

THE VERTEBRATE FOSSIL ASSEMBLAGE FROM STĂUCENI (BOTOȘANI COUNTY, NORTHEASTERN ROMANIA): A MIXTURE OF MIOCENE AND PLIOCENE–PLEISTOCENE ELEMENTS REVEALING A COMPLEX SEDIMENTARY EVOLUTION ALONG THE MARGIN OF THE EAST EUROPEAN PLATFORM

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Associate Editor: Lorenzo Rook.

To cite this article: Vasile Ș., Haiduc B.-S., Crespo V.D., Kovalchuk O., Torcărescu B.-A., Țăbără D. & Loghin S. (2026) - The vertebrate fossil assemblage from Stăuceni (Botoșani County, northeastern Romania): a mixture of Miocene and Pliocene–Pleistocene elements revealing a complex sedimentary evolution along the margin of the East European Platform. *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 132(3): 633-654.

Keywords: mixed vertebrate assemblage; small mammals; cetaceans; fish fauna; fossil reworking.

Abstract: The fluvial deposits exposed at Stăuceni (northeastern Romania) have traditionally been assigned to the Miocene, due to the presence of cetaceans and seals. However, further investigation of the site has yielded additional fossils indicating a more complex depositional history of the site. Several fossiliferous layers, from the bottom to the top of the succession, yielded a mixed vertebrate assemblage including Miocene (kentriodontid and cetotheriid cetaceans, hipparion equids, sparid and merlucciid fishes) and Pliocene–Pleistocene (bovid artiodactyls, soricid eulipotyphlans, arvicoline, murid, sciurid, and spalacid rodents, lagomorphs, esocid and cyprinid fishes) taxa. The occurrence of *Microtus* (*Microtus*) *nivaloides* and *Arvicola* cf. *A. mosbachensis* supports a Middle Pleistocene age for the sedimentary succession, which contains reworked Miocene vertebrates, and rare Miocene foraminifers. The occurrence of Upper Pliocene palynomorphs suggests that Upper Pliocene units are also present at the very base of the succession. The mixed vertebrate assemblage from Stăuceni is not only significant for a better understanding of the local depositional setting, but also represents the only known site in Romania east of the Carpathians where Middle Pleistocene small mammals have been identified, thus providing important palaeogeographic information for this group. The occurrence of merlucciid remains is also unique for the Eastern Paratethyan realm, adding to the palaeobiogeographic importance of the site.

Received: June 10, 2026; accepted: September 14, 2026

INTRODUCTION

Fossil vertebrate assemblages provide essential evidence for reconstructing palaeoenvironments and establishing robust biostratigraphic frameworks throughout the European Neogene and Quaternary. Among these, small mammals, particularly voles, play a crucial role in refining chronological correlations owing to their rapid evolutionary rates and sensitivity to environmental change (e.g., Markova & Puzachenko 2018; Krokmal' et al. 2021, 2023; Popova et al. 2025). Marine mammals likewise provide valuable insights into the evolution of ancient seaways and the palaeobiogeography of the Paratethys region (Gol'din & Startsev 2016; Gol'din et al. 2014, 2020). Continental Pliocene–Pleistocene mammals further complement these datasets by documenting faunal turnover and dispersal events associated with climatic oscillations and environmental changes across Eurasia (Agadzhanyan 2012; Crespo et al. 2023). Together, these groups provide complementary records of the terrestrial and marine processes that shaped the faunal and environmental history of southeastern Europe. The Moldavian Platform, positioned at the junction between the East European Craton and the Carpathian Orogen, preserves a complex sedimentary succession ranging from the Miocene to the Quaternary (Săndulescu 1984; Ionesi 1994). Despite its significance, many fossil localities within this region remain insufficiently studied. The Stăuceni site in northeastern Romania is of particular interest because it yields a rare combination of Quaternary small mammals, reworked Miocene marine vertebrates, and Pliocene–Pleistocene continental mammals. This unusual association provides an opportunity to investigate faunal composition spanning distinct temporal intervals and depositional contexts within a single locality.

In this study, we present new data on vertebrate assemblages of different geological ages recovered from Stăuceni. Detailed systematic identifications, integrated with biostratigraphic and palaeoenvironmental analyses, allow us to refine the chronological framework of the site and better understand the depositional dynamics of the Moldavian Platform during the Middle and Late Pleistocene. The co-occurrence of reworked Miocene fossils and Pliocene–Pleistocene remains highlights the role of sedimentary processes on fossil redistribution and contributes to a broader understanding of

faunal dispersal and environmental change within the Eastern Paratethys.

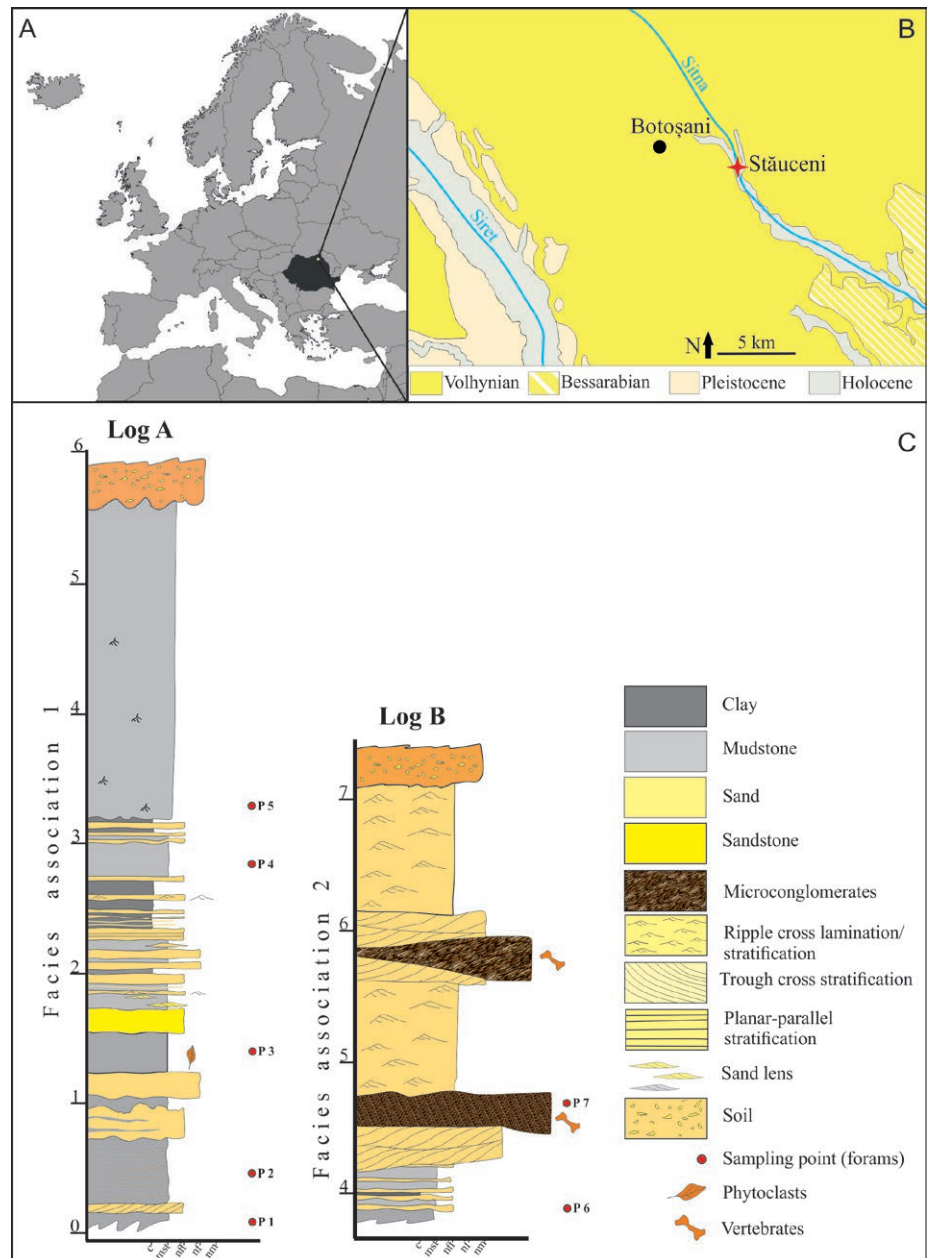
GEOLOGICAL SETTING

The village of Stăuceni, located in Botoșani County in northeastern Romania (Fig. 1A), lies within the Moldavian Platform, an area shaped by a long and complex geological evolution at the boundary between the East European Craton and the Carpathian Orogen (Săndulescu 1984). The region is dominated by Neogene and Quaternary sedimentary successions that rest upon a Precambrian–Paleozoic basement (Ionesi 1994).

The Moldavian Platform represents a stable cratonic unit characterised by a gently dipping sedimentary cover (Ionesi 1994). At Stăuceni, the exposed sedimentary succession encompasses both Miocene and Quaternary deposits (Fig. 1B). The lower part of the sequence belongs to the third accumulation megacycle, spanning the late Badenian (Kossovian) to the Maeotian, and corresponds to Volhynian (Middle Miocene) deposits of the Darabani-Mitoc clays and the Zlătunoaia limestone (Ionesi 1994; Brânzilă 1999; Ionesi et al. 2005; Gol'din et al. 2020). Overlying these units are Quaternary alluvial sediments (Badea et al. 1983; Brânzilă 1999). During the Middle Miocene, the Moldavian Platform functioned as part of a foreland basin system formed by the subduction of the western margin of the East European Platform beneath the Carpathian Orogen (Grasu et al. 1999, 2002). This tectonic setting generated four depozones – wedge-top, fore-deep, forebulge, and backbulge – *sensu* DeCelles & Giles (1996). The Stăuceni succession is interpreted as having accumulated within the backbulge depozone (Grasu et al. 2002).

Assigned by Brânzilă (1999) to the early Volhynian, the deposits from Stăuceni have, indeed, yielded a Miocene vertebrate assemblage including pinnipeds (indeterminate phocines) and cetaceans (kentriodontids) that agree with the Volhynian age (Gol'din et al. 2020). However, subsequent investigation, aimed at collecting additional specimens to increase the taxonomic diversity recorded from the site, led to the identification, in the same fossil beds bearing the Miocene marine mammals, of several vertebrate remains of strikingly different taphonomy. The newly found specimens were more fra-

Fig. 1 - A. Geographical location of the Stăuceni fossil site in northeastern Romania; B. General geological map of the area (after Saulea 1966); C. Sedimentary logs of the two main facies associations from Stăuceni (for the location of the two logs within the Stăuceni outcrop, see Supplementary Online Material 1).



gile, more brittle, and less mineralised when compared to the marine mammal remains that were much denser, heavier, and well mineralized. These new finds were followed by other, taxonomically more informative specimens that are described below, and were found to belong to Pliocene–Pleistocene continental vertebrates, which triggered a more thorough investigation of the outcrop that also led to the identification of small vertebrates, invertebrates, and palynomorphs.

The material described in this paper was collected from a single outcrop located northeast of Stăuceni village (Supplementary Online Material 1). The man-made outcrop, excavated in the flank of the hill to extract sand and gravel for local con-

structions, extends for about 60 m, largely on a northwest–southeast direction, facing southwest, and is around 8 m tall at its highest point. The sediments cropping out at Stăuceni do not exhibit lateral continuity, and, therefore, the entire outcrop was searched for vertebrate remains, six stratigraphic layers proving to yield more abundant fossil specimens (Supplementary Online Material 1): Layer A – a microconglomerate that yielded the first marine mammal remains described from the site (Gol'din et al. 2020), as well as additional marine and continental vertebrate remains described below; Layer B, also named ‘the ferruginous layer’ in the early field notes, consisting of iron-rich sandy deposits; Layer C, a layer of coarse sand, which appears to be the

lateral extension of Layer B, was also named ‘the metapodial layer’ in the field notes after yielding the hipparionine metatarsal described below; Layer D, a sandy mudstone bed, also named ‘the mollusc layer’, characterised by abundant molluscan remains; Layer E, the so-called ‘left layer’, a mudstone bed located on the left side of the quarry, as the viewer looks at the outcrop, and treated as an independent sampling unit; and Layer F, also from the left side of the quarry, a mudstone bed with fragmentary plant remains that was sampled for palynological analyses and yielded the only significant results in this respect. The heterolithic alternation of sands within mudstones indicates rhythmic sedimentation typical of floodplain environments (Miall 1982; Reading 1996). The presence of an incised channel truncating these deposits, along with trough cross-stratification, further points to fluvial processes and channel-bed dynamics consistent with sediment reworking and transport of older material (Fig. 1C, Log A). Such deposition is characteristic of overfilled foreland basins, where accumulation rates exceed subsidence (Galewski 1999). In the upper part of the outcrop, a second facies association – cross-stratified sands and conglomerates containing menilite clasts – records the activity of a fluvial depositional system (Fig. 1C, Log B). These deposits include mixed assemblages of Miocene and Pliocene–Pleistocene vertebrate remains (see below), reflecting continued sediment reworking and redistribution within the Quaternary landscape. The broader region is further mantled by widespread loess and alluvial sediments of Pleistocene and Holocene age, particularly along the valleys of the Prut and Jijia rivers (Badea et al. 1983).

MATERIAL AND METHODS

All fossil specimens were taxonomically identified through direct comparison to published reference material. In cases when species identification was impossible, the specimens were classified to higher taxonomic ranks. The descriptive osteological terminology follows Sturani & Sampò (1973), Szabó & Kocsis (2020), Szabó et al. (2021), and Dubikovska et al. (2025) for marine fishes, as well as Kovalchuk (2015) and Vasile et al. (2025) for freshwater fishes. The following comparative frameworks were used for small mammals: Michaux

(1971) for Muridae, Sarica & Sen (2003) for Spalacidae, Tesakov (2004) for Cricetidae, and Sinitsa & Pogodina (2019) for Sciuridae. Upper teeth of small mammals are referred to by capital letters (e.g., M1), whereas the lower ones are given in lowercase (e.g., m1). Specimens were examined under a stereomicroscope, and measurements were taken using digital callipers to the nearest 0.01 mm where preservation allowed. Dental morphology was recorded following standard terminology for each clade, including the assessment of crown height, enamel pattern, lobe configuration, cement distribution, and the presence or absence of roots. Marine mammal material was identified using diagnostic characters and comparative descriptions from the following sources: Gol’din et al. (2014) and Gol’din & Startsev (2016) for Cetotheriidae, and Kazár et al. (2004), Kazár (2005), Grigorescu & Kazár (2006), and Gol’din et al. (2020) for Kentriodontidae. In the case of seals (Phocidae), measurements follow Ericson & Stora (1999), whereas taxonomic criteria follow Koretsky (2001) and Otriazhyi et al. (2025). Postcranial elements were evaluated according to their state of preservation, surface morphology, centrum proportions, and the presence or absence of diagnostic structural features (e.g., neural arch). All vertebrate fossil material is housed at the Faculty of Geology and Geophysics, University of Bucharest, and catalogued under the specimen numbers provided in the Fossil vertebrate description section.

FOSSIL VERTEBRATE DESCRIPTION

Although not in systematic order, the fossil vertebrate remains are described below in the order in which they contributed to a better understanding of the stratigraphic context of the site: marine mammal remains were the first to be identified, leading to a first interpretation, in which the deposits have been considered Middle Miocene in age; continental large mammal remains, showing different taphonomy, and belonging to more recent (Pliocene–Pleistocene) taxa; continental small mammals, indicative of a Middle Pleistocene age; fish remains, also found by screen washing, like the small mammals remains, showing a mixture of older, Miocene, marine taxa, and more recent, likely Pliocene–Plei-

stocene freshwater taxa, adding information about palaeoenvironments and taxonomic composition of fish faunas during the two time intervals.

MARINE MAMMALS

Order **Carnivora** Bowdich, 1821

Family Phocidae Gray, 1821

Phocidae indet.

Figs. 2A1–4.

Material: One right distal tibial fragment (ST-21-21), lacking stratigraphic context (found *ex situ*, at the base of the outcrop).

Description and remarks. Distal epiphysis preserved; diaphysis long and slender. In distal view, the articular surface is slightly concave and rounded. Proximal condyles are missing, precluding a more precise diagnosis. Overall proportions and distal morphology are consistent with phocids (Chiriac & Grigorescu 1975; Koretsky 2001; Otriazhyi et al. 2025), although the lack of diagnostic characteristics only allows attribution to an indeterminate specimen within Phocidae.

Order **Cetacea** Brisson, 1762

Suborder **Mysticeti** Cope, 1891

Family Cetotheriidae Brandt, 1872

Cetotheriidae indet.

Figs. 2B1–2

Material: Layer A: one caudal vertebra (ST-01-21).

Description and remarks. Incomplete caudal vertebra with a short centrum bearing two circular articular faces; weak fusion indicates a juvenile. No lateral (transverse) processes; spinous process broken at base. Haemal arch facets present ventrally; pachyosteosclerosis is evident. Two lateral foramina pierce the centrum. Morphologically, this specimen resembles a similar vertebra also discovered in Stăuceni and described by Gol'din et al. (2020, Fig. 5H). The lack of diagnostic features makes an exact taxonomic assignment difficult. Based on pachyosteosclerosis, the specimen can be assigned to Cetotheriidae.

Suborder **Odontoceti** Flower, 1867

Family Kentriodontidae Slijper, 1936

Kentriodontidae indet.

Figs. 2C1–E2

Material: Layer A: nine caudal vertebrae (ST-02-21; ST-02-22; ST-04-21; ST-05-21; ST-06-21; ST-08-21; ST-11-21; ST-12-21; ST-41-22), seven lumbar vertebrae (ST-02-21, ST-07-21, ST-09-21, ST-10-21, ST-43-22, ST-44-22, ST-45-22), and two phalanges (ST-01-22A, ST-01-22B).

Description and remarks. All elements are fragmentary to moderately preserved and described below.

Several caudal morphotypes are recognised. Morphotype 1 (ST-04-21; ST-08-21; ST-12-21): small vertebrae with very short, high centra. ST-04-21 shows a small neural canal dorsally and paired foramina adjacent to haemal arch facets ventrally; ST-08-21 is heavily eroded; ST-12-21 bears a slightly longer centrum (likely due to better preservation), lacks transverse processes, retains a basal spinous remnant, and exhibits two small lateral foramina. These features indicate a position within the posterior caudal series. Small size and absence of pachyosteosclerosis support referral to kentriodontids (cf. Gol'din et al. 2020: Fig. 5D). Morphotype 2 (ST-05-21; Figs. 2E1–2): short-centered caudal vertebra, not as tall as Morphotype 1; articular surfaces and most processes missing; paired foramina at bases of the transverse processes; eroded haemal arch facets ventrally. Morphology consistent with small odontocetes; referred to Kentriodontidae indet. (cf. Gol'din et al. 2020: Fig. 5F). Morphotype 3 (ST-06-21; ST-11-21, Figs. 2D1–2; ST-41-21): better-preserved caudal vertebrae with long and slender centra; processes absent except for bases; narrow neural canal; distinct haemal arch facets. Overall proportions resemble those in the small delphinoid *Sophianaecetus commenticius* (Kazár, 2005). The specimens analysed were assigned to Kentriodontidae indet. as the closest identification is not possible for isolated vertebrae lacking reliable species- or even genus-specific diagnostic features.

Lumbar vertebrae (ST-02-21; ST-07-21, Figs. 2C1–2; ST-09-21; ST-10-21; ST-43-22; ST-44-22; ST-45-22) are all incomplete, with elongate, slender centra and circular articular facets; neural arches represented only by bases; transverse processes absent (bases only); long and narrow neural canals; no centrum foramina observed. Proportions and lack of pachyosteosclerosis indicate small odontocetes (cf. Gol'din et al. 2020: Fig. 5b, c) and support the assignment of these specimens to indeterminate taxa within the family Kentriodontidae.



Fig. 2 - Marine mammal remains from Stăuceni: A1–4 - Phocidae indet.: distal right tibia (ST-21-21) in anterior (A1), medial (A2), posterior (A3), and distal (A4) views; B1–2 - Cetotheriidae indet.: caudal vertebra (ST-01-21) in anterior (B1) and left lateral (B2) views; C1–E2 - Kentriodontidae indet.: C1–2. lumbar vertebra (ST-07-21); D1–2 - caudal vertebra (ST-11-21); E1–2 - caudal vertebra (ST-05-21), in anterior (C1, D1, E1) and left lateral (C2, D2, E2) views.

Specimens ST-01-22A and ST-01-22B represent two well-preserved, short, slender phalanges with dorsoventrally flattened diaphyses; articular surfaces are missing. Small size and dorso-ventral flattening are consistent with delphinoids (Kazár 2005); assigned to Kentriodontidae indet.

CONTINENTAL LARGE MAMMALS

Order **Artiodactyla** Owen, 1848

Family **Bovidae** Gray, 1821

Bovidae indet.

Figs. 3A1–D2

Material: Layer A: four molar fragments (ST-15-21; ST-18-21; ST-25-21; ST-26-21) and one premolar fragment (ST-20-21); Layer C: one second phalanx fragment (ST-33-22, Figs. 3C1–3), one complete M2 (ST-30-22, Figs. 3D1–2), and one distal humeral fragment (ST-22-21, Figs. 3A1–3); Layer D: two distal humeral fragments (ST-27-21; ST-40-22, Figs. 3B1–3).

Description and remarks. Humeri large but eroded and incomplete. In anterior view, the trochlea

and capitulum lie on an approximately straight line, contrasting with the slight obliquity typical of *Bison bison* (Linnaeus, 1758), and thus supporting attribution to *Bos primigenius* Bojanus, 1825 (cf. Bibikova 1958; Olsen 1960; Breda et al. 2010). The second phalanx, though partly eroded distally, shows a gentle U-shaped dorsal margin in lateral view – feature diagnostic of the genus *Bos* Linnaeus, 1758 rather than *Bison* Hamilton Smith, 1827 (Olsen 1960). The M2 crown morphology in occlusal view accords with *Bos primigenius* (Brudnicki et al. 2012). Measurements are not decisive owing to overlap with *Bison* (e.g., Breda et al. 2010). Due to the considerable overlap in the size and morphology of teeth and postcranial remains, although some evidence support the presence of *Bos primigenius* at Stăuceni, the scarcity and fragmentary nature of the material lead us to refrain from a definitive taxonomic assignment of the large bovid remains. We prefer to maintain an open designation until diagnostic material becomes available.

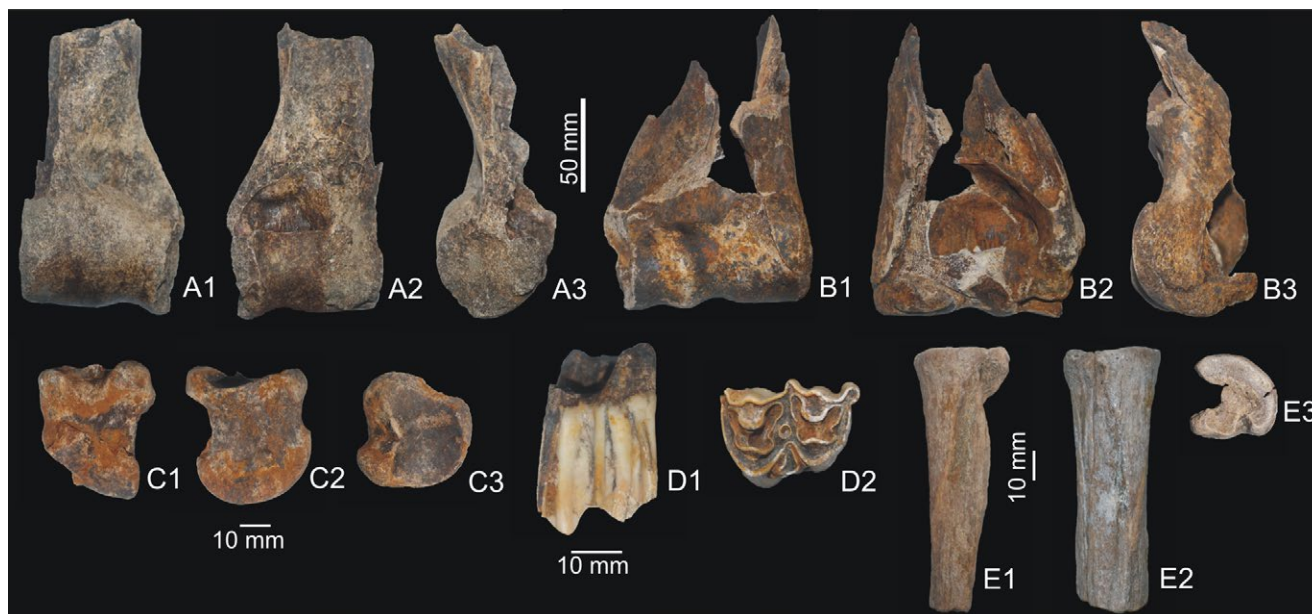


Fig. 3 - Continental large mammal remains from Stăuceni: A1–D2 - Bovidae indet. (*Bison priscus* or *Bos primigenius*): A1–3 - left distal humerus (ST-22-21); B1–3 - right distal humerus (ST-40-22); C1–3 - second phalanx (ST-33-22) in anterior (A1, B1), posterior (A2, B2, C1), lateral (A3, C2), medial (B3), and proximal (C3) views; D1–2 - left upper M2 (ST-30-22) in buccal (D1), and occlusal (D2) views; E1–3 - *Hipparion* sp.: proximal left third metatarsal (ST-23-21) in lateral (E1), anterior (E2), and proximal (E3) views.

Order **Perissodactyla** Owen, 1848

Family Equidae Gray, 1821

Genus *Hipparion* de Christol, 1832

Hipparion sp.

Figs. 3E1–3

Material: Layer C: one proximal metatarsal (ST-23-21).

Description and remarks. Proximal articular surface partly missing; diaphysis incomplete but slender and subcylindrical rather than flattened. Proximally, the articular surface is broad and well-developed. Only the third metatarsal is present; the second and fourth elements are not fused to MtIII, excluding *Equus* Linnaeus, 1758 (cf. MacFadden 1997; Janis & Bernor 2019). The combination of slender proportions and the lack of fusion of the lateral metapodials support an assignment to *Hipparion* sp.

CONTINENTAL SMALL MAMMALS

Order **Eulipotyphla** Waddell, Cao, Hauf &

Hasegawa, 1999

Family Soricidae Fischer, 1814

Soricidae gen. et sp. indet.

Material: Layer E: one fragment of a lower incisor (ST-Mm-001).

Description and remarks. A basal fragment

of a soricid incisor lacking diagnostic features; no further taxonomic resolution is possible.

Order **Rodentia** Bowdich, 1821

Family Cricetidae Fischer, 1817

Subfamily Arvicolinae Gray, 1821

Genus *Microtus* Schrank, 1798

Subgenus *Microtus* Schrank, 1798

Microtus (Microtus) nivaloides Forsyth Major, 1902

Figs. 4A1–2

Material: Layer C: three m1 (ST-Mm-002; ST-Mm-003: L: 2.89; M: 1.11, A: 1.59, H: 0.38, D: 0.31, E: 0.78, W: 0.98, C: 0.05; ST-Mm-004), two m2 (ST-Mm-005: L: 1.7, M: 1.13; ST-Mm-006: L: 1.55, W: 0.98), two m3 (ST-Mm-007: L: 1.48, M: 0.86; ST-Mm-008: L: 1.47, M: 0.88), two M1 (ST-Mm-009; ST-Mm-010), two M2 (ST-Mm-011: L: 1.63; M: 1.10; ST-Mm-012: L: 1.15, W: 0.85), one M3 (ST-Mm-013: L: 1.93, M: 0.98); Layer D: five m1 (ST-Mm-014: L: 2.78; M: 1.1, A: 1.26, H: 0.37, D: 0.16, E: 0.75, W: 0.92, C: 0; 3-2; ST-Mm-015; ST-Mm-016: L: -; M: -, A: 1.34, H: 0.51, D: 0.23, E: 0.59, W: 0.8, C: 0; ST-Mm-017; ST-Mm-018: L: -; M: -, A: 1.64, H: 0.49, D: 0.19, E: 0.82, W: 1.03, C: -; 4-15), five m2 (ST-Mm-019; ST-Mm-020; ST-Mm-021: L: 1.46, M: 1.02; ST-Mm-022: L: 1.56, M: 0.90;), two m3 (ST-Mm-023: L: 1.26, M: 0.75; ST-Mm-024), three M1 (ST-Mm-025: L: 1.90, W: 1.04; 2021-1-8: L: 1.90, W: 1.21; ST-Mm-026: L: 2.04, W: 1.21), two M2 (ST-Mm-027; ST-Mm-028), two M3 (ST-Mm-029; ST-Mm-030); Layer B: one m1 (ST-Mm-031: L: -; M: -; A: -; H: 0.70; D: 0.08; E: 0.83 W: -; C: -), one m3 (ST-Mm-032), one M1 (ST-Mm-033), one M3 (ST-Mm-034: L: 2.12; W: 1.14).

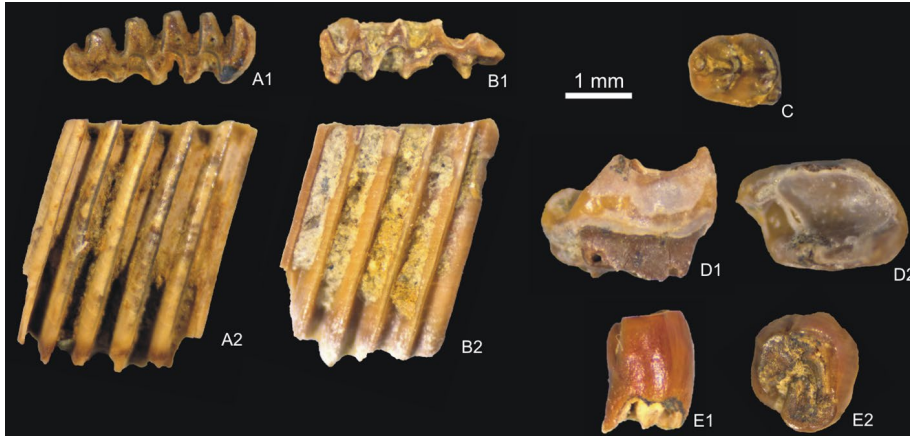


Fig. 4 - Continental small mammal remains from Stăuceni. A1–2 - *Microtus* (*Microtus*) *nivaloides*: left m1 (ST-Mm-003) in occlusal (A1) and buccal (A2) views; B1–2 - *Arvicola* cf. *A. mosbachensis*: right m3 (ST-Mm-036) in occlusal (B1) and lingual (B2) views; C - *Apodemus* ex. gr. *A. sylvaticus-flavicollis*: left m2 (ST-Mm-047) in occlusal view; D1–2 - *Spermophilus* cf. *S. nogaici*: left m1 (ST-Mm-048) in buccal (D1) and occlusal (D2) views; E1–2 - *Spalax* sp.: right M3 (ST-Mm-050) in buccal (E1) and occlusal (E2) views.

Description and remarks. The most common arvicoline at Stăuceni. The m1 typically bears five lingual and four labial salient angles; re-entrant angles, and the anterior cap is weakly developed. Teeth possess cement and lack roots. Overall morphology accords with *Microtus* (subgenera *Microtus* or *Terricola* Fatio, 1867), with the orientation of LRA3 and BRA2 excluding *Terricola*. The A/L ratio is borderline, lying on the boundary between *Microtus* (*Microtus*) *nivaloides* and *Microtus* (*Microtus*) *arvalis* (Pallas, 1779), whereas the D/E ratio is typical of *M. (M.) nivaloides*; the assemblage corresponds to the most derived evolutionary stage of *M. (M.) nivaloides* (Krokhmal' et al. 2021, 2023). Dimensions fall within the known range of the species (Pazonyi et al. 2018).

Genus *Arvicola* Lacépède, 1799

Arvicola cf. *A. mosbachensis* (Schmidtgen, 1911)

Figs. 4B1–2

Material: Layer C: one m3 (ST-Mm-035); Layer D: one m3 (ST-Mm-036: L: 1.05, W: 0.8), one M3 (ST-Mm-037: L: 2.65, W: 1.43); Layer B: one m1 (ST-Mm-038); Layer E: one M1 (ST-Mm-039: L: 2.46, W: 1.49).

Description and remarks. Fragmentary arvicoline remains are distinguished by large size, relatively rounded lobes, and reduced cement relative to *Microtus*. The M3 closely matches *Arvicola mosbachensis* as described and illustrated by Maul et al. (2000). Absence of roots excludes *Mimomys* Forsyth-Major, 1902 (Maul et al. 2000). Therefore, the material is best referred to as *Arvicola* cf. *A. mosbachensis*.

Genus *Lagurus* Gloger, 1841

Lagurus lagurus (Pallas, 1773)

Material: Layer C: four m2 (ST-Mm-040: L: 1.89, W: 1; ST-Mm-041: L: 2.02; W: 1.15; ST-Mm-042; ST-Mm-043); Layer D: one m1 (ST-Mm-044: L: 2.75; M: 0.95, A: 1.59, H: 0.71, D: 0.09, E: 0.88, W: 0.96, C: 0.04), one m2 (ST-Mm-045: L: 2.16, W: 1.30), one M3 (ST-Mm-046: L: 1.62, W: 0.68).

Description and remarks. Scarce Material: The m1 possesses a “laguroid” anteroconid type (Popov & Marinska 2007), with a characteristic dentine tract on the anterior lobe and no cement (Santel & von Koenigswald 1998). The A/L ratio is 0.57, within the range of *L. lagurus* (after Krokhmal' et al. 2021). *Lagurus transiens* Jánossy, 1962 is excluded by the presence of distinct re-entrant folds on the anterior cap (Santel & von Koenigswald 1998), absence of cement, and smaller size.

Family Muridae Illiger, 1811

Genus *Apodemus* Kaup 1829

Apodemus ex gr. *A. sylvaticus-flavicollis*
(Linnaeus, 1758/Melchior, 1834)

Fig. 4C

Material: Layer C: one m2 (ST-Mm-047: L: 1.40×W: 1.10).

Description and remarks. The tooth exhibits a well-developed tE and a very small c2; c1 and the external cingular margin are absent. Cusps tD–tC and tB–tA form convergent V-shaped connections. The medial crest is absent, and the cp is well-developed. The pattern is consistent with *Apodemus*, in which longitudinal cusp connections are rare and chevrons common (Martín-Suárez & Mein 1998). *Apodemus mystacinus* (Danford & Alston, 1877) is excluded (prominent external cin-

gular margin; Popov 1988); *Apodemus uralensis* (Pallas, 1811) and *Apodemus atavus* Heller, 1936 are ruled out by their smaller size (Hordijk & de Bruijn 2009; Knitlová & Horáček 2017). Separation of *A. sylvaticus* and *A. flavicollis* requires additional elements (Knitlová & Horáček 2017); the external cingular margin criterion (Jeannet & Mein 2016) is equivocal here. The identified material is, therefore, assigned to the *sylvaticus*–*flavicollis* group.

Family Sciuridae Fischer, 1817
Genus *Spermophilus* Cuvier, 1825

Spermophilus cf. *S. nogaici* (Topachevsky, 1957)
Figs. 4D1–2

Material: Layer D: one m1 (ST-Mm-048: L: 2.12, W: 2.57); Layer C: one upper molar fragment (ST-Mm-049).

Description and remarks. Subquadrangular crown; hypoconulid and entoconid weak, forming an almost continuous ridge to a robust metaconid; hypoconid is connected to protoconid by a strong ridge and a faint mesoconid; short but distinct metalophid; anterolophid enclosing a small trigonid basin. Size and morphology fit *S. nogaici* (Sinita & Pogodina 2019), but the limited material warrants a cautious assignment.

Family Spalacidae Gray, 1821
Genus *Spalax* Güldenstädt, 1770

Spalax sp.
Figs. 4E1–2

Material: Layer D: one M3 (ST-Mm-050: L: 1.82, W: 2.13).

Description and remarks. Subquadrangular M3 with a narrower posterior part. The anteroloph is well-developed and wide, and the two labial valleys are connected, although the anterior one is closed labially. The posterior valley is very deep, resulting in the mesoloph being isolated. The sinus is short and the posterior part of the tooth is unified. Sarica & Sen (2003) and Nowakowski et al. (2018) described a series of characters for the M3 of this family. Due to these characteristics, the specimen we are studying here is more similar to those of the genus *Spalax*, and we can include it in this genus. Additionally, we can rule out other genera, such as *Nannospalax* Palmer, 1903, due to their

size (Popov 2017). However, dental morphology in this family is highly variable due to wear, making species discrimination difficult (Skandalos & van der Hoek Ostende 2023).

Order **Lagomorpha** Brandt, 1855
Lagomorpha indet.

Material: Layer E: one tooth fragment (ST-Mm-051).

Description and remarks. Fragmentary element showing lagomorph dental morphology; insufficient for further identification.

FISHES

Class ACTINOPTERYGII Klein, 1885
Subdivision TELEOSTEI Müller, 1846
Order **Cypriniformes** Bleeker, 1859
Family Cyprinidae Bonaparte, 1832
Genus *Rutilus* Rafinesque, 1820

Rutilus sp.
Figs. 5A1–B2

Material: Layer C: two pharyngeal teeth (ST-Pi-001, Figs. 5A1–2; ST-Pi-067, Figs. 5B1–2).

Description and remarks. The assemblage includes two distinct morphotypes of pharyngeal teeth. The first morphotype is characterised by a robust crown with a gently arched dorsal margin that rises towards the apex, which terminates in a low, blunt hook (Figs. 5A1–2). The grinding surface is smooth and slopes gently towards the convex ventral surface. The second morphotype is markedly compressed laterally and exhibits a partially concave crown (Figs. 5B1–2). Its dorsal margin is straighter and more obliquely oriented, and an apical hook is absent. The grinding surface is narrow and concave, with slightly elevated and gently rounded margins relative to the central furrow. Several folds are present along the mesial margin near the ventral surface, whereas the lateral margin is entirely smooth. Constriction in the neck region is more pronounced than in the first morphotype. Overall, the morphology of these specimens is consistent with isolated pharyngeal teeth and allows their parsimonious attribution to *Rutilus* sp. (Kovalchuk 2015; Vasile et al. 2020, 2025).

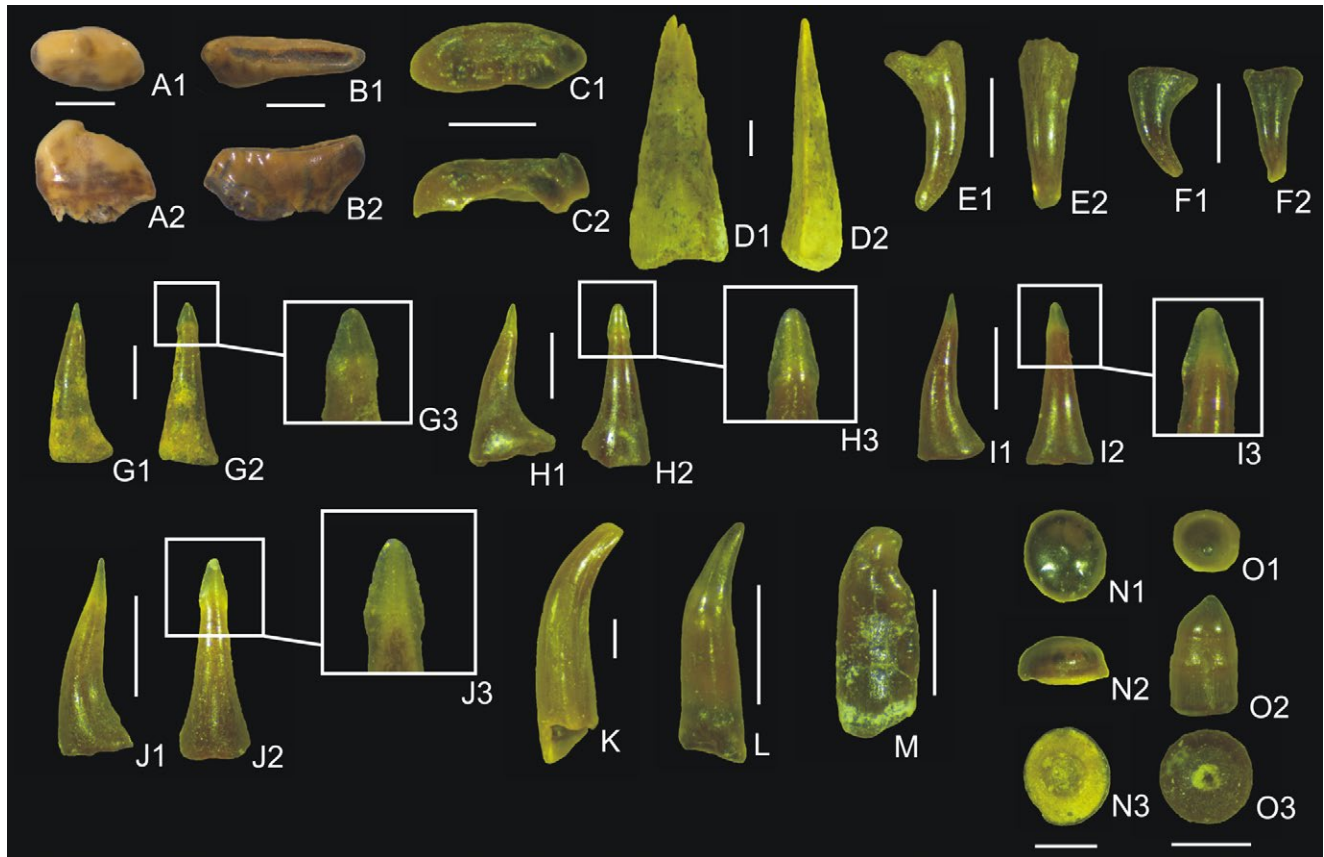


Fig. 5 - Fish remains from Stăuceni. A1–B1 - *Rutilus* sp.: pharyngeal teeth (A1–2: ST-Pi-001; B1–2: ST-Pi-067) in occlusal (A1, B1) and lateral (A2, B2); C1–2 - *Tinca* sp.: pharyngeal tooth (ST-Pi-002) in occlusal (D1) and lateral (D2) views; D1–F2 - *Esox* sp.: dentary tooth (D1–2: ST-Pi-003) and palatal teeth (E1–2: ST-Pi-005; F1–2: ST-Pi-006) in lateral (D1, E1, F1) and anterior (D2, E2, F2) views; G1–J3 - *Merluccius* sp.: teeth (G1–3: ST-Pi-012; H1–3: ST-Pi-014; I1–3: ST-Pi-013; J1–3: ST-Pi-015), in lateral (G1, H1, I1, J1) and anterior (G2, H2, I2, J2) views, with detailed views of the apical hook (G3, H3, I3, J3); K–M - *Dentex* sp.: teeth (K: ST-Pi-007; L: ST-Pi-040; M: ST-Pi-009) in lateral views; N1–O3 - Sparidae indet.: teeth (N1–3: ST-Pi-010; O1–3: ST-Pi-011) in apical (N1, O1), lateral (N2, O2), and basal (N3, O3) views.

Genus *Tinca* Cuvier, 1817

Tinca sp.

Figs. 5C1–2

Material: Layer B: one pharyngeal tooth (ST-Pi-002).

Description and remarks. Only the upper portion of the isolated tooth crown is preserved; the pedicle and neck are broken. The crown is anterodorsally compressed. A shallow, elongated depression extends along the entire length of the straight grinding surface and terminates laterally in a small hook with an upward-directed apex. The lateral margin of the grinding surface is smooth, whereas the mesial margin is distinctly wrinkled. The tooth belly is rounded. In its overall morphology, the pharyngeal tooth closely corresponds to specimens previously described as belonging to the genus *Tinca* (Gaudant 1994; Böhme 2002; Rückert-

Ülkümen & Yiğitbaş 2007; Kovalchuk 2015; Trif et al. 2016, 2022; Vasile et al. 2020, 2025). However, given the poor state of preservation, the specimen is left in open nomenclature.

Order **Esociformes** Bleeker, 1859

Family Esocidae Cuvier, 1817

Genus *Esox* Linnaeus, 1758

Esox sp.

Figs. 5D1–F2

Material: Layer C: two dentary teeth (ST-Pi-003, Figs. 5D1–2; ST-Pi-004), two palatal teeth (ST-Pi-005, Figs. 5E1–2; ST-Pi-006, Figs. 5F1–2).

Description and remarks. The dentary teeth are large and characterised by straight or slightly curved crowns that are strongly compressed laterally. A narrow cutting ridge extends along both the

anterior and posterior edges. Near the base, the teeth are lenticular in cross-section. In contrast, the palatal teeth are smaller, strongly curved, and nearly circular in cross section; their crowns are broad at the base and taper distally to a pointed tip. The tooth surface is smooth and convex and lacks cutting ridges. Overall, the specimens are indistinguishable from those of pikes (*Esox*), although species-level identification based on isolated teeth remains uncertain (Trif et al. 2016; Kovalchuk et al. 2017; Codrea et al. 2018; Vasile et al. 2020, 2025). Accordingly, the material is herein referred to as *Esox* sp.

Order **Gadiformes** Goodrich, 1909
Family Merlucciidae Rafinesque, 1815
Genus *Merluccius* Rafinesque, 1810

***Merluccius* sp.**

Figs. 5G1–J3

Material: Layer C: four teeth (ST-Pi-041–044); Layer D: five teeth (ST-Pi-45–49); Layer B: 28 teeth (ST-Pi-012–39).

Description and remarks. The isolated teeth are elongated, robust, and caniniform, with a thick and nearly cylindrical crown over most of their length. In lateral view, the teeth are gently curved, with the curvature becoming more pronounced towards the distal end. The crown tapers gradually apically and terminates in a sharp, pointed tip. A small but distinct distal barb is present at the apex, projecting slightly posteriorly; this feature is clearly visible in several specimens and represents a key diagnostic character of hakes (*Merluccius*). In cross-section, the crown is subcircular to weakly oval and shows no marked lateral compression. The basal part of the crown is noticeably expanded relative to the shaft, giving the tooth a stout appearance. The transition between the crown and the basal attachment area is gradual, and no distinct neck is developed. The basal surface is irregular and broken, indicating post-mortem damage or detachment from the jaw; the pedicle is not preserved. The enameloid surface is smooth, glossy, and homogeneous, lacking ornamentation, cutting edges, or longitudinal ridges, and no carinae are present along the margins. The pronounced surface sheen suggests relatively thick enameloid. Minor colour variation is observed, ranging from light brown to dark amber, likely reflecting diagenetic alteration rather than

original histological differences. In overall profile, the teeth closely resemble the anterior jaw dentition of hakes, which is characterised by stout, curved caniniform teeth with a terminal barb adapted for grasping prey. The combination of a thick, cylindrical crown, smooth enameloid, apical curvature, and the presence of a distal barb supports attribution to the genus *Merluccius*. However, because isolated gadiform teeth exhibit considerable interspecific overlap and lack reliable species-level diagnostic characters, assignment beyond the generic level is not possible based on the available material.

Order **Spariformes** Bleeker, 1876
Family Sparidae Rafinesque, 1810
Genus *Dentex* Cuvier, 1814

***Dentex* sp.**

Figs. 5K–M

Material: Layer C: two teeth (ST-Pi-009, Fig. 5M; ST-Pi-040, Fig. 5L); Layer B: two teeth (ST-Pi-007, Fig. 5K; ST-Pi-008).

Description and remarks. The caniniform teeth vary in size and are characterised by a curved profile and a circular cross-section. They are taller than wide, with the greatest width near the base, from where they taper gradually towards the apex. The tooth surfaces are covered by smooth enameloid and lack any ornamentation or cutting edges. Each tooth contains a distinct pulp cavity surrounded by a thick layer of dentine. The specimens attributed to *Dentex* sp. resemble those reported from the Middle Miocene of Hungary (Szabó & Kocsis 2020) and Ukraine (Dubikovska et al. 2025) in overall shape and proportions.

Sparidae gen. et sp. indet.
Figs. 5N1–O3

Material: Layer D: one tooth (ST-Pi-011, Figs. 5O1–3); Layer B: one tooth (ST-Pi-010, Figs. N1–3).

Description and remarks. The specimens exhibit molariform morphology, with hemispherical crowns that are circular in cross-section. The teeth are covered by smooth, thick enameloid, and each bears a large basal pulp cavity. All specimens display morphological features typical of sparid teeth. However, owing to the low diagnostic value of

isolated sparid teeth (Jonet 1975; Szabó & Kocsis 2020; Dubikovska et al. 2025), the material can be confidently assigned only at the family level.

TELEOSTEI indet.

Material: Layer C: one bone fragment (ST-Pi-050); Layer D: three rib fragments (ST-Pi-051–053); Layer B: 11 vertebrae centra (ST-Pi-054–064), two bone fragments (ST-Pi-065–066).

Description and remarks. The small vertebral centra, ribs, and other bone fragments are highly fragmentary and display only very general morphological features. Consequently, they cannot be identified even at the order level.

DISCUSSION

Marine mammals are represented at Stăuceni by fragmentary remains embedded within ferruginous sandy gravels (Layers A and B). Their high density, strong mineralization, and poor preservation contrast sharply with the condition of the Pliocene–Pleistocene terrestrial remains. These taphonomic attributes, together with their exclusively Miocene affinities, indicate that the marine mammal fossils were reworked from older Paratethyan deposits and incorporated into younger Pliocene–Pleistocene fluvial or alluvial sediments. Although their fragmentary nature prevents precise taxonomic assessment, the presence of phocids, cetotheriids, and kentriodontids is consistent with previously documented Middle Miocene marine vertebrate assemblages of the Eastern Paratethys (Gol'din et al. 2014; Gol'din & Startsev 2016; Gol'din et al. 2020). Their occurrence at Stăuceni thus reflects local sedimentary reworking rather than contemporaneous marine conditions.

Continental large mammals are only represented by a few specimens of taxonomic relevance. Dental and postcranial remains found in Layer A have been assigned to an indeterminate bovid, either the steppe bison, *Bison priscus* (Bojanus, 1825), or the aurochs, *Bos primigenius*, two large bovids widespread across Europe during the Middle Pleistocene–Late Holocene interval (e.g., Petronio et al. 2011; Masini et al. 2013). The steppe bison and aurochs are present in numerous Late Pleistocene faunal assemblages of Romania (e.g., Apostol & Vicoveanu 1970; Apostol 1976, 1981; Apostol & Cacoveanu 1980),

and aurochs remains are also frequently encountered in Neolithic-to-Mediaeval zooarchaeological assemblages (Bejenaru et al. 2012). The presence of *Bison priscus* or *Bos primigenius* remains in Layers A, C, and D of the succession from Stăuceni (Tab. 1) shows the deposits must have accumulated sometime between the Middle Pleistocene and the Holocene. A single proximal metatarsal, found in Layer C, was assigned to an indeterminate *Hipparion*. Hipparions are a common find in Upper Miocene to Lower Pliocene faunal assemblages of the Mediterranean and East European regions, reaching high taxonomic diversity (e.g., Bernor et al. 2021). The westernmost part of the Eastern European Platform, including the Moldavian Plateau of eastern Romania and Moldova, is no exception, hipparions representing some of the most common herbivores of the Middle and Late Miocene, also occurring during the Early Pliocene (for a list of hipparion occurrences in Romania, see Macarovici 1978 and references therein). The fragmentary third metatarsal from Stăuceni offers no diagnostic features for a more precise assignment, and is assigned to *Hipparion sensu lato*, broadly including all Miocene to Pliocene taxa known from the region. It is, nonetheless, a rare find in the region, since hipparions are more often found in sites of the central and southern Moldavian Plateau, farther south. Though most Romanian hipparion faunas are of Late Miocene age, it is worth noting that two of the oldest occurrences in the country, from Păun and Răducăneni (both localities in Iași County), also the two northernmost sites, closer to Stăuceni, date back to the Middle Miocene (Khersonian and, respectively, Bessarabian; Macarovici 1957; Codrea et al. 1992). Since hipparions were present in eastern Romania from the Middle Miocene to the Pliocene, with peak abundance during the latest Miocene, the hipparion metatarsal from Stăuceni, found in Layer C alongside geologically younger taxa, is, like the marine mammal remains, considered to have been redeposited from older formations.

The small mammal assemblage from Stăuceni provides the most reliable biostratigraphic indicators for the site, as arvicolids remain the principal group used for correlating Middle Pleistocene faunas of Europe (Markova & Puzachenko 2018; Krokhmal' et al. 2021, 2023). The dominance of *Microtus* (*Microtus*) *nivaloides* is particularly informative. Its morphological traits correspond to the

Tab. 1 - Fossil vertebrate taxonomic distribution for each layer of the Stăuceni succession and the age indicated by each taxon.

Age/Layer Taxon	Age	Layer A	Layer B	Layer C	Layer D	Layer E
Phocidae indet. (<i>ex situ</i>)	Miocene	-	-	-	-	-
Cetotheriidae indet.	Miocene	x	-	-	-	-
Kentriodontidae indet.	Miocene	x	-	-	-	-
Bovidae indet. (<i>Bison priscus</i> / <i>Bos primigenius</i>)	Pleistocene–Holocene	x	-	x	x	-
<i>Hipparion</i> sp.	Middle Miocene–Pliocene	-	-	x	-	-
Soricidae gen. et sp. indet	-	-	-	-	-	x
<i>Microtus</i> (<i>Microtus</i>) <i>nivaloides</i>	Middle Pleistocene	-	x	x	x	-
<i>Arvicola</i> cf. <i>A. mosbachensis</i>	Middle Pleistocene	-	x	x	x	x
<i>Lagurus lagurus</i>	Middle Pleistocene–Holocene	-	-	x	x	-
<i>Apodemus</i> ex gr. <i>A. sylvaticus</i> – <i>flavicollis</i>	Middle Pleistocene	-	-	x	-	-
<i>Spermophilus</i> cf. <i>S. nogaici</i>	Late Pliocene–Middle Pleistocene	-	-	x	x	-
<i>Spalax</i> sp.	middle Pliocene–Holocene	-	-	-	x	-
Lagomorpha indet.	Pliocene–Holocene	-	-	-	-	x
<i>Rutilus</i> sp.	Pleistocene?	-	-	x	-	-
<i>Tinca</i> sp.	Pleistocene?	-	x	-	-	-
<i>Esox</i> sp.	Pleistocene?	-	-	x	-	-
<i>Merluccius</i> sp.	Middle Miocene	-	x	x	x	-
<i>Dentex</i> sp.	Middle Miocene	-	x	x	-	-
Sparidae gen. et sp. indet.	Middle Miocene	-	x	-	x	-
Teleostei indet.	-	-	x	x	x	-

most advanced evolutionary stage of the species described by Krokmal' et al. (2021), which is characteristic of deposits dating to the upper part of the Chibanian (MIS 11–7). This would place part of the Stăuceni small mammal assemblage within a relatively young Middle Pleistocene interval. In contrast, *Arvicola* cf. *A. mosbachensis* is represented at Stăuceni by specimens that fall within the primitive morphological range of the species, comparable to material belonging to MIS 9 (Krokmal' et al. 2021, 2023). Although *Arvicola* is an important biostratigraphic marker within the Middle Pleistocene, the reduction in size and the evolutionary progression of *A. mosbachensis* are not strictly linear across Europe, and local environmental factors may also influence morphological variation (Desclaux et al. 2026). Nonetheless, the occurrence of such an early morphotype at Stăuceni complicates the biostratigraphic signal and suggests mixing of material from slightly different Middle Pleistocene intervals.

Other small-mammal taxa recovered from the site provide limited biostratigraphical refinement. The taxon *Apodemus* ex gr. *A. sylvaticus*–*flavicollis* comprises modern species groups that emerged early in the Middle Pleistocene (Jeannet & Mein 2016) and, therefore, do not further narrow the age range. *Spermophilus* cf. *S. nogaici* similarly spans a broad temporal interval from the Late Pliocene to the Middle Pleistocene (Sinita & Pogodina 2019;

Crespo et al. 2023), whereas the genus *Spalax* has a long history extending from the mid-Pliocene to the present day (Topachevsky 1969; de Bruijn 1984; Şen & Sarica 2011). These taxa corroborate a Middle Pleistocene age but cannot constrain the chronology more precisely.

In addition to the important biostratigraphic information, which helps understand the depositional history of the site, the small mammal assemblage from Stăuceni is also important from a palaeobiogeographic viewpoint, as it is the only fossil locality in Romania east of the Carpathians to have yielded Middle Pleistocene small mammals. The occurrence of the above-mentioned taxa at Stăuceni enhances the knowledge on their palaeobiogeographic distribution, confirming their presence in northeastern Romania.

The fish assemblage from Stăuceni is relatively small, comprising 67 specimens, including 41 from Layer B, 15 specimens from Layer C, and 11 specimens from Layer D. Preservation is generally poor, and the diagnostic potential of the material is limited; none of the recovered skeletal elements could be identified to species level. Nevertheless, 48 specimens (71.6%) could be assigned to the generic level. Such a proportion of taxonomically informative material is relatively high for assemblages dominated by isolated teeth and highly fragmentary bones and allows for cautious palaeoecological interpretation.

Despite their fragmentary condition, the assemblage is notable in consisting of remains attributable to both marine and freshwater taxa. This taxonomic heterogeneity points to a complex depositional and post-depositional history of the site.

Several observations can be made at the family level. Layer D yielded exclusively marine fishes, represented by Sparidae and Merlucciidae. This association is consistent with deposition under fully marine conditions and agrees well with the abundant mollusc shell fragments present in this layer. However, co-occurrence with Middle Pleistocene-indicative small mammals (Tab. 1) argues for a redeposition of older, marine fish specimens in a Middle Pleistocene freshwater environment. A comparable pattern is observed in Layer B, which contains the same taxa, together with a single pharyngeal tooth of tench *Tinca* sp. In contrast, Layer C differs markedly from the other two samples: sparids are entirely absent, hakes are represented only sporadically, and freshwater and/or brackish-water taxa – namely roach *Rutilus* sp. and pike *Esox* sp. – dominate the assemblage. This shift in taxonomic composition suggests substantially different environmental conditions during the formation of Layer C. Such a mixed ichthyofaunal composition suggests that at least part of the osteological material may have been redeposited from older, most likely Middle Miocene, strata. Reworking of Neogene material is a well-documented phenomenon in many Pleistocene and upper Neogene deposits of Europe. However, this interpretation appears less likely for Layer C, particularly given the presence of pike teeth derived from both the dentary and palatine. The occurrence of elements from different parts of the jaw argues against long-distance transport and supports a more local origin of these remains.

Isolated skeletal elements of sparids are frequently recorded in the fossil record of Central and Eastern Europe (Jonet 1975; Böhme & Ilg 2003; Gregorová 2009; Schultz et al. 2010; Mikuž et al. 2013, 2017; Trif & Codrea 2017; Szabó & Kocsis 2020; Szabó et al. 2021; Schwarzhans et al. 2022, 2024; Dubikovska et al. 2025; Vasile et al. 2025). They have also been reported from Pleistocene deposits within the Eastern Paratethys (Šoster & Kovalchuk 2016; Kovalchuk 2017), although they are interpreted as reworked Neogene material. The repeated occurrence of sparid remains in reworked contexts highlights their high preservation potential

and resistance to post-depositional destruction.

The precise age of the cyprinid and esocid remains from Stăuceni cannot be confidently established owing to the absence of biostratigraphically diagnostic fish taxa. Both families are commonly recorded from deposits spanning a wide temporal range across the studied region. Cyprinids and esocids have long stratigraphic ranges in Eurasia (Kovalchuk 2017) and show limited morphological change at the level of isolated teeth, further complicating age assessment. Although Pleistocene age for these remains is conceivable, the poor preservation and high degree of fragmentation of the material preclude a more definitive interpretation, and we therefore refrain from advancing speculative age assignments based on the composition of the fish assemblage.

The discovery of numerous isolated hake teeth in the Stăuceni material is particularly noteworthy. Skeletal remains of *Merluccius* are quite rare in the Neogene of Europe and are predominantly known from Messinian (7.2–6.0 Ma) and Piacenzian (3.6–2.0 Ma) deposits in the Mediterranean region (Gaudant 2002; Gaudant et al. 2010; Carnevale et al. 2022). To our knowledge, remains of these fishes have not yet been reported from the Paratethyan area. Thus, the Stăuceni material potentially represents the first documented discovery of hake skeletal elements in Eastern Europe. This finding substantially expands the known palaeogeographic range of the genus during the Neogene. Meanwhile, numerous (though often fragmentary or juvenile) *Merluccius* otoliths have been described from Europe. Based on the comprehensive systematic review by Schwarzhans (2024), several species occur in European deposits of different ages: *Merluccius aequipar* Schwarzhans, 2024, *Merluccius albidus* (Mitchill, 1818), *Merluccius brevis* Leriche, 1926, *Merluccius kokeni* Schwarzhans, 2024, *Merluccius leptus* Schwarzhans, 2024, *Merluccius merluccius* (Linnaeus, 1758), and *Merluccius rattaxzii* Lin, Brzobohatý, Nolf & Girone, 2017. The detailed tooth morphology described above closely resembles that of *Merluccius merluccius*, but we refrain from assigning the Stăuceni material to that species due to its fragmentary condition and the fact that *M. merluccius* is the only species represented in our comparison collection. Although there are numerous records of *M. merluccius* from the Miocene of Europe, most are based on misidentified otoliths and in fact belong to differ-

ent extinct species (see Schwarzhans 2024 for more details).

The hake tooth finds from Stăuceni may signal historic marine connections within the Paratethys, possibly linked to Late Miocene sea-level fluctuations. Such connections may have facilitated episodic dispersal of marine taxa into marginal basins otherwise dominated by restricted or brackish conditions. Reviewing the Stăuceni assemblage for associated otoliths could significantly advance taxonomic resolution following Schwarzhans (2024). Future discoveries of more complete skeletal material would also be critical for clarifying the taxonomic status of *Merluccius* in the Paratethyan realm. Radiometric or biostratigraphic dating of the layers may also refine their age within marine episodes of the Paratethys.

Palynological analyses conducted on two samples from the base of the Stăuceni outcrop, Layer F, provide additional environmental insights. Although total palynomorph abundance is low, the assemblage is dominated by the freshwater phytoplankton *Sigmopollis laevigatoides* Krutzsch & Pacltová, 1990 (Figs. 6A–B), a taxon characteristic of freshwater facies and known to reach peak abundance in Dacian age (i.e. Late Pliocene) deposits of the central Dacian Basin (Casas-Gallego et al., 2020). Angiosperm pollen, including *Tricolporopollenites microhenrici* (Potonié, 1931) Potonié et al., 1950 (oak; Fig. 6C), Gramineae (grass; Fig. 6D), and *Carpinipites carpinoides* (Pflug, 1953) Nagy, 1985 (hornbeam; Fig. 6G), as well as rare gymnosperm (*Ginkgo* sp. Lubert & Waltz, 1941; Fig. 6F) and fern spores (*Laevigatosporites gracilis* Wilson & Webster, 1946; Fig. 6E), indicate a mixed mesophytic forest in the surrounding region (Țabără 2008). The presence of well-preserved *Tytthodiscus* Norem, 1955 phytoplankton specimens (Fig. 6H) is best explained as reworking from Sarmatian or older (Oligocene) deposits. Overall, the dominance of freshwater algae and the composition of the palynofacies, including rare cuticles (Fig. 6J) and fossil resin (amber, Fig. 6I), support a lacustrine to deltaic palaeoenvironment with a strong freshwater influence. Layer F, the only bed in the succession to have yielded palynomorphs, is located at the very base of the succession, representing a distinct facies, dominated by mudstone, rich in phytoclasts. The occurrence of Late Pliocene taxa suggests a more complex architecture of the Stăuceni succes-

sion, one in which Pliocene deposits also occur beneath the Middle Pleistocene ones. The exact relation between these deposits is, however, not clear, as no evident unconformity could be seen on site.

The identified micropalaeontological assemblage (Figs. 7A–I) contains typically Sarmatian foraminifera and mysid statoliths. Their state of preservation showing corroded and/or abraded tests is indicating a postmortem transport, as described by Holcová (1996, 1999) for the Middle Miocene of Central Paratethys. The *Elphidium rugosum* (d'Orbigny, 1846) and *Elphidium macellum* (Fichtel & Moll, 1798) species are typical for the Volhynian deposits from the Eastern Carpathians Foreland Basin, indicating that the source of the sediments from Stăuceni was represented by pre-existent emerged upper Middle Miocene sedimentary formations.

CONCLUSIONS

Together, the combined faunal, palynological, and sedimentological evidence indicate a complex depositional history at Stăuceni. The coexistence of reworked Miocene marine and continental fossils (mammals, fishes, forams), Pleistocene continental mammals, and Middle Pleistocene small mammals, and Upper Pliocene palynomorphs highlights the dynamic nature of sediment transport within the Moldavian Platform. Fluvial incision, channel migration, and redeposition processes have mixed material from different ages, creating a palimpsest assemblage. Nevertheless, the small mammal assemblage, particularly the evolutionary stages of *Microtus* and *Arvicola*, provides the most reliable chronological indicator, suggesting that the primary accumulation of small-mammal remains took place during the Chibanian. This mixed assemblage thus offers a valuable window into both local depositional processes and broader faunal and environmental developments across the Eastern Paratethys during the Middle Pleistocene.

The fossil assemblage from Stăuceni, in which Middle Miocene (Volhynian) vertebrate remains have been redeposited in a Middle Pleistocene setting, where they are found alongside Pleistocene terrestrial large and small mammals (Tab. 1), bears striking similarities to the fossil as-

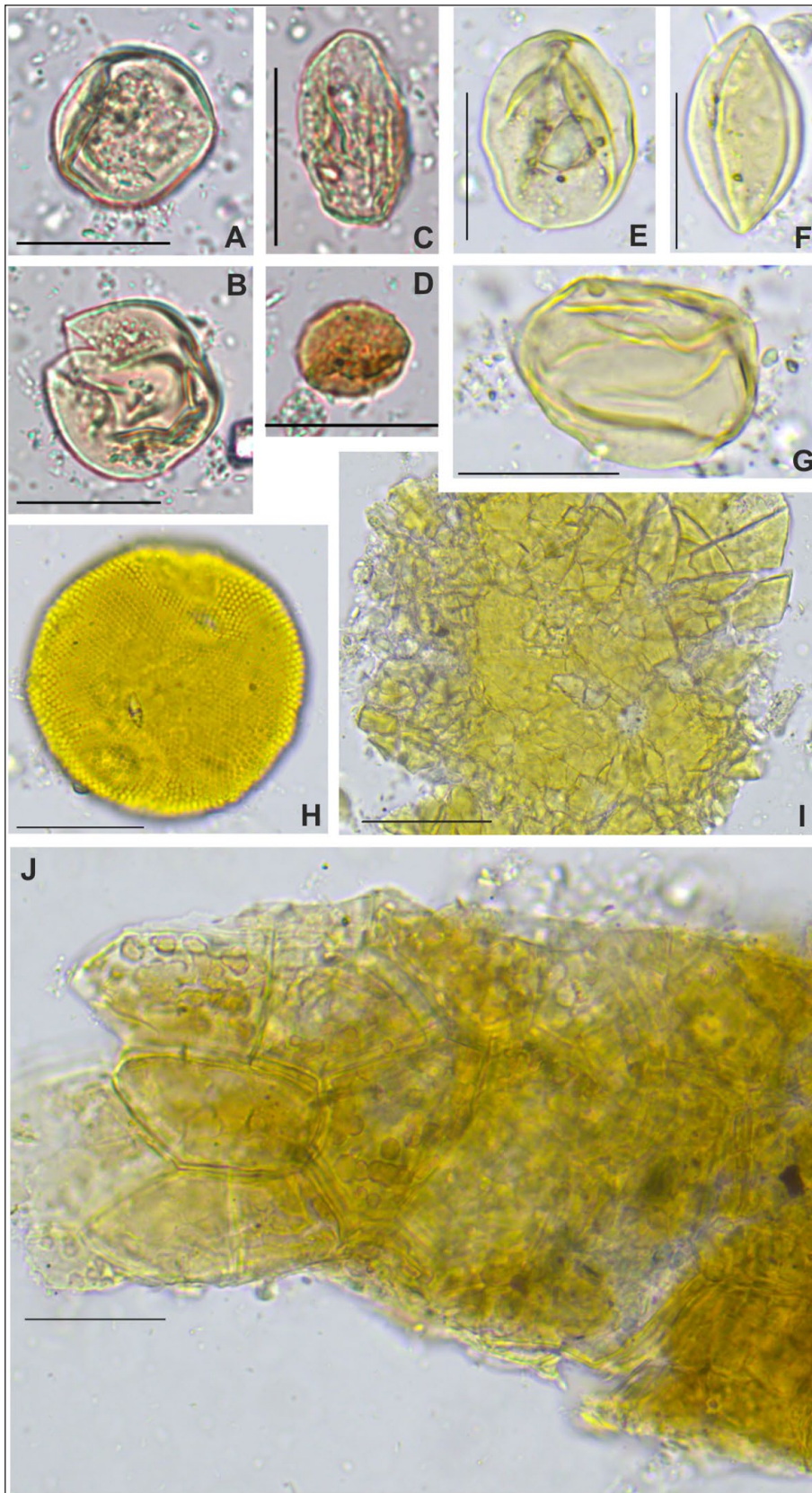
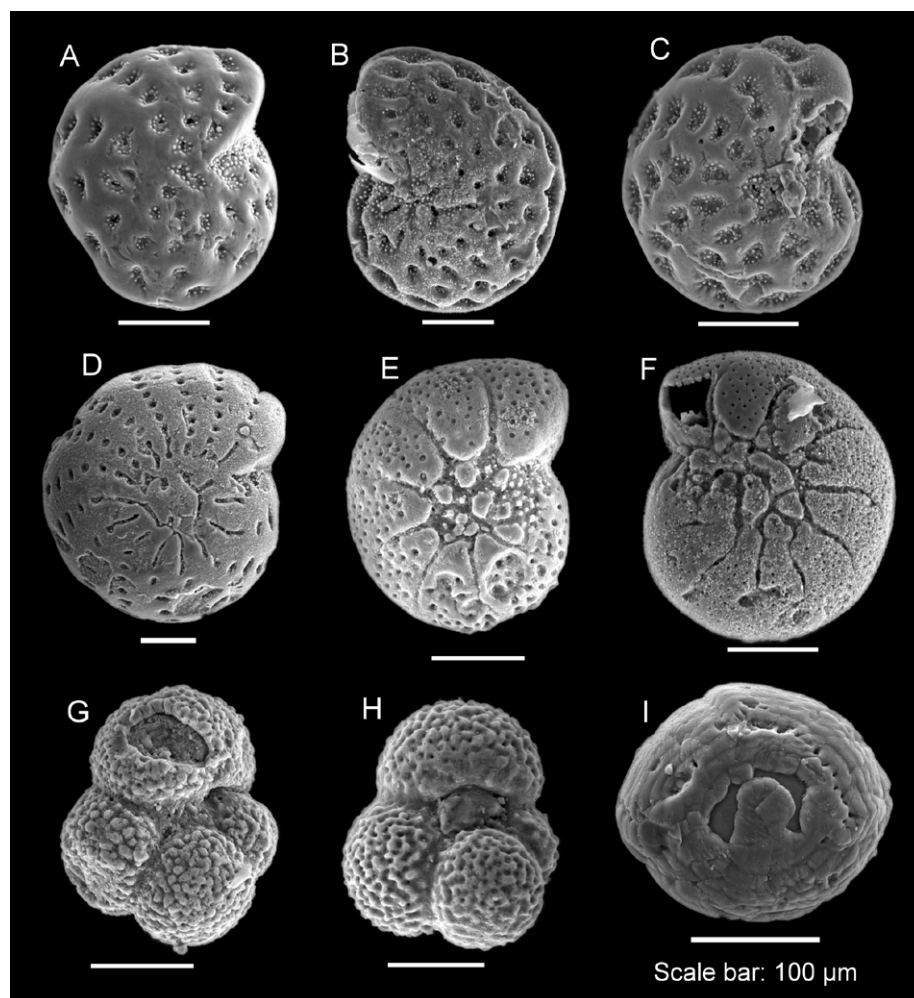


Fig. 6 - Palynomorph assemblage from Stăuceni, Layer F. A–B - *Sigmopollis laevigatoides*; C - *Tricolporopollenites microbenrici*; D - Gramineae; E - *Laevigatosporites gracilis*; F - *Ginkgo* sp.; G - *Carpinipites carpinoides*; H - *Tyttobdiscus* sp. (probably reworked); I - fossil resin; J - cuticle. All scale bars = 30 μ m.

semblage of Pécs-Danitzpuszta sand pit from the Pannonian Basin (Botfalvai et al. 2022). Marine Sarmatian taxa similar to those found at Stăuceni (phocines, kentriodontids), and even older, Bade-

nian, ones, are found alongside Pannonian (i.e., Late Miocene) terrestrial taxa (see Botfalvai et al. 2002 and references therein for a taxonomic list and age estimates). Although redeposition occur-

Fig. 7 - Reworked Sarmatian micro-palaeontological assemblage from Stăuceni. Each taxon is followed by the sampling point from which it was obtained (P1 to P6), as shown in Fig. 1C. A - *Elphidium jukovi* Serova, 1955 P1; B–C - *Elphidium macellum*, B – P4, C – P6; D - *Elphidium rugosum*, P3; E–F - *Porosonion subgranosus* (Egger, 1857), E – P6, F – P3; G–H - *Globigerina praebulloides* Blow, 1859, G – P2, H – P6; I. mysid statolith, P1.



red earlier at Pécs-Danitzpuszta than at Stăuceni, the two sites share many similarities and point to similar sedimentary settings both inside and outside the Carpathians, following the emplacement of the last major tectonic nappes during the Miocene (Badenian or Sarmatian – Săndulescu 1984).

The Middle Pleistocene small mammal assemblage from Stăuceni is unique for the area of eastern Romania, where Middle Pleistocene deposits are generally rare, and small mammal assemblages of this age were previously unknown. Similarly, although reworked from Miocene strata, the presence of merlucciid remains also appears to be unique for the Eastern Paratethys. The occurrence of mixed vertebrate fossil assemblages in the area underlines the importance of more detailed studies when assessing the age of the deposits. Because Miocene marine mammal remains can be readily reworked, their occurrence alone does not provide sufficient evidence for assigning the host deposits a Miocene age, as was initially proposed for Stăuceni.

Acknowledgements. All the authors contributed to this work in equal amounts to the contribution of the first author. The research of B-SH was supported by the National Research Subprogramme 01.09.01 of the Republic of Moldova through the Institute of Geology and Seismology of the Moldova State University, as well as by a project funded by NARD (Project No. 25.80012.7007.28SE). BSH and SL also acknowledge the support of Project PNRR C9-I19 “Multiproxy reconstruction of Eurasian Megalakes, connectivity and isolation patterns during Neogene – Quaternary times” code 97/15.11.2022, Contract No. 760115/ 23.05.2023. The research of OK was partially supported by the grant “Species composition and paleobiogeographic analysis of Miocene fish assemblages of the Forecarpathian Basin” from the National Academy of Sciences of Ukraine for research groups of early-career scientists. VDC. thanks the Stimulus of Scientific Employment, Individual Support – 2021 Call grant by the Fundação para a Ciência e a Tecnologia (Portugal, CEECIND/03080/2021; DOI: 10.54499/2021.03080.CEECIND/CP1657/CT0007) and FCT – Fundação para a Ciência e a Tecnologia, within the framework of UID GeoBioTEC UIDB/04035/2020 (DOI: 10.54499/UIDB/04035/2020). We are thankful to A. Dubikovska (Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine) for her kind help with the interpretation of sparid remains. We would like to thank the two anonymous reviewers and the editors for the valuable comments and suggestions that helped us improve the content of this paper.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access.

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