A new species of *Nitidiclavus* (Neogastropoda: Drilliidae) from the Miocene Paratethys and an overview of the paleoecology and distribution of related species in the Cainozoic of Europe

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ABSTRACT

A new Paratethyan species of the middle Miocene (Serravallian) conoidean gastropod of the family Drilliidae Olsson, 1964 is described. Rare finds of *Nitidiclavus senesi* spec. nov. have been obtained from the marine sediments exposed in the eastern marginal part of the Vienna Basin in Slovakia (Western Carpathians). The shells were collected from the calcareous clays of the upper Badenian Studienka Formation exposed in the former clay pit of the locality Rohožník-Konopiská. Under UV light, the shell surface of some specimens had residual colour patterns, which represent the first known evidence of these exceptional features for the genus *Nitidiclavus*. The species from Rohožník is also compared with other similar taxa from the European Cainozoic. As suggested by the sedimentology at the studied locality, *N. senesi* spec. nov. lived on a soft, muddy bottom in the circalittoral zone, in a habitat influenced by lowered water dynamics and occasional hypoxia. Preferred paleoecological conditions and geographic and stratigraphic distribution of *Nitidiclavus* in the North-East Atlantic and circum-Mediterranean regions are briefly discussed and summarized.

Key words: Conoidea, Drilliidae, *Nitidiclavus senesi*, new species, residual colour patterns, paleoecology, Miocene, Badenian, Central Paratethys, Slovakia

INTRODUCTION

Nitidiclavus Bernasconi & Robba, 1984 is a conoidean Neogastropod genus belonging to the family Drilliidae Olsson, 1964, and it is known only from the fossil record (e.g., Scarponi & Della Bella, 2003; Lozouet, 2017; MolluscaBase, 2021a). Representatives of the family Drilliidae are marine carnivorous gastropods characterized by their high diversity, with about 661 fossil and Recent species currently described (Tucker, 2004). In the present-day seas, they are widespread, almost worldwide, with highest diversity mostly in tropical and subtropical waters of the Eastern Pacific, South and West African, New Zealand, Western Atlantic, and Caribbean regions (Kilburn, 1988; Wells, 1995; Tucker, 2004; Kilburn & Dekker, 2008; Kilburn et al., 2014; Fallon, 2016).

Nitidiclavus is a relatively rare and species-poor genus, with only five species currently known from several localities in Europe. Although most species were initially established in other genera, their current placement in *Nitidiclavus* was made by Bernasconi & Robba (1984). The stratigraphic and geographic distribution of *Nitidiclavus* is restricted to the Paleogene and Neogene marine deposits of the European Eastern Atlantic, Proto-Mediterranean, and Paratethyan regions. This genus is known from the Oligocene of France (Lozouet, 2017), Miocene of the North Sea Basin (e.g., Rasmussen, 1956; Anderson, 1964; Nordsieck, 1972; Janssen, 1984; Wienrich, 2007; Moths et al., 2010), and also from the Pliocene of France (Chirli & Richard, 2008), Italy (e.g., Cavallo & Repetto, 1992; Chirli, 1997; Scarponi & Della Bella, 2003; Brunetti & Cresti, 2018), and Spain (Vera Peláez, 2002). From the middle Miocene of the Central Paratethys, it has been recorded only from the Badenian marine deposits of Romania (Boettger, 1902, 1906; Zilch, 1934), Hungary (Csepreghy-Meznerics, 1953; Strausz, 1966) and Poland (Bałuk, 2003).

The members of the genus *Nitidiclavus* are characterized by their small, fusiform shells, usually with a short siphonal canal; the whorls almost lacking spiral sculpture, are polished and decorated by flexuous, strongly developed axial ribs; anal sinus is typically shallow and wide (Bernasconi & Robba, 1984). The genus is characterized by its multispiral protoconch bearing a microsculpture of small papillae or granules in the embryonic shell, and abapical belt of granules developed in the larval shell (Bernasconi & Robba, 1984; Della Bella & Tabanelli, 1990). Adult shells of relevant species are morphologically almost invariant and

very similar in shell shape and size, whorls profile and axial sculpture. Nevertheless, they can be reliably distinguished on morphological features of the early shell; primarily on protoconch morphology, number of protoconch whorls and the presence of specific surface microsculpture of the embryonic and larval shell. Hence, for a clear and correct identification of respective species belonging to the *Nitidiclavus*, it is necessary to have well-preserved shells including the protoconchs.

GEOLOGICAL SETTING

The locality (Fig. 1) is situated near the village of Rohožník, in the eastern margin of the Vienna Basin, near the western edge of the Malé Karpaty Mountains (Slovakia). The paleontological site of Konopiská is comprised of an old clay pit and its surrounding area and is located approximately 1 km south to the Rohožník railway station (48°26′39″N, 17°9′53″E). At the present, the clay pit is abandoned, completely overgrown, and flooded by water. Miocene beds in this area are Langhian to Tortonian (Čierna, 1973), which correlate to the regional Paratethyan middle Badenian, upper Badenian, lower Sarmatian, and Pannonian stages (cf. Harzhauser & Piller, 2007; Piller et al., 2007; Kováč et al., 2004, 2017, 2018). Marine sediments that were exposed in the former clay pit have been assigned to the upper Badenian Studienka Formation and lower Sarmatian Holíč Formation (Fordinál et al., 2012). The upper Badenian (Serravallian) marine sediments comprise clays, organodetritic corallinacean marls, sandy clays, and sands and belong to the foraminiferal *Bulimina–Bolivina* Biozone (Biskupič, 2020). Several transitional facies between the Sandberg Member facies and the pelitic strata of the Studienka Formation are characterized by the occurrence of species-rich and abundant micro- and macrofauna and represent different shallow- to deep water depositional paleoenvironments (Biskupič, 2020). The lower Sarmatian sediments of the Holíč Formation comprise grey to greenish calcareous clays, pale-grey to yellowish clays, and layers of fine- to coarse-grained bioclastic yellow to ocherous sands with the occurrence of typically monotypic assemblages of bivalves and gastropods. Previous studies of the high diverse associations of marine organisms confirmed the presence of foraminifers (Čierna, 1973), ostracods (Kučerová, 1986), molluscs (e.g., Švagrovský, 1971; Hladilová, 1991; Fehse & Grego, 2012; Ruman & Hudáčková, 2015; Studencka, 2018; Biskupič, 2020), decapods (Fuksi et al., 2011; Hyžný & Gašparič, 2014), serpulid polychaetes (Biskupič, 2017), and fish otoliths (Holec, 1973, 1975). Very rare remnants of marine and terrestrial mammals were reported from the locality, including finds of a baleen whale (Holec, 1987), a toothed whale of the platanistid subfamily Pomatodelphininae (Lambert et al., 2008), and a cervid artiodactyl (Holec et al., 2007). Abundant and taxonomically diverse assemblages of bryozoans, brachiopods, scleractinian corals, cirripeds, echinoids, ophiuroids, and elasmobranchs were observed too. For more information about lithology and marine faunas of the upper Badenian section and previous research of the locality see Biskupič (2020).

Figure 1. Location of the studied locality in Slovakia and position of the Konopiská clay pit near Rohožník.

The shells of *Nitidiclavus senesi* spec. nov. were mainly found in the homogenous grey calcareous clays with bioturbation that formed the lowermost part of the upper Badenian section exposed in the clay pit. These strata are characterized by the occurrence of *Gyrolithes*-like trace fossils. An assemblage of molluscs (gastropods, bivalves, scaphopods) is dominated by the bivalves *Neopycnodonte navicularis* (Brocchi, 1814) and *Corbula gibba* (Olivi, 1792), and also by the gastropod *Euspira helicina* (Brocchi, 1814) and by the common scaphopod *Fissidentalium mutabile* (Hörnes, 1856). Fossil remnants of foraminifers, serpulid polychaetes, bryozoans, ahermatypic corals, cidaroid echinoids (spines), scalpelliform barnacles (isolated valves), brachyuran decapods (remains of carapaces, isolated cheliped fingers), sharks (teeth), and bony fishes (otoliths, teeth) were recovered as well. As mentioned by Hladilová (1991), Hladilová et al. (1998), Lambert et al. (2008), and Biskupič (2020), occasional, unfavourable, paleoenvironmental conditions near the sea bottom, such as episodical hypoxic events and lowered water dynamics, are assumed. Towards the southwest, the grey calcareous clays with bioturbation gradually laterally and partly also vertically pass into the yellow to brown-yellow clays with a similar malacofauna. A single shell of *N. senesi* spec. nov. has been found in these deposits.

MATERIAL AND METHODS

Most of the studied shells of this drilliid were collected in a former clay pit of the site Konopiská near Rohožník by the author in the period 2001–2004. A single specimen was retrieved during fieldwork by fossil collector Štefan Meszároš (Bratislava, Slovakia) in the 1980s. The examined material includes seven adult specimens, of which four are moderately to poorly preserved. Only three are well-preserved with minimum signs of breakage. The protoconchs are preserved in nearly all specimens but variably abraded, with only one shell showing an extraordinarily well-preserved protoconch including micro-ornamentation. Under UV light the surfaces of several shells showed residual colour patterns.

The shells of *Nitidiclavus senesi* spec. nov. are stored in the collections of the Natural History Museum of Slovak National Museum, Bratislava, Slovakia and are labelled as the inventory numbers SNM-PM Z 40193 to Z 40199.

The photographs were taken with a digital camera Nikon D 5600 and an AF-S Micro Nikkor 60mm f/2.8G ED macro lens under a low-angle light source. The protoconchs were photographed with the additional help of Kenko extension tubes (12/20/36 mm). Measurements of the shells were taken with a Leica DVM6 digital microscope; the scanning electron micrographs (SEM) of morphological details of protoconchs were made using a Jeol JSM-6390LV. The shells with well-preserved residual colour patterns were photographed under UV light.

Descriptive terminology of conoidean gastropod shells follows the works of Bernasconi & Robba (1984), Scarponi & Della Bella (2003), and Scarponi et al. (2011). I counted the number of protoconch whorls using the method proposed by Bouchet & Kantor (2004). Depending on shell preservation, the following morphometric parameters are provided and studied here: protoconch diameter, protoconch height, shell height, maximum shell diameter, spire height, the height of the body whorl, aperture height, spire angle, and apical angle (Fig. 2). When possible, additional morphometric data were given by statistical methods: mean and standard deviation.

Morphometric and statistic abbreviations referenced in the text: PH = protoconch height, PD = protoconch diameter, SH = shell height, SD = maximum shell diameter, SPH = spire height, BWH = the height of the body whorl, AH = aperture height, SA = spire angle, AA = apical angle, AS = anal sinus, LV = labial varix, DV = dorsal varix, *n* = number, μ = mean, σ = standard deviation.

SYSTEMATIC PART

The higher systematics of gastropods used herein follow Bouchet et al. (2017). The genus *Nitidiclavus* Bernasconi & Robba, 1984 was originally placed into the family Turridae H. Adams & A. Adams, 1853 (see Bernasconi & Robba, 1984; Della Bella & Tabanelli, 1990); however, it was later transferred to the family Drilliidae Olsson, 1964 (see Scarponi & Della Bella, 2003; Lozouet, 2017; MolluscaBase, 2021b), which is adopted in this study. Although Della Bella & Tabanelli (1990) disputed the validity of the genus *Nitidiclavus* and considered it as a junior synonym of the genus *Cerodrillia* Bartsch & Rehder, 1939 based on similarities in morphology of shell and protoconch, this proposal was later disclaimed and *Nitidiclavus* was accepted as a valid taxon (e.g., Scarponi & Della Bella, 2003; Wienrich, 2007; Lozouet, 2017; MolluscaBase, 2021a). *Nitidiclavus* has a typically simple, shallow, and wide anal sinus, which is its defining generic character, whereas the anal sinus of *Cerodrillia* is more pronounced and more deeply incised. Following the morphological characters defined by Bernasconi & Robba (1984) the new species described here is placed in *Nitidiclavus*.

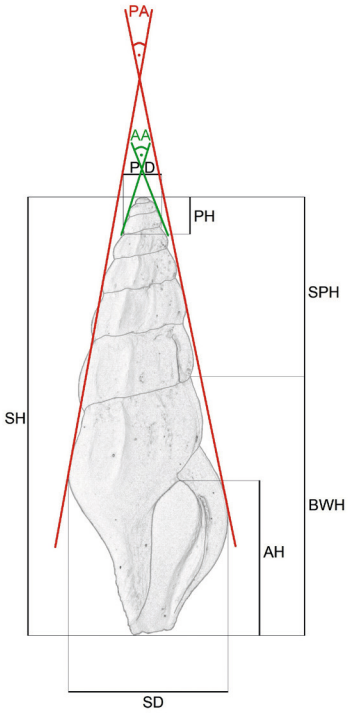


Figure 2. *Nitidiclavus senesi* spec. nov. shell measurements.

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

Order Neogastropoda Wenz, 1938

Superfamily Conoidea J. Fleming, 1822

Family Drilliidae Olsson, 1964

Genus *Nitidiclavus* Bernasconi & Robba, 1984

Type species: *Mangilia maitreja* Koenen, 1872, by original designation, middle Miocene, Germany.

***Nitidiclavus senesi* spec. nov.**

Figures 3–13

Type material and dimensions. — Holotype: SNM-PM Z 40193, SH: 9.70 mm, SD: 3.44 mm, PH: 735 µm, PD: 800 µm (Figs 3a–d, 9a–b, 10a–d, 11a–b); Paratype 1: SNM-PM Z 40194, SH: 9.80 mm, SD: 3.86 mm, PH: 750 µm, PD: 770 µm (Figs 4a–d, 12a–b) (donation of Štefan Meszároš, Bratislava, Slovakia); Paratype 2: SNM-PM Z 40195, SH: 8.68 mm, SD: 3.12 mm, PH: 700 µm, PD: 790 µm (Figs 5a–d, 13a–b); Paratype 3: SNM-PM Z 40196, SH: 7.46 mm, SD: 3.08 mm, PH: 730 µm, PD: 790 µm (incomplete specimen) (Fig. 8a–b); Paratype 4: SNM-PM Z 40197, SH: 8.80 mm, SD: 3.85 mm (incomplete specimen) (Fig. 7a–b).

Additional material. — Maximum height: 8.65 mm. SNM-PM Z 40198, SNM-PM Z 40199.

Etymology. — Named in memory of Ján Seneš (1924–1992), Slovak palaeontologist, geologist, and researcher of the Miocene molluscan faunas of the Western Carpathians, as well as a proponent and co-author of designation of the regional stratigraphic concept of the Central Paratethys.

Type locality. — Konopiská clay pit near Rohožník, Vienna Basin, Slovakia.

Type stratum. — Grey calcareous clays with bioturbation, brown-yellow to yellow clays of the Studienka Formation, middle Miocene, upper Badenian (= lower Serravallian), *Bulimina–Bolivina* Biozone.

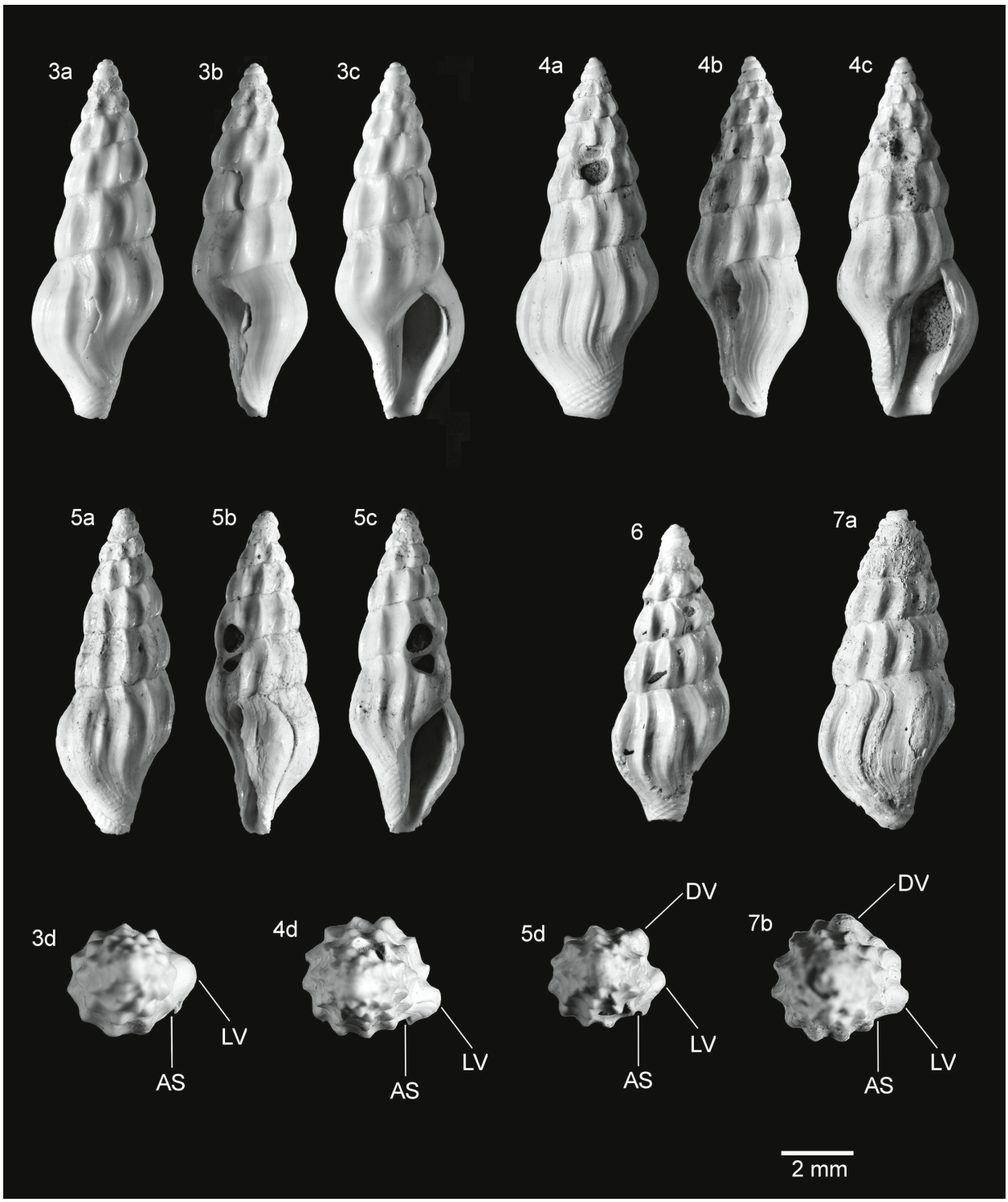
Diagnosis. — Shell slender, fusiform, elongate, large for the genus. Protoconch acuminate, conical-shaped, relatively tall, multispiral of 2.75 smooth convex whorls covered by a fine microsculpture, embryonic shell bears fine granulation, in larval shell the abapical belt developed close the abapical suture. Teleoconch of 5–5.5 convex whorls sculptured by 9–12 axial ribs, axials opisthocyrt, well defined, prominent abapically, shell surface polished and smooth, with lack of spiral sculpture, last adult whorl rounded, moderately prolonged, varicose, dorsal side of body whorl with 1–2 strong, broad, round-crested varices, labial varix situated nearby outer lip, dorsal varix developed occasionally about ¼ turn from the edge of the outer lip, siphonal canal short to moderately long, well developed and with delicate spiral cords, aperture lanceolate, anal sinus poorly developed, shallow and wide, columellar lip smooth; residual colour patterns composed of 2–3 pale spiral strips on spire whorls, increase to 4–7 bands on last adult whorl.

Description. — Protoconch conical, slightly acuminate, turriculate, multispiral, of 2.75 convex whorls covered with delicate micro-ornaments, reaching about 770–800 µm in diameter. Embryonic shell of circa 1 whorl, well recognised by unevenly sparse, tiny granules that cover entire surface; granules coarse, nonuniform, rather angular. Junction between embryonic shell and larval shell marked by absence of granulation. Surface of larval shell mostly smooth; microsculpture more or less poorly developed, visible only close to abapical suture. A relatively narrow abapical belt is developed there and bears peculiar micro-ornamentation consisting of oblique, uneven, scrappy, short cords and elongated granules. Its upper margin marked by an irregular, chain-like cord, its abapical edge bordered by the suture. On last protoconch whorl, abapical belt attenuated and completely absent. Protoconch–teleoconch boundary well-delimited by beginning of axial sculpture and defined by a few fine, sigmoid riblets.

Shell slender, fusiform, elongated, glossy, large for the genus, up to 9.80 mm in length. Spire relatively tall; last teleoconch whorl generally 60% of total height. Teleoconch composed of 5–5.5 convex-sided, well-demarcated whorls separated by a shallow but distinct suture. Sutural ramp poorly delimited, sometimes with slightly concave profile. Shell surface polished, smooth, lacking spiral sculpture. Teleoconch whorls with well-developed fold-like opisthocyrt axial ribs which extend from suture to suture; axial ribs slightly curved on spire. In adapical half of whorls, axial ribs sharp-crested, narrow, and low, whereas on abapical half of whorls axial ribs rounded, broad, and prominent. Early teleoconch whorls initially bear 9–10 axial ribs, but ribs increase to 9–12 on penultimate whorl. Last adult whorl moderately elongated, rounded at periphery, oblong to shell base, passing into the short neck, and bearing 9–11 axial ribs and 1–2 varices. Varices large and relatively broad, variable in thickness, prominent, wider than adjacent ribs, sigmoidal, round-crested, usually cup-handle-like, and developed

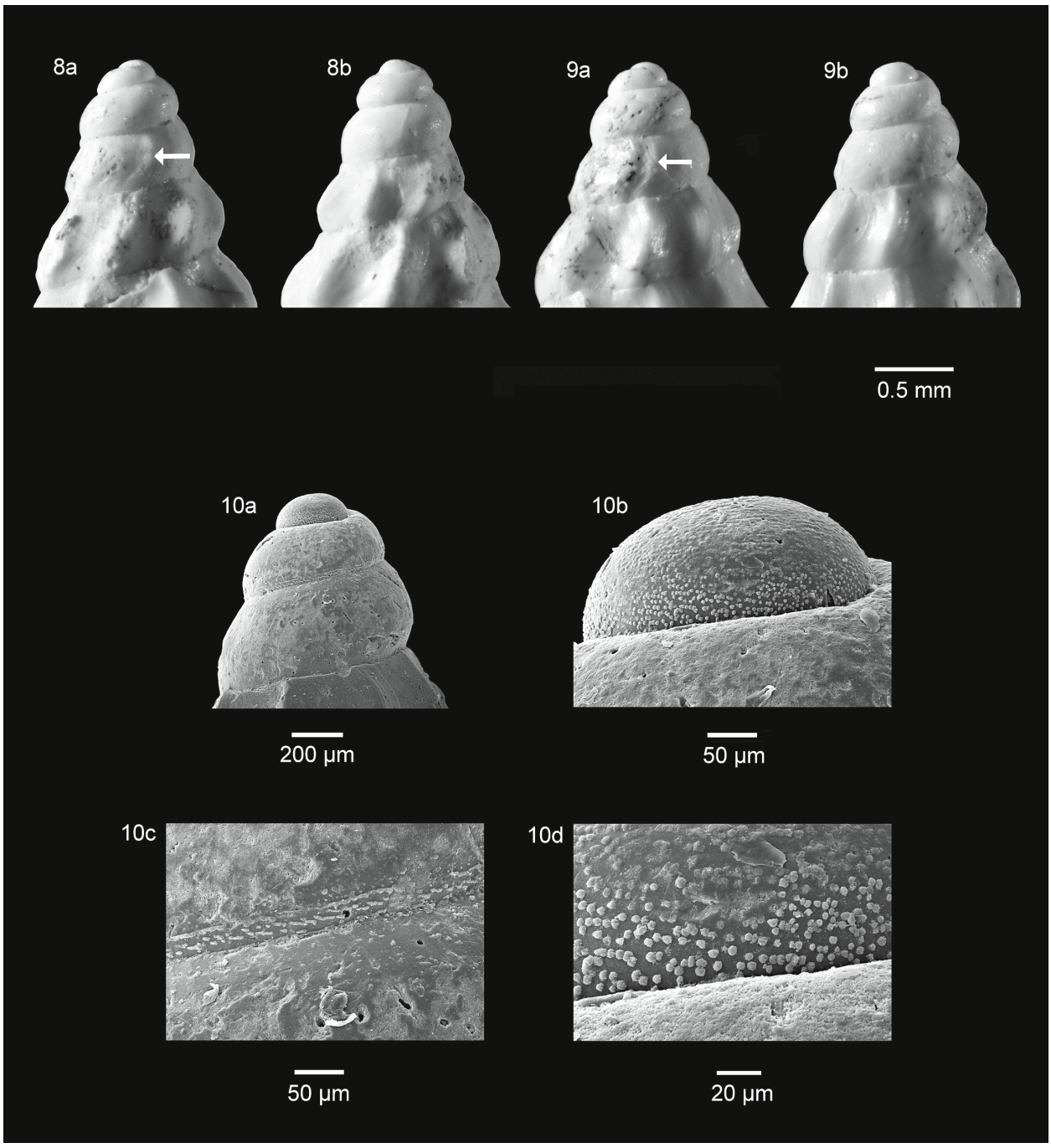
Table 1. Measurements of *Nitidiclavus senesi* spec. nov.

Specimen	SH (mm)	SD (mm)	SPH (mm)	BWH (mm)	AH (mm)	PD (mm)	PH (mm)	PA	AA
Holotype SNM-PM Z 40193	9.70	3.44	4	5.70	3.72	0.800	0.735	24°	44°
Paratype 1 SNM-PM Z 40194	9.80	3.86	4.13	5.67	3.95	0.770	0.750	27°	48°
Paratype 2 SNM-PM Z 40195	8.68	3.12	3.58	5.10	3.37	0.790	0.700	23°	49°
Paratype 3 SNM-PM Z 40196	>7.46	>3.08	—	—	—	0.790	0.730	28°	50°
Paratype 4 SNM-PM Z 40197	>8.80	3.85	—	5.60	3.70	—	—	26°	—
SNM-PM Z 40198	>8.66	>3.43	—	—	—	—	—	25°	—
SNM-PM Z 40199	>8.44	3.35	—	5.40	3.60	—	—	22°	—



Figures 3–7. *Nitidiclavus senesi* spec. nov., from Rohožník-Konopiská (clay pit), upper Badenian (middle Miocene). **3a–d.** Holotype, SNM-PM Z 40193. **4a–d.** Paratype 1, SNM-PM Z 40194. **5a–d.** Paratype 2, SNM-PM Z 40195. **6.** SNM-PM Z 40198. **7a–b.** Paratype 4, SNM-PM Z 40197.

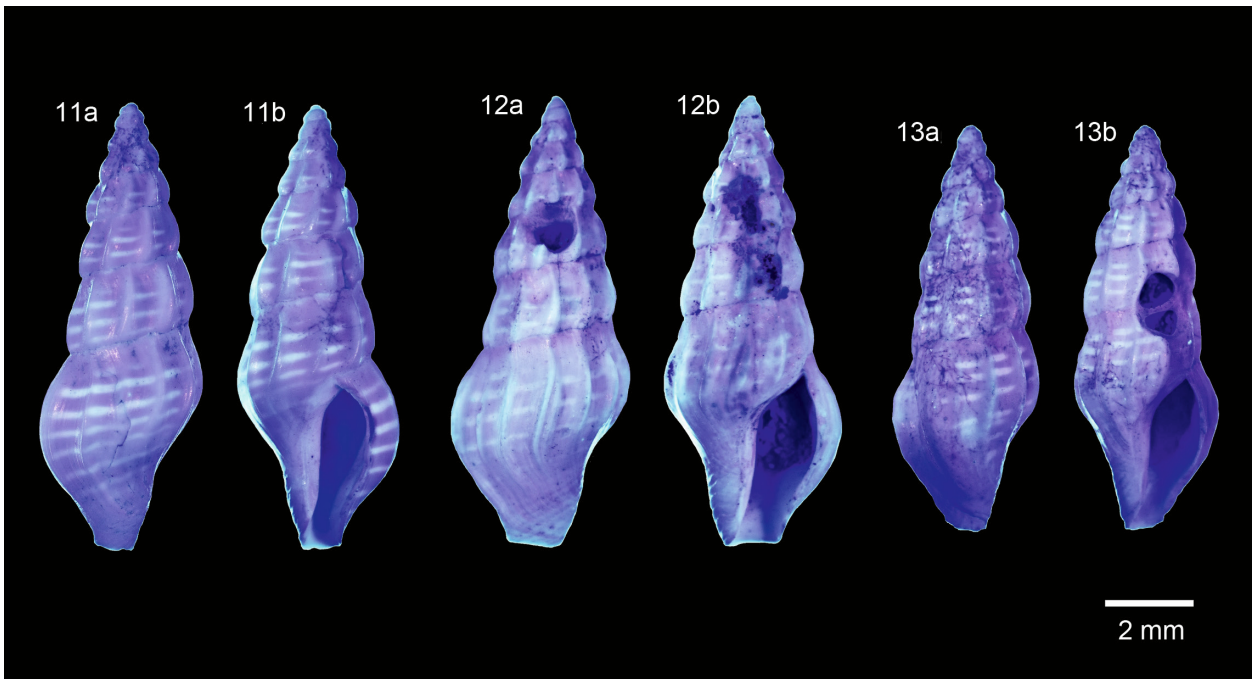
on dorsal side of the last whorl in fully grown individuals. Labial varix well developed in all shells, running from suture to base and positioned closely behind anal sinus, about 0.10 turn from outer lip. Dorsal varix rather rarely developed, extending from suture to shell base; its position variable, approximately 0.25–0.33 turn from outer lip. Hardly visible, very narrow growth lines and weak, narrow, fold-like striae decorate surface of last adult whorl in parallel to outer lip. Anal sinus rather poorly defined, simple, shallow, broad, and positioned in sutural ramp. Aperture lanceolate, oblong-oval,



Figures 8–10. *Nitidiclavus senesi* spec. nov., Rohožník-Konopiská (clay pit), upper Badenian (middle Miocene). **8–9.** Detail of protoconchs and the early teleoconch whorls. White arrows indicate protoconch-teleoconch transition. **8a–b.** Paratype 3, SNM-PM Z 40196; **9a–b.** Holotype, SNM-PM Z 40193. **10.** SEM images of protoconch and microsculpture. Holotype, SNM-PM Z 40193. **10a.** Protoconch. **10b.** Embryonic shell. **10c.** Detail of abapical belt in the larval shell. **10d.** Detail of granulate microsculpture in the embryonic shell.

narrowed abapically. Columellar lip straight and smooth; parietal callus lacking. Outer lip sharp, thin at the edge but thickened at back by a strong labial varix. Siphonal canal short to moderately long, well developed, bearing 7–9 delicate but clearly defined spiral cords; in cross-section spiral cords form very small, indistinctive pustules where they cross axial ribs.

Residual colour patterns, present on teleoconch whorls visible under UV light, composed of very clear, white, narrow spiral bands of relatively equal strength. Early teleoconch whorls initially with 2 spiral bands; penultimate whorl with 2–3 bands. Uppermost band on adapical half of whorl mostly weakly developed and hardly discernible or entirely absent. Last adult whorl ornamented with 4–7



Figures 11–13. *Nitidiclavus senesi* spec. nov., Rohožník-Konopiská (clay pit), upper Badenian (middle Miocene). Residual colour patterns in shells under UV light. **11a–b.** Holotype, SNM-PM Z 40193. **12a–b.** Paratype 1, SNM-PM Z 40194; **13a–b.** Paratype 2, SNM-PM Z 40195.

almost uniform bands; 2 bands, on adapical half of whorl, more clearly and better defined; other bands weaker and somewhat less pronounced. Uppermost and lowermost spiral bands usually faint and barely visible. On siphonal canal, colour pattern completely absent. Colour bands prevailingly continuous, or sometimes intermittent and developed only in interspaces between axial ribs.

Shell measurements. — SH (n = 3): μ = 9.39 mm (σ = 0.50 mm), SD (n = 5): μ = 3.52 mm (σ = 0.28 mm), SPH (n = 3): μ = 3.90 mm (σ = 0.23 mm), BWH (n = 5): μ = 5.49 mm (σ = 0.22 mm), AH (n = 5): μ = 3.66 mm (σ = 0.18 mm), PD (n = 4): μ = 0.787 mm (σ = 0.010 mm), PH (n = 4): μ = 0.728 mm (σ = 0.018 mm), PA (n = 7): μ = 25° (σ = 2°), AA (n = 4): μ = 47.75° (σ = 2.27°).

Remarks. — On the basis of morphological features as diagnosed by Bernasconi & Robba (1984), the new species is placed into the genus *Nitidiclavus*. However, in overall shell morphology, the new species is very similar to other conoidean genera, such as *Cerodrillia* Bartsch & Rehder, 1939, *Crassopleura* Monterosato, 1884, and *Haedropleura* Bucquoy, Dautzenberg & Dollfus, 1883. *Cerodrillia* does seem very similar to *Nitidiclavus*, mainly in its elongate-turreted shape, size, and ornamentation. Despite some similarities, the shells of *Cerodrillia* are characterized by their well-defined, deeply notched, mostly U-shaped anal sinus, and the protoconch has fewer whorls and its surface is smooth (Bernasconi & Robba, 1984; Scarponi & Della Bella, 2003; Fallon, 2016). The drilliid genus *Crassopleura* is also closely similar in overall shell morphology but differs from *Nitidiclavus* in its deeper, narrower, U-shaped anal sinus and in having opisthocline axial ribs; the protoconch morphology is also considerably different (Bernasconi & Robba, 1984; Scarponi & Della Bella, 2003). *Haedropleura* is placed in the family Horaiclavidae Bouchet, Kantor, Sysoev & Puillandre, 2011 and resembles the genus *Nitidiclavus*, whose representatives were previously often included within *Haedropleura* (e.g., Boettger, 1906; Rasmussen, 1956; Anderson, 1964; Strausz, 1966; Janssen, 1984; Bałuk, 2003). Species of *Haedropleura* are almost identical to *Nitidiclavus* but differ primarily in having a delicate sculpture of very fine spiral threads over the entire surface of the teleoconch; furthermore in *Haedropleura* the protoconch is completely smooth and lacks any microsculptural elements (Scarponi & Della Bella, 2003; Scarponi et al., 2011).

Nitidiclavus senesi spec. nov. is closely similar to two middle Miocene congenerous drilliids described from the Central Paratethys. *Nitidiclavus pseudosigmoidea* (Boettger, 1902), recorded from the Badenian clayey deposits of Romania, is similar to the new species in shell shape (cf. Zilch, 1934; Della Bella & Tabanelli, 1990). However, this Romanian congener is considerably smaller (cf. Boettger, 1902, 1906) than the new species, has rounder teleoconch whorls, a dome-shaped, markedly lower, depressed, and less prominent protoconch, and the protoconch whorls more convex-sided, broader; additionally, the second protoconch whorl is weak and apparently smaller. Furthermore, as reported by Bernasconi & Robba (1984), the protoconch diameter of *N. pseudosigmoidea* ranges from 900–1000

μm, whereas in the new species the maximum protoconch diameter attains about 800 μm. Bałuk (2003: pl. 15, figs 4–6) figured specimens from Korytnica, Poland identified as *Haedropleura pseudosigmoidea*, which appears very similar to *N. senesi* spec. nov., especially in its large size, tall and prolonged profile, number of teleoconch whorls, and markedly similarly shaped protoconch. The Polish specimens differ from the new speices in having a somewhat shorter and wider siphonal canal and fewer axial ribs (7–9). Moreover, no data are available on protoconch microsculpture and varices in the Korytnica specimens. *Nitidiclavus crystallina* (Boettger, 1906) is another allied Badenian species which has been recorded from Romania. It is reminiscent of *N. senesi* spec. nov. but is clearly distinguishable from it mainly by its shell profile and number of axial ribs (cf. Zilch, 1934; Della Bella & Tabanelli, 1990). Although shells are almost identical in size, the main difference is that the last adult whorl and siphonal canal are clearly shorter, the teleoconch whorls exhibit fewer axial ribs (7–8) and are a little more rounded, and interspaces between axial ribs are wider. The Pliocene Proto-Mediterranean *Nitidiclavus exiguus* (Della Bella & Tabanelli, 1990) resembles *N. senesi* spec. nov. primarily by its fusiform shape and sculptural elements on the teleoconch. The shells of this taxon differ primarily in their smaller size; fully grown adult specimens commonly reach about 5–6 mm long (e.g., Bernasconi & Robba, 1984; Chirli, 1997; Scarponi & Della Bella, 2003; Chirli & Richard, 2008), and the largest known specimen is 6.8 mm long, as noted by Della Bella & Tabanelli (1990). The shell shape of *N. exiguus* is moderately broader, and teleoconch whorls are more convex and fewer in number. In addition, the microsculpture on the larval shell is considerably different. The abapical belt near the abapical suture bears small, delicate granules, whereas *N. senesi* spec. nov. has the abapical belt composed of somewhat coarser sculpture defined by the oblique oriented, uneven, scrappy, short cords and elongated granules, and its upper margin is delimited by an irregular, chain-like cord. The new species is also closely similar to the middle Miocene *Nitidiclavus maitrejus* (Koenen, 1872) described from the North Sea Basin. Although both species are large and similarly elongate, *N. maitrejus* has little in common with *N. senesi* spec. nov. and is characterized by a taller and more elongated spire, somewhat shorter body whorl, weak and indistinct siphonal canal, and the axial ribs are more curved. Moreover, in the last adult whorl, the axial ribs are often become reduced, attenuated, and hardly developed, suggestive of the specimens figured by Janssen (1984), Della Bella & Tabanelli (1990), and Wienrich (2007). *Nitidiclavus oligocaenicus* Lozouet, 2017, reported from the upper Oligocene of the Aquitaine Basin in France, differs from *N. senesi* spec. nov. mainly in having a tall and slender spire and in its smaller size. As mentioned by Lozouet (2017), the largest shell reaches only 6.2 mm in length. This French drilliid is also easily distinguishable by its overall ornamentation: axial ribs are depressed and less prominent and in the last adult whorl are suppressed, weak, and hardly visible. In comparison to the practically smooth and lustrous body whorl of the new species, the last adult whorl of *N. oligocaenicus* bears very fine, almost barely visible spiral threads, and the siphonal canal shows slightly coarser, well-defined spiral cords.

DISCUSSION

Residual colour patterns in shells

In fossil shells of Cainozoic gastropods, traces of original colouration are recognised only in extraordinary cases (cf. Hörnes, 1851; Hoernes & Auinger, 1879, 1880; Fehse & Vicián, 2008; Kovács & Vicián, 2013; Kovács, 2018; Harzhauser & Landau, 2021a, 2021c). Some shells bear well-preserved residual patterns of original colouration that can only be observed by means of UV light (e.g., Caze et al., 2010, 2011; Landau et al., 2013; Harzhauser & Landau, 2016, 2021b; Pacaud & Vicián, 2018). These rare features are important characters for the differentiation and recognition of fossil gastropods. In Miocene conoidean fossil gastropods, colour patterns have been also seen, mainly in species belonging to the families Conidae, Borsoniidae, Mangeliidae, Pseudomelatomidae, Clavatulidae, and Terebridae (e.g., Bohn-Havas, 1973; Scarponi & Della Bella, 2010; Landau et al., 2013; Harzhauser & Landau, 2016).

Under UV light *Nitidiclavus senesi* spec. nov. shows conspicuous remnants of colouration and represents the first known evidence of pigmentation in fossil shells for the genus and also probably for the family Drilliidae. Teleoconch whorls are decorated with distinctive, pale, narrow spiral bands of a relatively equal width (Figs 11–13). The preserved remnants of pigmentation represent one of the important diagnostic features that characterize *N. senesi.*

For comparison, the present-day representatives of the family Drilliidae are variable in shell decoration, and their colour patterns consist of various bands, lines, spots, and irregular patches, or are uncoloured (Kilburn, 1988; Wells, 1995; Kilburn & Dekker, 2008; Kilburn et al., 2014; Fallon, 2016).

Paleoecology

Nitidiclavus Bernasconi & Robba, 1984 is an extinct gastropod genus, and, therefore, its preferred ecological conditions can only be interpreted from the fossil record based on the paleoecological reconstructions of the respective habitats in which it appeared. Paleoecology of the genus is poorly known and was briefly commented only by Scarponi & Della Bella (2003).

Specimens of *Nitidiclavus senesi* spec. nov. were found exclusively in basinal pelitic facies of the Studienka For-

mation at Konopiská, which points to this species' strong preference for a relatively deep-water habitat. As reported by Biskupič (2020), sedimentation took place in fully marine conditions, in moderately deep sublittoral settings (circalittoral zone) on a soft, muddy bottom affected by episodical hypoxic events and lowered water circulation near the sea-floor. In addition, the presence of some typical thermophilic gastropod genera such as *Schilderia*, *Mitrella*, *Tosapusia*, and *Splendrillia* suggest a warm-water marine setting. The multispiral protoconch of the species reflects its planktotrophic larval development.

Based on the subsequent evidence from other Cainozoic localities of Europe, *Nitidiclavus* was adapted to a variety of environments. According to Scarponi & Della Bella (2003), the Pliocene Proto-Mediterranean *Nitidiclavus exiguus* (Della Bella & Tabanelli, 1990) typically occupied deeper circalittoral to upper bathyal depths. Its occurrence in deep-water marine paleoenvironments was also reported by Moni (2006), Ceregato et al. (2007), and Tabanelli (2008). Preference for deep-water conditions was also confirmed by the occurrence of *N. pseudosigmoidea* and *N. crystallina* in offshore clays of the Făget Basin in Romania. At Coşteiu de Sus (= Kostej) and Lăpugiu de Sus (= Lapugy), Harzhauser et al. (2011) estimated the water depth to range around 300m. The middle to outer neritic environments and soft-bottom habitats of both localities were also proposed by Harzhauser & Landau (2019). However, in contrast, at the Badenian locality in Szob (Hungary) shallow-water conditions are assumed from the seagrass habitat in the infralittoral zone and the soft, sandy-muddy bottom (Dulai, 1996). Similar paleoecological settings is believed to have existed in Korytnica, Poland; a fine, clayey sea-floor overgrown with seagrasses in a relatively shallow sublittoral zone is thought to be the habitat of *Nitidiclavus* there (Bałuk & Radwański, 1977). Records of *Nitidiclavus maitrejus* (Koenen, 1872) from the middle Miocene deposits of the North Sea Basin were associated with soft, sandy-clayey and clayey sea bottoms, which may be regarded as its preferred habitat (Kautsky, 1925; Rasmussen, 1956, 1968). From a bathymetric point of view, *N. maitrejus* probably inhabited greater depths, which is also supported by Janse & Janssen (1983). According to them, at Stemerdink in the Netherlands, sedimentation took place in an open marine, relatively deep part of the shelf sea.

This overview points to the broad bathymetric ranges of the genus, with occurrence from infralittoral to bathyal depths in soft-bottom, sandy-clayey and clayey habitats, and with some tolerance to episodic lowered oxygen content near the sea-floor.

Distribution of *Nitidiclavus* in the Central Paratethys Sea

The geographic and stratigraphic distribution of the newly described species *Nitidiclavus senesi* spec. nov. is restricted to the upper Badenian Studienka Formation at of Rohožník-Konopiská. Its presence in the eastern part of the Vienna Basin represents the first records of the genus in the Miocene of Slovakia and also in the upper Badenian of the Central Paratethys.

The genus *Nitidiclavus* rarely occurs in the middle Miocene marine gastropod assemblages of the Central Paratethys and is traditionally represented by two species: *N. pseudosigmoidea* and *N. crystallina*. Since the beginning of the 20th century, their first fossil records are known from this territory, namely from the lower Badenian fossiliferous sites of Romania. From the marine clayey deposits at Coşteiu de Sus and Lăpugiu de Sus, both situated in the Făget Basin, Boettger (1902) originally described species *Drillia (Haedropleura) pseudosigmoidea*. Later, in 1906, he described *Haedropleura crystallina*, however, both without any illustrations, only descriptions were published. Boettger's extensive conchological type material from Romania including the above mentioned two new species was subsequently summarized and figured by Zilch (1934).

Other finds were recorded from the lower Badenian of Hungary and Poland. Csepreghy-Meznerics (1953) identified a single shell as *Haedropleura cristallina* from Szob (Börzsöny Mountains, Hungary), but later, the same specimen was treated as *Haedropleura septangularis pseudosigmoidea* by Strausz (1966). Bałuk (2003) reported *Haedropleura pseudosigmoidea* (Boettger, 1902) and *H. cristallina* Boettger, 1906 from the fossil-bearing clays at Korytnica (Korytnica Basin, Poland). Nevertheless, the affiliation of Bałuk's shells to the respective taxa is questionable and will need verification. The specimens recognised as *H. cristallina* bear a spiral sculpture composed of very delicate and thin but distinct spiral lines and grooves (see Bałuk 2003; pl. 15, figs 4–6) which are relevant morphological characters indicating affinity with the genus *Haedropleura*. Consequently, these shells are certainly not conspecific with those presented from Romania by Boettger (1906), Zilch (1934) and Bernasconi & Robba (1990) and belong to another taxon. Also, the specimens treated as *H. pseudosigmoidea* have a different, slightly conical shaped protoconch and the shells are much larger (Bałuk 2003; pl. 15, figs 7–9) than material studied by Boettger (1902), Zilch (1934), and Bernasconi & Robba (1990). These shells are similar to the new species from Rohožník, but probably represent another species of *Nitidiclavus*. Furthermore, the protoconch morphology of both species from Poland was not studied and important specific characters were probably overlooked. For that reason, the fossil material from Poland and also from Hungary will need revision.

As outlined in this short synopsis, *Nitidiclavus* species were obtained only at a few localities in the Paratethyan region and there only in rather low abundance. It is obvious that the stratigraphic distribution of the genus in the Central Paratethys was strictly delimited to the Badenian (= Langhian

to lower Serravallian), which is characterized by an extensive increase of species richness of marine molluscan faunas.

CONCLUSION

A new species of conoidean gastropod of the family Drilliidae, *Nitidiclavus senesi* spec. nov. is described from the middle Miocene (Serravallian) of the Central Paratethys. Fossil shells were recovered from the marine clayey deposits of the upper Badenian Studienka Formation that were revealed at the paleontological site of Rohožník-Konopiská in the Slovak part of the Vienna Basin. The presence of *N. senesi* spec. nov. at Rohožník represents the first records of the genus in the upper Badenian of the Central Paratethys.

Extraordinary preservation of residual colour patterns in shells of *N. senesi* spec. nov. are first evidence of these rare feature for the genus. The occurrence of this species in the grey calcareous clays with bioturbation, suggest that this drilliid was adapted to the moderately deep sublittoral settings with a preference for soft muddy substrate and occasional low bottom water oxygenation, and normal salinity and warm-water conditions are assumed. The early ontogenic stages of this species are characterized by a long-term planktotrophic larval phase, which is demonstrated by its multispiral protoconch.

The temporal and spatial distribution of *Nitidiclavus* was limited in the North-East Atlantic region from Oligocene to Miocene, persisted in the Proto-Mediterranean until the Pliocene, but was restricted in the Central Paratethys to the Badenian (middle Miocene). The genus *Nitidiclavus* can be regarded as a strictly European taxon, based on its geographical distribution as sketched in this study. Generally, from a paleoecological point of view, *Nitidiclavus* appears to have been well adapted to a broad bathymetric range and occurred from infralittoral to bathyal depths in the soft seabottom, sometimes with some tolerance to episodic lowered oxygen content near the sea-floor.

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