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ALLOSOREX STENODUS FEJFAR, 1966 (EULIPOTYPHLA, SORICIDAE): RE-DESCRIPTION OF TYPE MATERIAL AND RE-INTERPRETATION OF ITS FOSSIL RECORD

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Abstract: The original fossil record of *Allosorex stenodus* Fejfar, 1966 from Ivanovce (late Ruscinian, MN 15b) is redescribed and supplemented by the description of so far unpublished fossil remains, including upper dentition (P4 and M3) and a humerus fragment as well as the enamel microstructure analysis of m2. Based on the critical evaluation of other fossil remains from sites in Romania, Hungary, and France, the Ivanovce fossils are so far the only unquestionable recorded finds of *A. stenodus* in Europe, which can be considered as a local early Pliocene (MN 15) endemic species. Its occurrence is connected with the forested karst area along a broad valley of "pre-Váh" River, ecologically and climatically resembling the environment of modern karst areas in south-eastern Asia. Based on enamel microstructure analysis and unique mandible and dentition morphological characters, a separate taxonomical status of the species is also discussed.

Key words: *Allosorex stenodus*, Pliocene, late Ruscinian (MN 15b), Ivanovce, Slovakia

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Introduction

Allosorex stenodus, originally described by Fejfar in 1966 as a new genus and a new species of soricid, remains the only described insectivore taxon from the Ivanovce Pliocene primate site. This site is located in western Slovakia, approximately 12 km south-west of the town of Trenčín at 48°49′30″ N and 17°54′14″ E (Text-fig. 1). Although fossil remains of other insectivore taxa have also been found in the reddish clays of tectonically disturbed vertical and horizontal karst fissures in Triassic limestone, these are only mentioned in the faunal lists (Fejfar 1961, Fejfar and Heinrich 1985, Fejfar and Sabol 2005). Moreover, their description and evaluation is still in progress (Fejfar et al., in preparation). Additional *A. stenodus* material has been detected during this revision, and it is described here with original material for a re-evaluation and re-interpretation of the species. The study also includes analysis of the enamel microstructure.

Allosorex stenodus is a highly specialised soricid and apart from the type locality it has only been sporadically reported from other European sites (Guerin and Mein 1971, Rădulescu et al. 1995, 1997, Mészáros 1999, Rzebik-Kowalska 2002, 2005). While attribution to this species of *Allosorex* for fossils found outside Ivanovce is very questionable, taxonomical re-interpretation can yield relevant data on its geographical distribution in Europe during the Pliocene and its significance for palaeoenvironmental reconstructions. The Ivanovce early Pliocene palaeoenvironment has generally been classified as a humid forest belt along a broad river valley, with a karstified limestone massif most likely surrounded by an open drier habitat at higher elevations.

Material and methods

The *Allosorex stenodus* remains were discovered in vertical and horizontal Ivanovce karst fissures (Fejfar

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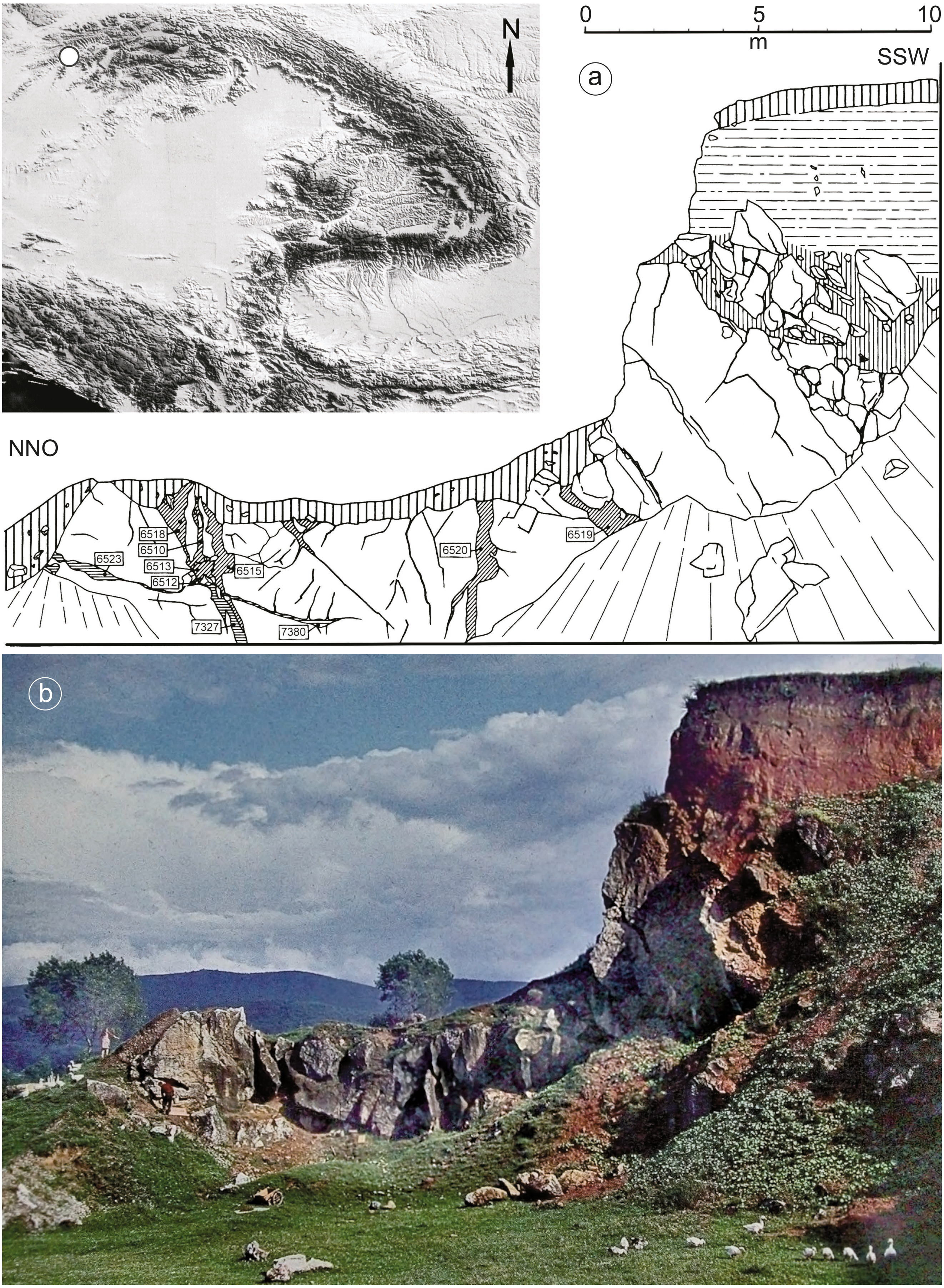


Text-fig. 1. Location of Ivanovce Pliocene primate site in Slovakia within the wider area of the Carpathians-Pannonian Basin (white circle). The northern wall of the former limestone quarry at Ivanovce near Trenčín in western Slovakia. Several karst fillings provided a rich early Pliocene vertebrate assemblage. a: schematic sketch of the site showing the location of different karst fillings, b: photo of the same site during the palaeontological research in 1960s.

1961, Fejfar and Heinrich 1985), originally numbered 6510, 6512, 6520 and 6523 by O. Fejfar (Text-fig. 1a). These were discovered during O. Fejfar's 1956–1959 and 1965 detailed research of the site organised by the Prague Central Geological Survey. The fossiliferous sediments were extensively screen-washed in the field to obtain small vertebrate species samples. All material studied and reported herein is deposited under museum numbers (Z number) and numbers of O. Fejfar's original collection (OF number) in the fossil vertebrate collections at the Slovak National Museum – Natural History Museum (SNM-NHM) in Bratislava, while the first four numerals in the original designation of O. Fejfar indicate the number of the fissure in which the studied material was found. The fossils presented in this paper were documented by Carl Zeis Jena and Leica binocular magnifiers and Meopta and Leica drawing aparatuses. They were scanned by SEM Hitachi S-3700N in the National Museum (NM) in Prague and by Quanta FEG250 at the Institute of Electrical Engineering of the Slovak Academy of Sciences (SAS) in Bratislava. The photos were then converted for figure portrayal by Corel-Photo Paint and Adobe Photoshop software. We adopted Repenning (1967) and McKenna and Bell (1997) taxonomy, and adapted the dental and jaw nomenclature and measurement methodology from Reumer (1984). Measurements of *Allosorex* remains were taken to the nearest 0.01 mm under the Leica binocular magnifying scale. All measured data are in millimetres and presented in the text and Tables 1–4. The upper teeth are referred to by capitals, as in "M3", the lower ones by normal letters, as in "m3".

The enamel microstructure analysis (W. v. Koenigswald) was also included in the fossil record re-description process. The analysis was performed on a fragment of left m2 (Z 28207 – OF 6512) with laboratory number KOE-4196. The Soricidae enamel microstructure ranges from a uniform enamel to a combination of different tooth-enamel types, and differentiation of these features enhances a discussion of genera characteristics and precise phylogenetic relationships. The mammalian enamel consists of hydroxyapatite crystallites that appear in bundles called as enamel prisms (P) or as interprismatic matrix (IPM). The arrangement of these components was extensively modified during mammalian evolution, thus forming different enamel types with different biomechanical properties. A combination of such different enamel types in a single tooth occurs in many mammals and it is defined as "schmelzmuster" (Koenigswald 1980). The English translation would be "enamel pattern". This term, however, is preoccupied for tooth surface morphological features. Therefore, the German term "Schmelzmuster" is generally used. The various tooth positions of a dentition may differ in schmelzmuster due to the biomechanical requirements.

Herein, the lower molar schmelzmuster was selected for comparison of the fossil and extant soricids. While the specialised incisors and upper molars have differentiated enamel, lower molars are obtainable from a greater number of genera for comparison purposes. In addition, transverse (horizontal) sections through the trigonid and talonid provide a great number of characters which enable genera characterisation and also positive arguments for their phylogenetic position. Moreover, the schmelzmuster variability in soricid molars enables identification of six schmelzmuster types at different evolutionary levels (Koenigswald and Reumer 2020).

The most basal schmelzmuster in Soricidae is found in *Soricella*, which has a single-layered enamel formed solely by radial enamel. This is the most simple schmelzmuster and it occurs also in several outgroups, e.g., in *Florinia*, *Lartetium*, *Miosorex*, *Paenelimnoecus*, *Paenesorex*, "*Petenyia*" *dubia*, *Soricella* and *Ulmensia*.

Three independent differentiations arose from this basal *Soricella*-schmelzmuster. One of these is the *Anourosorex*-schmelzmuster that is characterised by specific bending of the enamel prisms near the outer enamel surface and this is present, e.g., in *Paranourosorex*, *Crusafontina* and *Kordosia.* The second type is the *Crocidura*-schmelzmuster with its outer zone of prism-less enamel of variable thickness and this occurs, e.g., in *Scutisorex*, *Sylvisorex* and *Paracrocidura*. The third variation covers the Soricinae and their schmelzmuster is generally two-layered, with an inner layer of radial enamel with inter-row sheets and an outer layer of undifferentiated radial enamel. This, however, is also pigmented by iron which prevents normal preparation. Within this third group, three levels of increasing complexity can be differentiated: (1) the *Notiosorex*-schmelzmuster, (2) the *Sorex*-schmelzmuster and (3) the *Blarina*-schmelzmuster. These differ in increasing lateral inclination of the inner radial enamel and *Blarina* has the most derived schmelzmuster within the Soricidae (Koenigswald 2019, Koenigswald and Reumer 2020).

Knowledge of these differentiations in soricid enamels inspired our research in specifying the *Allosorex* position. Prior to its investigation under the scanning electron microscope (SEM – Camscan MV 2300) at the University of Bonn, the fragmented left m2 was imbedded in epoxy resin and sectioned parallel to the intended ground section. The resin block was then ground from this cut until the required paralophid horizontal section was exposed. Etching with 10% hydrochloric acid (HCL 2n) for approximately three seconds was followed by washing and drying the section for the subsequent sputter-coating. This was inspected and documented in SEM at magnifications from 500× to 2000×. The paralophid between the paraconid and protoconid created special interest in our enamel microstructure analysis because enamel differentiations are also observed in derived soricids. Finally, our different angled photographs were combined to cover the entire length of the paralophid and thus provide a large mosaic of this lophid.

Abbreviations

Measurements of teeth

H	crown height
L	crown length
LT	length of the talon
TAW	talonid width
TRW	trigonid width
W	crown width

Measurements of mandibles

H	height of the coronoid process

HC	height of the condyle
L	length between the posterior rim of the mental foramen and the point where the angular process connects with the mandible ramus
LLF	length of the condylar lower facet
Lm1-m3	overall length of m1–m3
LUF	length of the condylar upper facet

Systematic palaeontology

Family Soricidae Fischer, 1814
Subfamily Allosoricinae Fejfar, 1966

Genus *Allosorex* Fejfar, 1966

***Allosorex stenodus* Fejfar, 1966**

Text-figs 2–7, 9, 10

1966 *Allosorex stenodus* nov. gen., nov. sp.; Fejfar, pp. 227–237, Taf. 23–27, Abb. 1–9.
1985 *Allosorex stenodus*; Fejfar and Heinrich, p. 220.

Holotype. Right mandible with the incisor and alveoli for a2–m3, without the angular process (Z 28208 – OF 651273; Fejfar 1966: Abb. 1, Taf. 23.1–3, Taf. 24).

Paratype. Incomplete right mandible with antemolar (currently absent), m1 and m2, and alveoli for m3, without the angular process (Z 28209 – OF 652356; Fejfar 1966: Abb. 2, Taf. 23.4, Taf. 25, Taf. 26.5).

Type locality. Ivanovce, fissures 6512, Slovakia (early Pliocene, late Ruscinian, MN 15).

Emended diagnosis. Large soricid (Lm1 = 2.59–2.88 mm) with dental formula 1.?.3./1.2.3. The fissident I1 has a curved cutting edge on the talon; the P4 parastyle with its high and sharp paracone is larger than the protocone; M3 is short and wide. The acuspulate to bicuspulate hook-shaped i1 has a distinct lingual groove; a2 is single-rooted; low molars lack the entoconid, the long paralophid forms a distinct sharp cutting edge (except in m3) and the low metaconid is situated close to the high protoconid; the m3 talonid is distinctly reduced. The molar enamel exhibits the *Soricella*-schmelzmuster. The coronoid process is low; the interarticular area is very short to almost absent; the triangular to rectangular upper condylar facet is positioned caudally and the lower condylar facet is strongly displaced forward (see also Fejfar 1966: 224–226 and Reumer 1984: 18).

Stratigraphical distribution. Early Pliocene, late Ruscinian (MN 15).

Geographical distribution. Central Europe (probably an endemic form, which so far is known maybe only from Ivanovce locality).

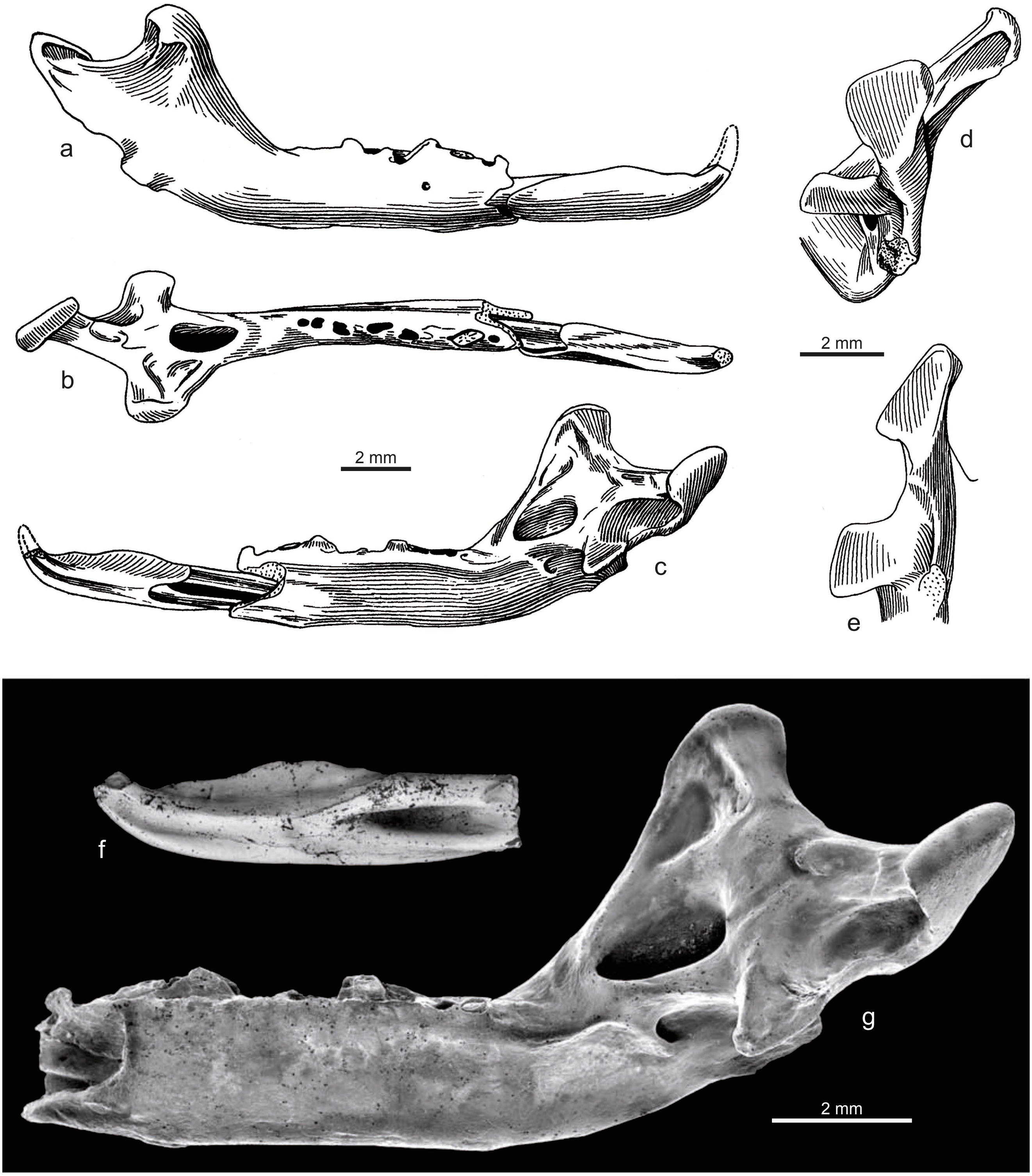
Site. Ivanovce, vertical fissures 6510 and 6520, and horizontal fissures 6512 and 6523 (paratype locality) (early Pliocene, late Ruscinian, MN 15), Slovakia.

Material. I dext. fragment (Z 28191 – OF 6512); I dext. (Z 28192 – OF 6523); I sin. (Z 28193 – OF 652360); 2 fragmented right upper incisors and 2 fragmented left upper incisors (Z 28194/1–4 – OF 6523); 2 fragmented i dext. (Z 28195 – OF 652361, Z 28196 – OF 652362); i dext. fragment (Z 28197 – OF 652363); i sin. fragment (Z 28198 – OF 6510); i sin. without the root (Z 28199 – OF 6523); i sin. fragment (Z 28200 – OF 6523); P4 sin. (Z 28201 – OF 6523); M3 sin. (Z 28202 – OF 6523); 3 m1 dext. (Z 28203 – OF 652364, Z 28204 and Z 28205 – OF 6523); m2 dext. (Z 28206 – OF 652); m2 sin. fragment (Z 28207 – OF 6512); right mandible with incisor and alveoli of a2 to m3 (Z 28208 – OF 651273, holotype); incomplete right mandible with m1 and m2 (antemolar is lost) and alveoli of m3 (Z 28209 – OF 652356, paratype); incomplete toothless right mandible with alveoli of m1 to m3 (Z 28210 – OF 652358); 2 right mandible fragments (Z 28211 – OF 652357, Z 28212 – OF 6523); left mandible with the incisor, m1 and m3 (Z 28213 – OF 6523); fragment of left mandible with the fragmented incisor, antemolar (a2) and m2 (Z 28214 – OF 6523); left mandible with m1 (Z 28215 – OF 652366); toothless left mandible (Z 28216 – OF 6523); 3 left mandible fragments (Z 28217 – OF 651274 with alveoli of m2 and m3; Z 28218 – OF 6520; Z 28219 – OF 6523); and fragment of humerus dext. (Z 28220 – OF 6523).

The entire fossil record consists minimally of 7 individuals (MNI). The fragment of left m2 (Z 28207 – OF 6512) was used for the enamel microstructure analysis (W. von Koenigswald). The left m1 (OF 652367) previously mentioned in this collection (Fejfar 1966: 231–232, Abb. 7a–e, Taf. 26.3–4) is currently absent.

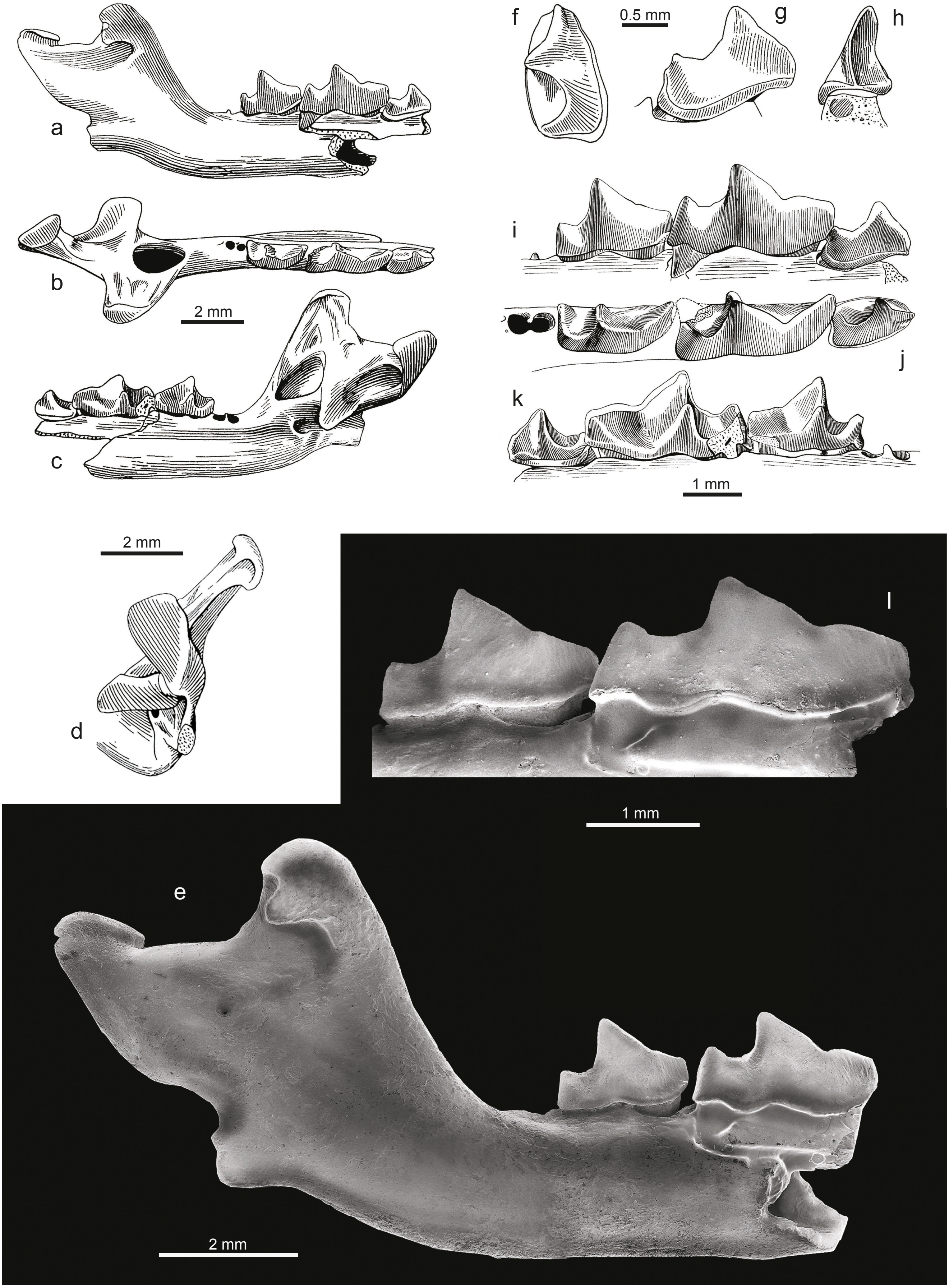
The teeth crowns are not pigmented, fossilized in white to yellowish-white. The fossilization of mandibles is brownish-white, with black manganese plaques.

Description of the holotype. The damaged right mandible, with the incisor and alveoli of a2 to m3 (Z 28208 – OF 651273; Text-fig. 2), is approximately as large as the mandible of large soricids such as *Beremendia fissidens* (Petényi, 1864). The incisor portion of the mandible is broken off and the horizontal ramus is slender. The small mental foramen is situated under the m1 middle portion and the mandibular foramen opens below the central part of the long and broad internal temporal fossa, which lies just above the level of the dental row. The fossa is oval shaped, very deep and distinctly bordered in its upper (dorsal) and lower (ventral) parts. The shallowly concave medial surface from the upper edge of this fossa to the wide top of the coronoid process has several irregular ridge-like tuberosities in its anterior half for the attachment of the temporal muscles. The concavity of the coronoid medial surface appears as a dorsal continuation of the internal temporal fossa and the upper edge of this fossa is thus homologous with the "limula" of other soricid types. The external pterygoid fossa is situated at the level of the internal temporal fossa and it has a completely unusual position between this fossa and the condyle. Its posterior boundary forms the lingual boundary of the upper condylar facet, and the fossa is also the deepest at this site. It gradually becomes more shallow anteriorly and slopes towards the back edge of the internal temporal fossa. Finally, the imprecisely-bounded external pterygoid fossa is generally deep and long. This ventrally borders the dorsal edge of the lower condyle and dorsally limits the lingual wall of the upper condyle process. This peculiar morphology has no similar analogy in other soricids. The external temporal



Text-fig. 2. *Allosorex stenodus* Fejfar, 1966 – holotype (Z 28208 – OF 651273), Ivanovce, fissure 6512. a–c: recontruction of the mandible with incisor (a – buccal view, b – occlusal view, c – lingual view), d–e: condylar facets (d – posterior view, e – ventral view), f: holotype lower incisor (SEM lingual view), g: holotype mandible (SEM lingual view).

fossa is a shallow depression, and this is also clearly visible in the paratype. The fossa lies on the lateral side between the broad coronoid process and the upper condylar facet, under the upper sigmoid notch. The coronoid process is relatively low, superiorly shortened and lies in a blunt 121° angle just behind the m3 alveolus. Its long base is the broadest at the upper level of the condyle and it is caudally and strongly laterally inclined, similar to the carnivore coronoid process. Its anterior edge is slightly concave and the posterior edge is very short, forming the anterior arm of the upper sigmoid notch. The coronoid process head is long, wide, and rounded with a distinct muscular bar and a caudally-oriented lateral coronoid spicule. Both mandible articulation facets on the condyle appear strange and these are very specialised being completely separated far from each other in vertical and horizontal directions; they are not joined to a lamina and



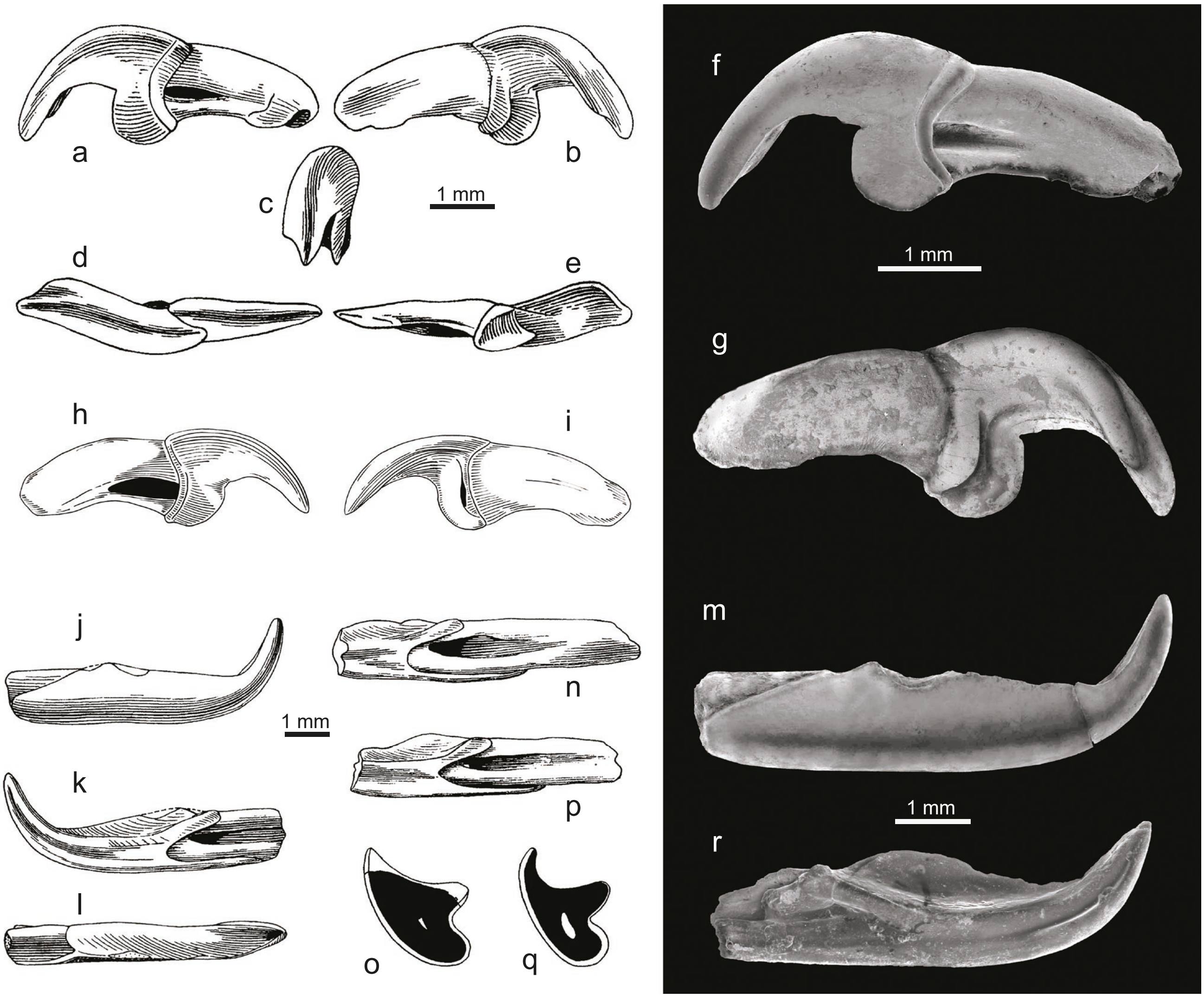
Text-fig. 3. ***Allosorex stenodus*** **Fejfar, 1966 – paratype (Z 28209 – OF 652356), Ivanovce, fissure 6523. a–c: recontruction of the mandible with antemolar, m1 and m2 (a – buccal view, b – occlusal view, c – lingual view), d: condylar facets (posterior view), e: paratype mandible without the antemolar (SEM buccal view), f–h: lost antemolar (f – occlusal view, g – buccal view, h – anterior view), i–k: detail view on the antemolar and molars (i – buccal view, j – occlusal view, k – lingual view), l: detail SEM buccal view on m1 and m2.**

there is no interarticular area for connection. The distinct and unusually thick triangular upper condylar facet is more caudally shifted. The lower condylar facet is strongly displaced forward and its medial portion is situated below the posterior margin of the internal temporal fossa. The relative height of the upper condylar facet is visible in caudal view, together with the lateral inclination of the coronoid process. The angular process is broken off and its base is laterally flattened, but the process was most likely medially-hooked.

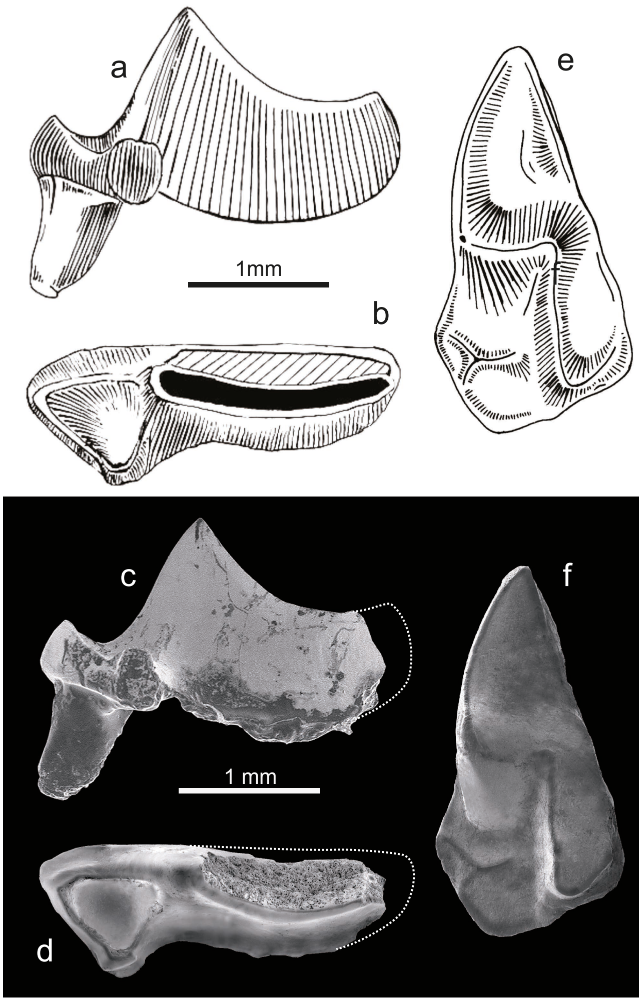
The crown of the narrow lower incisor (i1) is hook-shaped, with its upwardly curved apex broken off. It has a distinct longitudinal groove on the symphysial portion (a blood-groove?) and a sharp dorso-labial edge with an irregularly, weakly waved (bicuspulate-like) dorsal margin. The symphysial wall of this cutting edge is covered with very thin enamel and the crown buccal wall has short parallel vertical wrinkles. The crown length is 6.45 mm.

Based on the preserved alveoli, the a2 antemolar was only single-rooted. The well-preserved alveoli of the double-rooted molars indicate that especially the m1 and m2 were very weakly anchored in the mandible, and this is certainly related to their sectorial function of being mechanically unaffected by chewing processes.

Description of the paratype. The incomplete right mandible with antemolar (currently lost), m1 and m2, and alveoli for m3 and without the angular process (Z 28209 – OF 652356; Text-fig. 3) is approximately as large as the holotype. The incisor portion of the mandible is broken off, together with the anterior part of the slender horizontal ramus, which is also damaged below the m1 (currently separated from the mandible with a piece of its horizontal ramus). Although the mental foramen and angular process are unpreserved, the overall mandibular morphology is very similar to that of the holotype and differs only in the following details: the rounded fossa is broader; a small circular opening is situated in the posterior portion of the external pterygoid fossa; the coronoid process lies in a less blunt angle of 115° and its anterior edge is straight;



Text-fig. 4. ***Allosorex stenodus*** **Fejfar, 1966 – upper and lower incisors, Ivanovce, fissure 6523. a–g: upper left incisor (Z 28193 – OF 652360; a, f – buccal view, b, g – lingual view, c – anterior view, d – dorsal view, e – ventral view), h–i: upper right incisor (Z 28192 – OF 6523; h – buccal view, i – lingual view), j–m: lower right incisor (Z 28197 – OF 652363; j, m – buccal view, k – lingual view, l – dorsal view), n–o: lower right incisor (Z 28196 – OF 652362; n – lingual view, o – crown cross-section), p–q: lower right incisor (Z 28195 – OF 652361; p – lingual view, l – crown cross-section), r: lower left incisor (Z 28199 – OF 6523; lingual view).**



Text-fig. 5. ***Allosorex stenodus*** **Fejfar, 1966 – fragment of left P4 and left M3, Ivanovce, fissure 6523. a–d: P4 sin. (Z 28201 – OF 6523; a, c – lingual view, b, d – occlusal view, a–b – hypothetical reconstruction of the premolar), e–f: M3 sin. (Z 28202 – OF 6523; occlusal view).**

the coronoid process head is not so long and the caudally oriented postero-lateral coronoid spicule is more robust; and finally the upper condylar facet is smaller than the holotype facet and the lower one is larger.

The separated first lower molar (m1) is unusually slender in occlusal view and damaged in the postero-lingual portion. The typical soricid V-shaped trigonid basin is completely expanded here, and the long paralophid is transformed into a carnassial-like blade similar to that in predatory carnivores, and it has a shallow notch. The trigonid buccal wall is very steep and its lingual slope is only moderately inclined. The U-shaped talonid basin is slightly more open lingually than seen in the second lower molar. The oblique crest resembles the paralophid and begins at the posterior wall of the protoconid. Only part of the hypolophid is preserved because the whole postero-lingual crown portion is broken off. The protoconid is the highest cusp and the others are approximately the same height, with only the metaconid protruding slightly above them when unworn. This cone-like cusp, however, is the smallest of all trigonid cusps and is situated close to the protoconid. The cingulum is only indicated, or slightly developed, on the lingual side and also on the antero-buccal side under the paraconid. The anterior root is longer than the damaged posterior root and is more laterally flattened. Finally, the larger molar width lies at the distal part of the trigonid.

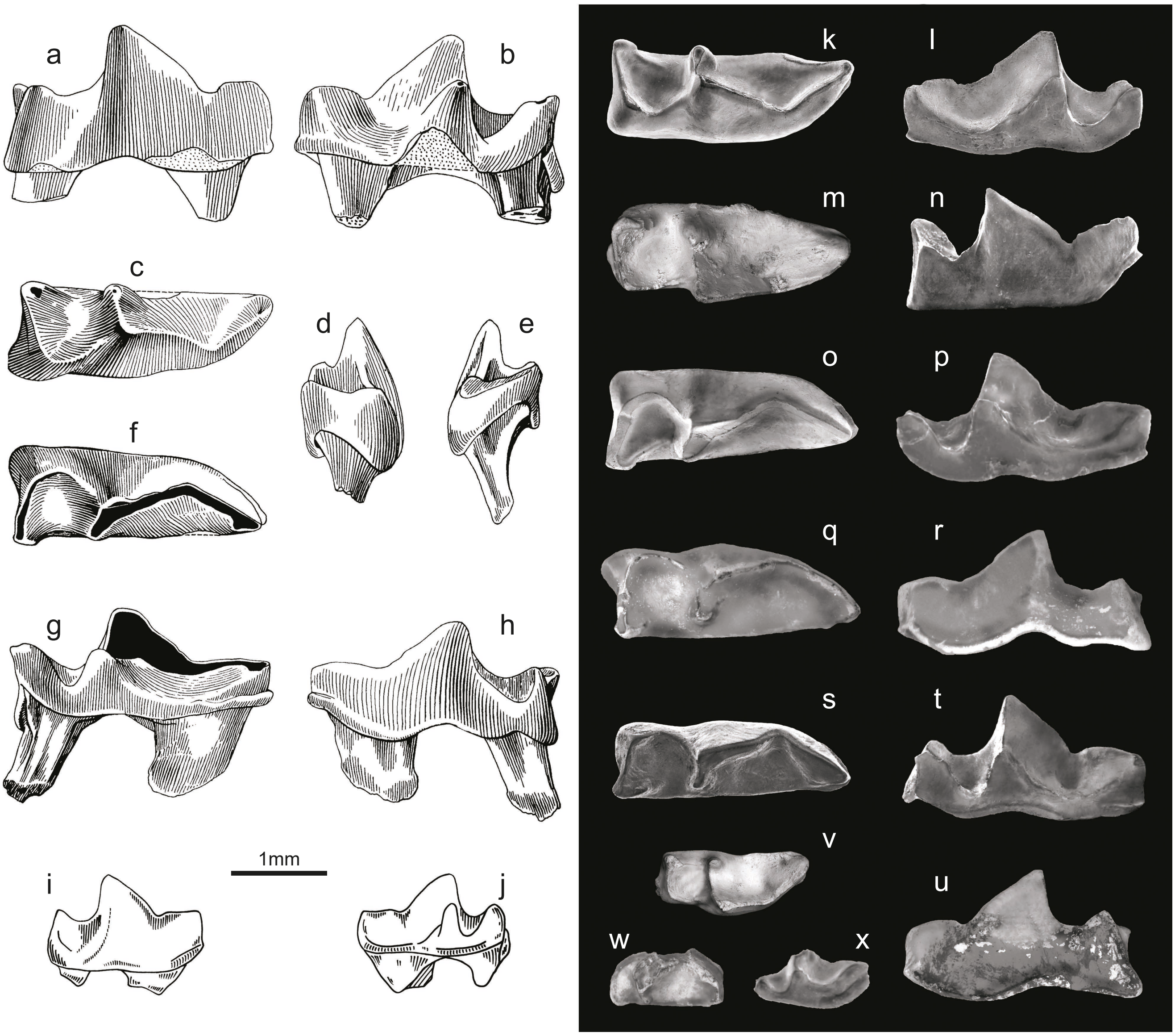
The second lower molar (m2) is similar in morphology to m1, but it is smaller. The trigonid basin is expanded, but not as much as in m1, and it is wide open lingually; the U-shaped talonid basin is also lingually open because no entoconid crest is developed. The oblique crest begins directly under the protoconid and passes through the low hypoconid into the straight hypolophid which ends in the distinct cone-like entostylid. The latter parallels the missing entoconid in both position and function. The protoconid is high and comparatively higher than in m1. The cone-like metaconid is situated close to the protoconid and although it is low, it is higher than the paraconid and the entostylid. The long paralophid with shallow notch resembles the carnassial cutting edge, but not as distinctly as in m1. The cingulum is only indicated on the lingual edge of the crown base and slightly developed on the antero-buccal side under the paraconid. Finally, the largest molar width is at the trigonid.

No mesoconid is developed on the preserved lower molars. Based on preserved alveoli, the third lower molar (m3) was double-rooted, with the anterior root larger than the posterior one.

Description of dentition. Twenty nine additional teeth of *Allosorex*, including upper and lower incisors, upper fourth premolar, upper third molar, lower antemolar, and lower molars are available (Text-figs 4–6, Tabs 1–3). The upper incisors (I sup.) in the explored sample comprise only two complete teeth and five fragmented specimens. The narrow apex is extremely sickle-like and transversely widened in shovel-like shape in ventral view. The teeth are not fissident, and instead of the usual soricid talon with a lateral tip, there is a strange blade developed with a semi-circular cutting edge which connects to the apical posterior edge. The cingulum on the crown base under the talon is less robust on the buccal side than on the medial one where a similar structure to the talon blade can be formed (as in Z 28192 – OF 6523). The laterally flattened root has a short longitudinal groove on the buccal side and a small opening for a blood vessel at the distal end.

Upper antemolars (A1–A3) are unknown in the fossil record of the species from this site.

The preserved portion of P4 sin. (Z 28201 – OF 6523) has a possible hypercarnivorous condition, not recognised in other soricids. Its long buccal edge makes almost a 45° angle with the anterior edge. The paracone is very high and narrow, laterally flattened cusp, with the long sharp posterior cutting edge, slightly curved medially, and most likely running into a metastyle crest. The metacone/metastyle part of the crown is unfortunately broken off, and while the buccal wall of the relatively high cutting blade is heavily worn (or damaged?), the inner wall is smooth with a worn narrow stripe along the cutting edge. This resembles the similar phenomenon in the lower carnassials of large felids or hyenids. The triangular parastyle is somewhat larger than the conical, lingually situated protocone and it is connected to the paracone by a distinct parastylar crest. A crest also connects the parastyle with the protocone and another one

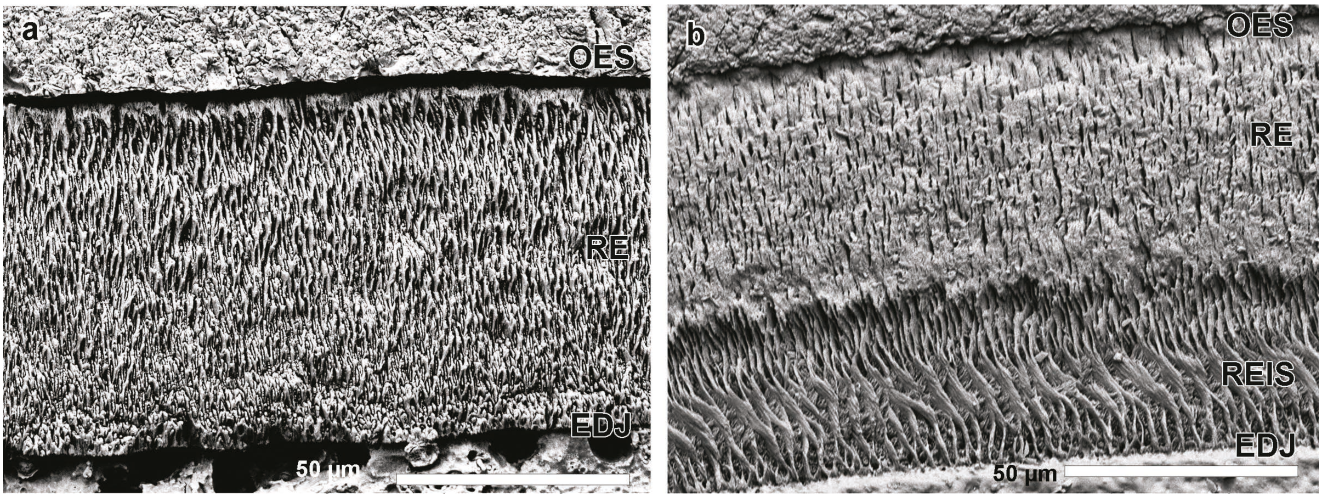


Text-fig. 6. ***Allosorex stenodus*** **Fejfar, 1966 – lower molars, Ivanovce, fissure 6523. a–d: m1 dext. (Z 28203 – OF 652364; a – buccal view, b – lingual view, c – occlusal view, d – distal view), e–h, o: lost m1 sin. (OF 652367; e – distal view, f, o – occlusal view, g – lingual view, h – buccal view), i–j, v: m2 dext. (Z 28206 – OF 6523; i – buccal view, j – lingual view, v – occlusal view), k–l: m1 dext. (Z 28204 – OF 6523; k – occlusal view, l – lingual view), m–n: m1 dext. (Z 28205 – OF 6523; m – occlusal view, n – buccal view), p–r: m1 sin. (Z 28213 – OF 6523; p –lingual view, q – occlusal view, r – buccal view), s–u: m1 sin. (Z 28215 – OF 652366; s – buccal view, t – lingual view, u – buccal view), w–x: m3 sin. (Z 28213 – OF 6523; w – occlusal view, x – lingual view).**

connects the protocone with the paracone. All these three crests bounds a conspicuous anterior basin. The hypocone and the hypoconal flange are not preserved; but based on the P4 morphology of the related *Viretia gracilidens* species, the hypocone could be reduced or even completely absent. This is consistent with the assumed hypercarnivorous appearance of the discovered tooth fragment. The pronounced short cingulum is present on the buccal side below the parastylar crest and it passes anteriorly into the parastyle anterior crest. The anterior root is small and the length of the preserved premolar portion on the buccal side is 2.17 mm.

Only one triangular M3 sin. (Z 28203 – OF 6523) was discovered at the site. The tooth is short and wide, with the large and well-developed paracone extended by a decreasingly distinct and moderately anteriorly bent crest that runs up to the pointed (parasytyle) buccal margin. The metacone is markedly weaker, but not low, and it is connected to the paracone by a blunt crest. The antero-lingual basin is almost flat, with only an indication of a tiny blunt accessory cusp and the basin is anteriorly and lingually surrounded by a cingular ridge. Of the four roots, only the robust but shorter buccal root and the antero-lingual root are preserved, while the postero-lingual and tiny central ones are broken off. The M3 crown is 1.36 mm long and 2.69 mm wide.

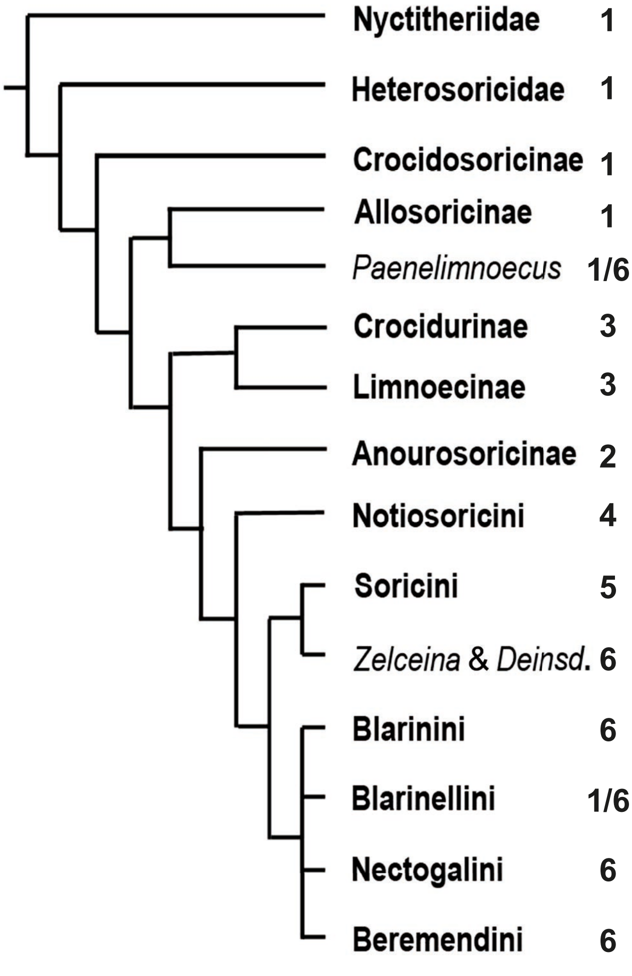
The most prominent characteristic of the lower incisors (i inf.; six isolated fragments and two fragmented teeth in mandibles) is the narrow crown apex which is extremely upwardly curved. The crown has a distinct longitudinal groove on the symphysial side which is wedged almost in the middle of the crown and branches distally. A very sharp enamel edge runs from the buccal base of the apex; its dorsal margin is straight in Z 28197 – OF 652363 or



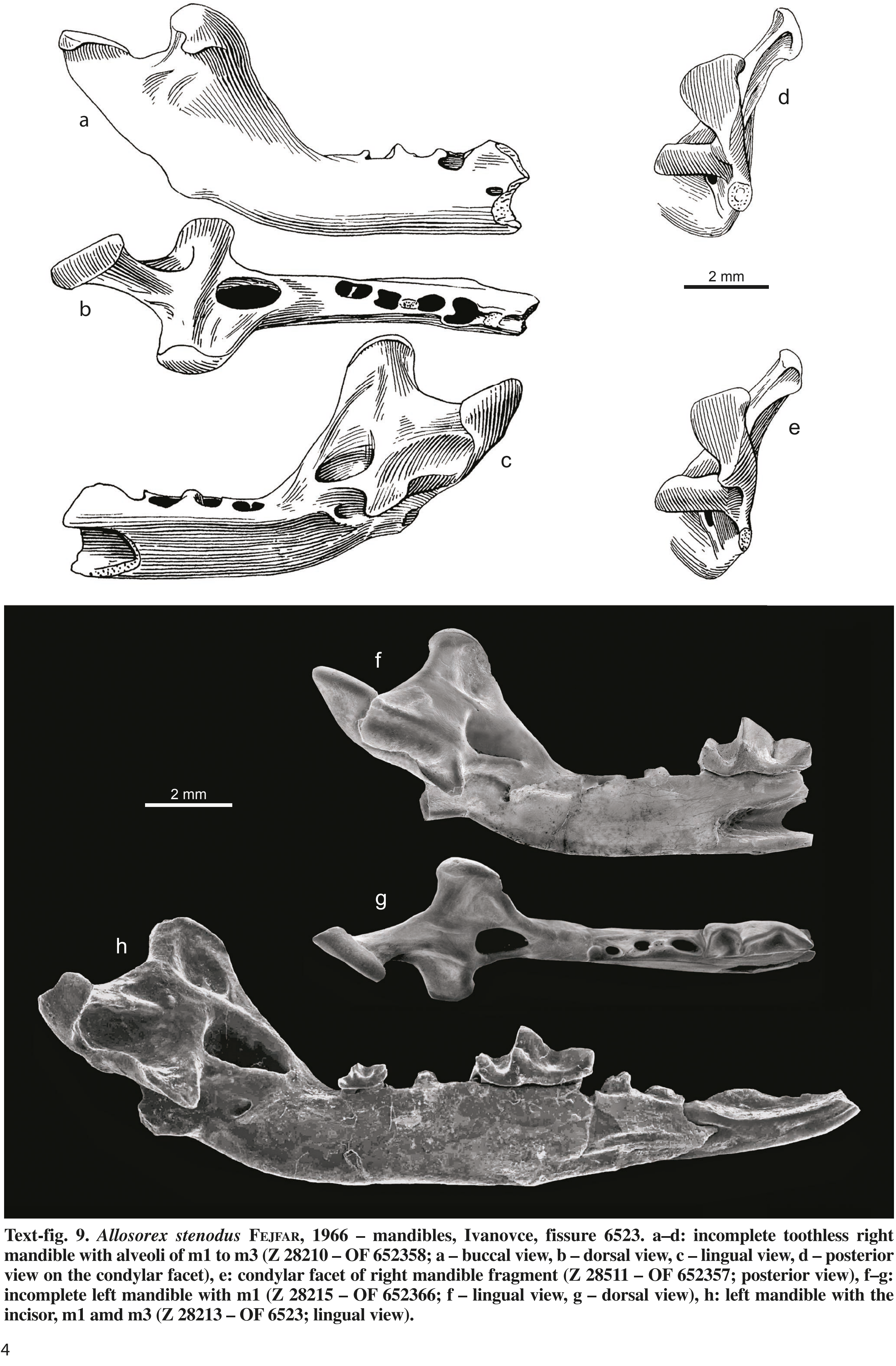
Text-fig. 7. Enamel microstructure in the molars of (a) *Allosorex stenodus* (KOE-4196 / Z 28207 – OF 6512) and (b) *Blarina brevicauda* (KOE-1435). SEM photos showing transverse sections of the paralophid in a lower molar. The schmelzmuster of *Allosorex* is one-layered and formed exclusively from radial enamel (RE), whereas the schmelzmuster of *Blarina* is two-layered, with an inner enamel of laterally inclined radial enamel with distinct interrow sheets (REIS). The radial enamel of the outer layer is heavily pigmented and therefore poorly etched. The pigmentation does not affect the schmelzmuster.

relatively weakly waved as in the Z 28195 – OF 652361 (holotype) or Z 28196 – OF 652362. Most teeth, however, have unserrated acuspulate crowns. The distal border of the crown is posteriorly elongated on the buccal side and extends below the middle of the second lower antemolar (a2/p4). In common with other soricids, the crown has a deep indentation (sinuosity) on the symphysial side and its anterior margin terminates in the first third of the crown. A deep longitudinal groove is situated at the root's symphysial side and the small opening for a blood vessel is visible at the distal end. Some incisors have no enamel on the crown dorsal side (see Fejfar 1966: Abb. 5e), and this lack is paralled in molars where the lingual walls of the trigonid or talonid basins have only very thin enamel or no enamel covering near the ridges.

From lower antemolars – a1 and a2 – only the latter one is preserved in the explored material and this is generally considered the p4 (Reumer 1984). An a1 alveolus can be seen in Z 28213 – OF 6523 and Z 28214 – OF 6523 and this indicates smaller size than a2. The a2 root is inclined posteriorly (similarly like a1 root) and a2 crown is slightly hidden below the mesial margin of the m1. The a2 and m1 crown bases are almost at the same level, and this feature differs from other soricids. The a2 outline is oval in occlusal view and has a shallow fold (indentation) at the slightly wider distal margin. The only relatively high and narrow main cusp (protoconid) is clearly bi-crested – both crests are sharp and while the anterior crest runs straight anteriorly, the posterior runs posteriorly and lingually. The cusp is slightly inclined lingually, and the lateral view identifies a mesially arched anterior crest and the concave posterior crest bounding a small shallow syncline which is a homologue of the talonid basin in molars. The cingulum is well developed and absent only on the mesial edge. The buccal wall is much smoother than the lingual. The a2 from the paratype (see Fejfar 1966: Abb. 2, 6, 10a, e) is now lost and the only (faintly damaged) a2 is preserved on the fragmented left mandible with the incisor fragment and m2 (Z 28214 – OF 6523). The crown length is 1.38 mm and the width is 0.91 mm.



Text-fig. 8. The limited differentiation the schmelzmuster in *Allosorex* (Allosoricinae) indicates its phylogenetic position in Soricomorpha. The numbers to the right refer to the different types of schmelzmuster found in Soricidae: 1 – *Soricella*-schmelzmuster, 2 – *Anourosorex*-schmelzmuster, 3 – *Crocidura*-schmelzmuster, 4 – *Notiosorex*-schmelzmuster, 5 – *Sorex*-schmelzmuster, and 6 – *Blarina*-schmelzmuster (ex Koenigswald and Reumer 2020).



Text-fig. 9. ***Allosorex stenodus*** **FEJFAR, 1966 – mandibles, Ivanovce, fissure 6523. a–d: incomplete toothless right mandible with alveoli of m1 to m3 (Z 28210 – OF 652358; a – buccal view, b – dorsal view, c – lingual view, d – posterior view on the condylar facet), e: condylar facet of right mandible fragment (Z 28511 – OF 652357; posterior view), f–g: incomplete left mandible with m1 (Z 28215 – OF 652366; f – lingual view, g – dorsal view), h: left mandible with the incisor, m1 amd m3 (Z 28213 – OF 6523; lingual view).**

Table 1. Measurements of upper incisors of *Allosorex stenodus* Fejfar, 1966 from Ivanovce and soricid from Dranic-0 (Rzebik-Kowalska 2002).

Upper incisors		L	H	LT
Ivanovce	**Z 28191**	–	1.88	0.91
	Z 28192	2.50	1.63	0.70
	Z 28193	2.63	1.93	0.83
	Z 28194/1	–	1.88	0.94
	Z 28194/2	–	1.89	0.88
	Z 28194/3	–	1.63	0.88
	min.	2.50	1.63	0.70
	max.	2.63	1.93	0.94
	mean	2.57	1.81	0.86
Dranic-0	**No. 1**	–	1.68	–
	No. 2	2.14	1.51	1.04

The lower molars gradually decrease from m1 to m3 in length, width, and height and the length difference between m1 and m2 is particularly significant. While the molars' lingual side is straight, the buccal side is slightly buccally arched. In occlusal view, their narrow shape related to the elongated trigonid is very striking compared to the normal molar shape seen in other soricids.

Three isolated right m1s and two left m1s remain in the mandibles, and these have similar morphology described in the paratype m1 above, with the difference that the crowns' posterior portions are preserved. The hypolophid is straight and connects the low hypoconid with the high entostylid (sensu Reumer 1984), and this feature parallels the entoconid of other insectivores in both position and function. Although the entoconid is absent, a weak entoconid crest can be developed. The cingulum is slightly developed on the mesial margin under the paraconid in all m1s. The m1 from the left mandible fragment (Z 28213 – OF 6523) has an almost indistinguishable metaconid and indication of a small entoconid in front of the conspicuous entostylid.

Table 2. Measurements of first lower molars (m1) of *Allosorex stenodus* Fejfar, 1966 from Ivanovce and soricids from Dranic-0 (Rzebik-Kowalska 2002) and Alsótelekes (Mészáros 1999).

m1		L	TRW	TAW
Ivanovce	**Z 28203**	2.71	–	1.01
	Z 28204	2.64	1.06	0.94
	Z 28205	2.69	1.00	0.88
	Z 28209	2.88	0.91	–
	Z 28213	2.75	1.03	0.99
	Z 28215	2.59	0.91	0.89
	OF 652367	2.70	(0.94)	1.10
	min.	2.59	0.91	0.88
	max.	2.88	1.06	1.10
	mean	2.70	0.98	0.97
Dranic-0		–	–	0.97
Alsótelekes		2.03	–	0.98

The m2 morphology resembles that described in the paratype. This is especially relevant in the left m2 analysed fragment (Z 28207 – OF 6512) and the damaged m2 from the left mandible fragment (Z 28214 – OF 6523), while the isolated right m2 (Z 28206 – OF 6523) has no notch on the paralophid.

The only preserved and slightly damaged m3 is still situated in a left mandible (Z 28213 – OF 6523). This is a strongly reduced tooth with its length approximately half the m2 length and a third of m1. The molar is tiny and narrow, with a lingually opened and distinctly reduced and posteriorly narrowed talonid where only a small cuspid is developed (entostylid?). The protoconid is relatively robust, while the metaconid is reduced and situated very close to the protoconid. The paraconid forms only a semi-arched anterior elevation with the flat inner surface, and there is no carnassial blade-shaped paralophid developed between the paraconid and the protoconid. The weak cingulum is indicated only at the antero-buccal margin. Of the two m3 roots, only the anterior one is laterally flattened. The m3 measurements are as follows: the crown length is 1.08 mm, the trigonid width is 0.56 mm, and the talonid width is approximately 0.35 mm.

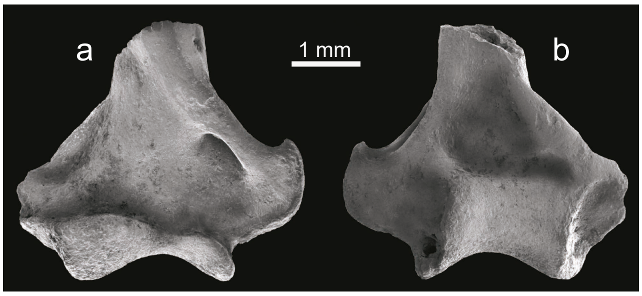
The position and shape of especially the two anterior lower molars in the mandible is certainly related to their sectorial (not-chewing) function. Moreover, this odontological specialisation correlates with the highly specialised morphological construction of the mandibles, and it is quite remarkable that the majority of the discovered mandibles are toothless, thus indicating weaker embedment in the jaws. While this phenomenon is rarely mentioned in other fossil soricids, edentulous insectivore mandibles are quite common in the fossil record.

The schmelzmuster of *Allosorex*. As previously mentioned, the microstructural character of paralophid enamel between the paraconid and protoconid is important in soricid differentiation (Koenigswald and Reumer 2020). The schmelzmuster in *Blarina*, and similarly differentiated genera, distinctly changes along the paralophid. The paralophid enamel in *Allosorex stenodus* from Ivanovce is one-layered and composed solely of radial enamel. The prisms in the transverse section are seen in oblique cross-sections, as they arise from the enamel-dentin-junction (EDJ) towards the outer enamel surface (OES). The crystallites of the interprismatic matrix (IPM) are oriented at an angle to the prisms and anastomose between them. This gives the typical appearance of radial enamel. No specializations could be recognized, neither a separated inner layer with interrow sheets or a prism-less outer enamel (Text-fig. 7a). Therefore, *Allosorex* represents the *Soricella*-schmelzmuster – the least derived schmelzmuster in soricids. The simplicity of this one-layered schmelzmuster is well recognizable when compared to the two-layered schmelzmuster of *Blarina brevicauda.* (Text-fig. 7b).

According to many investigated genera, the variability in the schmelzmuster is limited (Koenigswald 1980, 1997, Koenigswald and Reumer 2020). Therefore, the *Allosorex* genus can be characterised by the basal *Soricella*-schmelzmuster. Furthermore, the occurrence of the

Table 3. Measurements of second lower molars (m2) of *Allosorex stenodus* Fejfar, 1966 from Ivanovce and soricids from Dranic-0 (Rzebik-Kowalska 2002) and Alsótelekes (Mészáros 1999).

m2		L	TRW	TAW
	Z 28206	1.98	0.78	0.69
	Z 28207	–	0.78	–
	Z 28209	1.99	0.76	0.75
Ivanovce	**Z 28214**	–	0.81	0.75
	min.	1.98	0.76	0.69
	max.	1.99	0.81	0.75
	mean	1.985	0.78	0.73
Dranic-0		1.83	0.83	–
Alsótelekes		1.68	0.90	–



Text-fig. 10. *Allosorex stenodus* Fejfar, 1966 – fragmented right humerus (Z 28220 – OF 6523), Ivanovce; a – anterior view, b – posterior view.

Soricella-schmelzmuster can be used – in combination with other characters – to discuss *Allosorex* phylogenetic position. The presence of this underived *Soricella*-schmelzmuster excludes *Allosorex* from groups with a more differentiated schmelzmuster. *Allosorex* forms most likely an early side branch of Soricidae (Text-fig. 8). Thus, the enamel supports the isolated position of *Allosorex* among the late Miocene and Pliocene soricids and strengthens the separate Allosoricinae subfamily based on morphological reasoning (Fejfar 1966).

Description of mandibles. The mandible morphology (Text-fig. 9, Tab. 4) is very similar to both holotype and paratype; with only the following variations: the internal temporal fossa is ovally to triangularly rounded and very deep (Z 28217 – OF 651274, Z 28218 – OF 6520, Z 28211 – OF 652357, Z 28215 – OF 652366), distinctly bordered on all sides (Z 28217 – OF 651274, Z 28218 – OF 6520, Z 28213 – OF 6523, Z 28215 – OF 652366); the medial surface above the internal temporal fossa is less shallow than in the holotype (Z 28213 – OF 6523 and Z 28215 – OF 652366) and quite smooth without tuberosities (Z 28211 – OF 652357, Z 28210 – OF 652358, Z 28216 – OF 6523, Z 28219 – OF 6523); the coronoid process forms an angle from approximately 105° (Z 28218 – OF 6520) through 111° (Z 28215 – OF 652366), 116° (Z 28217 – OF 651274), 118° (Z 28216 – OF 6523), 120° (Z 28210 – OF 652358) to 140° (Z 28211 – OF 652357) and its anterior edge is straight (Z 28218 – OF 6520) or straight to slightly concave (Z 28217 – OF 651274); the caudo-ventrally oriented lateral coronoid spicule is more robust than in the holotype, but not as much as in the paratype (Z 28213 – OF 6523 and Z 28215 – OF 652366) or it can also be reduced (Z 28216 – OF 6523 and Z 28219 – OF 6523); a small circular opening is situated in the posterior portion of the external pterygoid fossa (Z 28218 – OF 6520) which can be uniformly deep throughout its length and distinctly bordered, especially on the ventral side (Z 28216 – OF 6523), or it can be almost as deep as the internal temporal fossa (Z 28219 – OF 6523); and the upper condylar facet is rectangular (Z 28213 – OF 6523).

Description of the humerus. The right humerus fragment (Z 28220 – OF 6523; Text-fig. 10) more or less consists only of the distal epiphysis with a spiral

Table 4. Measurements of mandibles of *Allosorex stenodus* Fejfar, 1966 from Ivanovce.

Mandibles		L	H	Lm1-m3	HC	LUF	LLF
	Z 28208	6.16	4.48	–	4.34	2.00	1.75
	Z 28209	(5.60)	4.34	–	3.78	1.50	1.75
	Z 28210	6.40	4.88	–	4.63	1.94	1.88
	Z 28211	–	4.40	–	4.13	1.56	1.75
	Z 28212	–	–	–	4.63	1.89	1.81
	Z 28213	7.13	4.88	5.63	3.88	–	1.81
	Z 28214	(5.52)	-	–	–	–	–
Ivanovce	**Z 28215**	6.63	4.50	–	3.88	1.75	1.56
	Z 28216	6.00	4.72	–	4.34	1.81	1.31
	Z 28217	–	4.50	–	-	-	-
	Z 28218	–	–	–	4.38	1.81	1.69
	Z 28219	–	–	–	4.44	1.75	1.63
	min.	6.00	4.34	–	3.78	1.50	1.31
	max.	7.13	4.88	–	4.63	2.00	1.88
	mean	6.46	4.59	5.63	4.24	1.78	1.69

fracture in the diaphyseal portion. The condyle has irregular hourglass-shape in cranial view and it is divided by a relatively distinct groove into a larger capitulum and smaller trochlea, and this latter is very high on the caudal side. The coronoid and radial fossae are shallow and indistinctly separated from one another. The triangular olecranon fossa is also shallow, but relatively larger than the fossae on the cranial side. While the lateral and medial supracondylar ridges are distinctly developed, the slightly damaged lateral epicondyle is smaller than the medial epicondyle which is hooked and has a distinct edge. The lateral supracondylar foramen is relatively large, roughly oval and ventrally narrow. The following measurements were determined: the maximum distal epiphysis transverse diameter is 4.44 mm, the trochlea diameter is 2.06 mm, the trochlea upper transverse diameter is 1.69 mm and the trochlea maximum height is 1.56 mm.

Comparison and conclusion

The morphological comparison, taxonomical position and stratigraphical occurrence of *Allosorex stenodus* have previously been discussed in details by Fejfar (1966: 237–246). Because the taxonomical position of the *Paenelimnoecus* genus in Allosoricinae is questionable (Storch et al. 1998, Fejfar et al. 2006), the subfamily currently contains only *Allosorex* and *Viretia* (Hugueney et al. 2012). The latter, however, differs from *Allosorex* in its much smaller size, the double-rooted a2, the larger metaconid and the well marked entoconid in lower molars, narrowing of whose can only be considered parallelism. Additionally, these two genera are separated by a time gap of seven million years. On the other hand, the possible *Viretia-Allosorex* phylogenetic line previously discussed by Fejfar (1966) and Repening (1967) is not excluded, and it may have been accompanied by talonid reduction in the connection with the developed carnassial specialisation, especially in m1.

In addition to the fossil record from Ivanovce, *Allosorex* remains are reported only from three localities in Romania, Hungary and France. The fossil record from the Romanian MN 15 site of Dranic-0 (Rădulescu et al. 1995, 1997, Rzebik-Kowalska 2002) is very limited with only three finds minimally from one individual. These finds comprise the following: an upper left incisor (I sin.), a fragmented upper incisor and a left mandible fragment with damaged m1 and complete m2. Unfortunately, the description and depiction of these fossil remains is insufficient for the detailed comparison. Despite the strong similarity, the depicted upper incisor from the Romanian locality differs from incisors in the type collection by its shorter and more rounded apex which is not hook-shaped, plus the slightly different shape of the talon and the more weakly developed buccal cingulum. In contrast, the Ivanovce incisors are larger and have proportionately smaller talon length than those from Dranic-0 (Tab. 1). While the depicted m2 from the mandible fragment also has similarities with type material, it differs in crown base shape on the buccal side, absence of the anterior buccal cingulum, presence of a postero-buccal cingulum and different shape of the paralophid cutting edge. This edge of Dranic-0 m2 has a shorter "paraconid portion" and more steeply directed "protoconid portion" and different shape of the protoconid itself. Moreover, the molar from Romania is shorter and wider than the Ivanovce m2s (Tab. 3) and thus loses the sectorial ("carnivorous") character so typical for the *Allosorex* first two lower molars from the type locality. While these features basically preclude attribution of the Dranic-0 finds to *A. stenodus* species, the possibility that it is a different species of this genus is not completely excluded. Without discovery of a complete m1, however, these finds can only be currently determined as ?*Allosorex* sp.

The other *Allosorex* finds (*A.* cf. *stenodus*) are recorded from the late Miocene (MN 9) site of Alsótelekes in Hungary (Mészáros 1999). However, the described fossil material (M1 dext., m1 dext., and m2 dext.) can be completely excluded from *Allosorex* genus relationship based on the description and depiction of morphological characteristics and metric data (Tabs 2, 3). Moreover, it also differs from the middle Miocene *Viretia gracilidens*.

Finally, Guerin and Mein (1971) reported *Allosorex* finds from French locality of Hauterive, dated to the early Pliocene (MN 14). However, the allosoricine record from this site is neither described nor depicted, but only listed as ?*Allosorex* sp.

Because of the vast uncertainties and insufficients noted in the above Romanian, Hungarian and French records, Ivanovce in Slovakia remains the only credible locality with the unquestionable *A. stenodus* fossil record. Without convincing evidence from other European sites, it is concluded that the Ivanovce species is a local early Pliocene (MN 15) endemic. Moreover, its occurrence (together with desmanine representatives) results from the unique position of the karst in Ivanovce vicinity which is directly in the inundation of the water surface, most likely a blind branch of the large "pre-Váh" River; ecologically and climatically resembling the environment of the modern karst areas in south-eastern Asia.

In conclusion, the enamel microstructure analysis results in combination with other unique characters, such as mandible and dentition morphological adaptations, confirm the *Allosorex* peculiar position in soricids. This now inspires futher discussion on its possible separate family status (Allosoricidae) which was originally considered in 1966 correspondence between one of authors (OF) and Charles Repenning.

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