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# Fossil turtles of Slovakia: New material and a review of the previous record

Igor G. Danilov<sup>1</sup>, Andrej Čerňanský<sup>2,3,\*</sup>, Elena V. Syromyatnikova<sup>1</sup>, Peter Joniak<sup>4</sup>

**Abstract.** This paper presents the first review of the fauna of fossil turtles of Slovakia. It is focused on the turtle assemblages from 11 localities (Sandberg Hill, Waitov Lom, Borský Svätý Jur, Kamenica nad Hronom, Ivanovce, Hajnáčka, Žiar nad Hronom, Bojnice, Dreveník, Gánovce, and Levice) dated from the Middle Miocene to the Pleistocene. In addition, we describe new turtle material from the Hajnáčka and Sandberg Hill localities and, for the first time, from the Borský Svätý Jur locality. This new data expands our knowledge of the composition of the fossil turtle fauna of Slovakia and the morphology of its representatives. It also enables a more detailed comparison of this fauna with the contemporaneous turtle faunas of Central and Eastern Europe.

**Keywords:** Europe, fossil turtles, Neogene, Slovakia.

## Introduction

This article deals with the fossil turtles of Slovakia. It represents a contribution to the knowledge of the Slovak fossil reptile fauna and obliquely refers to the paper of Čerňanský (2011) on the fossil squamate fauna from this area. Fossil turtles of Slovakia have been studied for over 150 years. Although this material is only from the Neogene and Pleistocene and is not rich and mainly fragmentary, it contains some taxonomically important specimens and it is extremely important for correlation of Neogene vertebrate assemblages of Central and Eastern Europe. This paper presents the first review of the fauna of fossil turtles of Slovakia which contains data on turtle assemblages from

11 localities dated from the Middle Miocene to the Pleistocene, as highlighted (see fig. 1 and appendix). In addition, we describe new turtle material from Hajnáčka and Sandberg Hill localities and, for the first time, from the Borský Svätý Jur locality. The aims of this paper are: 1) to provide detailed descriptions of the new Slovak turtle material, 2) revise previously described material, 3) to compare this fauna with contemporaneous Central and Eastern European turtle faunas in greater detail.

## History of the study of fossil turtles of Slovakia

The first fossil turtle described on Slovakian territory was *Psephophorus polygonus* Meyer, 1847 (type of the genus *Psephophorus* Meyer, 1847) from Neudorf an der March, which is now Devinská Nová Ves locality of Sandberg Hill (Badenian, Middle Miocene-Badenian). This was initially considered an undetermined animal (von Meyer, 1846, 1847) and it was only later recognized as a turtle closely related to *Sphargis* Merrem, 1820 (now *Dermochelys* Blainville, 1816, *Dermochelyidae* Fitzinger, 1843; Seeley, 1880; see the latter publication for the early history of study of *P. polygonus* and Kuhn [1964] for other references on this species). When von Meyer first gave a name to this genus (1846, p. 472), he first recog-

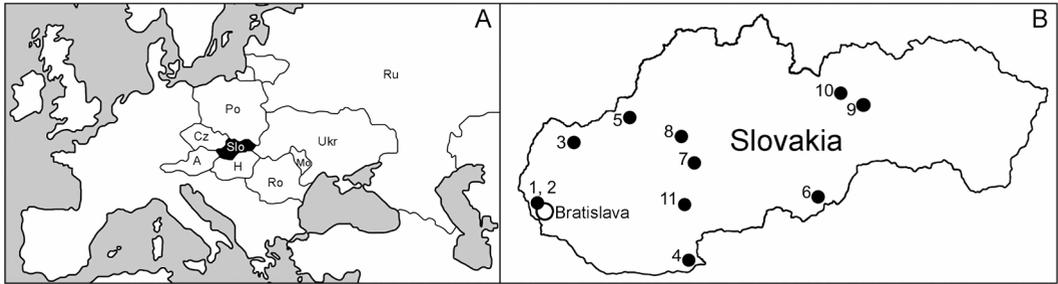
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**Figure 1.** Geographic position of localities of fossil turtles of Slovakia. (A) map of Europe with Slovakia filled with black; (B) map of Slovakia showing localities of fossil turtles: 1, Sandberg Hill; 2, Waitov Lom; 3, Borský Svätý Jur; 4, Kamenica nad Hronom; 5, Ivanovce; 6, Hajnáčka; 7, Žiar nad Hronom; 8, Bojnice; 9, Dreveník; 10, Gánovce; 11, Levice (see text for details).

nized it only by its isolated dermal plates, but subsequently a drawing was sent to him by Partsch, and based on that he made a further note in the 'Jahrbuch' for 1847 (p. 579). Soon after the description of *P. polygonus*, Hörnes (1848) reported findings of *P. polygonus*, *Trionyx* sp. and Testudinata gen. et sp. indet. in the same locality of Sandberg Hill. Kormos (1915) mentioned *Testudo* sp. from Hajnáčka (= Ajnácskö; Late Pliocene), and Szalai (1934) described and figured its partial plastron and correctly assigned it to *Emys orbicularis* (Linnaeus, 1758). The same year, Štěpánek (1934) described an internal core of the shell of *E. orbicularis* from the Pleistocene of Gánovce. Four years later, Petrbok (1938) mentioned a find of *Emys orbicularis* from the Pleistocene of Levice. Khosatzky (1956) assigned the material from Hajnáčka to *Emys orbicularis antiqua* Khosatzky, 1956, a subspecies described by him from the Pliocene of European Russia. Zázvorka (1957) described one neural similar to those of the genus *Testudo* Linnaeus, 1758 from Kamenica nad Hronom (Tortonian?; Late Miocene), and Skutil (1960) reported a finding of *E. orbicularis* from Bojnice (Pleistocene?; Fritz, 1995). Młynarski (1963) described fragmentary turtle remains from the localities of Hajnáčka (*Chelydra* aff. *decheni* and *Emys orbicularis*) and Ivanovce (*E. orbicularis*, Emydidae gen. et sp. indet. and ?Chelydridae gen. et sp. indet.), although only *Chelydra* aff. *decheni* and part of the Hajnáčka *Emys orbicularis* mate-

rial were figured in this paper. Later, Młynarski (1964) described a new species (*Geoemyda mossocznyi* Młynarski, 1964) from the lower Pliocene of Poland and also mentioned a form close to this species from Hajnáčka. Two shell fragments from this form were attributed to *Geoemyda* aff. *mossocznyi*, briefly described and partly figured by Młynarski (1966) in his study of fossil turtles from Hungarian collections, together with shell fragments of *Trionyx* sp. and *P. polygonus* from Sandberg Hill. Khosatzky and Młynarski (1966) in their review of the fossil *Geoemyda* Gray, 1834 (s. lat.) of Europe, mentioned *G.* cf. *mossocznyi* from Hajnáčka and ?*Geoemyda* sp. from Ivanovce. In the paper devoted to the review of Pliocene-Pleistocene turtles of Central Europe, Młynarski (1968) figured the carapace of *E. orbicularis* from Hajnáčka, which had been earlier described by Młynarski (1963). Ciesarik (1970) described remains of *E. orbicularis* from Žiar nad Hronom (Pliocene?, the exact age is unknown and may be even older; Fritz, 1995). The fossil record of the European *E. orbicularis*, including those from Slovakian localities, was reviewed by Ullrich and Młynarski (1978). Młynarski (1980) published a review of Neogene turtles of Central and Eastern Europe, where Slovakia was mentioned in the distribution of *Chelydropsis* (originally *Macrocephalochelys*) *pontica* (Pidoplichko and Tarashchuk, 1960), which is a chelydrid species primarily described from the Pliocene of Ukraine (Pidoplichko and

Tarashchuk, 1960). Contrary to this opinion, Chkhikvadze (1982, 1983) referred *Chelydra* aff. *decheni* from Hajnáčka, along with other chelydrid material from the Pliocene of Europe to *Chelydropsis* (orig. *Trionyx*) *nopcsai* (Szalai, 1934). This classification was utilized by Hutchison (2008) in his review of the chelydrid record. Krempaská (1993) described remains of *Emys orbicularis* from the travertine of Dreveník (Early Pleistocene), while Fritz (1995) reviewed the fossil record of *Emys* Duméril, 1806, including those from Slovakia, and suggested that post-Villafranchian records of *E. orbicularis* should be considered *E. orbicularis* sensu lato. Wood et al. (1996, their fig. 16) figured the “surviving portion” of a type of *P. polygonus*, and after discussing details of the morphology of this species, he included it in the phylogenetic analysis of dermochelyid turtles. Pipík and Holec (1998) mentioned, but failed to describe some turtle material (similar to Emydinae and ?*Geoemyda*) from Borský Svätý Jur (early Pannonian, Late Miocene). Holec and Schlögl (2000) described part of a carapace of a trionychid attributed to *Trionyx rostratus* Arthaber, 1898 from Sandberg Hill, a species initially described from the Middle Miocene of Austria (Arthaber, 1898; Karl, 1998). Holec (2006) described additional trionychid specimens of *Trionyx* sp. from Sandberg Hill and from Waitov Lom (Badenian). Finally, Delfino et al. (2012) reported new data about ossicle gross morphology and microstructure of *Psephophorus polygonus* based on type material.

## Material and methods

This study is based on turtle shell fragments and a humeral bone from several Neogene Slovak localities. Material from Sandberg and Borský Svätý Jur is housed in the collection of the Slovak National Museum in Bratislava, with the fossils prefixed by the acronym Z and the collection number following, while Hajnáčka material is housed in the collection of the Gemer-Malohont Museum, Rimavská Sobota. Here, the fossils are prefixed by the acronym B, followed by a collection number. These comprise the isolated elements collected by screen-washing or surface prospecting. All material was photographed using a Nikon D90 camera, and the

standard anatomical orientation system is used throughout this paper.

## Results

### Family Trionychidae Gray, 1825

#### Genus *Trionyx* Geoffroy, 1809 sensu lato (sensu Lapparent de Broin, 2001)

#### *Trionyx* sp. (fig. 2)

#### Material and locality

Z 15177, an almost complete costal 4 or 5; Z 26831, the left humeral bone; Sandberg Hill.

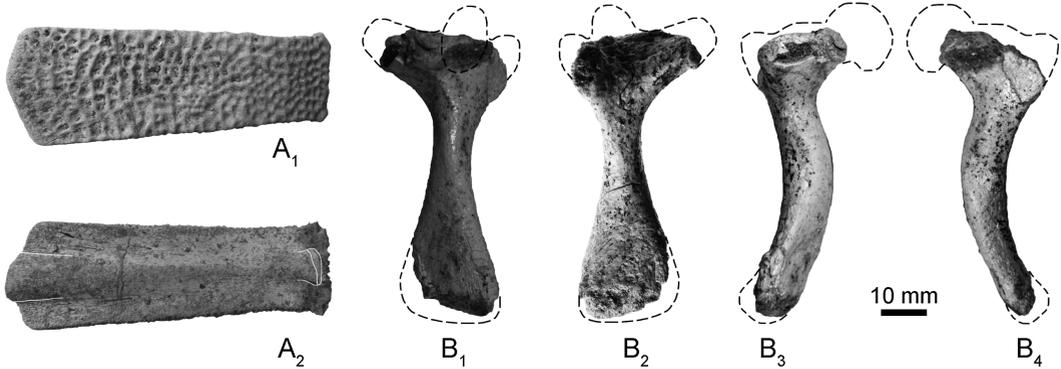
#### Description

The complete costal belongs to a turtle with an estimated shell length of approximately 20 cm. The costal is wider laterally than medially, with the lateral border angled. The free tip of the rib is broken off. The medial border of the costal is divided into three parts (short anterior, long central and short posterior), which correspond to contacts with three successive neurals, and such contacts are usually present in the middle (4 or 5) or posterior costals (Meylan, 1987). The costal sculpturing consists of small circular or polygonal pits, surrounded by ridges.

The humerus is devoid of the head and most parts of the lateral and medial processes, and the distal epiphysis is damaged. Despite poor preservation, the reconstructed outline of the bone is comparable with those of *Trionyx rostratus* (Arthaber, 1898, Taf. XXVIII, Abb. 16).

#### Discussion

The specimens described above closely correspond in size and morphology with other trionychid material from Sandberg Hill. These and previously described trionychid specimens from Sandberg Hill (Hörnes, 1848; Holec and Schlögl, 2000; Holec, 2006) are assigned to *Trionyx* sensu lato (sensu Lapparent de Broin, 2001) based on their similarities with *Trionyx* sensu stricto (and *Trionychina* sensu Meylan, 1987) in the following shell characteristics: the



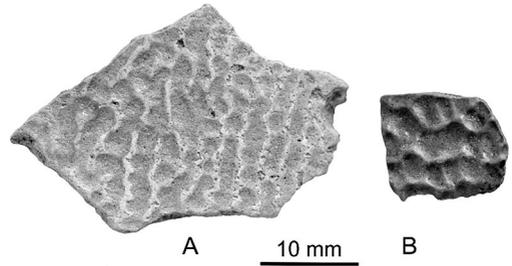
**Figure 2.** Shell fragments of *Trionyx* sp. from Sandberg Hill: (A) Z 15177, costal 4 or 5 in dorsal (A<sub>1</sub>) and ventral (A<sub>2</sub>) views; (B) Z 26831, left humerus in dorsal (B<sub>1</sub>), ventral (B<sub>2</sub>), lateral (B<sub>3</sub>) and medial (B<sub>4</sub>) views.

neural series contains one reversal of neural orientation; the presence of seven neurals and primitive retention of complete costals 8, see Meylan, (1987); and it is also based on their age and provenance (Lapparent de Broin, 2001). The attribution of the partial carapace from Sandberg Hill to *Trionyx rostratus* by Holec and Schlögl (2000) was based on similarity “in shape and size”. However, shell and size differences place doubt on this attribution. This specimen differs from *Trionyx rostratus* in the following shell characteristics: neural 1 is not widened anteriorly; neurals 4 and 5 are asymmetrically pentagonal, costal 8’s are wider than long; and the sculpturing consists of rounded pits rather than ridges and grooves. There is also size difference, where the carapace length is estimated at approximately 150 mm in the Sandberg specimen and 240 mm in *T. rostratus*. It is noteworthy that the systematic position of *T. rostratus* is not resolved, because Karl (1998) synonymised it with the living species *Amyda cartilaginea* Boddaert, 1770, whereas Lapparent de Broin (2001; pers. comm. to IGD, 2011) considered it to represent *Trionyx sensu lato*.

### Trionychidae indet. (fig. 3)

#### Material and locality

Z 27428/1a and Z 27428/1b, two undetermined shell fragments; Borský Svätý Jur.



**Figure 3.** Undetermined shell fragments of *Trionychidae* indet. from Borský Svätý Jur in external view: (A) Z 27428/1a; (B) Z 27428/1b.

#### Description and discussion

Fragments differ in the sculpturing, with smaller pits and lower ridges in Z 27428/1a, perhaps as a result of weathering, and larger pits and more pronounced ridges in Z 27428/1b. These differences may be a result of variation within the shell and/or variation in size of the individuals. The available character of the material allows determination only to the family level, although all fossil trionychids from the Neogene of Europe are referred to as *Trionyx sensu lato* and *Trionychinae indet.* (Lapparent de Broin, 2001).

### Family Testudinidae Batsch, 1788

#### Genus *Testudo* Linnaeus, 1758 sensu lato *Testudo csakvarensis* Szalai, 1934 (fig. 4)

#### Material and locality

Z 27429/a-b, nuchals; Z 27429/c-g, neurals; Z 27429/h, suprapygals 2; Z 27429/i, a pygal;

Z 27429/j-k, fragments of undetermined costals; Z 27429/l, the left peripheral 2; Z 27429/m, the left peripheral 7; Z 27429/n, a right peripheral 9 or 10; Z 27429/o, a partial right epiplastron; Z 27429/p-s, entoplastra; Z 27429/t, partial hyoplastra; Z 27429/u, the left xiphiplastron; Borský Svätý Jur.

### Description

The larger nuchal (Z 27429/a) is more elongated and narrowed anteriorly than the smaller one (Z 27429/b). The medial notch of the anterior border is present in the larger nuchal but not preserved on the smaller one. The cervical scale is absent on the dorsal and ventral surfaces of the nuchal in both specimens. The smaller nuchal has very small overlapping by pleurals 1 at the lateral corners, whereas the larger one lacks this.

The neurals are presented in five elements: an asymmetrical tetragonal neural 1 (Z 27429/c); an octagonal neural 2 (Z 27429/d), a tetragonal neural 3 (Z 27429/e); two hexagonal neurals (Z 27429/f-g) with shorter anterior sides from the posterior portion of the neural series. All neurals, except Z 27429/d, are crossed by intercentral sulci.

The suprapygal 2 (Z 27429/h) is lens-shaped with strongly convex anterior and slightly convex posterior borders. The sulcus between vertebral 5 and the supra-caudal scute crosses suprapygal 2 exactly parallel and very close to the posterior border of the plate.

The pygal (Z 27429/i) is a narrow trapezoid, wider anteriorly than posteriorly. The pygal is almost straight in lateral view, suggesting that it belongs to a female. The inter-marginal sulcus (between marginals 12) is absent both on the dorsal and ventral surfaces of the pygal.

Costals are represented by two lateral fragments of even plates, two medial fragments of odd plates and a number of undetermined costal fragments. The lateral fragments of the even costal (Z 27429/j) are widened laterally with an interpleural sulcus situated closer to the posterior border of the plate. Externally, the costals

bear growth lines parallel to their lateral borders. The proximal fragments of two odd costals (Z 27429/k) are narrowed laterally.

Peripheral 2 (Z 27429/l) is characterized by the overlapping of pleural 1 on to its dorsal surface.

Peripheral 7 (Z 27429/m) is very high and narrow in lateral view. Posteriorly, on its internal surface, there is an oblique sutural groove for attachment to the inguinal buttress. This groove crosses the posterior border of peripheral 7 at the centre of its height, indicating that the buttress also contacted peripheral 8.

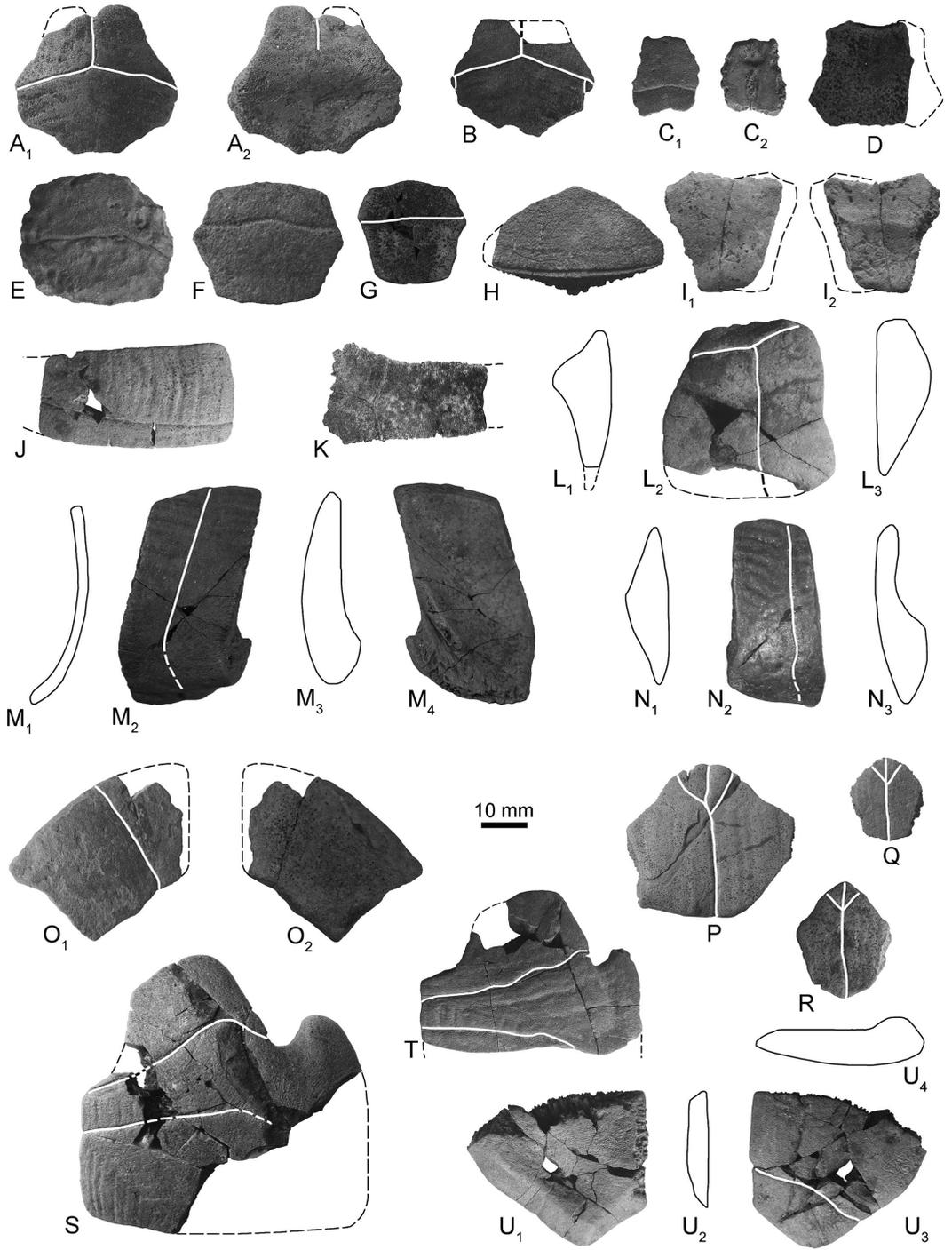
Peripheral 9 or 10 (Z 27429/n) is also high and narrow; its free edge is not upturned.

The epiplastron (Z 27429/o) is poorly preserved, lacking its medial portion, and with a damaged dorsal surface. Based on the preserved part, the gular projection was weak. The gulo-humeral sulcus crosses the entoplastral border of the plate. Part of this sulcus is also visible on the dorsal surface of the epiplastron.

The entoplastra are represented by three elements of different size. Two smaller elements (Z 27429/r-s) are hexagonal and longer than wide. The bigger specimen (Z 27429/p) is almost pentagonal and wider than long. All entoplastra demonstrate strong overlapping by gular scales, but are not crossed with humero-pectoral sulci. However, this type of crossing was noted in some *T. csakvarensis* specimens (Chkhikvadze, 1983, his fig. 67).

The hyoplastra are incomplete. They supported pectoral scales, which are long laterally and more than twice as short medially. In Z 27429/t, the pectoral comes very close to the entoplastral notch, whereas in Z 27429/u it is more distant. Similar variation in shape and position of pectoral is recognized in *T. csakvarensis* (Chkhikvadze, 1983, his figs 63 and 64).

The xiphiplastron (Z 27429/v) is complete; it is wider than long and relatively shorter than the xiphiplastron of *T. csakvarensis* figured by Chkhikvadze (1983, his fig. 66). This suggests that it belongs to a male. The anterior border of the xiphiplastron is slightly convex and with a



normal suture, implying the absence of a hypoxiphiplastral hinge. The anal scale covers almost the entire posterior third of the xiphiplastron. The femoro-anal sulcus is parallel to the posterior border of the plate, which participated in the formation a wide and angled anal notch.

### Discussion

The described material is assigned to *Testudo csakvarensis* on the basis of both the morphology of the nuchal (in proportions and the absence of the cervical scute), and also on the morphological congruency of the remaining shell parts. The morphology and variation in the described nuchals generally correspond with the material published as *T. csakvarensis* (Chkhikvadze, 1983, his figs 61a, 62a), although the cervical may be preserved on the internal surface of the nuchal in some specimens of this species (Młynarski, 1966, Abb. 11). This species was previously recorded from the Late Miocene (Sarmatian) of Hungary and Moldavia (Szalai, 1934; Młynarski, 1966; Chkhikvadze and Lungu, 1973; Chkhikvadze, 1983; Khosatzky and Redkozubov, 1989). Despite these numerous records, the known morphology of this species is restricted to the nuchal and the plastron, and this presents a problem for accurate generic attribution of *T. csakvarensis*. Some authors (Chkhikvadze and Lungu, 1973; Chkhikvadze, 1983; Khosatzky and Redkozubov, 1989; Böhme and Ilg, 2008) place it in the genus *Protestudo* Chkhikvadze, 1970 (type species: *T. bessarabica* Riabinin, 1935 from the Late Miocene [Meotic] of Moldavia and Ukraine).

According to Chkhikvadze (1973), this classification unites numerous species from the Neogene and Pleistocene of Eurasia, including the living *Testudo hermanni* Gmelin, 1789. By contrast, Lapparent de Broin et al. (2006, p. 345, 353) considered that *T. csakvarensis* is “incertae sedis probably *Eurotestudo* lineage”. However, the genus *Eurotestudo* Lapparent de Broin et al., 2006, based on *T. hermanni* as type species, is nomenclaturally an objective junior synonym of *Chersine* Merrem, 1820 (Fritz and Bininda-Emonds, 2007; Fritz and Kraus, 2008) and considered as taxonomically invalid by some authors (Fritz and Bininda-Emonds, 2007; Fritz and Kraus, 2008; Delfino et al., 2012). According to Lapparent de Broin et al. (2006), “*Eurotestudo*” (i.e. *Chersine*) also includes *T. pyrenaica* and allied taxa, which are characterized by a cervical scale on the dorsal and ventral surfaces of the nuchal. It is suggested that the following species are also allied with *T. pyrenaica*: *T. amberiacensis* Deperet, 1994 (MN 10-12, Late Miocene, France), *T. burgenlandica* Bachmayer and Młynarski, 1983 (Turolian, Late Miocene, Austria), *T. pyrenaica* Deperet and Donnezan, 1890 (MN 15, Pliocene, France) and *Testudo* sp. of Bachmayer and Młynarski (1983) from the Late Miocene of Austria (Lapparent de Broin et al., 2006). Meanwhile, Delfino and Göhlich (2009) reported variations in the presence and absence of the cervical in *T. burgenlandica*, and similar variation is reported in *T. csakvarensis*, as noted in the Description herein. For this reason, we propose that *T. csakvarensis* also belongs to the *T. pyrenaica* group.

**Figure 4.** Shell fragments of *Testudo csakvarensis* from Borský Svätý Jur: (A) Z 27429/a, nuchal in dorsal (A<sub>1</sub>) and ventral (A<sub>2</sub>) views; (B) Z 27429/b, nuchal in dorsal view; (C) Z 27429/c, neural 1 in dorsal (C<sub>1</sub>) and ventral (C<sub>2</sub>) views; (D) Z 27429/d, neural 2 in dorsal view; (E) Z 27429/e, neural 3 in dorsal view; (F, G) Z 27429/f-g, posterior neurals in dorsal view; (H) Z 27429/h, suprapygals 2 in dorsal view; (I) Z 27429/i, a pygal in dorsal (I<sub>1</sub>) and ventral (I<sub>2</sub>) views; (J) Z 27429/j, lateral fragment of the right even costal in dorsal view; (K) Z 27429/k, medial fragment of the right odd costal in dorsal view; (L) Z 27429/l, left peripheral 2 in dorsal view (L<sub>2</sub>) and its cross sections at anterior (L<sub>1</sub>) and posterior (L<sub>3</sub>) borders; (M) Z 27429/m, left peripheral in external (M<sub>2</sub>) and internal (M<sub>4</sub>) views and its cross sections at anterior (M<sub>1</sub>) and posterior (M<sub>3</sub>) borders; (N) Z 27429/n, peripheral 9 or 10 in external view (N<sub>2</sub>) and its cross sections at anterior (N<sub>1</sub>) and posterior (N<sub>3</sub>) borders; (O) Z 27429/o, right epiplastron in ventral (O<sub>1</sub>) and dorsal (O<sub>2</sub>) views; (P-R) Z 27429/p-s, entoplastra in ventral view; (S, T) Z 27429/t-u, partial left hyoplastra in ventral view; (U) Z 27429/v, left xiphiplastron in dorsal (U<sub>1</sub>) and ventral (U<sub>3</sub>) views and its cross sections at medial (U<sub>2</sub>) and anterior (U<sub>4</sub>) borders. A-K, L<sub>2</sub>, M<sub>2</sub>, 4, N<sub>2</sub>, and O-U<sub>1, 3</sub>: photographs; L<sub>1, 3</sub>, M<sub>1, 3</sub>, N<sub>1, 3</sub>, U<sub>2</sub>, and U<sub>4</sub>: drawings.

**Family Geoemydidae Theobald, 1868**  
**Geoemydidae indet. (fig. 5)**

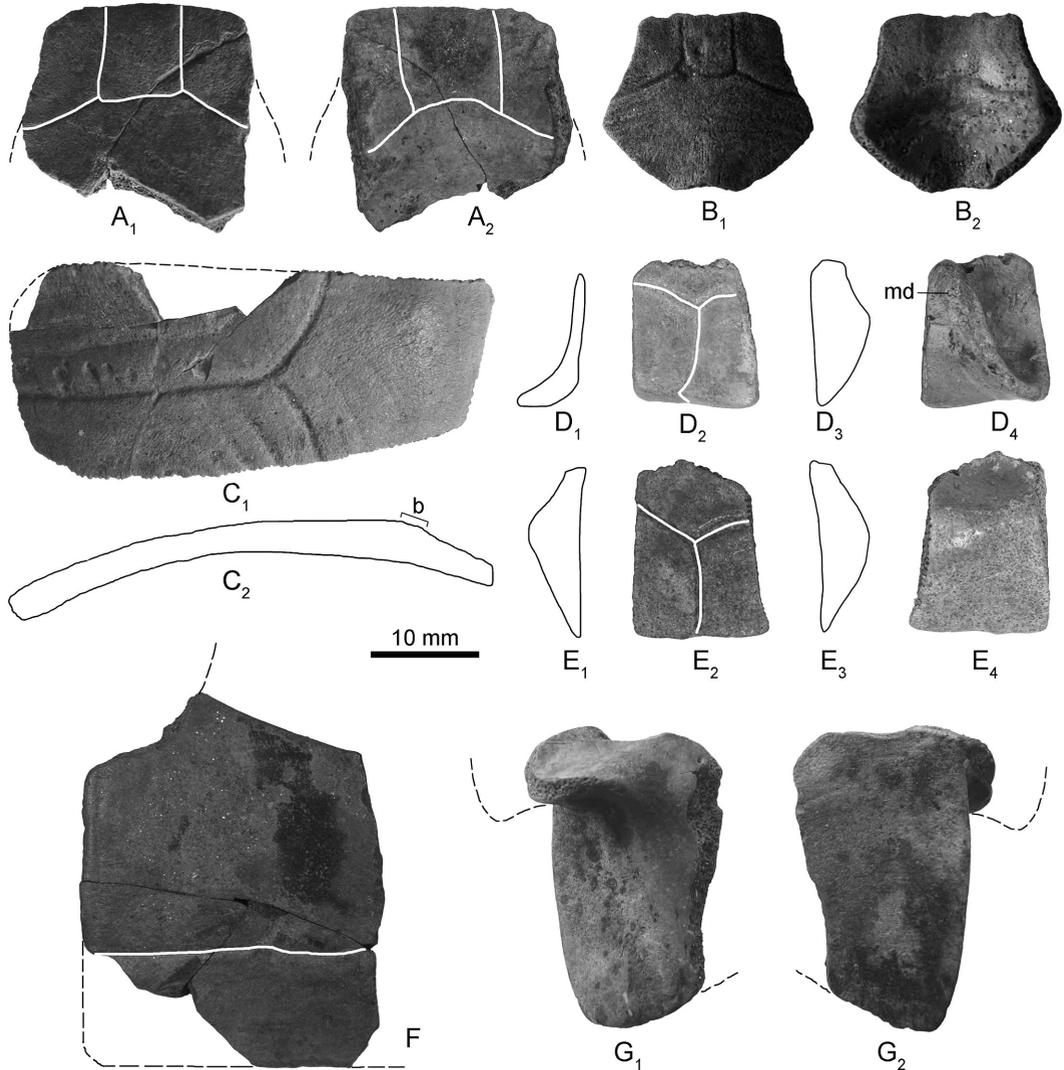
*Material and locality*

Z 27428/2b, complete nuchal; Z 27428/2a, a nuchal fragment; Z 27428/2c, left even costal (2 or 4); Z 27428/2d, left peripheral 7; Z 27428/2e, left peripheral 9; Z 27428/2f, a partial left hy-

oplastron; Z 27428/2g, a partial left hypoplastron; Borský Svätý Jur.

*Description*

Based on all available specimens, the estimated shell length of this form is up to 15 cm.



**Figure 5.** Shell fragments of *Geoemydidae* indet. from Borský Svätý Jur: (A) Z 27428/2a, nuchal fragment in dorsal (A<sub>1</sub>) and ventral (A<sub>2</sub>) views; (B) Z 27428/2b, complete nuchal in dorsal (B<sub>1</sub>) and ventral (B<sub>2</sub>) views; (C) Z 27428/2c, left even costal (2 or 4) in dorsal (C<sub>1</sub>) view and its cross section at the level of the bulge (C<sub>2</sub>); (D) Z 27428/2d, left peripheral 7 in dorsal (D<sub>2</sub>) and ventral (D<sub>4</sub>) views and its cross sections at anterior (D<sub>1</sub>) and posterior (D<sub>3</sub>) borders; (E) Z 27428/2e, left peripheral 9 in dorsal (E<sub>2</sub>) and ventral (E<sub>4</sub>) views and its cross sections at anterior (E<sub>1</sub>) and posterior (E<sub>3</sub>) borders; (F) Z 27428/2f, partial left hypoplastron in ventral view; (G) Z 27428/2g, a partial left hypoplastron in dorsal (G<sub>1</sub>) and ventral (G<sub>2</sub>) views. A-C<sub>1</sub>, D<sub>2,4</sub>, E<sub>2,4</sub>, F, and G: photographs; C<sub>2</sub>, D<sub>1,3</sub>, and E<sub>1,3</sub>: drawings. Abbreviations: b, bulge; md, musk duct.

The complete nuchal (Z 27428/2b) is hexagonal and with a straight anterior border. The ratio of the nuchal's anterior width to its maximum width is 0.67. The cervical is tetragonal, comprising approximately one third of the anterior width of the nuchal and one third of its length. There is no overlapping of the nuchal by pleurals 1, but there are growth lines visible on it in the vertebral 1 area.

The nuchal fragment (Z 27428/2a) is represented by the anterior portion from a larger individual than Z 27428/2b.

The even costal (Z 27428/2c) is widened laterally; its medial edge is divided into a short antero-lateral border and a long postero-lateral one. This morphology suggests contact with two neurals, which are hexagonal and short-sided posteriorly when the costal is correctly orientated. In the medial part of the costal close to its anterior border, there is a small bulge, indicating the presence of interrupted lateral keels on the carapace. The vertebral scale occupies more than 1/3 of the costal width. The inter-pleural sulcus is parallel and closer to the posterior border of the plate, and there are traces of growth lines in the vertebral and pleural scales.

Peripheral 7 (Z 27428/2d) is penetrated by a musk duct, typical for geoemydids. The pleuro-marginal sulcus is rather close to the medial border of the plate. Peripheral 9 (Z 27428/2e) has a divided and angled medial border for contact with costals 6 and 7. The pleuro-marginal sulcus is more distant from the medial border of the plate than it is in peripheral 7.

The hyoplastron (Z 27428/2f) has no anterior, lateral and part of the posterior portions. The preserved part of its entoplastral border is not crossed by the humero-pectoral sulcus, suggesting that this sulcus is situated more anteriorly. The pectoro-abdominal sulcus is straight and distant from the posterior border of the plate for about 1/3 of its medial length.

The hypoplastron (Z 27428/2g) is represented by its postero-lateral portion. Its free lateral border is slightly convex while the posterior border faces postero-medially. The position

of the abdomino-femoral sulcus is unclear, but it was most likely located more anteriorly. The base of a rather weak inguinal buttress is visible on the dorsal surface of the hypoplastron, together with strong overlapping of the femoral scale on the plate's dorsal surface.

### Discussion

This material is assigned to Geoemydidae based on the presence of the musk duct foramina on peripheral 7 (geoemydid synapomorphy; Hirayama, 1985; Yasukawa et al., 2001). This is supported by the general correspondence of the other elements to the morphology of this group. The bulge on the costal indicates the presence of lateral keels on the carapace, which are characteristic of some European members of the *Palaeochelys* sensu lato-*Mauremys* group (Hervet, 2004b). The far anterior position of the humero-pectoral sulcus on the hyoplastron is characteristic of some advanced members of this group, including *Mauremys* Gray, 1869, and also to genera *Sakya* Bogachev, 1960 and *Sarmatemys* Chkhikvadze, 1983 which may belong to the same group, but are sometimes placed in *Sakyini* Chkhikvadze, 1968 (see Danilov, 2005). The morphology of the nuchal, combining absence of the nuchal emargination with the shape of the cervical, is reminiscent of *Sakya*, *Sarmatemys* and *Clemmydopsis* Boda, 1927 (the latter genus is placed either in *Ptychogasterini* De Stefano, 1917 or in *Sakyini*; Hervet, 2004a; Danilov, 2005), whereas *Mauremys* usually has the nuchal emargination and a relatively smaller and trapezoid cervical. However, the correctly recognized relatively narrow vertebral scales allow the exclusion of all forms with wide vertebrals, such as *Clemmydopsis*, *Sakya* and *Sarmatemys*. The hexagonal and posteriorly short-sided located neurals can be present as a variation in some *Mauremys* (McDowell, 1964; Hervet, 2004b). We cannot exclude the possibility that the described material belongs to more than one geoemydid taxon, and this somewhat contradictory evidence enables determination of this material only at the family level.

**Family Chelydridae Swainson, 1839**

**Genus *Chelydropsis* Peters, 1868**

***Chelydropsis* sp. (fig. 6A)**

*Material and locality*

B-4106, a left peripheral 8; Hajnáčka.

*Description*

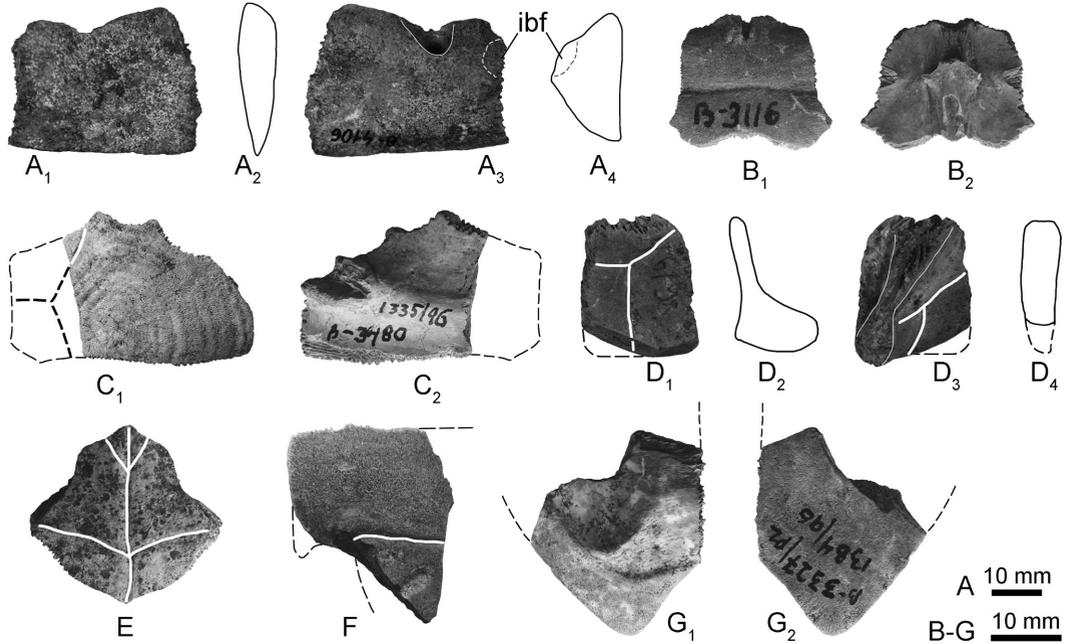
The peripheral lateral border is 3.9 mm in length, and it is longer than wide with the anterior border being narrower than the posterior one in dorsal view. The cross-section of the peripheral at the anterior border is at least twice as thick as it is at the posterior border. The posterior part of the inguinal buttress fossa is visible on the internal surface of the plate near its anterior border. The medial border of the plate bears no suture, thus indicating the presence of costo-peripheral fontanelles. This border has an incision in its middle portion where the pit for the costal free rib is located. The free lateral bor-

der of the plate is straight, rather than serrated, and due to weathering the inter-marginal sulcus is not visible either on the internal or external surface of the plate.

*Discussion*

This specimen is assigned to Chelydridae based on the general similarity of its shape to corresponding peripherals in chelydrids. It was assigned to *Chelydropsis* Peters, 1868, only because all chelydrids from the Neogene of Europe belong to this genus (see Hutchison, 2008).

The first chelydrid material from Hajnáčka was initially described as *Chelydra* aff. *decheni* (Młynarski, 1963), but later it was assigned to *Chelydropsis pontica* or *Chelydropsis nopscai* (Młynarski, 1980; Chkhikvadze, 1982, 1983; Hutchison, 2008). These two latter names are generally considered to be synonymous, and used for the Pliocene species of *Chelydropsis* (see Hutchison, 2008). According to Hutchi-



**Figure 6.** Shell fragments of *Chelydropsis* sp. (A) and "*Melanochelys*" cf. *mossoczyi* (B-G) from Hajnáčka: (A) B-4106, left peripheral 8 in dorsal (A<sub>1</sub>) and ventral (A<sub>3</sub>) views and its cross sections at posterior (A<sub>2</sub>) and anterior (A<sub>4</sub>) borders; (B) B-3116, odd neural in dorsal (B<sub>1</sub>) and ventral (B<sub>2</sub>) views; (C) B-3480, partial right costal 1 in dorsal (C<sub>1</sub>) and ventral (C<sub>2</sub>); (D) B-6198, left peripheral 3 in dorsal (D<sub>1</sub>) and ventral (D<sub>3</sub>) views and its cross-sections at anterior (D<sub>4</sub>) and posterior (D<sub>2</sub>) borders; (E) B-3573, entoplastron in ventral view; (F) B-3646, antero-lateral fragment of the right hypoplastron in ventral view; (G) B-3327, posterior fragment of the left xiphoplastron in dorsal (G<sub>1</sub>) and ventral (G<sub>2</sub>) views.

son (2008), the diagnostic characteristics of *Chelydropsis nopscai* include: a large size carapace size up to 70 cm; simple rather than doubled sulci which are only present within the vertebrals and pleurals; the absence of costal-peripheral fontanelles in adults; strongly serrated peripherals 8 and 9; the presence of supra-marginals, and the position of the posterior margin of vertebral 5 on or near the pygal-suprapygal suture. Since none of these characteristics are observable on the *Chelydropsis* material from Hajnáčka (Młynarski, 1963; this paper), we designate this material to *Chelydropsis* sp.

**Family Geoemydidae Theobald, 1868**  
**Genus “*Melanochelys*” Gray, 1869 sensu**  
**Chkhikvadze, 1973**  
**“*Melanochelys*” cf. *mossocyi***  
**(Młynarski, 1964) (fig. 6B-G)**

*Material and locality*

B-3116, an odd neural; B-3480, a partial right costal 1; B-6198, the left peripheral 3; B-3573, an entoplastron; B-3646, an antero-lateral fragment of the right hypoplastron; B-3327, a posterior fragment of the left xiphiplastron; Hajnáčka.

*Description*

The neural (B-3116) is hexagonal, wider than long, with convex anterior and concave posterior borders. There is a long and narrow notch at the middle of the anterior border. The short sides of the neural face posteriorly, as proven by the position and shape of the intervertebral sulcus which is located closer to the posterior border of the plate and arched slightly forward. The ventral surface of the plate bears a partial thoracic vertebra and sutured scars for the costal rib-heads in the middle of the lateral borders.

Costal 1 (B-3480) is represented by the lateral 2/3 of the plate. It has concave (emarginated) borders for contact with the nuchal and peripherals 1 and 2 and a convex border for

contact with peripheral 3 and most likely with part of peripheral 4. The posterior border of the costal is slightly s-shaped, and it is arched backward in the lateral part of the plate and forward in its medial part. The vertebral 1/pleural 1 sulcus crosses the nuchal border of the plate, indicating that pleurals 1 overlapped the lateral parts of the nuchal. A minimum of seven growth lines are clearly visible within pleural 1, and parallel to its borders. The axillary buttress fossa occupies approximately 1/4 of the costal width, thus indicating a rather weak axillary buttress.

Peripheral 3 (B-6198) is wider than long. The pleuro-marginal sulcus lies distant from the medial border of the plate anteriorly but approaches it posteriorly. Internally, the plate is pierced by a musk duct and has an oblique sutural surface for contact with the axillary buttress.

The entoplastron (B-3573) is bell-shaped, narrower anteriorly than posteriorly, and as wide as it is long with a length/width ratio of approximately 1.00; the postero-lateral borders are shorter than the antero-lateral ones at a ratio of 0.84. Gulars overlap the entoplastron for about 1/4 of its length. The humero-pectoral sulci cross the entoplastron at the level of its posterior fourth.

The fragment of the right hypoplastron (B-3646) shows the lateral part of the abdomino-femoral sulcus at the base of the posterior lobe.

The fragment of the xiphiplastron (B-3327) has a triangular xiphiplastral process, indicating a rather narrow and triangular anal notch. There is a rounded and posteriorly elevated site for pelvic attachment on its dorsal surface.

*Discussion*

The genus *Melanochelys* includes two living species distributed in South and South-East Asia (Fritz and Havaš, 2007). Chkhikvadze (1973) assigned some Neogene geoemydids of Eastern Europe “without the pointed xiphiplastron”, to this genus which had previously been referred to as *Geoemyda* (*Heosemys* Stejneger, 1902) by Khosatzky and Młynarski (1966). This assignment was based on the following shared

characteristics (Chkhikvadze, 1973): a weakly developed gular projection, small entoplastron, the similar ratio of squares covered by gulars and humerals, a shallow anal notch and the xiphiplastral processes not pointed. Later, Chkhikvadze (1983) mentioned the similarity of the Neogene "*Melanochelys*" of Europe to some representatives of the genus *Temnoclemmys* Bergounioux, 1957, which is now considered to be a subgenus of *Ptychogaster* Pomel, 1847 (Lapparent de Broin, 2001; Hervet, 2004a). However, available data on the shell morphology of Neogene "*Melanochelys*" of Europe shows considerable differences to the extant representatives of *Melanochelys* in carapace scale, and the shape of the cervical and vertebrals, which suggests their probable generic distinctness.

"*Melanochelys*" from Hajnáčka is most similar to "*Melanochelys*" *mossocznyi* (sensu Khosatzky and Redkozubov, 1989) in the proportions of the entoplastron, the position of the humero-pectoral sulcus and degree of development of the xiphiplastral process (see Description). The nuchal of "*Melanochelys*" from Hajnáčka figured by Młynarski (1966, Abb. 6) is not overlapped by pleurals 1, whereas the costal 1 described in this paper indicates the presence of such overlapping. Khosatzky and Redkozubov (1989) considered the latter characteristic diagnostic for "*M.*" *pidoplickoi* (Khosatzky, 1946), a species initially described as *Clemmys pidoplickai* from the Pliocene of Ukraine (Khosatzky, 1946), but later recognized with "*M.*" *mossocznyi* in many Pliocene localities of Moldavia and Ukraine (see Khosatzky and Redkozubov, 1989). Some authors consider "*M.*" *mossocznyi* and "*M.*" *pidoplickoi* to be synonyms and explain differences between them as only intraspecific variations (Taraschuk, 1971; Chkhikvadze, 1983). Until the quandary of "*M.*" *mossocznyi/pidoplickoi* is solved, we consider "*Melanochelys*" from Hajnáčka to be "*Melanochelys*" cf. *mossocznyi*.

## General discussion and conclusions

The review of the fossil turtles of Slovakia shows that they belong to at least the five following successive assemblages dating from the Middle Miocene (MN 6) to the Pleistocene (table 1): 1) Middle Miocene, Badenian, MN 6-MN 7-8: Sandberg Hill and Waitov Lom: *Trionyx* sensu lato and *Psephophorus polygonus*; 2) Late Miocene, Pannonian, MN 9: Borský Svätý Jur: Trionychidae indet., Geoemydidae indet. and *Testudo csakvarensis*; 3) Early Pliocene, Ruscinian, MN 15b: Ivanovce: *Chelydropsis* sp., *Emys orbicularis antiqua* and Geoemydidae indet. (two forms); 4) Late Pliocene, early Villafranchian, MN16a: Hajnáčka: *Chelydropsis* sp., *E. orbicularis antiqua* and "*Melanochelys*" cf. *mossocznyi*; 5) Pleistocene: Bojnica, Dreveník, Gánovce, Levice: *E. orbicularis* sensu lato. The precise ages of the turtle remains from Kamenica nad Hronom (Tortonian?; Zázvorka, 1957) and *Emys orbicularis* sensu lato from Žiar nad Hronom (possibly Pliocene or older; Fritz, 1995) are currently unknown.

Representatives of *Trionyx* sensu lato or Trionychidae are recognized from different European Neogene localities up to the MN 17-18 zones (Lapparent de Broin, 2001). However in Central and Eastern Europe, Trionychidae are known only below MN13 zone (see table 1).

In addition to its presence in Slovakia, *Psephophorus polygonus* is also known from the Miocene (Burdigalian-Messinian, MN 3-MN 13) of the Pietra Leccese locality in Italy (Chesi et al., 2007). This assemblage includes two cheloniid sea turtles in addition to dermochelyid.

Outside Slovakia, turtle findings from the MN 6 zone in Central and Eastern Europe are recognized from Austria, Hungary and Poland, and these are represented by members of *Trionyx* sensu lato or Geoemydidae ("*Melanochelys*" *eureia*) (table 1).

Turtle findings from MN 7-8 zones are absent in Slovakia but present in the Central and Eastern Europe countries of Austria, Hungary,

**Table 1 A-D.** Some Neogene turtle assemblages of Central and Eastern Europe. See text for the Slovakian record. Data about ages and composition of assemblages of other territories are as follows: Austria: Bachmayer und Mlynarski, 1983; Gemel and Rauscher, 2000; Delfino and Göhlich, 2009; Gross et al., 2010; Hungary: Mlynarski, 1966; Bernor et al., 2004; Moldavia: Khosatzky and Redkozubov, 1989; Redkozubov, 1991, 1994; Poland: Mlynarski, 1964, 1984; Romania: Vremir, 2004; Russia: Chkhikvadze, 1983; Danilov et al., 2010; Tesakov et al., 2010; Syromyatnikova et al., 2011; Ukraine: Chkhikvadze, 1983, 1989; Kordikova, 1994. Abbreviations: *A.*, *Agriemys*; *Ch.*, *Chelydropsis*; *Cl.*, *Clemmydopsis*; *E.*, *Emys*; *G.*, *Geoemyda*; *Ma.*, *Mauremys*; *Me.*, *Melanochelys*; *Pr.*, *Protestudo*; *Pt.*, *Ptychogaster*; *Ps.*, *Psephophorus*; *Sak.*, *Sakya*; *Sar.*, *Sarmatemys*; *Te.*, *Testudo sensu lato*; *Tr.*, *Trionyx*.

(A)

	Biozones	Austria	Hungary	Moldavia	Poland
Pleistocene	MQ 1-2 (= MN 18)	<i>E. orbicularis</i>	Süttő: <i>E. orbicularis</i> ; <i>Te. süttöensis</i> .	Salchiya: <i>E. orbicularis antiqua</i> ; <i>Ma. salčiensis</i> ; “ <i>Me.</i> ” <i>etuliensis</i> ; “ <i>Me.</i> ” <i>mossocznyi</i> ; <i>Sak. riabinini</i> ; <i>Te. sp.</i>	
	MN 17		Dunaalmás & Kisláng: <i>E. orbicularis</i> ; Nagyharsány-hegy: <i>Te. lambrechtii</i>		
Pliocene	MN 16		Beremend: <i>Te. lambrechtii</i>	Chishmikiy: <i>E. orbicularis antiqua</i>	Rębielice Królewskie: <i>E. orbicularis antiqua</i> ; “ <i>Me.</i> ” <i>mossocznyi</i> ; Weze II: <i>E. orbicularis antiqua</i>
	MN 15		Csarnóta: <i>Te. lambrechtii</i>	Moldavian assemblage: <i>Ch. nopscai</i> ; <i>E. orbicularis antiqua</i> ; “ <i>Me.</i> ” <i>etuliensis</i> ; “ <i>Me.</i> ” <i>mossocznyi</i> ; “ <i>Me.</i> ” <i>pidoplickoi</i> ; “ <i>Me.</i> ” <i>sakyaformis</i> ; <i>Sak. riabinini</i>	Weze I: <i>E. wermuthi</i> (as <i>E. orbicularis wermuthi</i> ); “ <i>Me.</i> ” <i>mossocznyi</i> (as <i>Geoemyda mossocznyi</i> ), <i>Te. globosa</i> , <i>Te. sp.</i>

(B)

	Biozones	Romania	Russia (European part)	Slovakia	Ukraine
Pleistocene	MQ 1-2 (= MN 18)	<i>E. sp.</i> ; <i>Te. graeca iberica</i> ; <i>Te. sp.</i>	<i>E. orbicularis</i> s.l.	Bojnice, Gánovce, Levice: <i>E. orbicularis</i> s.l.	<i>E. orbicularis</i> s.l.
	MN 17	Chelydridae indet.; <i>E. orbicularis</i> ; <i>E. sp.</i> ; Geoemydidae indet. (as aff. <i>Sak. “G.” cf. mossocznyi</i> and aff. <i>Sak. “G.” malustensis</i> ); <i>Te. aff. graeca</i> ; <i>Te. kalksburgensis</i> ; <i>Te. macarovicii</i> ; <i>Te. sp.</i> ;		Dreveník: <i>E. orbicularis</i>	
Pliocene	MN 16	Testudinidae indet. (as <i>Testudininei</i> indet.); Testudines indet. (as <i>Chelonii</i> indet.)		Hajnáčka: <i>Ch. sp.</i> ; <i>E. orbicularis antiqua</i> ; “ <i>Me.</i> ” cf. <i>mossocznyi</i>	
	MN 15			Ivanovce: <i>Ch. sp.</i> ; <i>E. orbicularis antiqua</i> ; Geoemydidae indet. (two forms)	Kotlovina: <i>E. orbicularis antiqua</i>

Poland and Romania, where they are represented by *Chelydropsis* sp., various Geoemydidae, *Testudo sensu lato* and Trionychidae (table 1).

The Central and Eastern European turtle assemblages of the MN 9 zone are generally similar to the Borský Svätý Jur assemblage in the presence of geoemydids, testudinids and tri-

Table 1 A-D. (Continued.)

(C)

	Biozones	Austria	Hungary	Moldavia	Poland
Miocene	MN 13	Gramatneusiedl: "Ma." <i>ukoi</i> (as <i>Ma. ukoi</i> )	Polgárdi: Geoemydidae indet. (as Emydinae indet.); <i>Te.</i> <i>kalksburgensis</i>		
	MN 12		Baltavar (= Berbaltavar): <i>Te. sp.</i>	<i>Pr. bessarabica</i>	
	MN 11	Kohfidisch: <i>Ma. aff.</i> <i>gaudryi</i> ; <i>Te.</i> <i>burgenlandica</i> ; Testudines gen. et sp. indet.; Prottes: <i>Manouria</i> ( <i>Hadrianus</i> ) sp.; <i>Te.</i> cf. <i>promarginata</i> ; <i>Te. sp.</i>	Csakvar: Geoemydidae indet. (as "Clemmys" <i>hungarica</i> ; as <i>Geoemyda sp.</i> ); <i>Te.</i> <i>csakvarensis</i>		
	MN 10				
	MN 9	Atzelsdorf: <i>Ma. sp.</i> ; <i>Te. cf.</i> <i>burgenlandica</i> ; Testudines indet.; <i>Trionyx s.l.</i> ; Götzen- dorf/Sandberg: <i>Te.</i> sp.; <i>Tr. sp.</i> ; Vösendorf: <i>Cl.</i> <i>mehelyi</i> ; <i>Te. sp.</i>	Rudabánya: Geoemydidae indet. (as <i>Geoemyda sp.</i> ); <i>Tr. sp.</i> ; <i>Te. cf.</i> <i>kalksburgensis</i> ; <i>Te.</i> sp. I & II; Sopron: <i>Cl. sopronensis</i>	Kalfa assemblage: <i>Ch. murchisoni</i> ; "Me." <i>moldavica</i> ; <i>Pr. moldavica</i> ; <i>Sar.</i> <i>lungui</i> ; <i>Te.</i> <i>csakvarensis</i> ; <i>Tr.</i> <i>moldaviensis</i>	
	MN 7-8	Gratkorn: <i>Ch. sp.</i> ; ?Geoemydidae (as Emydidae indet.); <i>Te. sp. 1 &amp; 2</i> ; Loretto: Testudines indet. (as <i>E.</i> <i>loretana</i> ); Trionychidae indet. (as <i>Tr. partschii</i> ); Sauerbrunn: <i>Te. sp.</i> ; Mataschen: <i>Cl.</i> <i>turnauensis</i> ; "Türkenschanze": <i>Ma. sarmatica</i>	Mad: <i>Ma. sp.</i> ; Szurdokpüspöki: Testudines indet. (as <i>Te. strandi</i> )		Opole II: "Me." <i>eureia</i> (as <i>Geoemyda eureia</i> ); Przeworno: <i>Pt.</i> <i>emydoides</i> <i>buechelbergense</i> ; <i>Te. sp.</i>
	MN 6	Göriach: <i>Tr.</i> <i>boulengeri</i>	Varpalota: <i>Tr. sp.</i>		Nowa Wies Krolewska: "Me." <i>eureia</i> (as <i>Geoemyda eureia</i> )

onychids (table 1). However, the closest similarity is established between the Borský Svätý

Jur assemblage and the Kalfa assemblage of Moldavia in the presence of one common

Table 1 A-D. (Continued.)

(D)

	Biozones	Romania	Russia (European part)	Slovakia	Ukraine
Pliocene	MN 14		Kosyakino: <i>E. orbicularis antiqua</i> ; “ <i>Me.</i> ” <i>pidoplickoi</i> ; <i>Sak. riabinini</i>		Kuchurgan assemblage: <i>Ch. nopscai</i> ; “ <i>Me.</i> ” <i>mossoczzi</i> (= “ <i>M.</i> ” <i>boristhenica</i> ); “ <i>Me.</i> ” <i>pidoplickoi</i> ; <i>Sak. riabinini</i> ; <i>Te. cernovi</i> ; <i>Te. kuchurganica</i>
	MN 13	<i>Ch. cf. decheni</i> ; <i>Ch. sp.</i> (as <i>Chelydra sp.</i> ); <i>E. orbicularis</i> ; <i>Te. sp.</i> ; <i>Tr. sp.</i> (s.l.)	Nizhniy Vodyanoy: <i>A. caucasica</i> ; Geoemydidae indet.; <i>Pr. sp.</i> ; <i>Te. cernovi</i> ; Testudinidae indet.; Solnechnodol’sk: Geoemydidae indet.; <i>Sak. sp.</i>		Naumovka: <i>Sak. riabinini</i>
	MN 12		Morskaya: Chelydridae indet.; <i>E. sukhanovi</i> ; “ <i>Me.</i> ” <i>mossoczzi</i> ; <i>Sak. riabinini</i> ; Testudinidae indet. 1 & 2		Belka assemblage: <i>E. sukhanovi</i> ; “ <i>Me.</i> ” <i>mossoczzi</i> ; <i>Sak. sp.</i> ; <i>Pr. bessarabica</i> ; <i>Te. bosporica</i> ;
Miocene	MN 11				Krivoy Rog: <i>E. tarashchuki</i>
	MN 10				Grebeniki: <i>Pr. bessarabica</i>
	MN 9		Maikop: Emydidae or Geoemydidae indet. (as Emydidae indet.); <i>Tr. khosatzkyi</i>	Borský Svätý Jur: Geoemydidae indet.; <i>Te. csakvarensis</i> ; Trionychidae indet.	Sevastopol: Geoemydidae indet. (as Emydidae); Testudinidae indet.; Trionychidae indet.
	MN 7-8	Testudines indet. (as <i>Chelonii</i> indet.); <i>Tr. sp.</i> (s.l.) (cf. <i>plioopedemontanus</i> ); <i>Tr. stiriacus</i> (s.l.)			
	MN 6			Devinská Nová Ves, Sandberg Hill: <i>Ps. polygonus</i> ; <i>Tr. s.l.</i> ; Waitov Lom: <i>Tr. s.l.</i>	

species – *Testudo csakvarensis* (Khosatzky and Redkozubov, 1989).

Turtle findings from MN 10-14 zones are absent in Slovakia, but present in other areas of Central and Eastern Europe (table 1): Austria (MN 11 and 13), Hungary (MN 11-13),

Moldavia (MN 12), Romania (MN 13), Russia (MN 12-14) and Ukraine (MN 10-14). In general, this interval is characterized by the presence of Chelydridae, Emydidae (Romania, Russia, Ukraine), various Geoemydidae and Testu-

dinidae and also the last occurrence of Trionychidae (Romania).

The Central and Eastern European turtle assemblages of MN 15-17 zones are represented by Chelydridae, *Emys* spp., various Geoemydidae and Testudinidae (table 1). Among these assemblages, the Ivanovce and Hajnáčka assemblages of Slovakia are most similar to the MN 15 Moldavian assemblage (Khosatzky and Redkozubov, 1989) in the shared presence of *Chelydropsis*, *Emys orbicularis antiqua*, at least two forms of Geoemydidae and the absence of Testudinidae.

Finally, the Pleistocene (MQ 1-2) assemblages of Slovakia contain a single turtle taxon (*E. orbicularis sensu lato*) widely distributed in the Pleistocene of Europe, including the Central and Eastern Europe areas (Fritz, 1995).

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## Appendix. Turtle localities of Slovakia

1. Sandberg Hill, near Devínska Kobyla Mountain, northern vicinity of Bratislava, south-western Slovakia.

*Geology and age.* Sandberg layers, upper Badenian, Middle Miocene, MN 6 (see e.g., Holec and Schlögl, 2000; Sabol and Holec, 2002; Fejfar and Sabol, 2005, Holec, 2006).

*Material and references.* Costal fragments of Trionychidae indet. (as *Trionyx* sp.; Młynarski, 1966, p. 233, 275) and a partial carapace and a posterior part of the carapace of *Trionyx* sensu lato (as *Trionyx* sp.; Hörnes, 1848; Holec, 2006, p. 67, fig. 2; as *Trionyx rostratus* Arthaber, 1898; Holec and Schlögl, 2000); a complete costal 4 or 5, and a humeral bone of *Trionyx* sensu lato (fig. 2; see Results); a portion of shell mosaic and several vertebrae of *Psephophorus polygonus* (type material), isolated epithelial plates and their fragments of the same species (Meyer, 1846, p. 472; 1847, p. 579; Seeley, 1880, 406, pl. XV; Bachmayer, 1958, p. 715, Abb. 7; Młynarski, 1966, p. 233, 271; Wood et al., 1996, p. 279, figs 16, 17); and Testudinata gen. et sp. indet. (see Hörnes, 1848).

2. Waitov Lom, a stone quarry, near Devínska Kobyla Mountain, northern vicinity of Bratislava, south-western Slovakia.

*Geology and age.* Sandberg layers, upper Badenian, Middle Miocene, MN 6 (Holec, 2006).

*Material and references.* A fragment of costal of *Trionyx* sensu lato (as *Trionyx* sp.; Holec, 2006, p. 67, fig. 3).

*Remarks.* The material is assigned to *Trionyx* sensu lato because it comes from the same Sandberg layers as the trionychid material from Sandberg Hill.

### 3. Borský Svätý Jur, south-western Slovakia.

*Geology and age.* Lacustrine basin deposits at an abandoned brickyard, Early Pannonian, Late Miocene, MN 9 (see Joniak, 2005).

*Material and references.* Shell fragments of Trionychidae indet., *Testudo csakvarensis* Szalai, 1934 and Geoemydidae indet. (figs 3, 4, 5; see Results). For other material see Remarks.

*Remarks.* The correct systematic attribution of the material from Borský Svätý Jur mentioned as Emydinae and *?Nicoria* (= *?Geoemyda*) sp. by Pipík and Holec (1998) is unclear. The trionychid material mentioned from this locality cannot be determined below the family level, although all fossil trionychids from the Neogene of Europe are referred to as *Trionyx* sensu lato and Trionychinae indet. (Lapparent de Broin, 2001).

### 4. Kamenica nad Hronom, southern Slovakia.

*Geology and age.* Sand clay and conglomerate, Tortonian?, Late Miocene (unfortunately, a more precise age is unknown, due to the absence of information about the exact location of the find in the lithological section; see Zázvorka, 1957).

*Material and references.* One isolated neural element similar to those of the genus *Testudo* (in Zázvorka, 1957; his fig. on p. 96).

### 5. Ivanovce, near Trenčín, western Slovakia.

*Geology and age.* Fissure fillings along tectonic lines, Late Ruscinian, Early Pliocene, MN 15b (Fejfar et al., 1998; Fejfar, 2001; Fejfar and Sabol, 2005).

*Material and references.* Neural 1 and peripheral 6 or 7 of *Chelydropsis* sp. (as *?Chelydridae* gen. et sp. indet.; Młynarski, 1963, p. 240); shell fragments of *Emys orbicularis antiqua* (as *E. orbicularis*; Młynarski, 1963, p. 239; Ullrich and Młynarski, 1978, p. 99; as *E. orbicularis antiqua*; Fritz, 1995, p. 255); shell fragments of two forms of Geoemydidae indet. (as Emydidae gen. et sp. indet., two forms; Młynarski, 1963, p. 239; as *?Geoemyda* sp.; Khosatzky and Młynarski, 1966, p. 403 (caption to map 1)).

*Remarks.* The material from Ivanovce, described as *?Chelydridae* gen. et sp. indet. (Młynarski, 1963, p. 240), is here considered as *Chelydropsis* sp., only because all chelydrids from the Neogene of Europe belong to this genus (Hutchison, 2008). Młynarski (1963) mentioned two forms of Emydidae gen. et sp. indet. from this locality, one of which showed similarity with the genus *Clemmys* Ritgen, 1828 (sensu lato); and the second one similar to the genus *Geoemyda* Gray, 1834. According to later revisions (McDowell, 1964; Khosatzky and Młynarski, 1966), *Clemmys* was placed in the subfamily Emydinae Rafinesque, 1815 (now Emydidae) and restricted to North America, whereas its former Eurasian representatives were placed in different genera of the subfamily Batagurinae Gray, 1869 (now Geoemydidae Theobald, 1868); similarly, *Geoemyda* was divided into several genera or subgenera within Batagurinae. *?Geoemyda* sp. mentioned by Khosatzky and Młynarski (1966) corresponds to the second of the forms discussed above.

### 6. Hajnáčka (= Ajnácskö), near Rimavská Sobota, southern Slovakia.

*Geology and age.* Infill of a maar lake (with lacustrine sands, lacustrine tuffites and subaeric tuffs) during alkaline (basaltic) volcanic activity, early Villanyian (= Villafranchian), Late Pliocene, MN 16a (see Fejfar and Sabol, 2005).

*Material and references.* Numerous skull, shell and non-shell postcranial fragments of *Chelydropsis* sp. (as *Chelydra* aff. *decheni* H.v.

Meyer, 1852; Młynarski, 1963, p. 233, Tab. 23-25, 26, figs 3, 4; 1966, p. 237, 244; 1968, p. 352; as *Chelydropsis pontica* Pidoplichko et Taraschuk, 1960; Młynarski, 1980, p. 18; as *Chelydropsis nopscai* Szalai, 1934; Chkhikvadze, 1982, p. 16; 1983, p. 28; Hutchison, 2008, p. 24); peripheral 8 of *Chelydropsis* sp. (fig. 6A; see Results); a partial plastron (right hypoplastron + xiphiplastron), a carapace with a well preserved stone core, neural 4 or 5, a medial fragment of costal 6, peripherals 3, 9, 11 and two articulated xiphiplastra of *Emys orbicularis antiqua* (as *Testudo* sp.; Kormos, 1915; as *E. orbicularis*; Szalai, 1934, p. 111, Tab. III, fig. 4; Młynarski, 1963, p. 236, Tab. 26, figs 1, 2; 1966, p. 237, 254; 1968, p. 353, Abb. 2; Ullrich und Młynarski, 1978, p. 99; Młynarski, 1980, p. 31; *E. o. antiqua*; Khosatzky, 1956, p. 325; Fritz 1995, p. 255); a nuchal and right hypoplastron of “*Melanochelys*” cf. *mossoczyi* (as a form close to *Geoemyda mossoczyi* Młynarski, 1964, p. 340; as *G. cf. mossoczyi*; Khosatzky and Młynarski, 1966, p. 403 (caption to map 1), p. 408, 409; as *G. aff. mossoczyi*; Młynarski, 1966, p. 237, 252, Abb. 7; as *G. mossoczyi*; Młynarski, 1968, p. 352); shell fragments of the same taxon (fig. 6B-G; see Results).

7. Žiar nad Hronom, central Slovakia.

*Geology and age.* Pliocene? (the age is unknown, and it may be older; Ciesarik, 1970).

*Material and references.* *Emys orbicularis* sensu lato (Fritz 1995, S. 255).

8. Bojnice, central Slovakia.

*Geology and age.* Pleistocene? (Skutil, 1960).

*Material and references.* *Emys orbicularis* sensu lato (as *E. orbicularis*; Skutil, 1960; Ullrich and Młynarski, 1978, p. 99; as *E. orbicularis* sensu lato Fritz, 1995, p. 255).

9. Dreveník, near Spišské Podhradie town, eastern Slovakia.

*Geology and age.* Early Pleistocene, MN 17 (Tóth and Krempaská, 2008). Since the sediments presented are very thick, this age could be even younger (Holec, pers. comm.).

*Material and references.* *Emys orbicularis* (Krempaská, 1993, fig. 5; Tóth and Krempaská, 2008, p. 116).

10. Gánovce, northern Slovakia.

*Geology and age.* Travertines, Eemian Interglacial, Pleistocene (Štěpánek, 1934).

*Material and references.* An internal core of the shell of *Emys orbicularis* sensu lato (as *E. orbicularis*; Štěpánek, 1934, p. 219, pl. with two figures; Vlček, 1969, pl. with one figure; Ullrich und Młynarski, 1978, p. 99; as *E. orbicularis* sensu lato Fritz, 1995, p. 255).

11. Levice, southern Slovakia.

*Geology and age.* Travertines, Pleistocene.

*Material and references.* An internal core of the shell of *Emys orbicularis* sensu lato (Petrbok, 1938, his p. 85, fig. 1).