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Quaternary evolution of the river Danube in the central Pannonian Basin and its possible role as an ecological barrier to the dispersal of ground squirrels

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ABSTRACT

Large rivers can act as important ecological barriers for small mammals, but their exact role is debated. Here we examine the effect of the river Danube on populations of the European ground squirrel, an important representative of steppe communities, by studying the Quaternary history both of ground squirrels and of the Danube in the Pannonian Basin, in Hungary. The Danube experienced considerable channel changes during the Quaternary, with >100 km westward shift of its middle reach, interrupted by temporary eastward movements. Besides autogenic river processes, tectonically induced avulsions have played a role in re-routing channels. Three of the four *Spermophilus* species certainly extended their ranges on both sides of the Danube, referring to repeated river crossings during the Quaternary. Hydrological events, most importantly rapid river course changes (avulsions) but also meander cut-offs are viable mechanisms to enable ground squirrel populations to cross large rivers. On longer timescales, oscillating river course changes can maintain gene exchange across the river.

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Introduction

Ground squirrels are characteristic members of biotic communities in steppe environments. They play a key role in the steppe ecosystem and are often handled as indicators of the existence of steppe biome (e.g. Kryštufek et al. 2009). For ground squirrels and similar, relatively small-sized, non-flying and hibernating mammals geographical obstacles can act as barriers and limit their ranges. The role of large rivers as barriers for ground squirrels has been put forward several times and although this supposition is generally considered valid, contradictory data are calling for further discussion (Ćosić et al. 2013; Říčanová et al. 2013; Popova et al. 2019). One of the debated questions is the role of interspecific competition in relation to that of the geographical barrier itself in maintaining the separation of populations inhabiting opposite sides of large rivers (Popova et al. 2019). Among large rivers in general, especially the role of river Danube as a barrier is problematic, which flows through major *Spermophilus* ranges. This lead Popova et al. (2019) to propose that further research should focus on its Quaternary history and geomorphology to help to elucidate how ground squirrels were able to make repeated crossings of the river during the Pleistocene.

Ground squirrels (*Spermophilus* spp.) have been present in the Pannonian Basin for most of the Quaternary, represented by several species (Jánossy 1986). Their fossils are relatively widespread in the area, providing an opportunity to study the above questions in detail. In this paper, we examine the Quaternary history both of ground squirrels and of the Danube in the Pannonian Basin. We collect and re-evaluate all ground squirrel data in the central Pannonian Basin, considering both areal distribution and the temporal range they cover. We also present the Quaternary evolution and palaeogeographical changes in the middle reach of the Danube and discuss the mechanisms that can potentially transfer the animal populations to the other side of the river and thus ensure gene flow across the 'barrier'.

Materials and methods

To assess the areal and temporal range of *Spermophilus* species, all available palaeontological data, both in collections and in literature were gathered and reviewed that referred to the presence of this genus in Hungary during the Quaternary. The available material is considerably rich, specimens are known from 71 layers of 41 localities. The taxonomic revision of some sites – Jankovich Cave, Pilisszántó, Szelim Cave and Tokod II – with the re-identification of finds has also begun (Sinitsa et al. this issue) but is not complete yet. The exact timing of the appearance of *Spermophilus citellus* and the disappearance of *S. citelloides* in Hungary is therefore still uncertain. In the present paper, the revised sites are represented by the new data, while in case of the localities lacking revision literature data are used, indicating which of them need to be revised.

The Quaternary evolution of the Danube was studied in detail in the central Pannonian Basin, in the Great Hungarian Plain, which provides the best habitat for ground squirrels (Figure 1). New results were acquired during the geological research project of Paks II. Ltd. in 2015–2016. In this project, new boreholes were drilled and morphotectonic

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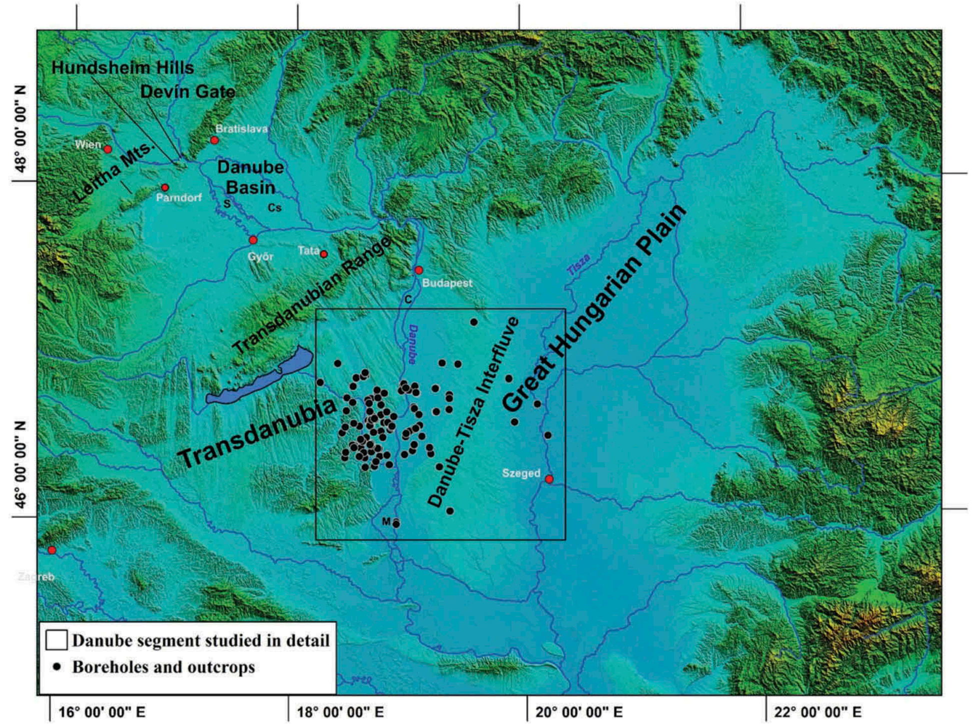

Figure 1. The Danube in the Pannonian Basin, with the Danube reach studied in detail. Islands: C – Csepel Island; Cs – Csallóköz/Žitný ostrov; M – Mohács Island; S – Szigetköz.

investigations were carried out to constrain the location of the main watercourses at given time points and possibly the drivers behind changes in the drainage network. Alluvial sediments in cores and outcrops were dated with optically stimulated luminescence (OSL), using the single aliquot regenerative dose (SAR-OSL) protocol for quartz and post-IR IRSL (290°C) protocol for feldspar. The ^{14}C method was used to date alluvial deposits if they contained measurable fossils. To construct geological cross-sections the documentations of archive boreholes, mostly from the 'Great Plain project' of the Geological Institute of Hungary in the 1970-80s, and of geological mapping campaigns since the 1950s were re-evaluated and used together with new data. Also archive palaeontological data reported from boreholes were used to date Lower and lower Middle Pleistocene Danube sediments by the means of biostratigraphy, mostly using mollusc and vertebrate remains.

Plio-quaternary evolution of the Danube in the Pannonian Basin

Prior to the recent terrestrial environment, the Pannonian Basin was occupied by Lake Pannon, which was filled up by deltaic to fluvial sediments from northwest to southeast between 10 Ma and 4 Ma (Magyar et al. 2013). With the regression of the lake the development of the modern drainage pattern of the Pannonian Basin started, with the paleo-Danube at its axis.

During the Early Pliocene the paleo-Danube flowed in a southerly direction across Western Transdanubia and discharged into the remnant of Lake Pannon (Slavonian Lake) occupying the Drava and Sava Basins (Szádeczky-Kardoss 1938; Somogyi 1961), where lacustrine, paludal, then alluvial environments prevailed (Saftić et al. 2003) (Figure 2). In the Late Pliocene, upon entering the Pannonian Basin, the Danube was diverted to an easterly flow direction across the Danube Basin, passing along the northern side of the Transdanubian Range (TR), which was a low hilly area during the Late Miocene and Early Pliocene (Tari et al. 1992; Horváth and Tari 1999; Magyar et al. 2013; Balázs et al. 2018). The river cut across the mountains through the Miocene volcanics of the Danube Bend area (Karátson et al. 2006), then turned to the south and left the TR in a south-easterly direction towards the Great Hungarian Plain. On the northern side of the Transdanubian Range, in the Gerecse Hills, the highest and oldest geomorphic horizon with Danube sediments was dated to 2.9 ± 0.5 Ma (Ruszkiczay-Rüdiger et al. 2018), this is the minimum age from when the Danube River occupied its recent course through the mountains. This shift of the Danube influenced the entire Transdanubian drainage network, forcing the smaller streams to follow the main river (Figure 2).

The course of the Danube in the Pannonian Basin can be divided into three main sections: the lowland areas of the Danube Basin and the Great Hungarian Plain, and the uplifting TR between them (Figure 2).

The river has always entered the Pannonian Basin from the NW through narrow passages: during the Early Quaternary the entrance point was between the Leitha Hills and Hundsheim Hills, at Parndorf (Zámolyi et al. 2017) and around 0.9 Ma it occupied its recent position through the Devín Gate (Šujan et al. 2018). In the subsiding Danube Basin alluvial sedimentation was continuous throughout the Quaternary with mostly braided river environment (Šujan et al. 2018). The river course consisted of a tens of km-s wide and constantly varying network of river

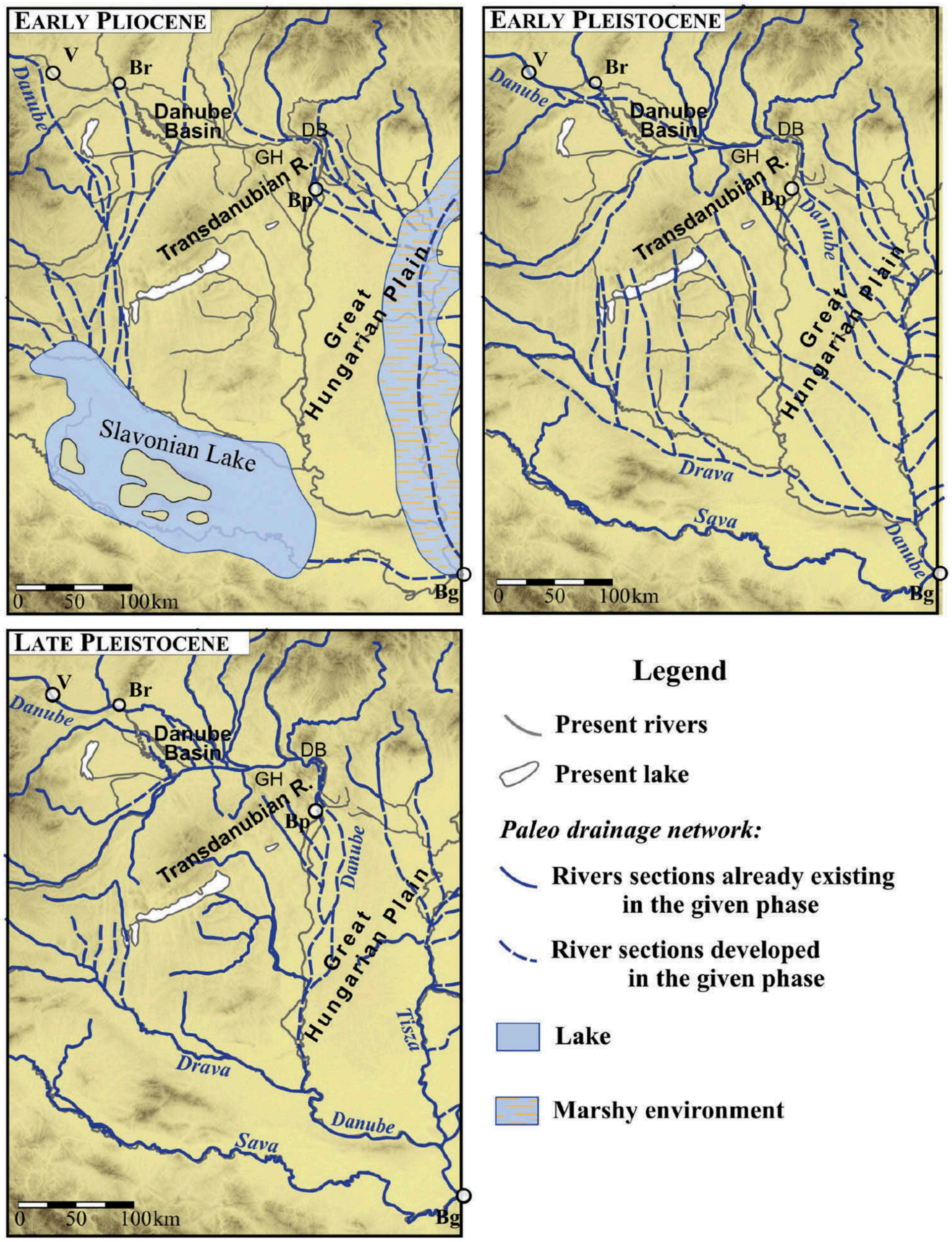

Figure 2. Drainage pattern evolution of the Western Pannonian Basin (after Sümeghy 1955, Somogyi 1961; Borsy 1989). GH: Gerecse Hills, DB: Danube Bend, V: Vienna, Br: Bratislava, Bp: Budapest, Bg: Beograd.

channels with small, often temporary islands between them. The main channel was followed by several anabranches of meandering style. According to historical records, prior to the river regulations, the lateral migration of the river channels was fast. Meanders could develop and cut off on a decadal timescale. Abrupt changes of the channel courses were frequently triggered by large floods caused by ice-damming (Pišút 2002; Pišút and Timár 2007; Timár and Pišút 2008). The south-eastern part of the Danube Basin (Győr-Tata Terraces) was a transitional zone between the lowland and the TR. According to dated fluvial terraces, the uplift of this area started at latest around 1 Ma (Ruszkiczay-Rüdiger et al. 2016, 2018). River terraces in the north-eastern embayment of the Danube Basin suggest that to the north of the Gerecse Hills the Danube might have shifted its course between the northern and southern sides of the valley, meaning up to ~10 km rapid river course changes (avulsions) of the main channel (Šujan and Rybár 2014).

The Transdanubian Range forms a 300–750 m high range composed of Palaeo-Mesozoic rocks with Neogene cover (sedimentary and volcanic lithology). The Danube is the only river cutting through the TR. Its incision kept pace with the uplift of the mountains and formed a terraced valley (Pécsi 1959; Ruszkiczay-Rüdiger et al. 2005; Gábris and Nádor 2007). At this valley section, the course of the Danube is considered to be relatively stable at least during the last ~3 Ma (Ruszkiczay-Rüdiger et al. 2018).

On the northernmost part of the Great Hungarian Plain, where the river is depositing its sediment load after leaving its incised valley in the TR, a terraced valley was formed by alternating alluvial sedimentation and incision. Here the river still has a braided character with constantly migrating channels, bars and islands. Decadal changes of the river bank positions and varying numbers and shapes of the islands have been reported during historical times (Timár et al. 2013).

Further to the south, since the Late Pliocene the Danube has built a large alluvial fan in the area currently situated between the Danube and Tisza Rivers (Danube-Tisza Interfluve) (Figure 2). During the Middle Pleistocene, the channel system of the Danube shifted gradually towards the west on its own alluvial fan. Scarce geochronological data are available about the timing of this shift. Based on mostly sedimentological observations of drillhole data the estimated age of the abandonment of the Danube-Tisza Interfluve alluvial fan occurred by the beginning of the last glaciation (~100 ka) (Borsy 1989). The width of the modern Danube in the central Pannonian Basin typically varies between 350 and 600 m. Quaternary meanders had dimensions comparable to modern ones (Tóth et al. 2017; Tóth 2019).

Results

Ground squirrel species in the central Pannonian Basin during the Quaternary

Geographically considered, the *Spermophilus* sites in Hungary are located in the hills and mountains, because they are mainly caves (Figure 3, Appendix 1). *Spermophilus citelloides* sites are the most common, but sites with *S. citellus* and *S. primigenius* also occur. One site of *S. major* (Uppony I rock shelter) is also known. The map displays all available literature data, modified according to the results of recent revision if these were available. So far only a part of these data have been revised; thus, a future revision might change the colour of some localities (e.g. Bivak Cave, Por-lyuk, Lambrecht Kálmán Cave, Subalyuk; see below). The areal distribution of the ground squirrel species is obviously not influenced by the Danube, all three species with more than one data occur both east and west of the river.

Temporally, the genus *Spermophilus* occurs almost continuously in the Quaternary of Hungary. Based on the stratigraphical ranges of the species (Figure 4), it can be stated that

1. this genus is regularly recorded in the Pleistocene, although it is lacking in the Holsteinian and rare in the Saalian;
2. in the Villanyian and Biharian *Spermophilus primigenius*, in the Toringian mainly *S. citelloides*, and in the Holocene *S. citellus* were the typical species in the area;
3. a further, larger species has also been reported from the area (namely *S. major*), which requires taxonomic re-consideration.

The local ranges of the species do not show longer gaps that would refer to the disappearance of ground squirrels from the area of Hungary (Figure 4). The only long gap is observed between 500 and 320 ka. However, this can be a result of the fact that from this interval only a single vertebrate site (Tar-kő, Bükk Mts.) is known in the country, which lies at an altitude of 850 m a.s.l., probably too high for ground squirrels.

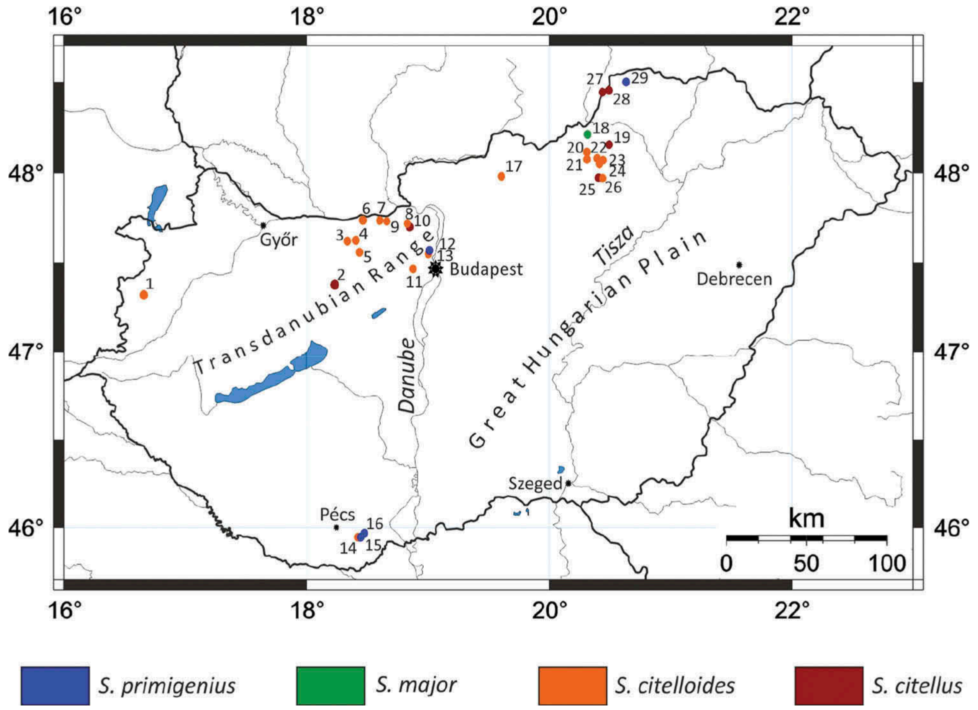

Figure 3. Areal distribution of Quaternary *Spermophilus* species in Hungary. Fossil sites: 1 – Gencsapáti; 2 – Rigó-lyuk; 3 – Tata; 4 – Vértesszőlős II; 5 – Tatabánya, Szelim Cave; 6 – Süttő; 7 – Jankovich Cave; 8 – Pilisszántó; 9 – Tokod; 10 – Bivak Cave; 11 – Érd; 12 – Újlaki-hegy; 13 – Várbarlang; 14 – Nagyharsányhegy; 15 – Villány; 16 – Somssich Hill 2; 17 – Függőkő Cave; 18 – Uppony I; 19 – Lambrecht Kálmán Cave; 20 – Istállóskő Cave; 21 – Peskő Cave; 22 – Kőrös Cave; 23 – Poros-lyuk; 24 – Pongor-lyuk; 25 – Subalyuk; 26 – Hórvölgy Cave; 27 – Nagyoldal Hole; 28 – Por-lyuk; 29 – Osztramos.

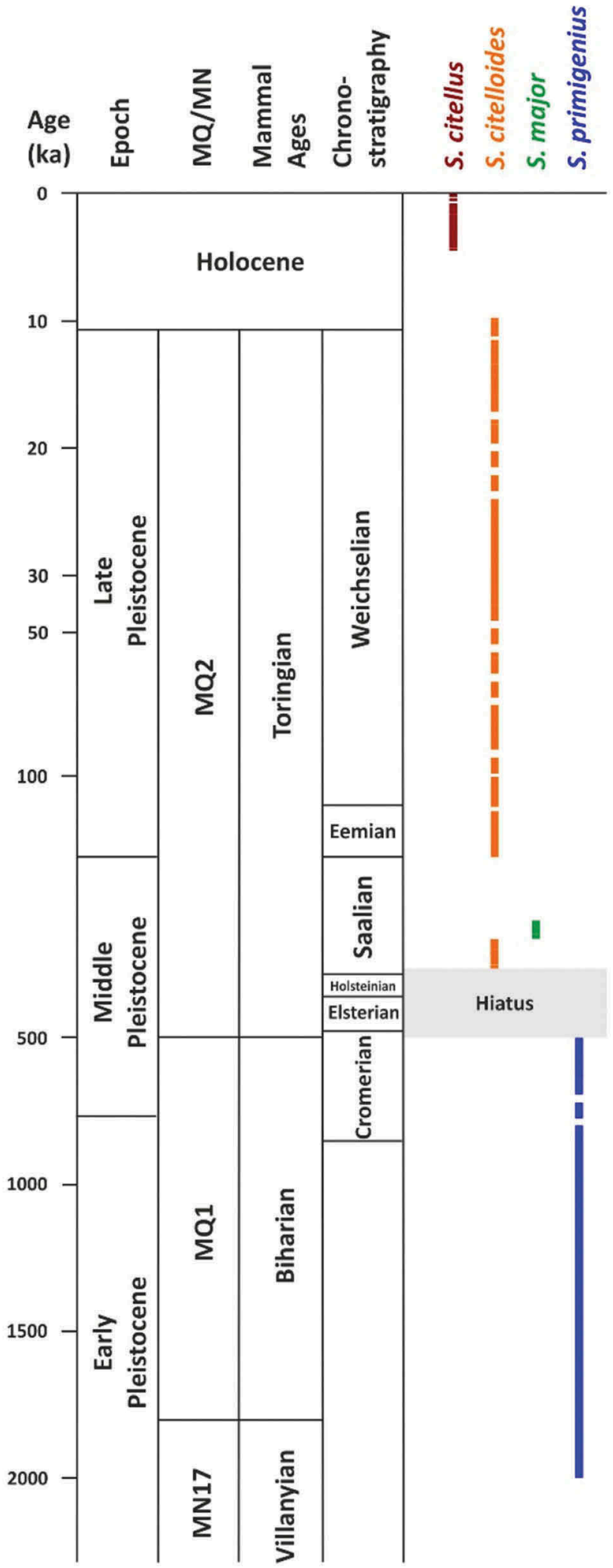

Figure 4. Stratigraphic range of Quaternary *Spermophilus* species in Hungary. For references containing ages see Appendix 1 and Pazonyi (2011).

In Figure 4 uncertain occurrences of *S. citellus* are not displayed. Uncertainty derives from two sources. First, based on literature data it is not possible to decide which species lived in the area during the last glacial maximum (LGM) and the end of the Pleistocene, since there exists a site (Bivak Cave) of a ~ 18–19 ka age (uncalibrated age 15,970 ± 270 BP, Pazonyi 2006) from where both *S. citellus* and *S. citelloides* were reported (Jánossy et al. 1957). However, in the faunas of already revised sites older (Pilisszántó, Szelim Cave; age LGM) and younger (Jankovich Cave, 17–15 ka) than the Bivak Cave only *S. citelloides* remains were found (Sinitsa et al. this issue), therefore it is supposed that the specimens found in the Bivak Cave and previously identified as *S. citellus* may also belong to the former species. Second, the validity of *S. citellus* occurrences can be questioned as well at sites where they appear as isolated points on the timeline, with *S. citelloides* occurring in older and younger sites (Porlyuk, ca. 120 ka; Lambrecht Kálmán Cave, ca. 82 ka; Subalyuk, ca. 64 ka). Previous palaeoecological investigations did not reveal any environmental changes at these time points, since the typical vegetation cover of the area was steppe between 190 and 102 ka and mammoth steppe between 90 and 27 ka (Pazonyi 2011). Furthermore, in the material of the locality Tokod II, almost coeval with the Lambrecht Kálmán Cave, exclusively *S. citelloides* fossils were found during the revision (Sinitsa et al. this issue), and this suggests that the isolated occurrences of *S. citellus* may result from erroneous identification.

Quaternary evolution of the middle course of the Danube

Early Pleistocene

In the Late Pliocene at latest the Danube occupied its present course across the Transdanubian Range and started building its alluvial fan in the Great Hungarian Plain. The area west of the fan was a moderately dissected hilly region, the older version of the present-day Transdanubia (Figure 5). Its surface was covered by thick pedogenic red clays, either in situ or slightly redeposited by slope processes, now classified into the Tengelic Red Clay Formation (Jámbor 2012). The TengelicRed clay marks the distribution of the Pliocene–Early Pleistocene elevated terrain of Transdanubia. This paleosurface can be followed on the surface in isolated erosional remnants – small hills – rising above the modern Danube floodplain and also in boreholes, far to the east of the present-day margin of Transdanubia (Figure 5). The previously larger extent of this paleosurface was first recognised by Erdélyi (1955, 1960) and Urbancsek (1963) and the boundary between Transdanubia and the Danube alluvial fan could now be drawn based on borehole data. Further sediments that can be used to map Transdanubia are deposits of small watercourses draining the hills towards the Danube. These were distinguished from Danube sediments by their finer grain size, poorer sorting, different lithologies (e.g. chert pebbles) and the lack of andesite grains (Franyó 1988). Transdanubian fluvial deposits have been reported from multiple boreholes (Figure 5, 7). In several boreholes (e.g. Tengelic K-15, Kalocsa K-43, Miske B-9; Jaskó and Krolopp 1991) their Early Pleistocene age was shown by a mollusc fauna belonging to the Viviparus boeckhi zone (~2–0.75 Ma sensu Krolopp 2014). In addition to the mollusc fauna, deposits of the palaeo-Danube tributaries are dated by small mammal findings: from the borehole Dávod K-47 (from 96 to 98 m depth) *Mimomys savini* was recovered, indicating an Early Biharian age (Kretzoi and Krolopp 1972), i.e. 1.8–0.9 Ma (Sala and Masini 2007; Virág 2013).

Danube sediments can be identified by andesite pebbles originating from the Danube Bend, and, if data are available, by their heavy mineral assemblage containing fresh, colourless or light red garnet, epidote, anthophyllite and actinolite (Molnár 1961; Gedeonné Rajetzky 1973; Thamó-Bozsó and Ó.Kovács 2007). The alluvial fan of the Danube had its apex approximately at its present-day location, in the area of Budapest, and spread to the SSE (Figure 2, Figure 5). The maximum width of the fan was 70–80 km. No detailed sedimentological descriptions are available from the studied cores, but it can be supposed that the alluvial fan had similar morphology as the modern fan in the upper reach of the river, in the Danube Basin (Figure 1).

Dating of the Danube sediments can be acquired using boreholes which contained age-indicating mollusc assemblages. These were classified into the Early Pleistocene Viviparus boeckhi zone (Krolopp 1974; Krolopp and Széles 1975; Krolopp 1980; Krolopp in Kovács 1992; Jaskó and Krolopp 1991) and included terrestrial (borehole Dánszentmiklós; Franyó et al. 1986) as well as lacustrine and fluvial taxa (boreholes Kerekegyháza and Jánoshalma; Krolopp and Széles 1975; Krolopp 1980; Franyó 1988). Deposits with Viviparus boeckhi zone mollusc fauna can be followed to the south into Serbia (Gaudenyi et al. 2013, 2018). Several boreholes containing this mollusc fauna were drilled on the western part of the alluvial fan, indicating that the Danube has wandered far to the west, very close to its modern position as early as the Early Pleistocene, in contrast with some previous opinions (Gábris and Nádor 2007). Vertebrate remains were found in a single borehole (Nyárlőrinc) near the eastern edge of the Danube alluvial fan and included *Mimomys* and other Arvicolidae fragments (Kretzoi in Franyó 1980). Based on them, the top of the Danube sediments is Early Biharian or older (≥0.9 Ma old), and the lower part (below 163 m depth) is Upper Villanyian or older (≥1.8 Ma old).

Oscillatory channel changes are also documented in the sedimentary record of the study area. The borehole Jánoshalma-1 exposed Danube sediments at the base of the Quaternary succession (below the depth 130.6 m), shown by andesite blocks originating from the Danube Bend (Franyó 1988). Upwards the deposits change into sediments of small watercourses (palaeo-Sió, palaeo-Sárvíz) from Transdanubia. Urbancsek (1963) also reported deposits of Transdanubian rivers in water wells around Jánoshalma. This means that after wandering to the west, the Danube moved backwards to the east, followed by the Transdanubian tributaries.

Middle Pleistocene

During the Middle Pleistocene, the Danube was drifting westward, as stated by Franyó (1980). The axis of its alluvial fan changed from NNW-SSE to approximately N-S. The fan became narrower than previously, maximum ~30 km wide,

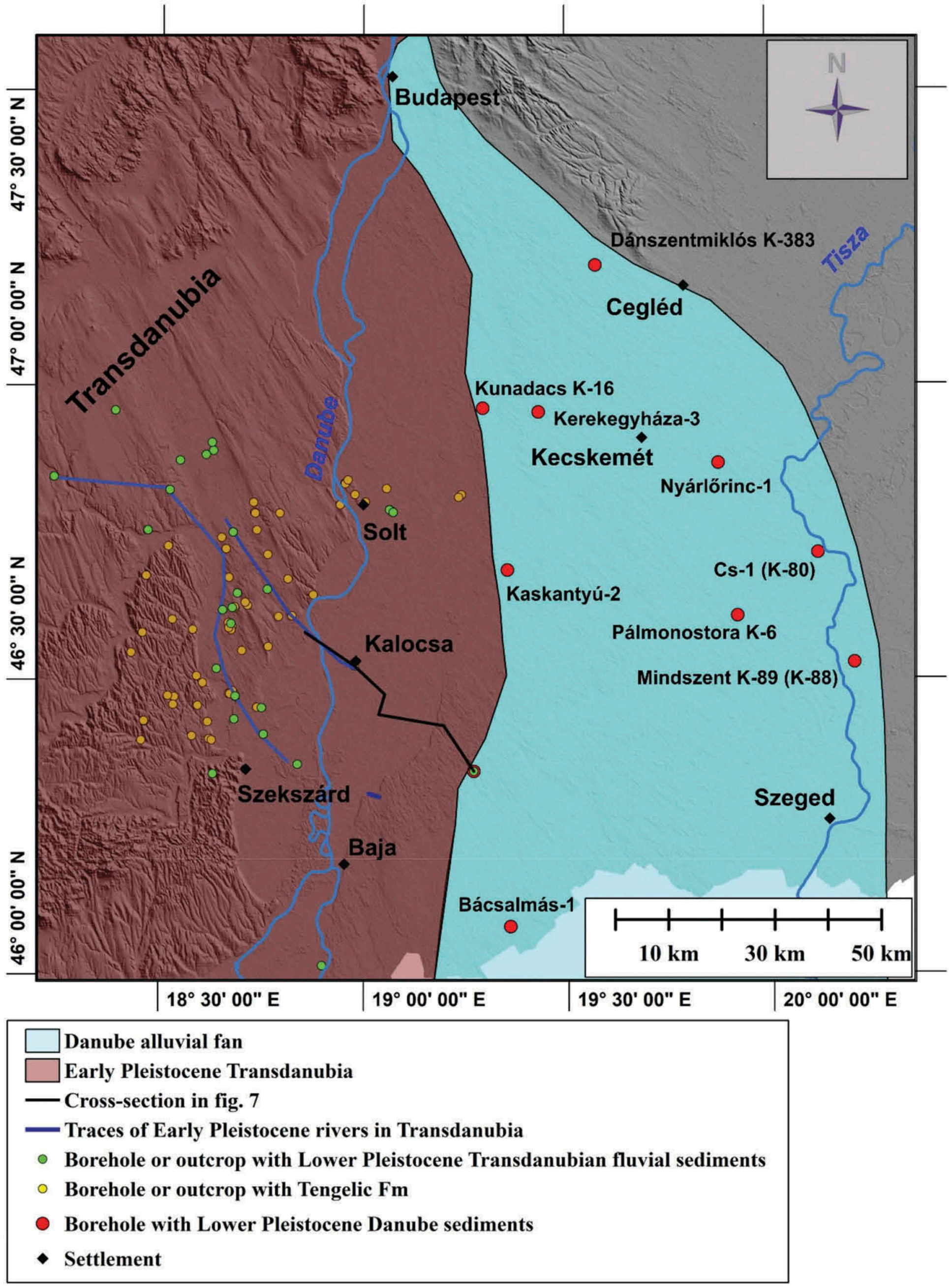

Figure 5. The Early Pleistocene alluvial fan of the Danube.

and covered the eastern part of the modern floodplain and the area east of it (Figure 6). Transdanubian watercourses continued to deposit their load until they reached the Danube, partly under the area of the modern floodplain.

The river Tisza started to prograde from the east onto the eastern margin of the Lower Pleistocene Danube alluvial fan. Tisza deposits are recognisable by their characteristic heavy mineral assemblage. They appear above Lower Pleistocene Danube sediments in the borehole Pálmonostora ('artesian well', probably well K-6, at 105–108 m depth) and some surrounding wells (Molnár 1961). The nearby Nyárlőrinc well contains Middle Pleistocene deposits between the depths 48–71 m, well dated by the gastropod *Neostyriaca corynodes* (Krolopp in Franyó 1980). Their lower segment is built up of sediments of a smaller river and its floodplain and contains fluvial (floodplain) molluscs. Being close to the wells with surely identifiable Tisza deposits, this one probably also exposed the Middle Pleistocene Tisza river. These data suggest that the Danube alluvial fan had moved to the west and left this area by the Middle Pleistocene. Based on the joint interpretation of both mollusc and small mammal data reported from the Nyárlőrinc well (Krolopp in Franyó 1980 and Kretzoi in, 1980, respectively), the temporal gap between the Lower Pleistocene Danube deposits and the Middle Pleistocene Tisza sediments is at least 120 ka here, but can even be more than 1 Ma.

The eastern boundary of the Danube floodplain during the Middle Pleistocene is represented among others in the borehole Bácsalmás-1. Here the Middle Pleistocene sediments reach

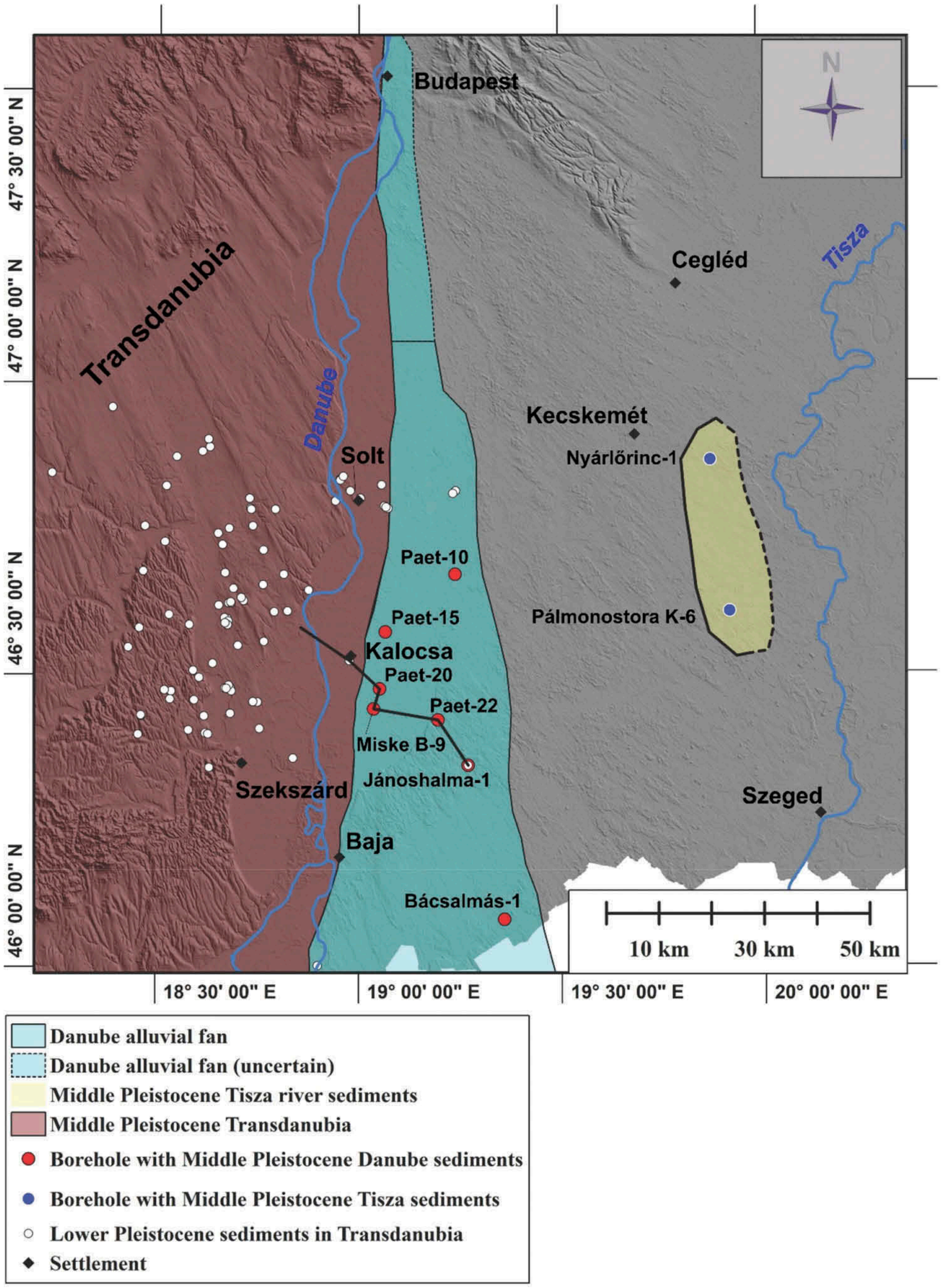

Figure 6. The Middle Pleistocene alluvial fan of the Danube.

a thickness of >50 m, from the top of the Viviparus boeckhi zone (at 107.4 m depth) to the somewhat uncertain Middle/Upper Pleistocene boundary somewhere between 43 and 57 m (Krolopp in Kovács 1992). Molluscs in this interval indicate lacustrine, slow-flowing fluvial or wet terrestrial environments, rather a floodplain than a river channel. River channel deposits from this period were recognised only to the west of this drilling. The westward shift of the Danube was remarkable: it not just left the southern part of the Lower Pleistocene alluvial fan but occupied a large terrain built up of pre-Quaternary sediments and partly of Quaternary Transdanubian deposits (Figure 7). The fact that the Danube incised into its own older sediments (Figure 7) suggests that the trigger behind its leaving the previous, eastern alluvial fan was that subsidence ceased in that area. The new OSL measurements provided a good tie-point for the sediments of the westward shifted and incised Middle Pleistocene Danube, they gave an age of 190.0 ± 17.9 ka for the sample taken from the borehole Paet-10 at 31.1 m depth (Thamó-Bozsó 2016a). Unfortunately, malacological data of older, more eastern Middle Pleistocene deposits do not allow for a more precise dating; therefore, it can only be stated that the westward displacement of the river happened some time during the Middle Pleistocene before 190 ka, and the duration of the process is not known.

Late Pleistocene

The formation of the modern Danube flood plain started in the Late Pleistocene (Figure 7, 8). On this 10 to 40 km wide

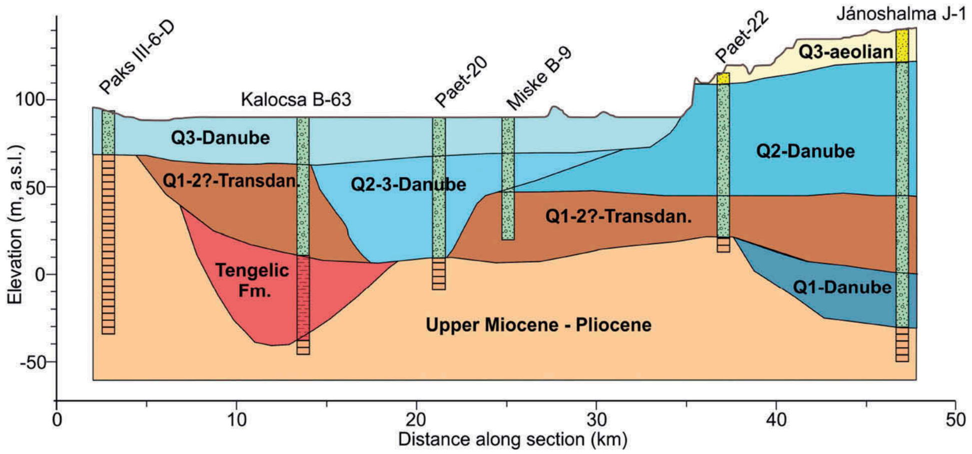

Figure 7. Geological cross-section across the Danube valley based on borehole data. For the location see Figures 5, 6 or 8. Q1, 2 and 3: Lower, Middle and Upper Pleistocene, respectively; Danube: sediments of the Danube; Transdan.: Transdanubian fluvial sediments; Q3-aeolian: – Upper Pleistocene to Holocene wind-blown sand. Note strong vertical exaggeration.

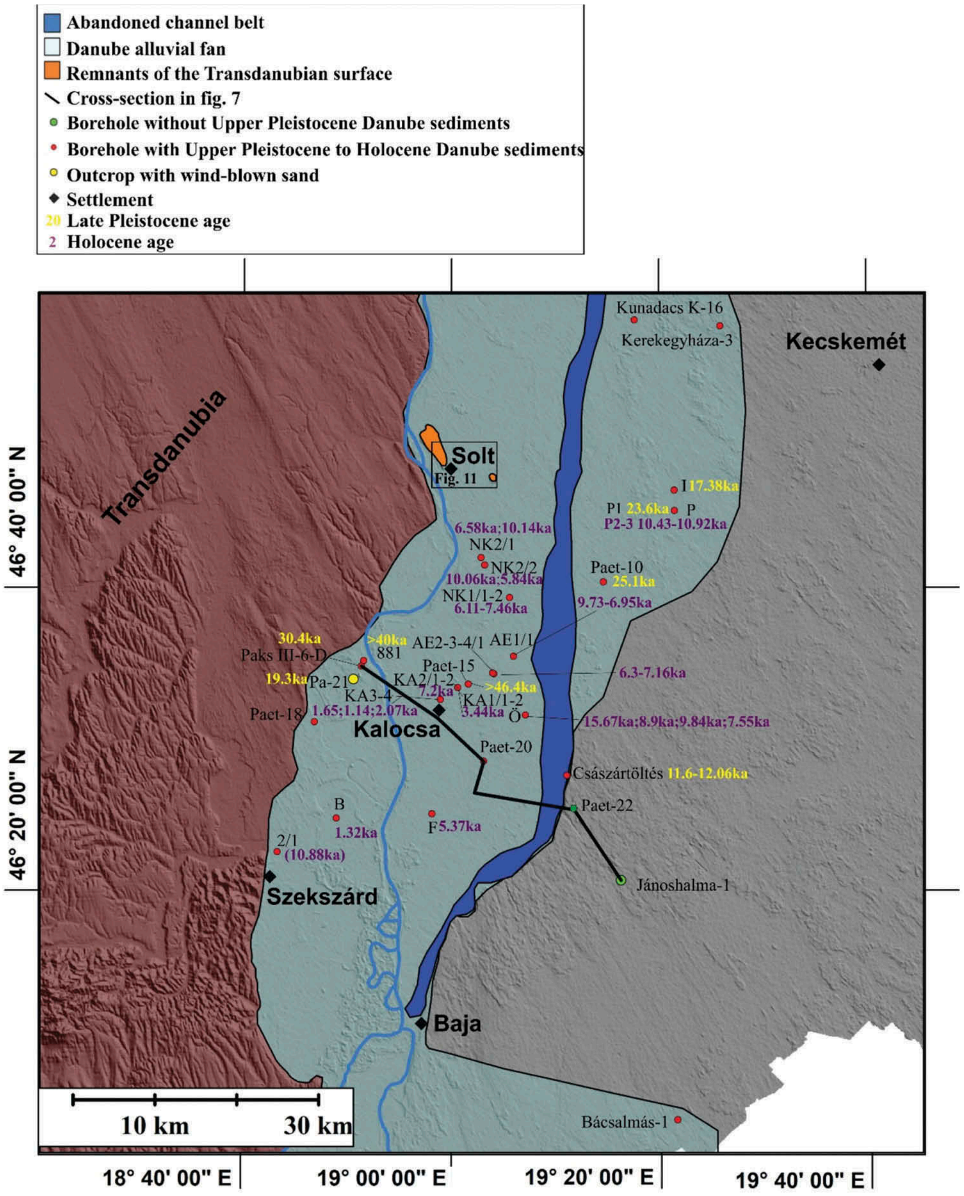

Figure 8. The Late Pleistocene alluvial fan of the Danube, with available numerical age data (from Hertelendi et al. 1989; Thamó-Bozsó 2016a, b, Isotoptech 2016; Törőcsik et al. 2018; Tóth 2019). Where ^{14}C is not indicated, measurement was performed using OSL method. For the geochronological data refer to Appendix 2.

plain the river created numerous channels, partly existing coevally, and this state ceased only by the river regulations in the 19th-20th centuries. Interestingly, the thickness of the Upper Pleistocene to Holocene Danube sediments on most of this wide floodplain is only around 30 m (max. 50 m) (Jaskó and Krolopp 1991). The position of the eastern margin of the floodplain is outlined by the thin (<10 m), malacologically dated floodplain succession of the Kunadacs well (Krolopp 1974), by the borehole of Kerekegyháza, where 35 m of terrestrial sediments with Upper Pleistocene dryland molluscs are intercalated with short fluvial intervals (Krolopp in Franyó 1980), by floodplain mollusc fauna in the well Bácsalmás-1 (28.2–55.7 m, Krolopp in Kovács 1992), and by boreholes (e.g. Jánoshalma and several wells east of the town Baja) which already lack Upper Pleistocene Danube deposits (Franyó 1988).

Several segments of the modern Danube follow areas of tectonically induced subsidence. The modern channel coincides with depressions in a horizon within the Upper Miocene Lake Pannon sediments (Figure 9, in bluish colours). This horizon, the top of the so-called Algyő Fm. (fine-grained sediments of the lake basin slope) was originally a flat surface, thus it, can be used to track uplift or subsidence of given areas. Tectonical subsidence disturbed the horizontal position of Lake Pannon sediments and attracted the modern Danube channel belt to its present position. The subsiding areas are typically small and bordered by faults. These fault have dominantly strike-slip kinematics (Bada et al. 2007; Koroknai et al. 2016), where steps and bends often induce the formation of laterally small but deep (pull-apart type) basins. East of the town Baja the marker horizon is significantly uplifted, and from the reconstructed palaeogeography, we see that the Danube bypassed this area in the Late Pleistocene (Figure 8), apparently diverted from here by local tectonic uplift.

Upper Pleistocene Danube sediments partly crop out on the modern floodplain, partly are covered by wind-blown sand. Beside the Holocene meanders, remnants of old, upfilled channels are still recognisable in the morphology. For instance, Figure 8 shows a long channel belt, which can be followed for tens of kms. For the Upper Pleistocene and Holocene fluvial deposits several numerical age data are available (Figure 8, Appendix 2). During the 2015–2016 research project OSL and ^{14}C measurements provided new data for Danube sediments in the Paet- and Paks III-6-D wells and for the overlying aeolian sands in the Pa-21 exploration trench (Isotoptech 2016; Thamó-Bozsó 2016b). Other projects acquired ^{14}C ages for the western part (wells Szekszárd 2/1 and Paks 881, Hertelendi et al. 1989) or for the entire width (Törőcsik et al. 2018; Tóth 2019) of the floodplain. From these the ~11 ka ^{14}C age in the borehole Szekszárd 2/1 at 23.3 m depth would require an unrealistically high subsidence rate and is thus not included in the interpretation. The spatial distribution of the age data displays no E-W trend. This can mean that in the past 50 ka the Danube has moved back and forth within its wide floodplain, or it had several parallel channels, or both of these are true. Measurements on Holocene deposits indicate that lateral shift of the channels was rapid, data from an interval of less than 6000 years (~11–5 ka) span the entire E-W width of the modern Danube valley (Törőcsik et al. 2018; Tóth 2019).

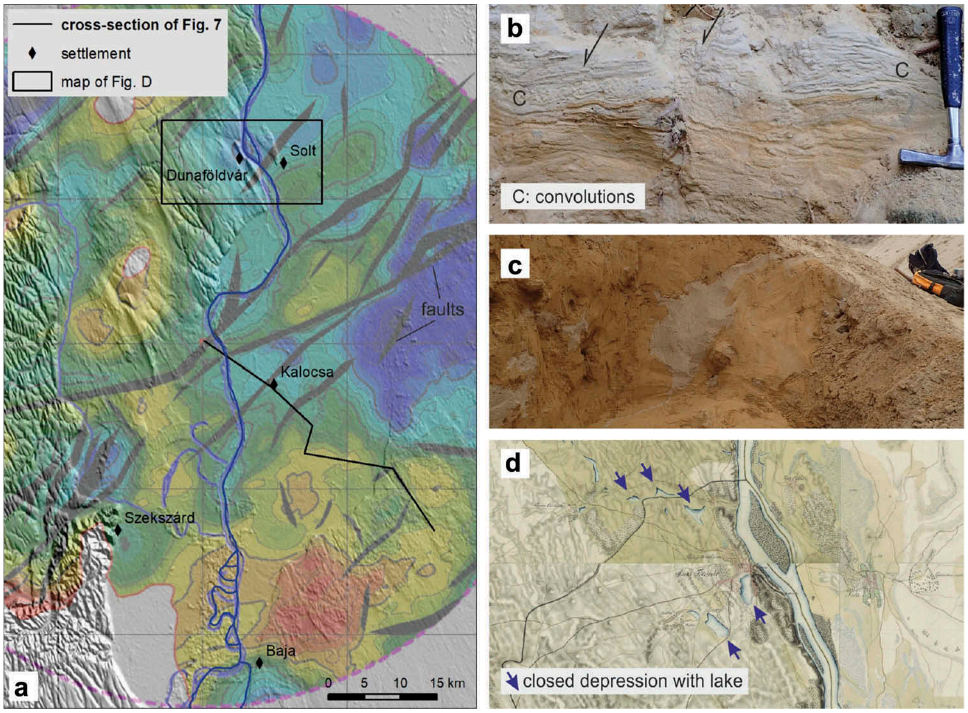

Figure 9. Linkage between tectonic movements and river channel changes along the Danube. (**A**) The modern course of the Danube above the elevation map of the top of an Upper Miocene Lake Pannon sedimentary unit (Algyő Fm.; source: Koroknai et al. 2016). Top of Algyő Fm. elevation ranges from −700 m (blue) to 0 m (red) and crops out in white areas. Thick black lines are faults mapped from seismic reflection profiles. (B-C) Seismically induced soft-sediment deformations: convolutions and small faults in Quaternary aeolian sand and silt in Dunaföldvár (B) and sand injectites in loess north of Solt (C). (D) Depressions filled by lakes (indicated by blue arrows) near Dunaföldvár in the map of the First military survey (1763–1787).

(source: Timár et al. 2011)

Along its eastern margin, small hills emerge above the Danube floodplain. These are relics of the ‘Transdanubian surface’, which have been separated from Transdanubia by the westward migrating river (Figure 8). These relics escaped obliteration by fluvial lateral erosion and thus prove that besides gradual channel shifts there occurred abrupt river course changes as well. Through these avulsions the channel was displaced into a completely new route, leaving an ‘island’ unaffected by fluvial processes on the opposite bank of the river. Re-routing is most probably tectonically induced in the above mentioned, fault-connected subsiding areas. Our field investigations revealed seismically induced soft-sediment deformations in Quaternary sediments among others on the two sides of one of these small basins, next to the relic Transdanubian surface by Solt (Figure 9(B,C)), which refer to the Quaternary activity of the faults. Small depressions with endorheic drainage and natural ponds (by now abolished by artificial draining) next to the river show that subsidence is still continuing (Figure 9(D)).

Discussion

Rivers as ecological barriers for ground squirrels

Large rivers are generally considered to be ecological barriers for ground squirrels (Popova et al. 2019 and references therein). Ground squirrels are small-bodied animals. *S. citellus* measures 18–24 cm (without tail) and weighs 170–430 g, and based on the size of its teeth, *S. citelloides* was also very close to these data. The two larger species, *S. primigenius* and the sexually dimorphic *S. major* (24.3–34 cm and 287–570 g) are not much larger either. With their small body suitable for steppe life and not for swimming, ground squirrels are refrained from crossing rivers. Besides, they spend the winters hibernating, when other animals are able to cross ice-covered watercourses. Molecular genetic investigations found a high level of genetic divergence between Little ground squirrel (*Spermophilus pygmaeus*) populations on the left and right banks of Volga river (Ermakov et al. 2006), showing that these populations have been isolated for thousands of year. The Dnieper separated the western and eastern forms of speckled ground squirrel (*Spermophilus suslicus* and *S. odessanus*) in the early Holocene (Brandler et al. 2015). The Danube has also been shown to be a barrier for recent gene flow for the European ground squirrel (*S. citellus*) (Ćosić et al. 2013; Říčanová et al. 2013). According to Popova et al. (2019), the geographical barrier effect can be reinforced by ecological factors (interspecific competition), if colonies of another ground squirrel species are present on the opposite river bank.

However, the above described geographic distribution of Quaternary ground squirrel species in Hungary indicates that during this period the Danube did not act as a significant barrier for them. Studies investigating the range dynamics of *Spermophilus* species showed that the range boundary between *S. citellus* and *S. citelloides* was of climatic/ecological nature, not a geographic barrier. The boundary experienced climatically induced oscillations, with *S. citelloides* expanding to the south during glacials, and *S. citellus* expanding to north during interglacials (Popova et al. 2019). This implies that both species had to cross the Danube several times. Phylogeographical investigations using mtDNA are in accord with this, stating that the Danube could not have been an unsurmountable obstacle for *S. citellus* on longer timescales (tens or hundreds of thousands of years) (Kryštufek et al. 2009; Říčanová et al. 2013; Németh et al. 2016).

It has been shown that the extant ground squirrel species of the area (*Spermophilus citellus*) is unable to swim across a river as wide as the Danube (Ćosić et al. 2013). Thus, it is reasonable to suppose that the extinct species (*S. citelloides, S. primigenius*), which were their close relatives, with very similar body size and behaviour, were likewise unable to accomplish this. For western Europe, it has been demonstrated that during cold periods of the Pleistocene many meandering rivers changed their flow patterns into braided (Mol et al. 2000). Braided rivers, with their more extreme discharge limits including very low base discharges, may be crossed more easily. However, in the Pannonian Basin, although rivers may also have partially changed their behavioural mode in response to climate changes, braided style was subordinate to meandering even during cold periods, and discharges could exceed even the interglacial values (Gábris and Nádor 2007; Nádor and Sztanó 2011, Cserkész-Nagy et al. 2012). Consequently, alternative solutions without swimming through rivers must be searched for to explain the distribution pattern of these animals.

Possible crossing mechanisms for ground squirrels

Ground squirrels – and other animals of similar size and unable to swim – can expand their ranges under normal circumstances maximum to the location of large rivers that act as barriers. They can get to the other side if the river is rerouted, cutting off a part of the population on the margin of the original range. In order to ‘transport’ sustainable (sub) populations across the river, two necessary conditions must be fulfiled:

1. the general direction of river course change (shifting) is opposite to the expansion direction of the population, and
2. a flood-free suitable habitat of sufficient size is maintained during the process.

These conditions can possibly be met during two scenarios.

Meander development

In meandering rivers overdeveloped meander loops are regularly cut off the main channel and transformed into an oxbow lake disconnected from the river. This process moves the inside of the loop to the other bank of the river (Figure 10), and if appropriate habitat is enclosed within the loop, animal populations can also be transported. The role of meander cut-offs in gene flow was demonstrated by Jackson and Austin (2013) for ground skinks on both banks of the Mississippi, a river with similar morphology and comparable discharge as the Danube. In case of the so-called entrenched rivers, whose meanders are deeply incised into plateaus, the meander loops can confine elevated, safely dry habitats. With lowland rivers like the Danube, meander development from a river curve is typically a continuous process, i.e. all parts of the area enclosed within a meander once were a channel, then

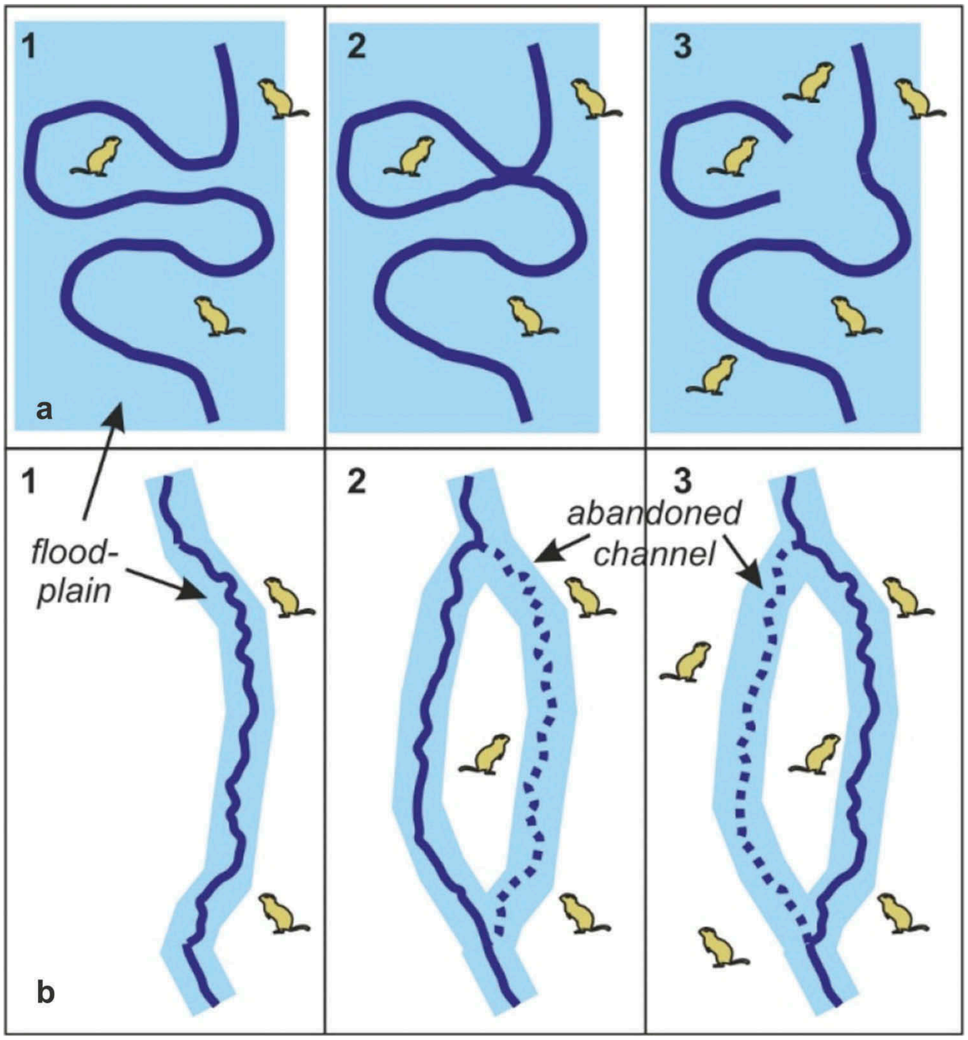

Figure 10. Mechanisms to cross a river through (A) meander cut-off; (B) avulsion.

a floodplain. Even after meander cut-off these terrains are flood-prone, thus not an ideal habitat for ground squirrels. Despite of this, small populations can survive in meander belts. These animals can excavate their burrows where the groundwater table is at a depth of minimum ~2 m (Katona et al. 2002). This may be fulfiled in a meander belt as well: in Hungary, some colonies live on the Danube floodplain, at spots hardly higher than other parts of the floodplain that still submerge every few years during great floods (Figure 11).

Avulsion

Avulsion means the diversion of flow out of an established river channel into a new permanent course (Slingerland and Smith 2004). It can occur if a new course offers a channel slope significantly steeper than the actual one. Avulsions are typically rapid events, often happening within a day (e.g. Ning 1990; Perignon 2007), though in other cases full avulsions may require centuries to complete (Slingerland and Smith 2004). Avulsion frequency varies widely, from a few decades to tens of thousands of years (Kraus and Aslan 1993; Slingerland and Smith 2004). Rivers with two or more interconnected channel belts on a floodplain termed anastomosing or anabranching in various terminology systems (e.g. Makaske 2001; Lewin and Ashworth 2014), are usually formed by avulsions (Makaske 2001). The individual channel belts of these rivers can be of any flow pattern, i.e. straight, meandering or braided. During avulsion events, the diverted flow often occupies pre-existing but inactive channels (Slingerland and Smith 2004). This means that the river has a tendency to switch back to previously abandoned channels. The oscillating channel changes can open a gateway for animal populations to cross the river (Figure 10).

In case of the Danube in the Pannonian Basin, its antecedent valley across the Transdanubian Range, i.e. the Danube Bend and its surroundings is inappropriate for crossing: here the river has had a single-thread, deep channel with steep rocky banks for at least the past 3 Ma. In contrast, long segments of its lowland reaches are characterised by large ‘islands’ encompassed by multiple river branches, like the Szigetköz and Csallóköz/Žitný ostrov areas in the Danube Basin, the Csepel Island at Budapest and the Mohács Island at the Hungarian-Serbian border (Figure 1). These segments with a multi-channel planform are known to have undergone river course changes during historical times (Pišút 2002; Pišút and Timár 2007; Timár and Pišút 2008; Faludi and Nebojszki 2008).

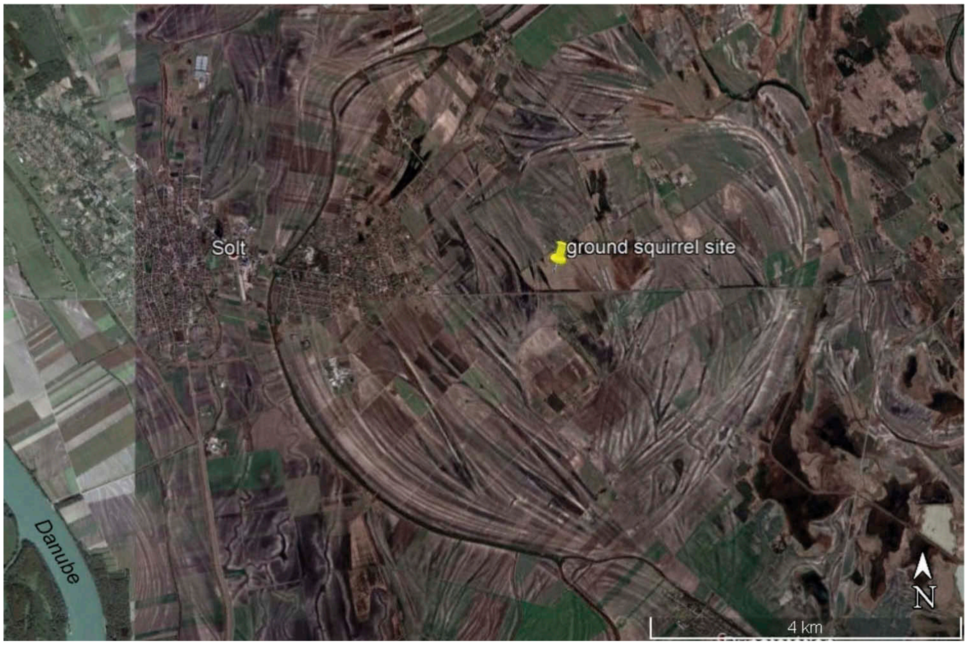

Figure 11. Geomorphological position of a ground squirrel habitat in the meander belt of the middle reach of the Danube. The colony lives among former point bar ridges, a landscape entirely transformed by the river. Satellite image from GoogleEarth. For location refer to Figure 8.

The dry areas between the shifting river branches can have been favourable habitats for ground squirrel colonies. Past switching of flow between river branches during geological and evolutionary timescales has been described in the previous chapters on the evolution history of the Danube. The largest shift of the river course occurred during the Pliocene, when in the NE Pannonian Basin the Danube moved from its southward flow direction to the current west-east one across the Danube Basin. In the Early Pleistocene the wide alluvial fan of the Danube was probably characterised by frequent channel changes. Boreholes around Jánoshalma (detailed above) record that the westward-moving Danube jumped back towards the east in this period, providing the counter-movement necessary for ground squirrel populations to get to the other side of the river. River course changes occurred not only the floodplains in a strict sense, but included more elevated areas ('islands') as well. For instance, the large shift during the Pliocene affected the entire Transdanubia (Figure 2). Similar, but smaller shifts were documented at the end of the Early Pleistocene, when the Danube moved from the Parndorf to the Devín Gate at its entrance to the Pannonian Basin (Šujan et al. 2018), or during the Late Pleistocene establishment of the modern channel west of the Solt Hill. These elevated topographical relics can be ideal stepping stones for animal populations due to their large areal extent and safely flood-free altitude, and can enable them to cross a large river. If after this physical opportunity for crossing a population does not colonise the terrain across the river, we cannot explain it by the geographical barrier. Instead, it is probably due to ecological factors, like the presence of a competitor species on the other bank, which can prevent the limited population of the new invader from taking roots, as illustrated by examples in Popova et al. (2019).

The evolution history of the Danube in the Pannonian Basin shows that besides autogenic river processes, at least some avulsions were triggered by tectonic movements. In uplifting areas tectonic movements influence and even drive speciation through the local topographic, climatic and drainage changes they cause (Craw et al. 2013, 2019; Szivák et al. 2017). The study presented here shows that in lowland areas tectonic movements are also capable of influencing biotic evolution, in this case by providing gateways for repeated gene exchange across a possible barrier.

Conclusions

- Four *Spermophilus* species lived in the Pannonian Basin during the Quaternary, without noticeable overlap in their temporal ranges: *S. primigenius* from 2 Ma to 500 ka, *S. citelloides* between 450 and 10 ka and *S. citellus* in the past 8 ka. There is a single record of *S. major* in the Middle Pleistocene (200–170 ka, Riss/Saale glaciation, MIS 6).
- All *Spermophilus* species having more than one paleontological record occurred on both sides of the Danube, implying that the animals were able to cross the Danube and extend their ranges on both sides.
- The course of the Danube in the central Pannonian Basin experienced considerable changes during the Quaternary. Its southern reach moved at least 100 km to the west, with most of this shift happening during the Early and Middle Pleistocene. The westward wandering was interrupted by temporary backward (eastward) movements of the river. The Middle Pleistocene saw an incision of the Danube valley as well.
- In the past 30 ka, the river has been using a ~ 40 km wide floodplain with several moving channels. Tectonically induced avulsions have played a role in re-routing the channels and in widening the floodplain towards the west.
- Hydrological events, most importantly rapid river course changes (avulsions) are a possible mechanism to enable ground squirrel and other small mammal populations to

cross a river. Meander cut-offs can also be effective, though probably they play a less important role due to less favourable character of habitats enclosed by floodplain meanders. River channel oscillation can ensure repeated gene exchange across the river, maintaining genetic similarity between populations on the opposite shores on the long run. Large rivers like the Danube can therefore be barriers on shorter – centennial or maximum millennial – timescales, but can be crossed and thus cease to be barriers after longer time intervals (tens/hundreds of thousands of years). These longer time intervals are defined by the recurrence time of hydrographic changes including channel reorganisations with avulsion.

- If large rivers as geographical objects are not necessarily unsurmountable barriers for small mammals, ecological factors (e.g. interspecific competition) may have more role in establishing rivers as apparent barriers than previously thought.
- In the Pannonian Basin, tectonically induced hydrographic changes seem to have played an important role in the phylogeographic evolution of ground squirrels. Their stabilising effect makes speciation in ground squirrels unlikely in the areas where channel oscillations allow river crossing. Tectonic processes in lowland areas can affect dispersal of animals and gene flow through river channel changes.

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Appendices

Appendix 1. Data of Quaternary *Spermophilus* occurrences in Hungary

	Ground squirrel species (number of specimens)					
Localities and layers with their estimated ages (ka)	*Spermophilus citellus*	*Spermophilus citelloides*	*Spermophilus major*	*Spermophilus primigenius*	References	Remarks
Bivak Cave yellow layer (18)	5				Jánossy et al. 1957	revision required
Bivak Cave yellowish grey layer (19)	2	1			Jánossy et al. 1957	revision required
Érd (73.5)		1			Gábori–Csánk and Kretzoi 1968	
Függőkő Cave layer 4 (25.5)		3			Jánossy et al. 1983	
Függőkő Cave layer 5 (25.5)		3			Jánossy et al. 1983	
Függőkő Cave layer 6 (25.5)		3			Jánossy et al. 1983	
Függőkő Cave layer 7 (25.5)		4			Jánossy et al. 1983	
Függőkő Cave layer 8 (25.5)		3			Jánossy et al. 1983	
Függőkő Cave layer 9 (25.5)		1			Jánossy et al. 1983	
Függőkő Cave layer I (25.5)		3			Jánossy et al. 1983	
Függőkő Cave layer II 26.2)		4			Jánossy et al. 1983	
Függőkő Cave layer III (27)		1			Jánossy et al. 1983	
Gencsapáti (26)		6			Kordos 1977	
Hórvölgy Cave (250)		7			Jánossy 1976a	
Istállóskő Cave (30)		5			Jánossy 1952	
Jankovich Cave (Kormos collection) (17)		211			Kormos and Lambrecht 1914; Sinitsa et al. this issue	
Jankovich Cave layer 1 (15)		2			Sinitsa et al. this issue	
Jankovich Cave layer 4 (15.3)		1			Sinitsa et al. this issue	
Jankovich Cave layer 6 (15.7)		12			Sinitsa et al. this issue	
Jankovich Cave layer 7 (15.9)		5			Sinitsa et al. this issue	
Jankovich Cave layer 8 (16)		11			Sinitsa et al. this issue	
Jankovich Cave layer 9 (16.5)		4			Sinitsa et al. this issue	
Jankovich Cave layer 10 (17)		3			Sinitsa et al. this issue	
Jankovich Cave layer 11 (17.5)		2			Sinitsa et al. this issue	
Kőrös Cave layer 5–7 (255)		2			Hír 1988	
Lambrecht Kálmán Cave (82)	8				Jánossy 1986	revision required
Nagyharsányhegy 4 (500)				*	Jánossy 1986	
Nagyharsányhegy 6 (250)		1			Jánossy 1976a	
Nagyoldal Hole (2)	1				Kordos 1981	
Osztramos 2 (1400)				2	Jánossy 1986	
Osztramos 3 (2000)				1	Jánossy 1986	
Osztramos 8 (1200)				15	Jánossy 1986	
Peskő Cave layer 11 (12)		1			Hír 1991	
Peskő Cave layer 16 (13)		1			Hír 1991	
Peskő Cave layer 19 (13.6)		1			Hír 1991	
Peskő Cave layer 20 (13.8)		1			Hír 1991	
Pilisszántó (20)		39			Kormos and Lambrecht 1915; Sinitsa et al. this issue	
Pongor-lyuk (270)		3			Hír 1986	
Por-lyuk (120)	9				Jánossy et al. 1972	revision required
Poros-lyuk (104)		7			Jánossy 1986	
Rigó-lyuk layer 1 (0.2)	6				Kordos 1984	
Rigó-lyuk layer 2 (0.3)	5				Kordos 1984	
Rigó-lyuk layer 3 (0.5)	4				Kordos 1984	
Rigó-lyuk layer 4 (0.8)	6				Kordos 1984	
Rigó-lyuk layer 5 (1.2)	3				Kordos 1984	
Rigó-lyuk layer 6–7 (1.8)	2				Kordos 1984	
Somssich Hill 2 (1000)				55*	Jánossy 1983	*unpublished data
Subalyuk layer 10–16 (64)	1				Jánossy 1986	revision required
Süttő 6 layer 2–3 (95)		10			Pazonyi et al. 2014	

(*Continued*)

(Continued).

Localities and layers with their estimated ages (ka)	Ground squirrel species (number of specimens) *Spermophilus citellus*	*Spermophilus citelloides*	*Spermophilus major*	*Spermophilus primigenius*	References	Remarks
Süttő 6 layer 4–5 (108)		3			Pazonyi et al. 2014	
Süttő 7 layer L (128)		4			Pazonyi et al. 2014	
Süttő 7 layer U (110)		2			Pazonyi et al. 2014	
Süttő 8 layer 2 (110)		5			Pazonyi et al. 2014	
Szelim Cave layer B (25)		84			Sinitsa et al. this issue	
Tata (100)		2			Kretzoi 1964	
Tatabánya, Kálvária-hegy 4 (105)		81			Kordos 1994b	
Tokod I (40)		10			Jánossy 1986	
Tokod II (80)		28			Gasparik 1993	
Újlaki-hegy (1200)				1	Jánossy and Topál 1990	
Uppony I layer 1 (170)			15		Jánossy 1986	
Uppony I layer 2 (175)			1		Jánossy 1986	
Uppony I layer 3 (180)			3		Jánossy 1986	
Uppony I layer 6 (205)			1		Jánossy 1986	
Várbarlang/Fortuna street 25 (310)		1			Jánossy 1986	
Várbarlang/Hotel Hilton (220)		15			Jánossy 1976a	
Várbarlang/Országház street 16 (320)		1			Jánossy 1986	
Vértesszőlős II (450)		1			Jánossy 1990	
Villány 3 (2000)				*	Jánossy 1986	
Villány 5 (1100)				14	Jánossy 1986	
Villány 6 (640)				5	Jánossy 1986	
Villány 8 (800)				7	Jánossy 1986	

Appendix 2. Geochronological data from Danube sediments cited in the text. For the location of boreholes, see Figures 5, 6 and 8

OSL data
Pleistocene

Site/drilling name	Depth (m)	Age (ka)	Reference
Paet-10	31.1	189.3 ± 17.9	Thamó-Bozsó 2016a
I	2.0	17.38 ± 0.6	Tóth 2019
Ö	4.75	15.67 ± 0.75	Tóth 2019
P1	2.0	23.6 ± 1,18	Tóth 2019
Pa-21	1.7–2.06	19.3 ± 1.5	Thamó-Bozsó 2016b
Paet-10	8.7–9.0	25.0 ± 2.1	Thamó-Bozsó 2016a
Paks III-6-D	18.7–19.2	30.0 ± 2.4	Thamó-Bozsó 2016a

Holocene

Site/drilling name	Depth (m)	Age (ka)	Reference
AE1/1	0.6	9.73 ± 0.42	Tóth 2019
AE1/2	1.3	9.19 ± 0.53	Tóth 2019
AE1/3	1.9	6.95 ± 0.71	Tóth 2019
AE/2	0.7	6.3 ± 0.37	Tóth 2019
AE/3	0.7	6.61 ± 0.34	Tóth 2019
AE/4	1.1	7.16 ± 0.62	Tóth 2019
B	2.0	1.32 ± 0.10	Tóth 2019
F	1.8	5.37 ± 0.24	Tóth 2019
KA1/1	2.2	3.44 ± 0.35	Tóth 2019
KA2/1	2.6	7.20 ± 0.46	Tóth 2019
KA3	0.8	1.65 ± 0.13	Tóth 2019
KA4	0.9	1.14 ± 0.14	Tóth 2019
KA4	2.4	2.07 0.17	Tóth 2019
NK1/1	1.1	7.46 ± 0.27	Tóth 2019
NK1/1	2.1	7.36 ± 0.27	Tóth 2019
NK1/2	1.0	6.11 ± 0.54	Tóth 2019
NK2/1	1.1	6.58 ± 1.22	Tóth 2019
NK2/1	2.6	10.14 ± 1.08	Tóth 2019
NK2/2	1.2	10.06 ± 0.43	Tóth 2019
NK2/2	2.0	5.84 ± 0.51	Tóth 2019
Ö	6.5	8.90 ± 0.35	Tóth 2019
Ö	7.75	9.84 ± 0.35	Tóth 2019
Ö	9.6	7.55 ± 0.28	Tóth 2019
P2	1.8	10.80 ± 0.66	Tóth 2019
P3	1.0	10.92 ± 0.04	Tóth 2019
P3	2.0	10.43 ± 0.71	Tóth 2019

Radiocarbon data
All ^{14}C ages appear as published

Site/drilling name	Depth (m)	conventional ^{14}C age (BP) (kyr)	^{14}C age cal BC (ka)	Reference
Paet-15	20.9–21.1	>49.40	1	Isotoptech 2016
Paet-22	22.5–26.8	>43.09	1	Isotoptech 2016
Paks-881	20.5	>40.00	1	Hertelendi et al. 1989
Császártöltés	2.6	11.96 ± 0.06	12.06–11.64	Törőcsik et al. 2018
Szekszárd-2/1	23.3	10.88 ± 0.15	2	Hertelendi et al. 1989

1. irrelevant for calibration due to old age.
2. not calibrated because of being an outlier providing uncomparably young age for its depth.