.
Key words: *Helminthia*, Gastropoda, paleoecology, protoconch, intraspecific variability, Miocene, Vienna Basin, Central Paratethys

1. INTRODUCTION

A comprehensive revision of the Turritellidae Lovén, 1847 from the Miocene of the Paratethyan Sea and redescription of the genus *Helminthia* Handmann, 1882 was presented by Harzhauser & Landau (2019).

The earliest occurrence of *Helminthia* in the Slovak part of the Western Carpathians is known from the Early Miocene (Burdigalian). Shells of *Helminthia taurobrocchii* (Sacco, 1895) were found in the Eggenburgian deposits of the Vaďovce Basin and the Novohrad-Nógrád Basin (Steininger et al., 1971; Ondrejičková, 1972; Harzhauser & Landau, 2019). Middle Miocene (lower Serravallian) occurrences come from the eastern Vienna Basin – Devínska Nová Ves where the upper Badenian deposits rich in Turritellidae including *Helminthia vermicularis* (Brocchi, 1814) and *Helminthia tricincta* (Borson, 1821) are exposed (cf. Kornhuber, 1865; Schaffer, 1897, 1908; Toula, 1900; Švagrovský, 1981; Hyžný et al., 2012). The first record from the locality Rohožník-Konopiská was published by Hladilová (1991), who mentioned a single *Helminthia* species under the name *Turritella tricincta*.

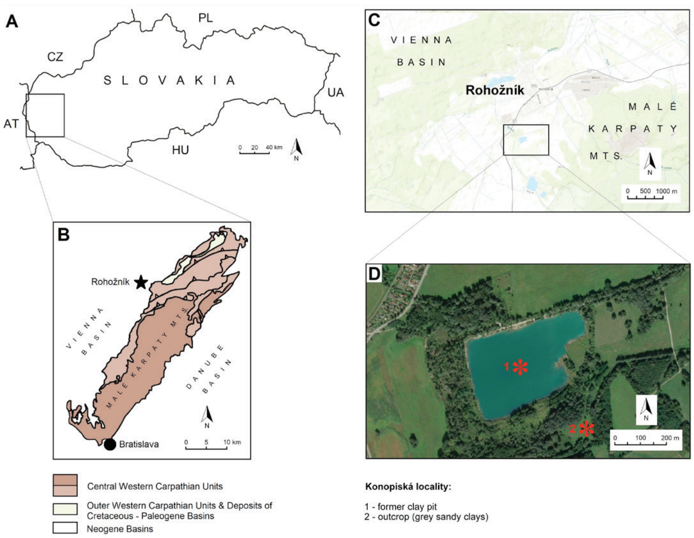

Fig. 1. A: Location of the eastern part of the Vienna Basin in Slovakia. B: Position of the Rohožník village in simplified geological map of south-western Slovakia with specified Pre-Neogene units and Neogene basins. C: Position of the surveyed locality. D: The Konopiská area with marked of the samples collecting. Map source: mapsfy.com, sk.wikipedia.org, Kováč et al. (2004) (modified).

2. GEOLOGICAL SETTING

The locality Rohožník-Konopiská is situated in the eastern Vienna Basin, at the western edge of the Malé Karpaty Mts. (Fig. 1), and comprises the area of a former clay pit and its vicinity (GPS coordinates: 48°26’39” N, 17°09’53” E). Exposed Middle Miocene deposits are of the Badenian and Sarmatian age (Figs. 2–3; Kučerová, 1986; Hladilová, 1991; Kováč et al., 1991; Fordinál et al., 2012). In the northern margin of the clay pit, the Badenian and Sarmatian deposits are situated on the same level, which has been caused by the tectonic lowering of one of the nearby tectonic blocks (Holec et al., 2007).

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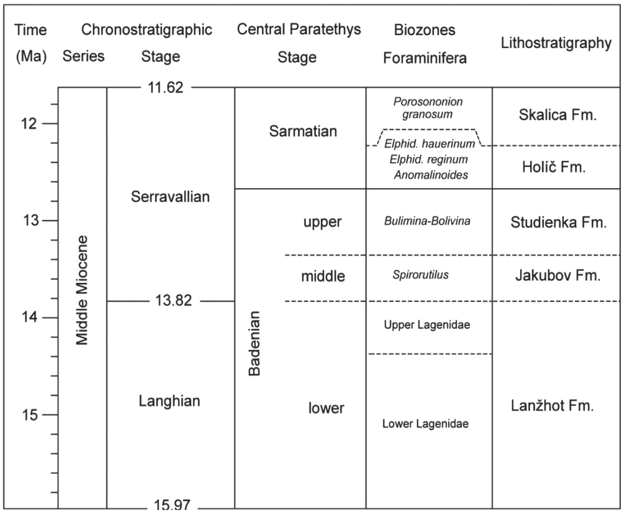

Fig. 2. The Middle Miocene chronostratigraphic and biostratigraphic zonation and lithostratigraphic units of the Vienna Basin. According to Harzhauser et al. (2018) (modified).

The studied upper Badenian (Serravallian) strata (Fig. 3) belong to the Studienka Fm. of the *Bulimina-Bolivina* Biozone that are represented by deep-water (circalittoral) clays, but also by sands, gravels, sandy clays and organodetritic marls and limestones of the Sandberg Member containing species-rich associations of marine faunas (Biskupič, 2020, 2021). While foraminifers (Čierna, 1973), molluscs (e.g., Hladilová, 1991; Fuksi et al., 2011; Fuksi, 2015a, 2015b; Ruman & Hudáčková, 2015; Studencka, 2018; Biskupič, 2020, 2021), ostracods (Kučerová, 1986), decapods (Fuksi et al., 2011; Hyžný & Gašparič, 2014), polychaetes (Biskupič, 2017), fishes (Holec, 1973, 1975) and cetaceans (Holec, 1987; Lambert et al., 2008) were studied from here, abundant bryozoans, brachiopods, scleractinian corals, cirripeds, echinoids, ophiuroids, elasmobranchs, coralline red algae and sporadically remains of terrestrial plants remain unpublished.

3. MATERIAL AND METHODS

The examined shells were collected in the clay pit between 1994 and 2004, and during excavation works south-east of the clay pit in 1996–1997.

Material of *Helminthia tricincta* (70 specimens) consists of moderately to poorly preserved shells, juvenile shells (9 specimens) possess well-preserved protoconchs. *Helminthia vermicularis* consists of 352 specimens, including 5 shells with preserved protoconch.

The protoconchs were documented by SEM microscope Jeol JSM-6390LV. Juvenile specimens and protoconchs were measured using a digital microscope Leica DVM6. Protoconch whorls counting follows Bouchet & Kantor (2004).

All measured and illustrated shells are stored in the collection of the Natural History Museum of Slovak National Museum, Bratislava, Slovakia (SNM-PM). The rest exemplars are housed in the collection of the author (RB/R–K).

The taxonomic concepts of turritellids, morphometric dimensions and abbreviations for shell morphology given by Harzhauser & Landau (2019) are adopted herein. The terminology of shell morphology is adopted from Allmon (1996), Landau et al. (2013), Van Dingenen et al. (2016), Landau et al. (2018) and Harzhauser & Landau (2019). The protoconch height and protoconch diameter are given for available specimens.

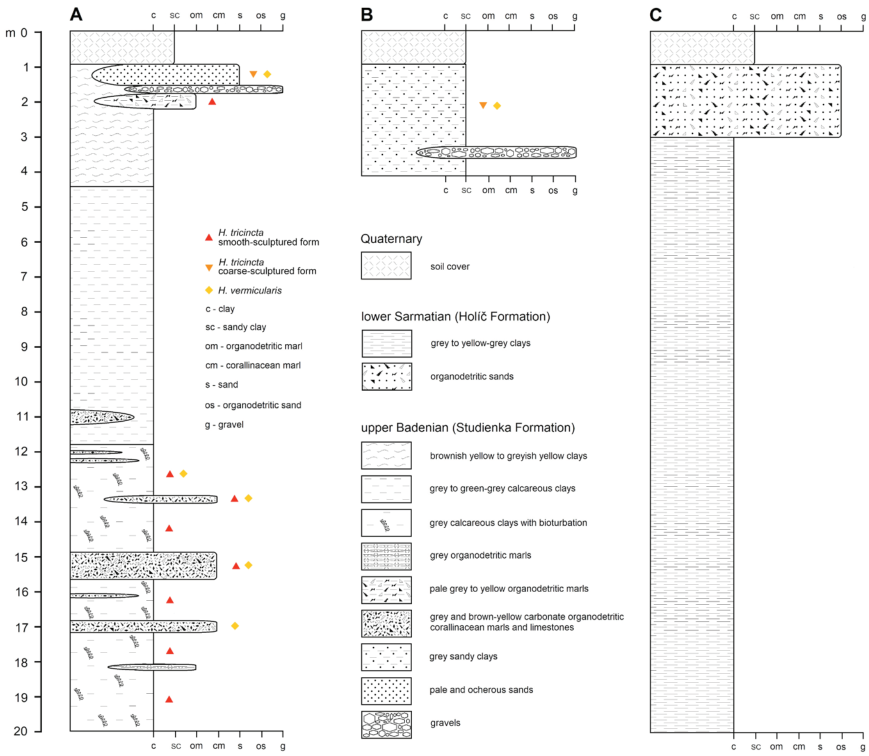

Fig. 3. Simplified schematic lithological profiles of the Middle Miocene group of beds of the locality Konopiská showing the distribution of respective *Helminthia* species. A: The main upper Badenian section exposed in the former clay pit (Studienka Formation), B: The upper Badenian profile of a temporary outcrop situated about 200 south-east of clay pit (Studienka Formation), C: The lower Sarmatian sequence exposed in the northern part of the former clay pit (Holíč Formation).

Morphometric abbreviations used in the text: SL= shell length, MD = maximum diameter, PH = protoconch height, PD = protoconch diameter.

4. RESULTS

4.1. Lithology and faunal assemblages of the Serravallian deposits

Three partial sections were studied in and around the former clay pit (Fig. 3). The lithostratigraphical columns were divided into pelitic and sandy members with documented even beds.

4.1.1. Section A (upper Badenian)

The lower part of the upper Badenian section (Fig. 3A) exposed in the former clay pit containing a rich assemblage of organisms (e.g., molluscs, scleractinian corals, polychaetes, echinoids, decapods, fishes) is formed by **grey calcareous clays with bioturbation**. These bioturbations formed of ferruginous, corkscrew-like structures probably belong to the *Gyrolithes*-like trace fossils. Bivalve association is dominated by suspension feeding *Corbula gibba* (Olivi, 1792) and *Neopycnodonte navicularis* (Brocchi, 1814). The assemblage of gastropods is characterized by abundant carnivorous *Euspira helicina* (Brocchi, 1814) and *Ringicula exilis* (Eichwald, 1830); deposit feeding scaphopods are represented by *Fissidentalium mutabile* (Hörnes, 1856). Southwestwards, these sediments gradually laterally and vertically pass into the yellow to brown-yellow clays with a similar taxonomic composition of malacofauna.

An interbed of **grey organodetritic marls** with a thickness from 20 to 30 cm accurs in the lowermost part of this pelitic member. It contains mixed shallow- to deep water species-rich malacofaunal assemblage. Bivalves, such as deposit feeder *Saccella commutata* (Philippi, 1844), and suspension feeding *Anadara diluvii* (Lamarck, 1805), *Striarca lactea* (Linnaeus, 1758), *Chama gryphoides* Linnaeus, 1758 and *Corbula gibba*, prevailed. Beside abundant micro-algal grazing *Bittium reticulatum* (da Costa, 1778) and *Cingula laevigata* (Eichwald, 1830), several *Alvania* species and a semi- infaunal deposit feeder *Fissidentalium mutabile* were identified. Foraminifers, polychaetes, echinoderms, decapods, and fishes were found as well.

Several finger-like beds of **grey and brown-yellow carbonate organodetritic corallinacean marls and limestones** (10–80 cm thick) occur in both the lower member and also in the basal part of the overlying pelitic member. These could represent an episodic redeposition of infralittoral facies by storm currents (Lambert et al., 2008) from the adjacent carbonate platforms or talus formed by coralline algae along the paleo-coast of the Malé Karpaty Mts. (e.g., Baráth, 1993; Hladilová et al., 1998; Lambert et al., 2008). They contain foraminifers, bryozoans, brachiopods, polychaetes, gastropods, bivalves, chitons, scaphopods, decapods, cirripeds, ahermatypic corals, echinoids, asteroids, sharks, and fishes. In the species-rich assemblage of gastropods, a mass occurrence of epifaunal suspension feeder *Petaloconchus intortus* (Lamarck, 1818) and epifaunal grazer *Bittium reticulatum* is accompanied by micro-algal grazers, e.g., *Tricolia eichwaldi* (Hörnes, 1855), *Alvania oceani* (d´Orbigny, 1852), *Cingula laevigata* and *Rissoina subconoidea* (Grateloup, 1847)). Abundant suspension feeding bivalves such as *Striarca lactea*, *Cosmetopsis anomala* (Eichwald, 1830), *Heteranomia squamula* (Linnaeus, 1758), *Ostrea digitalina* (Dubois, 1831), *Chama gryphoides* and *Hiatella arctica* (Linnaeus, 1767) are present as well.

Grey calcareous clays with bioturbation pass into **grey to green-grey calcareous clays**. These contain foraminifers, polychaetes, molluscs, decapods and fish remains. Relatively species-poor, a monotypic association of molluscs is characterized by the opportunistic suspension-feeding *Corbula gibba*, the scavenger *Tritia illovensis* (Hoernes & Auinger, 1882), micro-algal grazers *Alvania alexandrae* (Boettger, 1902), *A. productilis* Boettger, 1907 and carnivorous *Euspira helicina*. Infaunal deposit feeder *Saccella commutata* and epifaunal suspension feeder *Bathyarca pectunculoides* (Scacchi, 1835) are also abundant.

The upper part of the section A is made of **brownish yellow to greyish yellow clays** with the associations similar to those of the grey calcareous clays. It is dominated by suspension feeding *Corbula gibba*, scavenger *Tritia illovensis* and carnivorous *Euspira helicina*.

In the upper part of this member an elongated lens-like body of **pale grey to yellow organodetritic marls** containing taxonomically diverse assemblages of organisms, to a large extent consisting of molluscs, foraminifers, brachiopods, bryozoans, crustaceans, polychaetes, scleractinian corals and echinoderms occurs. Molluscs are represented mainly by deposit feeding *Nucula nucleus* (Linnaeus, 1758), and by sessile suspension feeders *Ostrea digitalina* and *Chama gryphoides*, associated with micro-algal grazers *Tricolia eichwaldi* (Hörnes, 1855), *Bittium reticulatum*, *Alvania oceani* and *Cingula laevigata*, and by semi-infaunal deposit feeder *Fissidentalium mutabile*.

Uppermost part of the member bears discontinuous intercalations and lenticular beds of **pale and ocherous sands and gravels** with fragments of corallinacean limestones mixed with bioclasts derived from the molluscan shells are developed. Fossils of gastropods, bivalves, scleractinian corals and tubes of polychaetes are mostly fragmented, which suggests their allochthonous origin and redeposition. The molluscan fauna is mostly composed of gastropods, of which suspension feeding turritellids and carnivorous *Amalda glandiformis* (Lamarck, 1810) are dominant.

4.1.2. Section B (upper Badenian)

Grey sandy clays with intercalations of gravels (Fig. 3B) represent shallow- water facies of the Sandberg Mb. and were exposed of about 200 m south-east of the clay pit. They yielded a highly diversified fauna, composed of gastropods, bivalves, scaphopods, bryozoans, echinoids, decapods, hermatypic corals, polychaetes, sharks and fishes. Gastropods are characterized by the mass occurrence of seagrass feeding *Smaragdia expansa* (Reuss in Hörnes, 1856) and by epifaunal grazers *Gibbuliculus pseudangulatus* (Boettger, 1907), *Rissoa acuticosta* (Sacco, 1895), *Gibborissoia varicosa* (Basterot, 1825), *Bittium spina* (Hörnes, 1855) and carnivore *Amalda glandiformis*. Among the bivalves, chemosymbiotic *Microloripes dentatus* (Defrance, 1823) dominated and was accompanied by suspension feeding *Anadara fichteli* (Deshayes, 1850), *A. diluvii*, *Ostrea digitalina*, *Cyclocardia scalaris* (J. de C. Sowerby, 1825), *Cardita partschi* Goldfuss, 1840 and *Megacardita hoernesi* La Perna, Mandic & Harzhauser, 2017.

4.1.3. Section C (lower Sarmatian)

The lower Sarmatian sediments of the Holíč Formation (Fig. 3C) are mostly composed of basinal pelites, represented by homogenous **grey to yellow-grey clays** exposed in northern part of the clay pit, with occurrence of specimen-rich communities of molluscs. Assemblages of gastropods and bivalves are dominated by epifaunal grazers *Granulolabium bicinctum* (Brocchi, 1814) and *Thericium rubiginosum* (Eichwald, 1830), and was accompanied by several species of rissoid and hydrobiid gastropods, and also by cardiid and lymnocardiid bivalves.

Some 2–3 m thick interval of **organodetritic yellow to ocherous sands** with mixed Badenian and Sarmatian malacofauna overlies the pelites. These fossiliferous deposits are very rich in shells of gastropods and bivalves, in many cases showing demonstrable traces of transport and abrasion. Taxonomically diverse assemblage of the Sarmatian gastropods consists of epifaunal grazers *Granulolabium bicinctum* and *Thericium rubiginosum*, scavengerous *Duplicata duplicata* (Sowerby, 1832), carnivorous *Olegia rumana* (Simionescu & Barbu, 1940), and grazing calliostomiids, rissoids and hydrobiids; the Badenian gastropods are characterized by the dominant suspension feeding *Archimediella carpathica* Harzhauser & Landau, 2019. Bivalves are represented by the abundant infaunal chemosymbiotic *Loripes dujardini* (Deshayes, 1850), accompanied by suspension feeding cardiid and lymnocardiid bivalves.

4.2. Systematic Paleontology

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Turritellidae Lovén, 1847
Subfamily Turritellinae Lovén, 1847
Genus *Helminthia* Handmann, 1882
Type species: *Turbo vermicularis* Brocchi, 1814, subsequent designation by Landau et al. (2013, 62). Miocene, Italy.

***Helminthia tricincta* (Borson, 1821)**
Figs 4A–H, 5A–F, 6A–F, 8A–B, 9A–D

1821 *Turritella tricincta* nob. – Borson, p. 342, pl. 6, fig. 11.
2019 *Helminthia tricincta* (Borson, 1821) – Harzhauser & Landau, p. 38, figs 6I,figs 6I, 13A, 13B1–B2, 13C (cum syn.).
?1968 *Turritella (Haustator) unipseudocarinata* Voorthuysen, 1944 – Hinculov, p. 132, pl. 31, fig. 15 [non *Haustator unipseudocarinata* (van Voorthuysen, 1944)].
?1971 *Turritella marginalis* Brocchi – Eremija, p. 70, pl. 6, fig. 5 [non *Haustator marginalis* (Brocchi, 1814)].

Material: 70 specimens, no complete specimen available (mostly fragments and juvenile shells). Illustrated material: Z 40136, SL: 91.50 mm, MD: 26.35 mm (Fig. 4A– B); Z 40137, SL: 57.75 mm, MD: 26.20 mm (Fig. 4C–D); Z 40138, SL: 44 mm, MD: 20.40 mm (Fig. 4E–F); Z 40139, SL: 45.20 mm, MD: 13.50 mm (Fig. 4G–H); Z 40142, SL: 7.94 mm, MD: 2.45 mm, PH: 430 μm, PD: 370 μm (Figs 5C–D, 8A–B); Z 40144, SL: 12.75 mm, MD: 4.20 mm (Fig. 9A); Z 40145, SL: 13.45 mm, MD: 3.60 mm (Fig. 9B); Z 40141, SL: 5.95 mm, MD: 2.03 mm, PH: 410 μm, PD: 360 μm (Fig. 5A–B); Z 40143, SL: 6 mm, MD: 2.10 mm, PH: 420 μm, PD: 370 μm (Fig. 5E–F); Z 40175, SL: 47.60 mm, MD: 20.10 mm (Fig. 6A); Z 40176, SL: 38.65 mm, MD: 18.45 mm (Fig. 6B); Z 40177, SL: 34.65 mm, MD: 15.20 mm (Fig. 6C); Z 40178, SL: 32.25 mm, MD: 16.55 mm (Fig. 6D); Z 40179, SL: 26.60 mm, MD: 12.10 mm (Fig. 6E); Z 40180, SL: 28.05 mm, MD: 10.40 mm (Fig. 6F); Z 40181, SL: 19.10 mm, MD: 6.15 mm (Fig. 9C); Z 40182, SL: 17.80 mm, MD: 7.20 mm (Fig. 9D). The material is derived from grey calcareous clays with bioturbation, grey and brown-yellow carbonate organodetritic corallinacean marls and limestones, pale grey to yellow organodetritic marls, pale and ocherous sands, and grey sandy clays.

Remarks: For a detailed description, discussion and full list of synonyms see Harzhauser & Landau (2019). Although the fossils from Rohožník-Konopiská are fragmentary and poorly preserved, they largely agree with the description and figures given by Hörnes (1855) and Harzhauser & Landau (2019).

In the examined material, the protoconch was preserved in several shells, which represents the first protoconch evidence for the species. The protoconch consists of 2.25–2.50 smooth, strongly convex whorls of 370 μm maximum diameter, with a

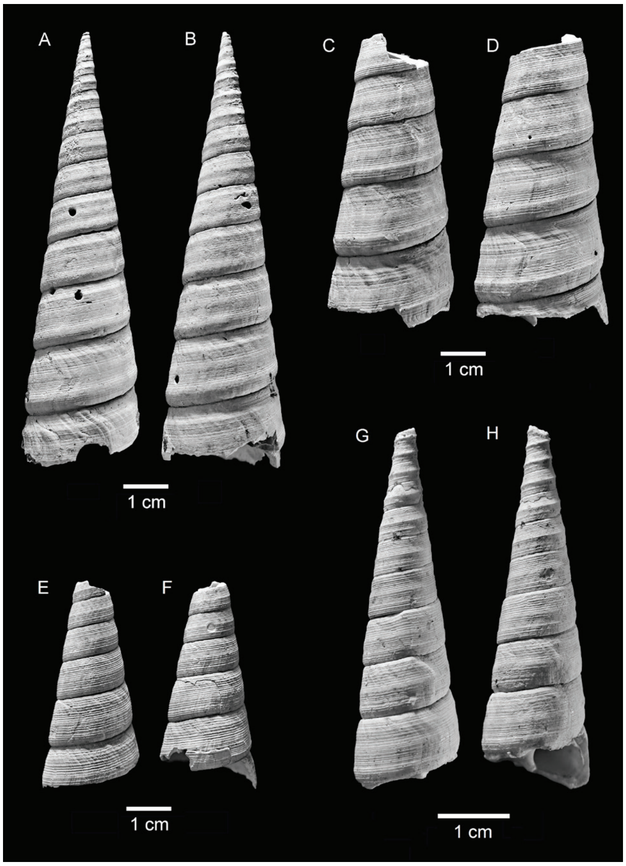

Fig. 4. A – H: *Helminthia tricincta* (Borson, 1821), smooth-sculptured form, Rohožník-Konopiská, upper Badenian. A – B: Z 40136; C – D: Z 40137; E – F: Z 40138; G – H: Z 40139.

large nucleus of 165 μm maximum diameter (Fig. 8A–B). The embryonic shell is not clearly distinct from the larval shell, and the boundary between them is not observed. Transition to the teleoconch is well-delimited, indicated by delicate microsculpture of small, regular-sized papillae, and by appearance of well-developed B spiral cord in the middle of the whorl, accompanied by C spiral cord. The first about 8 neanic teleoconch whorls are convex, strongly carinate and tricostate, with dominated sharply developed medial primary B, forming mid-whorl angulation separating moderately concave adapical and abapical halves of the whorl (Fig. 5A–F).

In several specimens, the primary spiral cords are strongly suppressed and hardly discernable (Fig. 4A–H), indicating wide intraspecific variability of the species. The shells are medium- to large-sized, turriculate, robust, and have a flat-sided profile of late teleoconch whorls. The latest adult whorls are stocky, with a slightly imbricate to frustate profile. Primary spiral cords (A, B, C) are weak, broad, flattened and strongly suppressed. The entire surface of the latest teleoconch whorls is covered by delicate 22–35 secondary and tertiary spiral cords. Interestingly, in coarse-sculptured specimens, their number is about 70 in the last whorl (cf. Harzhauser & Landau, 2019). Within *H. tricincta*, this strange smooth-sculptured form was recorded for the first time. In contrast, the typical form of *H. tricincta* has a robust, medium- to large-sized shell with flat-sided whorls and strongly developed spiral sculpture – the late teleoconch whorls are covered by three broad, low and convex primaries (cf. Hörnes, 1855, pl. 43, fig. 2; Schultz, 1998, pl. 21, fig. 7; Harzhauser & Landau, 2019, figs 13A–C).

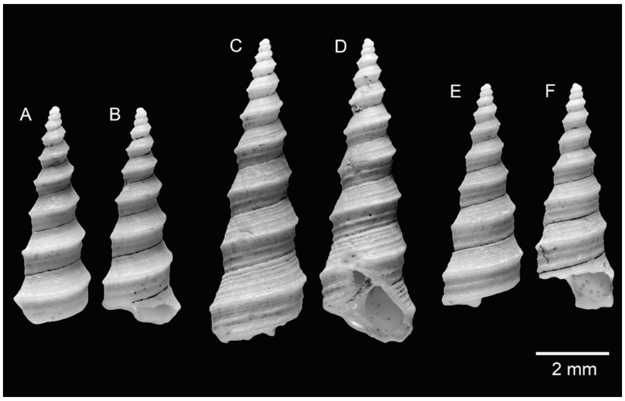

Fig. 5. Specimens with well preserved early apical whorls with protoconch. A – F: *Helminthia tricincta* (Borson, 1821), smooth-sculptured form, Rohožník-Konopiská, upper Badenian. A – B: Z 40141, C – D: Z 40142, E – F: Z 40143.

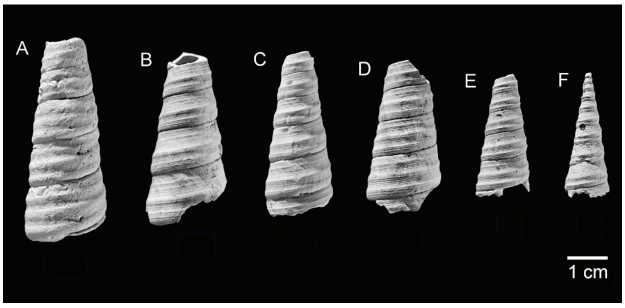

Fig. 6. A – F: ***Helminthia tricincta*** **(Borson, 1821), coarse-sculptured form, Rohožník-Konopiská, upper Badenian. A: Z 40175; B: Z 40176; C: Z 40177; D: Z 40178; E: Z 40179; F: Z 40180.**

The shells, most probably belonging to *H. tricincta*, characterized by flat-sided whorls with strongly suppressed spiral cords have also been found in other localities in the Central Paratethys. This is suggested by specimens recorded from Romania and Bosnia and Herzegovina. Hinculov (1968) reported an incomplete shell treated as *Turritella (Haustator) unipseudocarinata* from the Caransebeş-Mehadia Basin in Romania (p. 132, pl. 31, fig. 15). Although the figured specimen is poorly preserved, the shell shows several typical morphological features typical for specimens from Rohožník-Konopiská. It has stocky, flat-sided whorls with three reduced primary cords and with numerous, delicate secondary spiral cords. A shell identified by Eremija (1971) as *Turritella marginalis* Brocchi from the Prnjavor Basin (Bosnia and Herzegovina) (p. 70, pl. 6, fig. 5) has a flat-sided profile of the shell, teleoconch whorls are robust, bearing three suppressed primary spiral cords accompanied by fine spiral threads which agree with the overall morphology of the herein studied smooth- sculptured *H. tricincta*.

A shell described by Toula (1900) from the Badenian basinal pelites of the Devínska Nová Ves (= Neudorf an der March, Dévény – Ujfalu) – brickyard (Slovakia, Vienna Basin) under the name *Turritella neudorfensis* Toula, 1900 is similar to weakly sculptured specimens from Rohožník-Konopiská and slightly differs in its whorls shape and ornamentation. A poorly preserved shell described and illustrated by Toula (1900; 15, fig. 6 a–b) shows an imbricate, weakly bicarinate profile of the whorls and slightly concave sutural ramp, and its whorls bearing two primary spiral cords that are somewhat reminiscent of the genus *Oligodia*. Nevertheless, it is not excluded that this enigmatic turritellid represents the smooth-sculptured form of *H. tricincta*. Unfortunately, the type material is not available and probably is lost which does not allow its re-examination. In addition, the specimens belonging to *H. tricincta* (identified as *Turritella Riepeli* Partsch) were already found at the locality by Schaffer (1897).

Morphologically very similar *Helminthia vermicularis* is very frequent in the Miocene Paratethys and have often been misidentified with *H. tricincta* in the malacological literature which caused taxonomic confusions between these two taxa

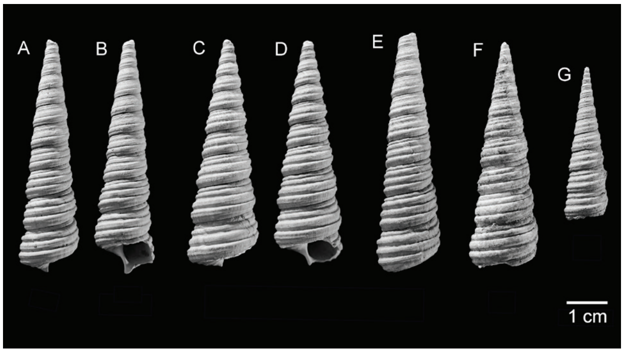

Fig. 7. A – G: ***Helminthia vermicularis*** **(Brocchi, 1814), Rohožník-Konopiská, upper Badenian. A – B: Z 40183, C – D: Z 40184, E: Z 40185, F: Z 40186, G: Z 40187.**

(see Harzhauser & Landau, 2019). From the Middle Miocene (Badenian) of the eastern Vienna Basin, the species was reported under the names *Turritella Riepeli* Partsch or *Turritella tricincta* (Borson), but usually without a detailed description, remarks, and illustration (e.g., Kornhuber, 1865; Horusitzky, 1917; Hyžný et al., 2012). Revision of specimens mentioned in Hyžný et al. (2012) and material from personal collection of the author confirm the presence of *H. tricincta* in the locality Devínska Nová Ves – Sandberg.

Buday (1939) determined *Turritella tricincta* from Kuchyňa and Stupava – Vrchná hora (Vienna Basin), but this identification is not possible to verify, because the fossil material is not accessible and probably is lost.

Seneš (1955; 31, pl. 3, fig. 10) presented a single specimen treated as *Turritella tricincta* from the Early Miocene (Eggenburgian) sandy marls of the Prešov Fm. exposed near Modra nad Cirochou (East Slovakian Basin). The illustrated shell has a convex outline of whorls with slightly mid-whorl angulation, and three primary spiral cords of a relatively equally thickness developed on teleoconch whorls. Although this shell shows some similarities with *Helminthia doublierii* (Matheron, 1842) (Seneš, 1955), probably belongs to other turritellid species and its generic placement in *Helminthia* will need verification.

Paleoecology: The smooth-sculptured form was recorded in biodetritic corallinacean marls and limestones and in pale grey to yellow organodetritic marls, originating in a shallow marine nearshore environment characterized by dominating corallinacean red algae (Biskupič, 2020). It was also found in grey calcareous clays with bioturbation, pointing to muddy seafloor and moderately deep sublittoral settings (circalittoral) influenced by low bottom water oxygenation (Biskupič, 2020). Based on the appearance of stenohaline organisms (e.g., scaphopods, scleractinian corals, brachiopods, echinoderms) and tropical/subtropical molluscs (plicatulids, carditids, costellariids), fully marine conditions and warm water settings are assumed in both paleoenvironments.

The coarse-sculptured form appeared in grey sandy clays and in pale and ocherous sands, both typical of co-occurring gravel intercalations. Mass occurrence of the gastropod *Smaragdia* (cf. Zuschin & Hohenegger, 1998; Zuschin et al., 2007; Harzhauser, 2014; Reich et al., 2014), presence of strombid gastropods (cf. Harzhauser & Kronenberg, 2013; Landau et al., 2013; Reich et al., 2015), and prevalence of lucinid bivalves, bittiinid gastropods and cone snails (cf. Reich et al., 2015), point to seagrass meadows. Abundant semi-infaunal suspension-feeding turritellids suggest a nutrient- rich environment (Allmon, 1988, 2011; Anderson et al., 2017; Harzhauser & Landau, 2019; Nebelsick et al., 2019), and shallow-water, soft bottom conditions (Zuschin et al., 2004). The shallow sublittoral settings are reflected by the bivalve *Acanthocardia turonica* (Hörnes, 1861) that prefer a water depth of 10–15 m (Harzhauser et al., 2014). Finds of articulated shells of the deep-burrowing bivalve *Panopea menardi* (Deshayes, 1829) refer shallow subtidal habitats down to 20 m and frequent disturbances of the seafloor by storms (Zuschin et al., 2007). The prevalence of thermophilic molluscs (e.g., carditids, strombids, costellariids, terebrids, clavatulids) indicate tropical or subtropical character of the environment. Normal marine conditions are reflected by the abundant stenohaline molluscs (e.g., pectinids, chamids, aporrhaids, clavatulids), scleractinian corals, and echinoderms.

Distribution: Middle Miocene (upper Badenian) of the Vienna Basin: Rohožník– Konopiská (this paper); vicinity of Bratislava – Devínska Nová Ves: Brickyard (Schaffer, 1897), Sandberg (Kornhuber, 1865; Horusitzky, 1917; Hyžný et al., 2012). Occurrences from the Caransebeş-Mehadia Basin (Romania) (Hinculov, 1968) and the Prnjavor Basin (Bosnia and Herzegovina) (Eremija, 1971) probably represent new records of this species in the Badenian of the Central Paratethys. A complete overview of the stratigraphic and geographic distribution of the species is given by Harzhauser & Landau (2019).

***Helminthia vermicularis* (Brocchi, 1814)**
Figs 7A–G, 8C–D, 9E–F

1814 *Turbo vermicularis* nob. – Brocchi, p. 372, pl. 6, fig. 13.
2019 *Helminthia vermicularis* (Brocchi, 1814) – Harzhauser & Landau, p. 41, figs 6K, 7G–H, 13D1–D2, 13E1–E2, 13F (cum n.).

Material: 352 specimens. Illustrated material: Z 40183, SL: 51.60 mm, MD: 18.10 mm (Fig. 7A–B); Z 40184, SL: 50.50 mm, MD: 15.40 mm (Fig. 7C–D); Z 40185, SL: 52.45 mm, MD: 19.35 mm (Fig. 7E); Z 40186, SL: 48.45 mm, MD: 15.30 mm (Fig. 7F); Z 40187, SL: 33.80 mm, MD: 9.55 mm (Fig. 7G); Z 40188, SL: 25.20 mm, MD: 7.35 mm (Fig. 9E); Z 40189, SL: 17.70 mm, MD: 5.45 mm (Fig. 9F); Z 40190, SL: 3.45 mm, MD: 1.35 mm, PH: 270 μm, PD: 360 μm (Fig. 8C–D). Additional material: Z 40191, SL: 3.50 mm, MD: 1.30 mm, PH: 320 μm, PD: 390 μm; Z 40192, SL: 4 mm, MD: 1.50 mm, PH: 260 μm, PD: 380 μm. The material is obtained from grey calcareous clays with bioturbation, grey and brown-yellow carbonate organodetritic corallinacean marls and limestones, pale grey to yellow organodetritic marls, pale and ocherous sands and grey sandy clays.

Remarks: A full list of synonyms and discussions on related species are presented in detail in Landau et al. (2013) and Harzhauser & Landau (2019). The specimens from

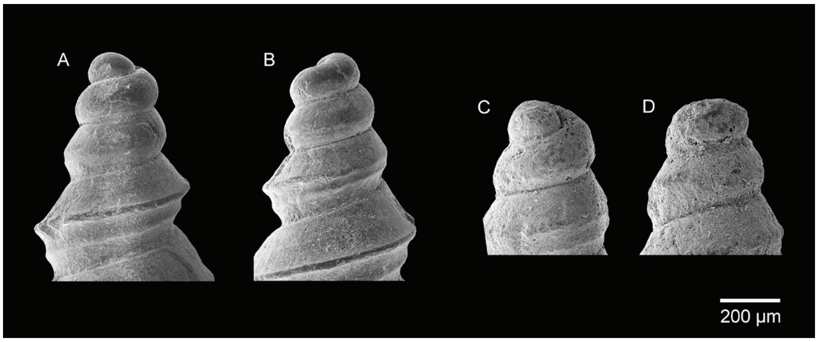

Fig. 8. Detail of protoconchs. A–B: *Helminthia tricincta* (Borson, 1821), smooth- sculptured form, Rohožník-Konopiská, upper Badenian, Z 40142. C–D: *Helminthia vermicularis* (Brocchi, 1814), Rohožník-Konopiská, upper Badenian, Z 40190.

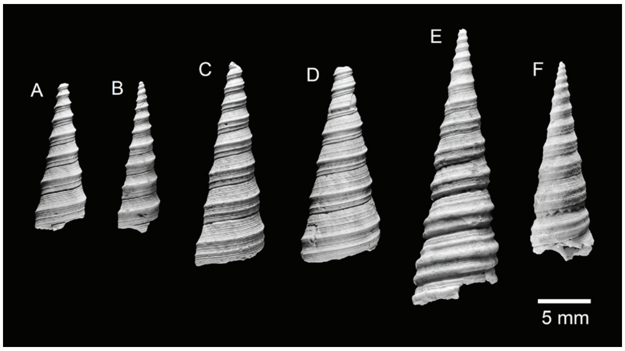

Fig. 9. A – B: *Helminthia tricincta* (Borson, 1821), smooth-sculptured form, Rohožník-Konopiská, upper Badenian. A: Z 40144, B: Z 40145; C – D: *Helminthia tricincta* (Borson, 1821), coarse-sculptured form, Rohožník-Konopiská, upper Badenian, C: Z 40181, D: Z 40182; E – F: *Helminthia vermicularis* (Brocchi, 1814), Rohožník-Konopiská, upper Badenian, E: Z 40188, F: Z 40189.

Rohožník-Konopiská comprise mostly of moderately preserved shells and are identical to the description and shell illustrated by Harzhauser & Landau (2019).

In the studied material, the protoconch was observed in some specimens. The species has a typical paucispiral protoconch consisting of 1.50 smooth convex whorls, with large-sized nucleus (Fig. 8C–D). The transition between the embryonic shell and the larval shell is not recognised. The protoconch-teleoconch boundary is shown by the initial spiral sculpture that is presented by well-defined spiral cord B accompanied by spiral cord C, both developed on the first teleoconch whorl. The first neanic whorls are typically corkscrew-like, convex-shaped, tricostate; medial primary spiral cord B forms mid-whorl angulation.

Morphological similarity of *Helminthia tricincta* and *Helminthia vermicularis* was already mentioned above. This often caused a confusion in identification (e.g. Švagrovský, 1981, Hyžný et al., 2012, Ruman & Hudáčková, 2015; see also Landau et al., 2013 and Harzhauser & Landau, 2019). Specimens studied by the above-mentioned Slovakian authors, housed in the Natural History Museum of Slovak National Museum, Bratislava, and in the personal collection of the author, were revised and a predominant part of the examined shells was assigned to *H. vermicularis*.

A single specimen was found in Pernek (Vienna Basin), representing the first occurrence of the species from this locality (collection of the author).

Several occurrences of poorly preserved turritellids reminiscent of *Helminthia vermicularis* are known from the Early Miocene (Eggenburgian) of Slovakia. A shell mould identified as *Turritella (H.)* cf. *vermicularis tricincta* Schaffer, 1912 was reported by Bílek (1966) from Chropov (Vienna Basin). Near Sverepec (Ilava Basin), fragments of shell moulds treated as *Turritella (Haustator)* cf. *vermicularis* were documented by Čtyroký (1960), and another specimen was also considered to be *Turritella (Haustator)* cf. *vermicularis* by Seneš (1960). However, the species identification of these fossils is relatively difficult due to their poor preservation. Consequently, they are not included in *Helminthia vermicularis* in this paper.

Paleoecology: This turritellid was found in grey sandy clays with intercalations of gravels, and in pale and ocherous sands with intercalations of gravels. As mentioned above, the assemblages of marine invertebrates show strong preferences for seagrass habitats and are characterized by a high abundance of thermophilic and stenohaline organisms which support the fully marine, shallow sublittoral, subtropical or tropical character of these paleoenvironments with sandy to sandy-clayey bottoms. The species was also common in biodetritic corallinacean marls and limestones and in pale grey to yellow organodetritic marls derived from infralittoral nearshore algae-dominated habitat (Biskupič, 2020).

Distribution: Middle Miocene (lower Badenian) of the Novohrad-Nógrád Basin: Kosihovce (Hano, 1950). Middle Miocene (upper Badenian) of the Vienna Basin: Rohožník-Konopiská (this paper), Pernek (this paper); Bratislava – Devínska Nová Ves: Brickyard (Schaffer, 1897; Toula, 1900), Sandberg (Kornhuber, 1865; Švagrovský, 1981; Hyžný et al., 2012), Bačnegovice (=Vineyard) (Švagrovský, 1981), Útočnice (Ruman & Hudáčková, 2015); Bratislava – Dúbravka: Fuchsov lom (Hyžný et al., 2012). For more information about the overall geographic and stratigraphic range of the species see Landau et al. (2013) and Harzhauser & Landau (2019).

5. DISCUSSION

5.1. Early ontogenetic development

Although the protoconch morphology and the neanic sculpture are important features to describe and distinguish turritellid species (e.g., Allmon, 1996; Landau et al. 2004, 2013, 2018; Harzhauser & Landau, 2019), their protoconchs are usually unknown or poorly preserved as their preservation is exceptional (e.g., Shiladri et al., 2018; Sang et al., 2019; Harzhauser & Landau, 2019). Sang et al. (2019) suggested the protoconchs are often abraded away in turritellines, even during the life of the organism. In the studied shells, the first neanic whorls and protoconchs are prevailingly broken or the neanic sculpture is eroded. Only in a few juvenile shells of *Helminthia tricincta* and *Helminthia vermicularis* the neanic whorls have been observed including protoconch.

Until now, the protoconchs of *Helminthia* from the Central Paratethys were unknown (Harzhauser & Landau, 2019) and were only observed in Proto-Mediterranean (Pliocene) specimens of *H. vermicularis* (Landau et al., 2004). For comparison, the protoconch consists of 1.50 whorls with a large-sized nucleus in *H. vermicularis* from Rohožník-Konopiská, whereas Landau et al. (2004) mentioned 1.75 protoconch whorls with a small to medium-sized nucleus.

In terms of protoconch type categorizing in turritellids defined by Allmon (1996, 2011) and Sang et al. (2019), planktotrophic species have relatively narrow, multispiral protoconchs suggesting long-term planktonic phases, and nonplanktotrophic species have larger, more rounded, paucispiral protoconchs which points to short planktonic phases. Similarly, as proposed by Thorson (1950), a large apex points to a nonpelagic development, while a narrowly twisted apex, often with delicate sculpture, points to a pelagic development. According to Shuto (1974), large, rounded, often paucispiral protoconchs indicate larvae that spent little or

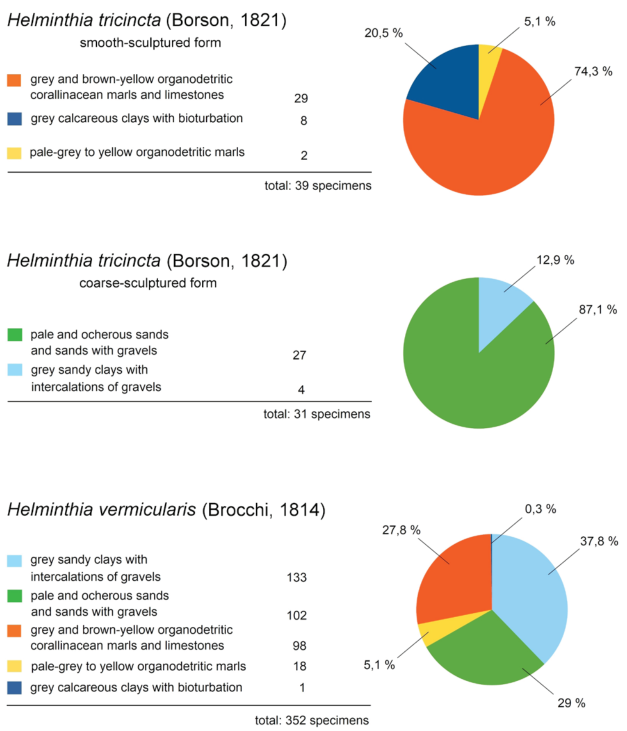

Fig. 10. Occurrence and percentage of studied *Helminthia* species in the upper Badenian marine facies of the locality Rohožník-Konopiská.

no time in the plankton, while narrow, polygyrate protoconchs suggest planktotrophic larvae.

Taking into account the morphological features defined by the abovementioned authors that differentiate planktotrophic and lecithotrophic development, the protoconch of *H. tricincta* characterized by its at most 2.50 convex smooth whorls with a large- sized nucleus reflects rather the nonplanktotrophy of the species. *H. vermicularis* has typically paucispiral protoconch (1.50 whorls) with a large-sized nucleus suggesting its short planktonic phase.

5.2. Paleoecology

As the results suggests, the herein discussed species of *Helminthia* were adapted to a broad spectrum of habitats, they were primarily adapted to the shallow-water nearshore paleoenvironments whereas in the deep sublittoral conditions reaches a lower abundance (Fig. 10). *H. tricincta* inhabited inner to middle neritic environments with organodetritic, sandy and muddy bottoms (this work). Its occurrences from the Paratethys are known mainly from offshore clays suggesting middle to outer neritic environments, but exceptionally also occurs in shallow water settings with seagrass meadows, indicating its broad habitat tolerance (Harzhauser & Landau, 2019). *H. vermicularis*, probably an only living species of this genus (see MolluscaBase, 2021), occurred in the seagrass meadows and the algae-dominated habitats at Konopiská (this work). As suggested by Harzhauser & Landau (2019), the species was common in shallow water settings, partly indicating seagrass meadows. According to Harzhauser & Landau (2019), this turritellid is still living along the coast of West Africa, which is supported by Talavera (1975) who mentioned it from the samples obtained in depths of 20–80 m at the continental shelf of Mauritania.

Helminthia is absent in the middle and upper pelitic members of the section A, characterized by a monotypic molluscan assemblage which indicates dysoxic conditions near the seafloor. The dominant opportunistic bivalve *Corbula gibba* accompanied by species-poor assemblages of molluscs and the sediment character (clays with only in places slight lamination without bioturbation) reflect a deterioration of paleoenvironmental settings (lowered water dynamics, occasional hypoxic events near the bottom) during the sedimentation (e.g., Hladilová, 1991; Hladilová et al., 1998; Lambert et al., 2008, Biskupič, 2020). As noted by Gallmetzer et al. (2017) and Tomašových et al. (2018, 2020), the turritelline gastropods are sensitive to deterioration of habitat and hypoxia conditions which causes decreasing abundance in turritellid populations or its complete absence in disturbed environments.

5.3. Intraspecific variability

Intraspecific variability in fossil turritellid shells is demonstrated in many species, as indicated by specimens illustrated in several papers (e.g., Harmer, 1916; Voorthuysen, 1944; Bałuk, 1975; Caprotti, 1975; Chirli, 2006; Van Dingenen, 2016; Harzhauser & Landau, 2019). This variability is manifested mainly by nonuniform spiral sculpture and the shape of whorls which is also observed in specimens within the respective *Helminthia* species, especially in *H. vermicularis* (cf. Harmer, 1916; Caprotti, 1975; Cavallo & Repetto, 1992; Chirli, 2006; Chirli & Linse, 2011; Harzhauser & Landau, 2019). Differences in morphological features, such as the number and thickness of spiral cords and the shape of whorls, are also seen in *H. vermicularis* from Rohožník-Konopiská (Fig. 7A–G).

Extreme variability in shell morphology is observed in shells of *H. tricincta*. Except for typical coarse-sculptured specimens characterized by well-defined, broad and convex primary spiral cords A, B, and C (Fig. 6A–F), several shells featured by strongly weakened spiral sculpture and somewhat different shape of later adult whorls (Fig. 4A–H). It seems that both forms were also ecologically separated, their co- occurrence in the same environment was not recorded (Fig. 10). At first sight, this peculiar form could represent a distinct species based on morphological and paleoecological differences, as deduced above. However, it possibly represents only an extremely smooth-sculptured regional morph of *H. tricincta* that most probably evolved due to adaptation to specific paleoenvironmental conditions prevailing in the eastern marginal part of the Vienna Basin during the upper Badenian.

6. CONCLUSIONS

From the upper Badenian deposits of Studienka Fm. in the Rohožník-Konopiská, a rich turritellid material comprise two species: *Helminthia tricincta* and *Helminthia vermicularis*.

H. tricincta was found in the marginal facies of the Sandberg Mb., as well as in the basinal pelites. It was adapted to the shallow marine nearshore settings affected by episodic storms currents and characterized by the dominance of coralline algae, and to the infralittoral seagrass paleoenvironments with fine-grained substrates but also occurred in moderately deep sublittoral settings with muddy seafloor and low bottom water oxygenation. Normal water salinity and warm water settings are expected. The first evidence of the protoconch for the species is recorded. It is the nonplanktotrophic species, its short-term planktonic phase during the early ontogenetic stages is assumed. In several specimens, considerable intraspecific variability of the shells was observed (suppressed spiral sculpture). These specimens represent an extremely smooth-sculptured regional morph of *H. tricincta* whose unusual shell morphology is probably the result of adaptation to the local paleoenvironmental conditions prevailing in the eastern Vienna Basin during the upper Badenian.

H. vermicularis was restricted to the shallow sublittoral seagrass habitats in the zone above the storm wave base characterized by well-aerated conditions, soft sandy to sandy-clayey bottoms, and fully marine and warm water settings, and also inhabited the algae-dominated habitats with fine- to coarse-grained bottoms. The finds of shells with rarely preserved protoconch represent the first protoconch evidence for the species in the Central Paratethys. It is the nonplanktotrophic species, its paucispiral protoconch suggests a relatively short planktonic phase of the larval development.

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