



## MYOTIS GERHARDSTORCHI SP. N. AND COMMENTS ON THE EUROPEAN FOSSIL RECORD OF MYOTIS FRATER GROUP (MAMMALIA, CHIROPTERA)

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**Abstract:** A new species, *Myotis gerhardstorchi* sp. n., supposedly close to *M. sicarius* and *M. frater* group, is described from MN 15 site Beremend 26 (Hungary). *M. frater* group, now restricted to vicariant ranges in E Asia, Siberia and Central Asia, is further reported from three Pliocene and two Early Pleistocene mass bat assemblages from the Czech Republic, Poland and Slovakia. The odontological diagnosis of the group is presented, together with comparisons of the fossil material with extant species of the group, and W Palearctic taxa of the genus, both fossil and Recent. Molecular phylogenetics reveals that the above-mentioned Asiatic taxa, together with the European species *M. daubentonii* and *M. bechsteinii*, the index fossil of the W Palearctic Late Cenozoic bat communities, compose a distinct phylogenetic entity called *Myotis* Clade III. Here we argue that the history of Clade III in the W Palearctics was contributed also by clades close to its stem line, and those related to the Asiatic forms that later disappeared from that region. Finally, a list of taxa, both fossil and Recent, composing the *Myotis* Clade III is provided.

**Key words:** *Myotis*, bats, Pliocene, taxonomy, distribution, Palearctic region

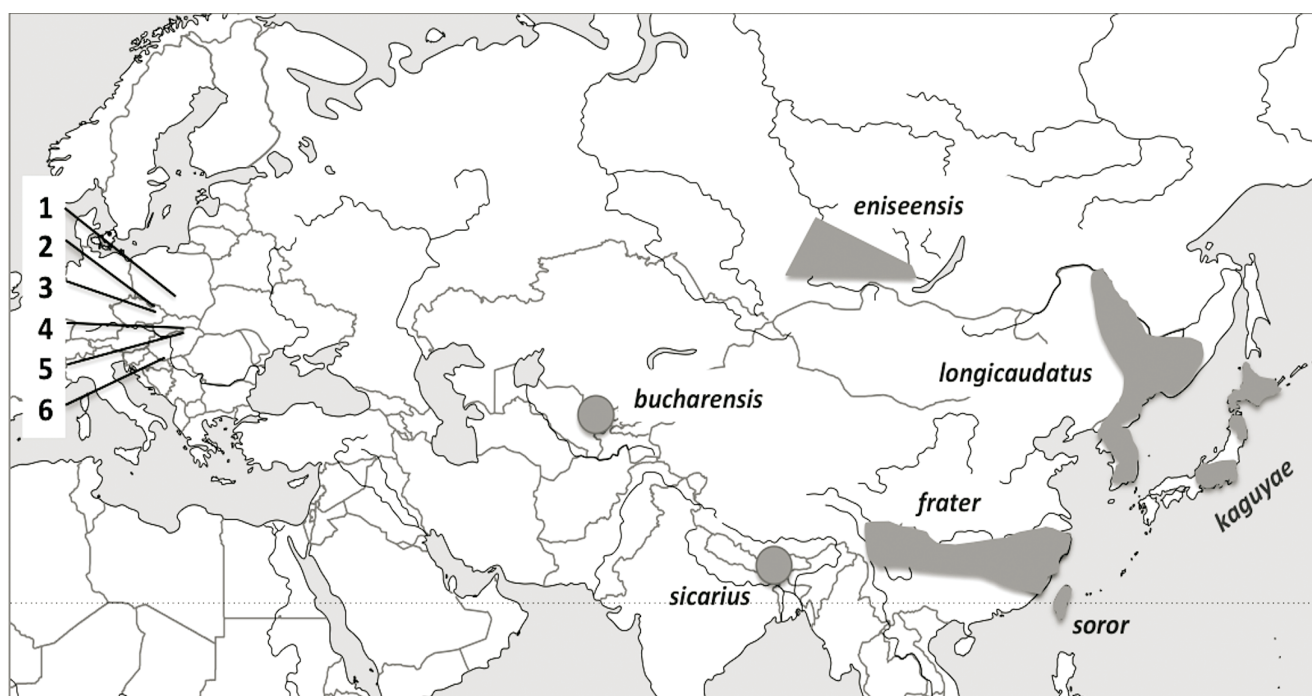
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### Introduction

Genus *Myotis*, one of two mammalian genera of cosmopolitan distribution, ranks with more than 120 extant species (Simmons 2005, Ruedi et al. 2013) among the most diversified clades of bats. All its members share the generalized state of nearly all dental and cranial characters, corresponding to plesiomorphic condition of the family, except for the myotodont pattern of lower molars (Menu and Sigé 1971), notwithstanding a few exceptions. No wonder that taxonomy of that genus and classification of more than 400 taxa named within that genus have traditionally presented the most puzzling topics of chiropteran systematics.

As generally admitted (comp. Findley 1972, Hill and Topál 1973, Topál 1983, Horáček et al. 2000), the phylogenetic morphocline common to the genus is characterised by shortening of rostrum and unicuspid row, reduction of size of small premolars and moderate reduction in size of M3 and m3 talonid, respectively. Based on the state of these characters, and particularly the external characters related to foraging strategies (auricle, hind leg and wing design etc.), Tate (1941), who first reviewed Eurasian forms of the genus in details, proposed subdividing the genus in seven subgenera (*Selysius*, *Isotus*, *Paramyotis*, *Chrysopteron*,

*Myotis*, *Leuconoe* and *Rickettia*). Findley (1972), based on profound analyses operating with multivariate phenetic comparisons, proposed three subgenera, generally delimited along major foraging strategies: ground and foliage gleaning (*Myotis*), aerial hawking (*Selysius*) and water trawling (*Leuconoe*). Despite often being considered provisional, that classification was generally accepted (comp. e.g. Koopman 1994), until a dramatic rearrangement was brought about by application of molecular methods. Ruedi and Mayer (2001) demonstrated that the phylogenetic structure of the genus is first of all linked to biogeographic factors, and the phenotypes characterising the traditional subgenera appeared at different biogeographic regions convergently from quite distant clades. After profound reexamination of almost all species of the genus, Ruedi et al. (2013) demonstrated quite robustly that molecular phylogenetics split the genus into ten distinct clades. Most of them are well delimited either by their biogeographic setting (e.g. Clade I – the American radiation) and/or common phenotype characters, or adaptive designs. Yet, there is one striking exception: Clade III, the most contra-intuitive output of the analysis. It is composed of *M. sicarius*, a large-sized species endemic to Nepal and Sikkim (formerly subgenus *Myotis*), *M. bechsteinii*, a medium-sized, long-eared European endemic (formerly



**Tex-fig. 1.** Current distribution of Asiatic *Myotis* Clade III and geographic position of the sites with its European fossil records. After Tsytulina and Strelkov (2001), Corbet and Hill (1992), Zhang et al. (1997) and Smith and Xie (2008). 1 – Urwista; 2 – Sovinec; 3 – Javoříčko; 4 – Včeláře 4D; 5 – Uppony; 6 – Beremend 17 and 26.

subgenus *Paramyotis*), *M. daubentonii*, the West Palearctic small, short-eared aerial forager trawling on water surface (subgenus *Leuconoe*), and the members of *M. frater* group (formerly *Selysius*) occupying the vicariant ranges in SE China, Taiwan, Japan, Far East, NW Siberia and Uzbekistan. Nevertheless, despite its obscurity, Clade III repeatedly received strong support (Kawai 2003, Horáček et al. 2006, Zhang et al. 2009, Kruskop et al. 2012, Ruedi et al. 2015, Chung et al. 2018).

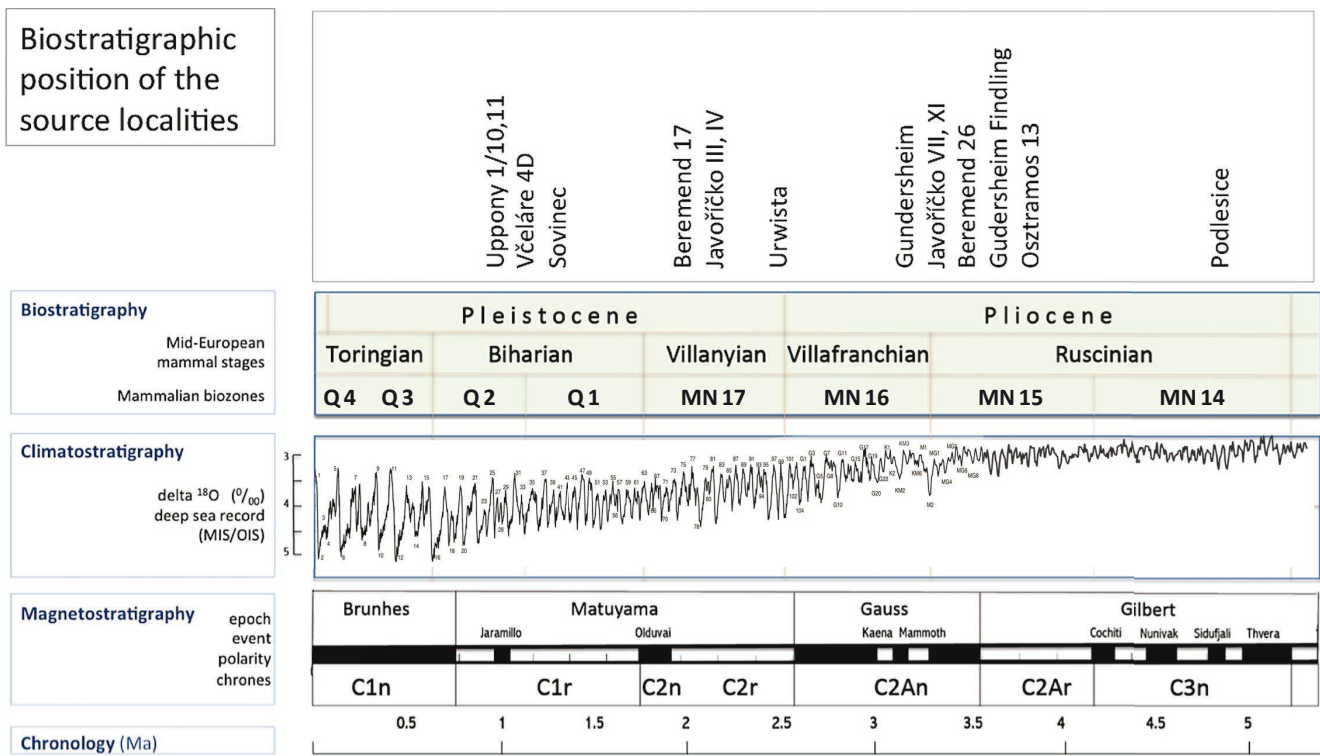
Some of the forms composing Clade III are well documented in the fossil record. First of all, this is true for *M. bechsteinii*, which represents the most abundant component of European bat assemblages throughout the Late Pliocene and Quaternary (Horáček et al. 2000: fig. 44), and for that reason can be regarded as an index fossil of that period. The same abundance pattern also characterises the Early Pliocene forms phenotypically close to *M. bechsteinii*, which were described as separate fossil species (*M. wuesti* KORMOS, 1934, *M. aemulus* HELLER, 1936, *M. kormosi* HELLER, 1936, *M. gundersheimensis* HELLER, 1936 etc.). Following some former authors (Heller 1936, Topál 1985), we tentatively consider these forms as closely related to the above-mentioned extant species, and denote the presumptive clade here as the *M. bechsteinii* group. The respective group is then reported from at least 84 localities of Pliocene and Pleistocene age (2 MN 14, 6 MN 15, 3 MN 16, 12 MN 17, 14 Q 1, 21 Q 2, 25 Q 3), and is also a dominant element in numerous Late Pleistocene and Holocene (Q 4) bat assemblages throughout Central Europe.

*Myotis daubentonii*, similarly to *M. bechsteinii*, is endemic to Europe, yet its Recent range extends to southern Scandinavia and eastward to Omsk Region in Western Siberia (Matveev et al. 2005). In contrast with *M. bechsteinii*, its European fossil record is quite scarce: it is reported as a

rare element from 6 Early Pleistocene sites and 15 Middle or Late Pleistocene sites; a few records from 3 MN 17 sites can be alternatively attributed to *Myotis paradoubentoni* TOPÁL, 1983, the species described from MN 15 Osztramos 13, Hungary (with further records from MN 14 Podlesice, Poland – Godawa 1993, and MN 15 Vitošov, the Czech Republic – Čermák et al. 2007). The latter form differs from the extant *M. daubentonii* by a more robust dentition, broader rostrum and a higher degree of P2, P3, p3 and M3 reduction, i.e. the dental characters obviously more derived than those of the extant species. Topál (1983) hence concludes that *M. paradoubentoni* cannot be considered an ancestor of *M. daubentonii*, though it is undoubtedly closely related.

As concerns the Asiatic representatives of Clade III (Text-fig. 1), to our knowledge, almost no fossil record is available, except for the Late Pleistocene appearance of *M. frater* in Yamaguchi Prov., Japan (Yoon et al. 1984) and the Far East (Tiunov 2016), its Holocene record in NW Altai (Rossina 2006) and listing of the form identified by the late György Topál as *M. frater* in faunal lists of Hungarian Early Pleistocene sites Q 2 Uppony 1/10–11 (Jánossy et al. 1968, Jánossy 1986) and MN 17 Beremend 17 (Jánossy 1996), and similar references in our localities Q 1 Včeláře 4D (Horáček 1985) and Q 1 Sovinec (Horáček and Ložek 1988), providing the material surveyed below.

Here we report further mid-European fossil records supposedly related to the Asiatic members of Clade III, namely the large form, which clearly differs from other species of the genus recorded in the European fossil record. It comes from a rich sample of bat remains from fossil cave deposits of the site Beremend 26 in the Villány Mts. (S Hungary). The abundant and greatly diversified vertebrate assemblage of that site indicates its Early Pliocene age



**Text-fig. 2.** Assumed stratigraphic context of the source assemblages of the fossil forms discussed in this paper. For details concerning standard biostratigraphic subdivisions see e.g. Mein (1975), Fejfar and Heinrich (1983), Fejfar and Storch (1990), Horáček and Ložek (1988), the climatostratigraphic curve compiled after global benthic  $\delta^{18}\text{O}$  record surveyed by Lisiecki and Raymo (2005), magnetostratigraphic standards and chronology after Berggren et al. (1995).

(biozone MN 15b – comp. Császár and Kordos 2004, Čermák 2007, Pazonyi 2011). The material was provided to us by László Pongrác, an enthusiastic private collector who during years of intensive work, assembled for his private museum in Harkány an extraordinary large collection of diverse fossils, first of all from Beremend 26, and some time ago asked one of us (IH) to analyze the bat material in detail. The respective bat assemblage consists of about 300 items, mostly well-preserved dental and cranial fragments. Among numerous remains belonging to at least 12 different species (*Rhinolophus* cf. *kowalskii*, *R.* cf. *mehelyi*, *R. variabilis*, *Miniopterus* sp., *Eptesicus serotinus* group, *M. blythii*, *M. baranensis*, *M. gundersheimensis*, *M. praevius*, *M. cf. paradaubetnoni*, *M. cf. exilis*, *Plecotus* cf. *crassidens*) two well-preserved rostral fragments and two other items exhibit a combination of dental characters by which they clearly differ from other forms of the genus, both fossil and Recent, and obviously represent an independent species, not yet described.

## Material and methods

A list of material and brief information on the source localities are in Appendix I and II, assumed biostratigraphic setting of individual source localities, mostly based on criteria summarized by Fejfar and Heinrich (1983) and Horáček and Ložek (1988) is indicated in Text-fig. 2. In text, the stratigraphic position is expressed in terms of MN zones after Mein (1975, 1990) and Q zones after Horáček (1981) and Horáček and Ložek (1988). All specimens under discussion were documented by optical (Olympus SZX 12

and SEM photography; measurements were taken mostly from the photographs with aid of TpsDig software using calibration by objective micrometer. The terms used for teeth descriptions follow the proposals by Van Valen (1966), Menu (1975) and Horáček and Špoutil (2012) with few modifications; for detailed explanation see Appendix III, Text-fig. A3. The techniques of measurement and particular abbreviations (uppercase letters for upper teeth, lowercase letters for lower teeth) are surveyed in Appendix III, Text-fig. A4, institutional abbreviations and specimen numberings are in Appendix II. Statistical analyses were computed with aid of Statistica 8.0 software.

## Systematic palaeontology

**Order Chiroptera** BLUMENBACH, 1799  
**Family Vespertilionidae** GRAY, 1821  
**Subfamily Myotinae** TATE, 1942 sensu Lack et al. (2010)

**Genus *Myotis*** KAUP, 1829

***Myotis gerhardstorchi* sp. n.**

Pl. 1, Figs 1, 2, Pl. 2, Figs 1, 2, Pl. 3, Fig. 1

**H o l o t y p e .** A nearly complete rostrum with preserved both left and right tooththrows (I1, 2) C–M3, compressed on dorsal side, partly cemented with flowstone incrustation. (Ber26/C1; Pl. 1, Fig. 1a–d)

I1M3 7.89, CM3 7.11, P4M3 5.05, M1M3 4.26, M2M3 2.79, M1M2 3.42, P4M1 2.74, CM1 4.84, P2P3 1.17, CH 2.42, CL 1.31, CW 1.15, P2L 0.81, P2W 0.76, P3L 0.57, P3W 0.52, P4L 1.33, P4W1 1.34, P4W2 1.27, P4W3 1.48,

M1L 1.81, M1W1 1.82, M1W2 1.91, M1W3 2.01, M2L 1.78, M2W1 2.01, M2W2 2.12, M2W3 2.16, M3L 0.95, M3W1 1.87, M3W2 1.65, M3W3 1.06 (measurements in mm).

All the material will be deposited in the collections of the Palaeontological Department, National Museum, Prague, the Czech Republic.

**Paratypes.** Ber26/C2: an incomplete rostrum (I1,2) CP2(P3)P4M1 on right side, (I1–C)P2(P3)P4–M3 on left side (Pl. 1, Fig. 2); Ber26/C4: fragment of left maxilla M1–M3 (Pl. 2, Fig. 2).

**Other material.** Ber26/C3: fragment of right mandible (i1–p3)p4m1(m2–m3) (Pl. 2, Fig. 6); Javoříčko VII/226: fragment of left maxilla (I2–P3)P4(M1–M2) (Pl. 2, Fig. 5); Javoříčko XI/547: fragment of right maxilla (C–P3)P4(M1) (Pl. 2, Fig. 4).

**Derivation nominis.** In memory of Gerhard Storch, one of the top personalities in the study of fossil bats, with a brilliant capacity to integrate both the neontological and palaeontological aspects of the topic.

**Type locality and stratum typicum.** Beremend 26 (Villány Mts., Hungary), Early Pliocene, MN 15b.

**Diagnosis.** A larger, medium-sized representative of the genus, resembling extant *M. dasyncneme* in skull size and proportions, from which it differs by robust unicuspid, higher degree of M3 reduction and less distinct M2 ectoflexus. In these characters it resembles *M. bechsteinii* (and related fossil forms such as *M. gundersheimensis*, *M. kormosi*, etc.), from which it differs by distinctly shortened unicuspid row with large but compressed premolars, P3 being displaced from toothrow, and by large, sharply pointed canine, round on section. In fine dental characters and shape of rostrum, it shows clear similarities to Asiatic forms *M. sicarius* (from which differs in smaller size, larger premolars and less reduced M3), and *M. frater*, which is of course much smaller.

**Description.** A larger, medium-sized form of *Myotis*, resembling *M. dasyncneme* in size and compression of unicuspid row. Rostrum is conspicuously broad and massive, with markedly shortened premaxillae, and short and narrow anterior palatal vacuity in between them. Its distal margin is situated at a level of middle of canine alveolus ( $\frac{2}{3}$  in the paratype, Ber26/C2). Canine is high (almost twice higher than P4), sharply pointed, round at its cingular base, with a sharp distal cutting ridge passing from the distal crown base to the crown tip, and a straight broad ridge at the mesioalatal crown corner. Labial wall is rounded without a trace of undulation. Cingulum continuous, moderately thick without distinct caspules or talonal extensions.

P2 is particularly massive, with sharp distal ridge and distinct cingulum, almost round on section. In lateral view its height amounts about  $\frac{2}{3}$  of P4 height. Also P3 is relatively large (about  $\frac{2}{3}$  of P2 size) and sharply pointed, but displaced palatally from the toothrow, and not visible in the lateral view.

P4 with a high labial crest, massive crown of subcircular outline with robust palatal heel, not extending into separate

talonal basin. Distal crown margin almost straight, without distinct undulation, mesial cingulum broadly rounded, buccal cingulum narrow and straight, without marked undulation. Molars are relatively high and massive, with sharp paraloph extended from the base of paracone and terminating in pronounced protoconules, clearly exceeding a level of preprotocrista. M1 and M2 are characterised by narrow postprotocrista continuing as a sharp crest to talonal base of metacone (note: this is a plesiomorphic state of postprotocrista design – comp. Horáček and Špoutil 2012). This arrangement is associated with a broad metaloph ridge passing from hypoconal extension of protoconal complex (“metaconule”) to base of metacone, attaining the occlusal level of postprotocrista. The hypoconal extension forms an undulation of the palatal wall of the protocone complex, at occlusal level marked by a short rudiment of transcrista, despite almost no undulation appearing at the palatal cingulum of the crown. Distal margin of the molar crown is almost straight, without marked separation of the protoconal complex. Both parastyle and metastyle wings of ectoflexus are markedly enlarged, and buccally they considerably exceed a level of mesostyle that makes the outline of the ectoflexus almost straight.

M3 is moderately reduced, its mesio-distal length is obviously smaller and the metacone is less distinct than in other compared species (Pl. 3). Paraconule and paraloph are well developed. In contrast to other species, M3 bears distinct hypoconal thickening with robust transcrista, by which the distal margin of the protocone complex is distinctly separated from the metacone.

All these characters are with minute variations pronounced in all three rostral fragments from the type locality. The maxillary fragments from Javoříčko VII and XI, which bear P4 only (Pl. 2, Figs 4, 5), correspond to them in alveolar conditions of unicuspid row, and in shape and size of P4.

The mandibular fragment from Beremend 26 (Pl. 2, Fig. 6), tentatively co-identified with the new species for roughly corresponding size and resemblance of *M. dasyncneme* (Pl. 5, Fig. 5) in proportions of p4 and m1, the only teeth preserved, differs from the extant species by narrower p4 and shape of m1, with elongated mesial wall of trigonid, broad trigonidal fovea with a low position of the fovea base, resembling the arrangements characteristic for the *M. frater* group (see below). By combination of a small and narrow p4 ( $0.81 \times 0.55$ ) and large m1 with elongated trigonid, it differs from the taxa of the *M. bechsteinii* group (*wuesti* KORMOS, 1934, *kormosi* HELLER, 1936, *gundersheimensis* HELLER, 1936, *aemulus* HELLER, 1936) and other fossil species of corresponding size (*schaubi* KORMOS, 1930, *steiningeri* KORMOS, 1934, *baranensis* KORMOS, 1934, *podlesicensis* KOWALSKI, 1956).

**Comparisons.** Of the extant European species, *M. dasyncneme* is the first to be taken in account. It resembles the above-described form in size, shape of rostrum and considerable compression of P2–P3. It differs, of course, in shape of canine (anterior position of mesiodistal ridge and flat palatal wall), smaller size and form of P2 and P3, slender heel of P4 with pronounced undulation of distal margin or lesser degree of M3 reduction. Its molars lack buccal

extensions of para- and metastyle wings of ectoflexus and metaloph thickening of distal postprotocrista.\*

In most species of *Myotis* (and most other vespertilionid genera), hypoconal extension of protoconal wall is relatively low compared to the protocone, and the metaloph is not developed. Consequently, the postprotocrista directly continues to presumptive hypocone and via the transcrista to the distal crown base, while the fossa gradually opens to the distal crown margin (comp. Pl. 3, Figs 4, 7, 8).

This is the case also in *M. bechsteinii* (and numerous fossil items co-identified with it and/or the fossil species supposedly related to it – see above). At the same time, of course, the forms of that group correspond to the new species in size of individual teeth, shape of the upper canine and premolars, though they markedly differ in size of premolars and arrangement of unicuspid row, position of P3 and in narrower rostrum prolonged in unicuspid section. M2 and M3 in *M. bechsteinii* as well as in *M. gundersheimensis* show a distinct extension of the metastyle wing of the ectoflexus, but the parastyle wing remains quite narrow (Pl. 3). Yet all these forms, as well as other European fossil species of corresponding size for which the maxillary dentitions are available (incl. *M. schaubi* and *M. podlesicensis* or numerous Miocene or Late Oligocene forms – comp. Horáček and Hanák 1984, Ziegler 2000, 2003, Rosina and Kruskop 2011, Rosina and Semenov 2012) differ significantly from the new species in arrangement of unicuspid row.

There is an extensive similarity between the new species and *M. sicarius* in the above-mentioned diagnostic characters, but the latter form, now endemic to Sikkim and Nepal, is

\* At this point we feel obliged to elucidate the usage of some terms applied in this paper, namely the term metaloph (or “premetaconule crista” by Aguiar Fracasso et al. 2011), commonly used to denote the crest between postprotocrista and base of metacone (comp. e.g. Menu 1985, Godawa Stormark 1998). Yet, following Cope-Osborn proposal, the term “loph” is to be applied to the thickened enamel ridges which perpendicularly interconnect the main cusps of tribosphenic design, i.e. paracone-protocone (paraloph) and metacone-hypocone (metaloph), respectively. Since in all early bats which lack hypoconal extension of protoconal complex (*Ageina*, *Icaronycteris*, *Archaeonycteris*, etc.) as well as in presumptive ancestors of this order (Nyctitheriidae, Adapisoriculidae) postprotocrista connects protocone with base of metacone, also in the modern bat the crest extending postprotocrista to base of metacone, though commonly denoted as metaloph (Menu 1985; or premetaconule crista by Aguiar Fracasso et al. 2011) is to be considered as part of postprotocrista and a distinct plesiomorphy of molar crown design (comp. Horáček and Špoutil 2012 for details). Of course, where hypocone and/or hypoconal extension of the protocone distal wall is developed (termed “metaconule” as a rule where it is shaped in form of a distinct cusp-like structure), the respective crest can be accompanied with a distally thickened ridge interconnecting that structure with the base of the metacone. This ridge, metaloph s. str., is obviously not identical with the above-mentioned crest (it is figured but not identified by Aguiar Fracasso et al. 2011: fig. 1b); in some clades it accompanies the crest, in others, one or both are absent. In *Myotis*-like bats, where taxonomically significant odontological criteria are rather scarce, a careful attention to fine morphology of upper molars incl. consequent distinguishing these structures can essentially improve the scope of comparative studies, particularly when the fossil record is taken in analysis.

considerably larger, and shows a higher degree of P2–P3 and M3 reduction (App. III, Tabs A1, A2). In *M. sicarius*, P2 is still relatively large, but infilling a narrow space between C and P4, it is mesiodistally compressed; P3 is dot-like, partly under the mesio palatal cingulum of P4. The metastyle wings of M1 and M2 ectoflexus are much less developed in *sicarius*, while mesostyles are prominent buccally to form a trilobate-like outline of the ectoflexus in the occlusal view.

A broad measure of agreement in the above-mentioned characters in shape of rostrum and relative sizes of individual teeth is also with members of the extant *M. frater* group (comp. Pls 4–7, and also Pl. 3, Figs 1, 2), which are, of course, much smaller (App. III, Tabs A1, A2).

Regarding all this, the new species, which reveals a mosaic of resemblances to all taxa composing Clade III, i.e. *M. sicarius*, *M. bechsteinii* group, *M. frater* group and *M. dasycneme-Leuconoe*-like traits characterising *M. daubentonii*, can be considered as the form closely related to the stem line of Clade III.

### ***Myotis frater* group in mid-European fossil record**

Bats of *M. frater* group bear an uncommon combination of characters for which their taxonomic position was considered uncertain (Tate 1941, Kuz'yakin 1950, Wallin 1969, Findley 1972, Tsytsulina and Strelkov 2001), but which at the same time allows distinguishing this group from other members of the genus: enlarged braincase, shortened but conspicuously broad rostrum, compressed unicuspid with displacement of P3 from the tooth row, greatly pronounced angulus mandibulae, mesially tapered processus coronoideus, etc.

The group, formerly denoted as a single species, was surveyed in detail by Tsytsulina and Strelkov (2001), who demonstrate that it is composed of several taxonomically distinct forms occupying isolated vicariant ranges: *Myotis f. frater* ALLEN, 1923 (China, Fujian Prov., Rong To Valley, Tibet and Taiwan), *Myotis f. kaguyae* IMAIZUMI, 1956 (Japan), *Myotis f. longicaudatus* OGNEV, 1927 (Russian Far East), *Myotis f. eniseensis* TSYTSULINA et STRELKOV, 2001 (Central Siberia). Similarly to Horáček et al. (2000), Tsytsulina and Strelkov (2001) demonstrated that *Myotis f. bucharensis* KUZ'YAKIN, 1950 (three localities in border region of Tajikistan and Uzbekistan) differs in more characters from the other forms of the group, and so represents a separate species. A detailed analysis by Ruedi et al. (2015) combining both molecular and morphological approach supplemented the *M. frater* group with a new species from Taiwan, *M. soror* (denoted as *Myotis* sp. 3 in Ruedi et al. 2013).

A tentative odontological diagnosis of the *Myotis frater* group (based on comparison of extant taxa) could be as follows:

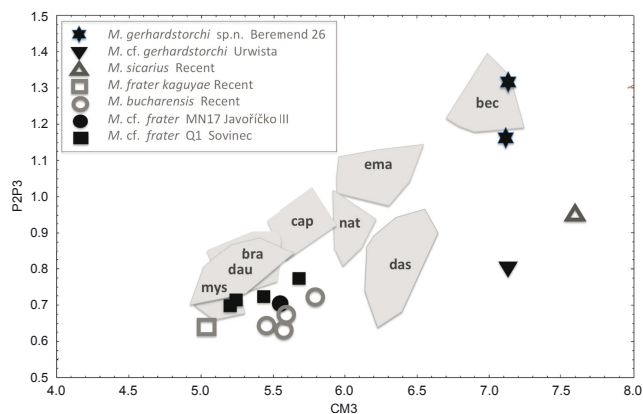
(i) A complete *Myotis* dentition with considerably reduced small premolars, shortened but broad rostrum, (ii) shortened premaxilla with a broad but short anterior palatal vacuity, with its distal margin at a middle level of canine alveolus, (iii) strong upper canine with a broad circular cingulum particularly distinct along labial edge of the crown, (iv) P2 is relatively large while P3 is displaced palatally from toothrow, so P2

appears nearly in contact with mesial cingulum of P4, (v) P4 relatively robust (compared to *M. daubentoni*, *M. dasynceme* or *M. mystacinus*), yet with only indistinct talonal extension, (vi) M1 and M2 with paralophs and protoconules (absent in M1 of *bucharensis*, indistinct in *eniseensis*; comp. Tsytulina and Strelkov 2001) and (vii) enlarged metastyle wings of ectoflexus, (viii) the crest between hypoconal extension of the protocone wall and metacone distinct (particularly high in *bucharensis* but low in *eniseensis*), accompanied by metalophus ridge (which is absent in *bucharensis*), (ix) M3 moderately reduced (more than in *M. daubentoni* or *M. dasynceme*) with retained protoconule.

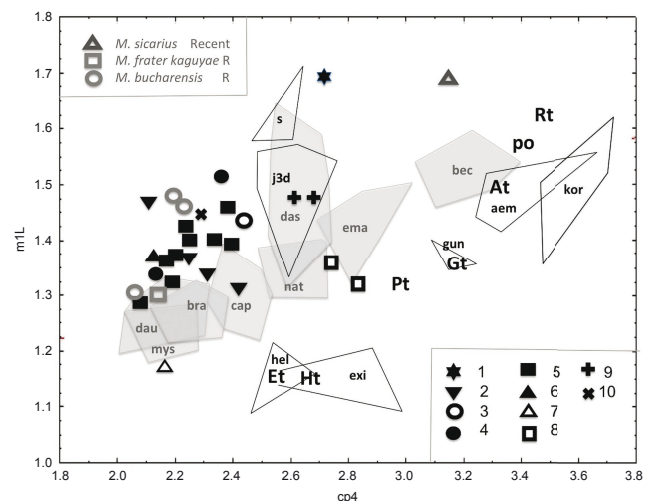
Mandible is characterised by (x) a pronounced angulus mandibulae, and (xi) anteriorly tapered processus coronoideus, clearly extending the mesial margin of ramus mandibulae, (xii) i3 is significantly larger than i1 and i2, with two large cusps at the labial side of the crown and two isolated cusps extending its crown lingually, (xiii) in contrast to most other species of the genus, i3 bears a distinct cingulum along its labial base, (xiv) the lower canine exceeds p4 in height only indistinctly, its lingual cingulum is conspicuously thick, and terminates in a robust cingular cuspid at the mesio-lingual corner of the crown, which attains almost half of the tooth height, (xv) p2 is about a half or 1/3 of p2 size and tends to be displaced lingually from a toothrow, (xvi) compared to m2 and m3 trigonid of m1 is enlarged with anteriorly extended mesial wall, (xvii) trigonid fovea of m1 is thus conspicuously broad and deep with a marked cingulids at its lingual base, (xviii) m3 is moderately reduced, its talonid is relatively narrow, but long, with high entoconid crest and robust postcristid.

The odontological differences of *M. bucharensis* lie particularly in shape of the upper canines, with an inflated distal cingulum laterally exceeding a level of P2 tip, and the distal margin of the protoconal complex of M1 and M2, with absence of a broad metalophus (vii, viii). In mandibular dentition, a robust elongated p4 is to be mentioned.

Studying extensive materials of fossil bats from a number of the Pliocene and Pleistocene localities of Central Europe (comp. e.g. Horáček and Ložek 1988), we found a set of items differing from other local forms, both extant and fossil, which show a broad measure of agreement with the characteristics of the *M. frater* group, as proposed above (including their size corresponding to respective extant



**Tex-fig. 3.** Maxillary variables C–M3 vs. P2–P3 in the reported fossil forms and extant Asiatic forms with clouds of variation of the extant W Palearctic representatives of the genus.



**Tex-fig. 4.** Mandibular variables cp4 vs. m1L in the reported fossil forms and extant Asiatic forms with clouds of variation of the extant W Palearctic representatives of the genus. 1 – *Myotis* cf. *gerhardstorchi* sp. n., Beremend 26; 2–6 – *M. frater* group: 2 – Urwista, 3 – Javoříčko VII, 4 – Javoříčko III, 5 – Sovinec 4; 6 – Včeláre 4D/12; 7 – *M. mystacinus* group, Včeláre 4D/12; 8 – *M. danutae*, Podlesice; 9 – *M. delicatus*, Gundersheim; 10 – *M. dasynceme subtilis*, Podlesice. At – *M. aemulus* holotype, Gundersheim; Et – *M. exilis* holotype, Gundersheim; Gt – *M. gundersheimensis* holotype, Gundersheim; Ht – *M. helleri* (*M. insignis* holotype), Gundersheim; Pt – *M. praevius* holotype, Gundersheim; Rt – *M. rapax* holotype, Gundersheim; aem – *M. aemulus*, Gundersheim; exi – *M. exilis*, Gundersheim; gun – *M. gundersheimensis*, Gundersheim; hel – *M. helleri*, Gundersheim; j3d – *M. delicatus/dasynceme*, Javoříčko III; kor – *M. kormosi*, Gundersheim; s – *M. dasynceme*, Sovinec 4.

species) – the complete list of them is in Appendix II, the best-preserved items are figured in Pls 4–7, their metrical characters are summarized in Appendix III (Tabs A1, A2). Yet, as is frequent in bat fossil assemblages, only few maxillary fragments are available, while the vast majority of the material is composed of mandibular fragments. On the other hand, this opens a possibility of comparison with other fossil species of the genus, described exclusively based on mandibular characters.

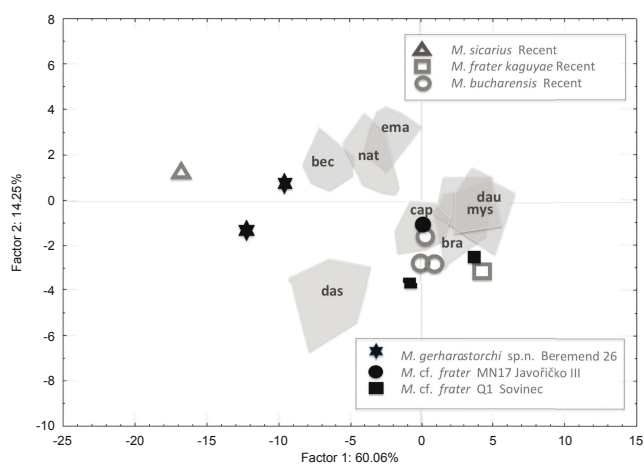
The largest collection comes from Q 1 site Sovinec 4 (northern Moravia, the Czech republic; three rostral fragments, three maxillary fragments and 38 mandibular fragments), a perfectly preserved specimen is available also from another Q 1 site – Včeláre 4D (SE Slovakia; one almost complete and three fragmentary mandibles), while the items found in MN 16 Urwista (Poland), MN 15 Javoříčko VII and MN 17 Javoříčko III (both north Moravia, the Czech Republic) are both less preserved and less frequent (comp. App. I). Both in dental phenotype and in measurements, these specimens fit impressively well to the conditions of extant form (comp. Pls 5–7 and App. III, Tab. A1). Yet all specimens from Urwista, several items in Sovinec 4 (Sov4/9, 19, 22), and other sites (Javoříčko VII: JavVII/29, Javoříčko III: JavIII/223) exhibit dimensions slightly larger, exceeding the upper limit of variation of extant forms (Tsytulina and Strelkov 2001) by 6–10 %. Some of them (e.g. Sov4/22, JavIII/233) also show certain differences in shape of the canine, which is conspicuously large, but mesio-distally

compressed at its base, though in indexing characters (xv–xviii) they exhibit good agreement with other forms of the *M. frater* group.

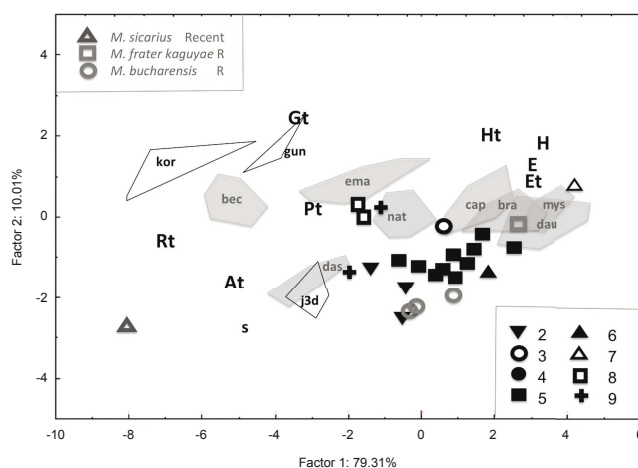
In morphometric space of uni-, bi- and multivariate comparisons, the fossil items attributed here to the *M. frater* group form a relatively compact cluster, close to extant forms of the clade (comp. Text-figs 3–6). It is situated quite apart from variation domains of most other W Palearctic members of the genus, not only the larger forms, both extant (*bechsteini*, *emarginatus*, *nattereri*, *dasycneme*) and fossil (*kormosi* HELLER, 1936, *aemulus* HELLER, 1936, *gundersheimensis* HELLER, 1936, *rapax* HELLER, 1936, *praeivius* HELLER, 1936, *podlesicensis* KOWALSKI, 1956 or *gerhardstorchi* sp. n.), but also from those of comparable or smaller size.

By some metrical characters, several items (particularly those from Urwista – comp. Pl. 7, Figs 1–2) fall into variation span of extant *M. capaccinii*. Yet *M. capaccinii* differs from the *M. frater* group (including the fossil items in question) by smaller lower incisors (incl. i3), low but elongated canine with enlarged and medially tapered talon and without mesiolingual cingular cusp, by large and high p2 and p3 amounting to 2/3 of p4 height, p4 square on section, narrow trigonid of m1 with a high base of trigonidal fossid, etc., notwithstanding the prolonged rostrum or unreduced premolars in the upper jaw. Similar differences, particularly the lesser degree of premolar reduction, narrower m1 trigonid and different shape of c1 and p4 also discriminate the *M. frater* group from *M. brandtii*, *M. mystacinus*, *M. daubentonii*, fossil taxa *M. paradoubentoni* TOPÁL, 1983, *M. janossyi* TOPÁL, 1983, *M. estramosensis* TOPÁL, 1983, *M. exilis* HELLER, 1936 and *M. helleri* KOWALSKI, 1962 (= *M. insignis* HELLER, 1936), all of which are also significantly smaller on average (comp. Godawa 1993 and App. III, Tab. A2).

*M. delicatus* HELLER, 1936, *M. dasycneme subtilis* KOWALSKI, 1956 and *Myotis danutae* KOWALSKI, 1956 are the other species which come in account, yet they all are somewhat larger than the discussed items, except for the above mentioned large specimens of our fossil material.



**Tex-fig. 5.** Plot of PCA Factor 1 and 2 scores (based on maxillary variables: CM3, P4M3, M1M3, M2M3, M1M2, P4C1, CM1, P2P3, length and width of individual teeth P4–M3, and proportions P2P3/P4 and W/L of individual teeth C–M3) of the reported fossil forms and extant Asiatic forms, with clouds of variation of the extant W Palearctic representatives of the genus.



**Tex-fig. 6.** Plot of PCA Factor 1 and 2 scores (based on mandibular variables cm3, p4m3, m1m3, cp4, p4m1, m1m2, m2m3, p4L, m1L) of the reported fossil forms and extant Asiatic forms, with clouds of variation of the extant W Palearctic representatives of the genus. For further explanations see Text-fig. 4.

The former two taxa were synonymized by Topál (1985) and interpreted as ancestor clade of *M. dasycneme* by Horáček and Hanák (1989), who suggested (with regards to remains from Javoříčko, Sovinec (both the Czech Republic), Urwista and Žabia (both Poland)) a gradual increase in size and degree of premolar reduction as the morphocline characterising the Pliocene history of that clade (comp. also Text-fig. 4). Of course, while the specimens of *delicatus* from MN 15 Gundersheim (incl. its holotype) conform well to characters of *dasycneme*-clade (small i3, elongated base of c1, compressed p3, narrow trigonid fossid of m1, broad molars), *M. dasycneme subtilis* KOWALSKI, 1956 from MN 14 Podlesice (emended to *M. delicatus subtilis* by Horáček and Hanák 1989) shows significantly smaller dimensions (comp. Godawa 1993), falling even into the variation span of large items of the *M. frater* group. The single paratype specimen of *subtilis* that was at our disposal resembles them even in shape of the lower canine. Also, the remaining species described from MN 14 Podlesice, *Myotis danutae*, could come in account as a taxon related to stem line of the *Myotis* Clade III, eventually. Kowalski (1956) and Topál (1983, 1985) mentioned suspected relations of this form to *M. emarginatus*, mostly based on elongated p4 and relatively short canine, yet at the same time it differs just in these characters from the extant species quite distinctly. When the senior author of this paper examined a paratype series of *danutae* many years ago, he concluded that the idea on its relationship to *emarginatus* seemed to be insufficiently substantiated, and *danutae* is to be looked upon as the form without apparent relations to any of the extant W Palearctic clades. In some characters it even resembles the *M. frater* group (e.g. in shortened premaxilla, relatively short and broad rostrum), yet its premolars are only slightly reduced, with no displacement and/or marked disproportions in degree of P2–p2/P3–p3 reduction characteristic, e.g. for the *M. mystacinus* group, or *M. dasycneme*.

In short, the status and phylogenetic relations of *subtilis* and *danutae* are worth being thoroughly re-examined, also in regards to the possibility of their relations to stem line of

Clade III. However, this topic is obviously beyond scope of the present paper.

Nevertheless, the possibility that the European Pliocene communities were enriched by more than one relic form related to the stem line of Clade III, not necessarily related to the extant species of that group, cannot be excluded. Also the fact that the phenotype variation observed among the fossil specimens surveyed above (e.g. in shape of lower canine) amounts to dental differences separating extant *M. longicaudatus* and *M. bucharensis*, put the assumed species homogeneity of the European *M. frater* group into question.

In any case, it seems clear that the forms attributed here to the *M. frater* group represented a quite rare component of fossil bat assemblages. In Sovinec, they are represented by 41 items of about 1,500 jaw fragments, in Javoříčko III 12 items of 1,360 jaws, in Javoříčko XI one of >2,000, in Javoříčko VII two items of ca. 300, in Urwista 9 items of 1,700 and in Včeláre 4D three items of ca. 300 jaws, i.e. 0.1–2 % of local bat community on average, notwithstanding absence of these forms in the vast majority of other fossil bat assemblages.

Of course, it should be remembered that the extant forms of that clade also rank in all regions of their appearance among very rare bats (comp. Wallin 1969, Tsytsulina and Strelkov 2000, Ruedi et al. 2015). For instance, *M. bucharensis* was found only in three localities in 1915, 1959 and 1960 (Kuzyakin 1950, Bogdanov 1960, Tsytsulina and Strelkov 2001, Benda et al. 2011), while no further record is available since 1963, when the colony discovered in 1960 disappeared, due to which the species is considered extinct (Horáček et al. 2000).

## Concluding remarks

Despite enormous enlargement of European fossil record of bats from beginning of the Pliocene and absolute predominance of the genus *Myotis* in the Pliocene and Pleistocene mass bat assemblages, the question, which was actual taxonomic diversity of that genus, presents even now a puzzling challenge not easy to resolve. In full, it holds also for actual status of the particular Pliocene taxa and their relations to the extant clades of the genus. It is not only due to conservative phenotype variation of the genus and parallel trends in phylogenetic morphoclines of different clades, i.e. the aspect which complicates taxonomy of the genus in general, but first of all due to the fact that the variation patterns within the Pliocene forms do not correspond to variation patterns characterising the extant clades. In any case, the Pliocene bat assemblages are in most instances dominated by forms somehow related to *M. bechsteinii* or resembling it, despite obvious differences, in their dental and cranial phenotypes. Remaining forms, mostly rare in fossil assemblages, include either those which obviously have no relations to any extant clade of the genus (*M. helleri*), or those sharing phenotype design with some W Palearctic extant species being often believed, despite faint support as a rule, to represent their ancestral clades (*M. praevius*-*M. nattereri*, *M. delicatus*-*M. dasyncneme*, *M. exilis*-*M. mystacinus*, etc.).

Very few clades of extant *Myotis* show the set of phenotype traits that would allow us to distinguish them

unambiguously from the other. One of them is the *Myotis frater* group, according to robustly supported molecular evidence (Ruedi et al. 2013, 2015), a sister clade of *M. bechsteinii*.

Here we demonstrated appearance of that clade in the European Pliocene and Quaternary fossil record, both with the forms obviously closely related to the extant Asiatic members of that group, and the forms which can be looked upon as a representative of the stem line of the *Myotis* Clade III, close to common ancestor of the Asiatic forms and the *M. bechsteinii* group. This concerns first of all the new species described here, *M. gerhardstorchi* sp. n., which shows a mosaic of phenotype characters distinguishing particular extant species of that clade (*M. sicarius*, *M. frater*, *M. bucharensis*, *M. daubentonii*, *M. bechsteinii*).

It can be hypothesized that retreat of ancient representatives of Clade III from the temperate Western Palearctic took place during the Late Pliocene or earliest Pleistocene, simultaneously with onset of current phenotypes in *M. bechsteinii* and *M. daubentonii*. The stratigraphic gap between the early MN 17 records (Javoříčko III, Urwista) of the *M. frater* group and its record in Q 1/Q 2 sites (supposedly close in stratigraphic position: Uppony 1/10 (Hungary), Včeláre 4D (Slovakia), Sovinec) conforms to a possibility of temporal westward range expansion of that clade during the middle to late Early Pleistocene.

In short, the present records suggest that a considerable part of *Myotis* Clade III history might have taken place in the W Palearctic, and this possibility opens an exciting topic for future research.

To provide a provisional basic platform for it, we propose here a tentative list of taxa composing Clade III, both fossil and Recent (the above mentioned hypotheses on *M. d. subtilis* and *M. danutae* not being taken in account):

- Myotis sicarius* THOMAS, 1915 (Recent, Nepal-Sikkim)
- +*Myotis gerhardstorchi* sp. n. (MN 15, Europe)
- Myotis bechsteinii* KUHL, 1818 (MN 15 – Recent, Europe)  
syn: +*wuesti* KORMOS, 1934, +*robustus* TOPÁL, 1963,  
+*intermedius* RYBÁŘ, 1976
- +*Myotis kormosi* HELLER, 1936 (MN 14–17, Europe)  
? syn: +*rapax* HELLER, 1936
- +*Myotis aemulus* HELLER, 1936 (MN 14–17, Europe)
- +*Myotis gundersheimensis* HELLER, 1936 (MN 14–17, Europe)
- Myotis frater* ALLEN, 1923 (Recent, SE China, Taiwan)
- Myotis soror* RUEDI et al., 2015 (Recent, Taiwan)
- Myotis daubentonii* KUHL, 1818 (Q 1 – Recent, Europe)
- +*Myotis paradaubentoni* TOPÁL, 1983 (MN 15–17?, Europe)
- +*Myotis cf. frater* (MN 16 – Q 2 Europe)
- Myotis longicaudatus* OGNEV, 1927 (Recent, Far East)
- Myotis longicaudatus kaguyae* IMAIZUMI, 1956 (Recent, Japan)
- Myotis (longicaudatus ?) eniseensis* TSYTSULINA et STRELKOV, 2001 (Recent, Central Siberia)
- Myotis bucharensis* KUZYAKIN, 1950 (Recent /?extinct/, Bukhara, Samarkand)

The arrangement of the list follows the refined topology of the Clade III tree, resulting from a comprehensive molecular and morphometric analysis by Ruedi et al. (2015). It suggests: (a) basal position of *M. sicarius* followed by (b) divergence of *M. bechsteinii* and (c) the clade containing



*M. f. frater* and *M. soror* and its sister group (d) the clade composed of *M. daubentonii* and *M. f. longicaudatus-kaguyae*. Unfortunately, to our knowledge, no molecular records are available for *bucharensis* and *eniseensis*. Their position as well as positions of some fossil forms remain thus matter of discussion.

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## Explanations to the plates

### PLATE 1

*Myotis gerhardstorchi* sp. n., MN 15, Beremend 26 (Hungary)

1. Holotype (Ber26/C1); a – dorsal view, b – lateral view, c – occlusal view, d – occlusal view of left toothrow.
2. Paratype (Ber26/C2); occlusal view.

### PLATE 2

Maxillary (1, 2, 4, 5) and mandibular (6) fragments attributed to the new species and maxillary dentitions of other forms (3, 7, 8, 9)

1. *Myotis gerhardstorchi* sp. n., holotype, MN 15, Beremend 26 (Ber26/C1).
2. *Myotis gerhardstorchi* sp. n., paratype, MN 15, Beremend 26 (Ber26/C4).
3. *Myotis dasyncneme*, Recent, the Czech Republic (ISZ 1328/73).
4. *Myotis* cf. *gerhardstorchi* sp. n., MN 15, Javoříčko XI (JavXI/547).
5. *Myotis* cf. *gerhardstorchi* sp. n., MN 15, Javoříčko VII (JavVII/226).
6. *Myotis* cf. *gerhardstorchi* sp. n., MN 15, Beremend 26 (Ber26/C3); a – occlusal, b – lingual view of a mandibular fragment.
7. *Myotis bechsteinii*, Holocene, Ponikleč cave, the Czech Republic (PonC24).
8. *Myotis* cf. *gundersheimensis*, MN 15, Beremend 26 (Ber26/30).
9. *Myotis* cf. *baranensis* MN 15, Beremend 26 (Ber26/18).

### PLATE 3

A detailed view on upper molar row of selected taxa (not to scale)

1. *Myotis gerhardstorchi* sp. n., holotype, MN 15, Beremend 26 (Ber26/C1).
2. *M. frater kaguyae*, Recent, Japan (ISZ N-101).
3. *M. daubentonii nathalinae*, Recent, France (ISZ F76/02).
4. *M. bechsteinii*, Holocene, the Czech Republic, (PonC24).
5. *M. dasyncneme*, Recent the Czech Republic (ISZ 128/73).
6. *M. aff. frater*, Q 1, Sovinec 4 (Sov4/16).
7. *M. cf. gundersheimensis*, MN 15, Beremend 26 (Ber26/30).
8. *M. blythii*, MN 15, Beremend 26 (Ber26/18).

### PLATE 4

Upper dentitions

1. *M. frater kaguyae*, Recent, Japan (ISZ N-101).
2. *M. bucharensis*, Recent, Samarkand, Uzbekistan (ISZ B-7).
3. *M. daubentonii nathalinae*, Recent, France (ISZ F76/02).
4. *M. daubentonii*, Recent, the Czech Republic (ISZ Voz2019/1).
5. *M. cf. frater*, Q 1, Sovinec 4 (Sov4/1).
6. *M. cf. frater*, Q 1, Sovinec 4 (Sov4/16).
7. *M. cf. frater*, MN 17, Javoříčko III (JavIII/11).

### PLATE 5

Mandibles

1. *M. frater kaguyae*, Recent, Japan (ISZ N-101).
2. *M. bucharensis*, Recent, Samarkand, Uzbekistan (ISZ B-7).
3. *M. daubentonii*, Recent, the Czech Republic (ISZ Voz2019/1).
4. *M. daubentonii nathalinae*, Recent, France (ISZ F76/02).
5. *M. dasyncneme*, Recent, the Czech Republic (ISZ 128/73).
6. *M. bechsteinii*, Recent, Bulgaria (ISZ B71/C21); a – upper dentition, b – mandible.
7. *M. cf. baranensis*, MN 15, Beremend 26 (Br26/C25).

### PLATE 6

Mandible fragments of *M. cf. frater* (1–4, 6) and *M. cf. mystacinus* (5) from Q 1 localities (a – labial view, b – occlusal view, c – lingual view)

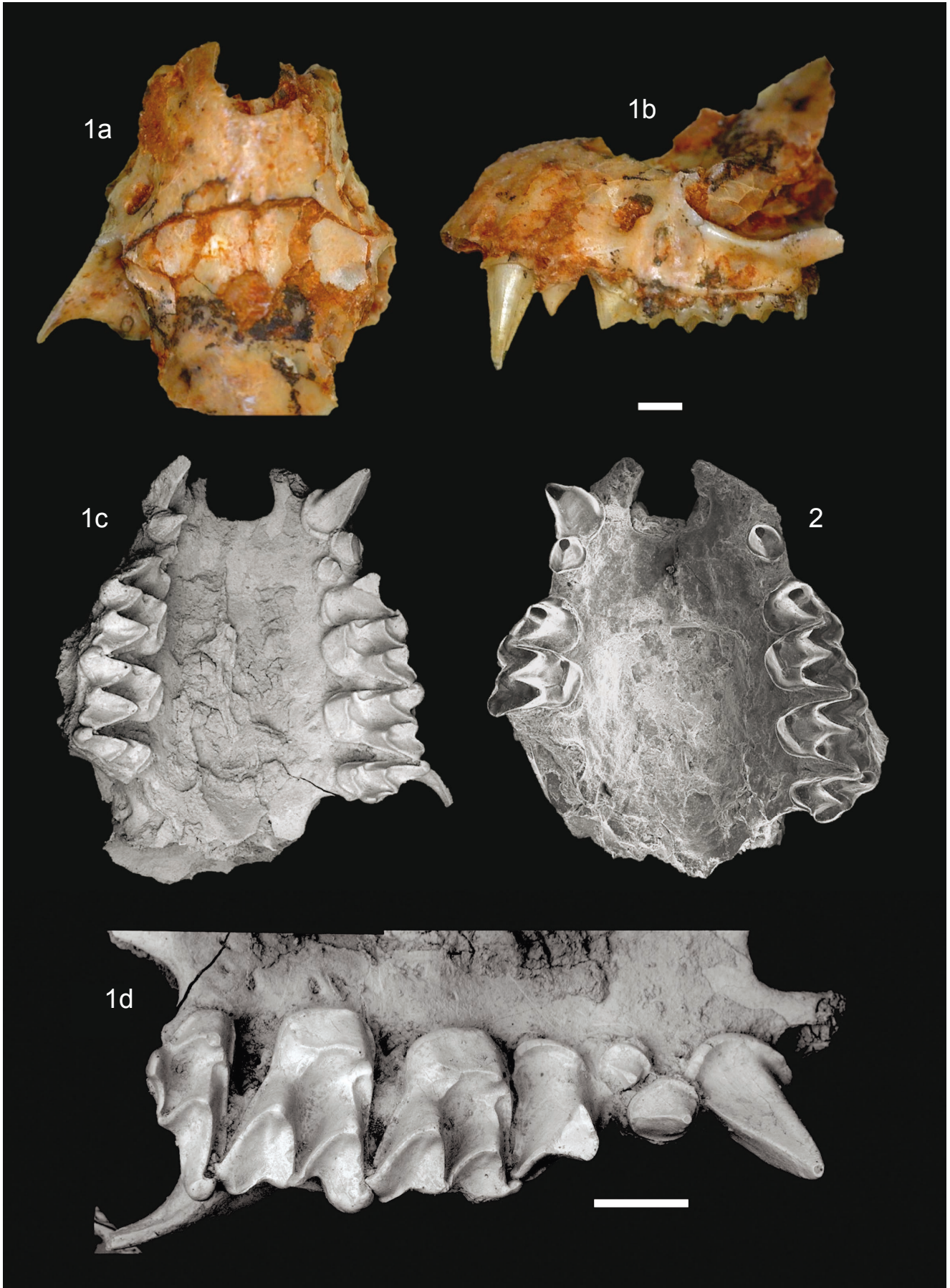
1. Sovinec 4 (Sov4/10).
2. Sovinec (Sov353/01).
3. Sovinec (Sov353/09).
4. Sovinec 4 (Sov4/22).
5. Včeláre 4D/12, Slovakia (Včel4D/12/02).
6. Včeláre 4D/12, Slovakia (Včel4D/12/01).

### PLATE 7

Mandible fragments of *M. cf. frater* from MN 17 (1–5) and MN 15 (6) localities (a – labial view, b – occlusal view, c – lingual view)

1. Urwista, Poland (Urw1/1/22).
2. Urwista, Poland (Urw1/1/23).
3. Urwista, Poland (Urw1/2/39).
4. Javoříčko III (JavIII/223).
5. Javoříčko III (JavIII/116).
6. Javoříčko VII (JavVII/39).

PLATE 1



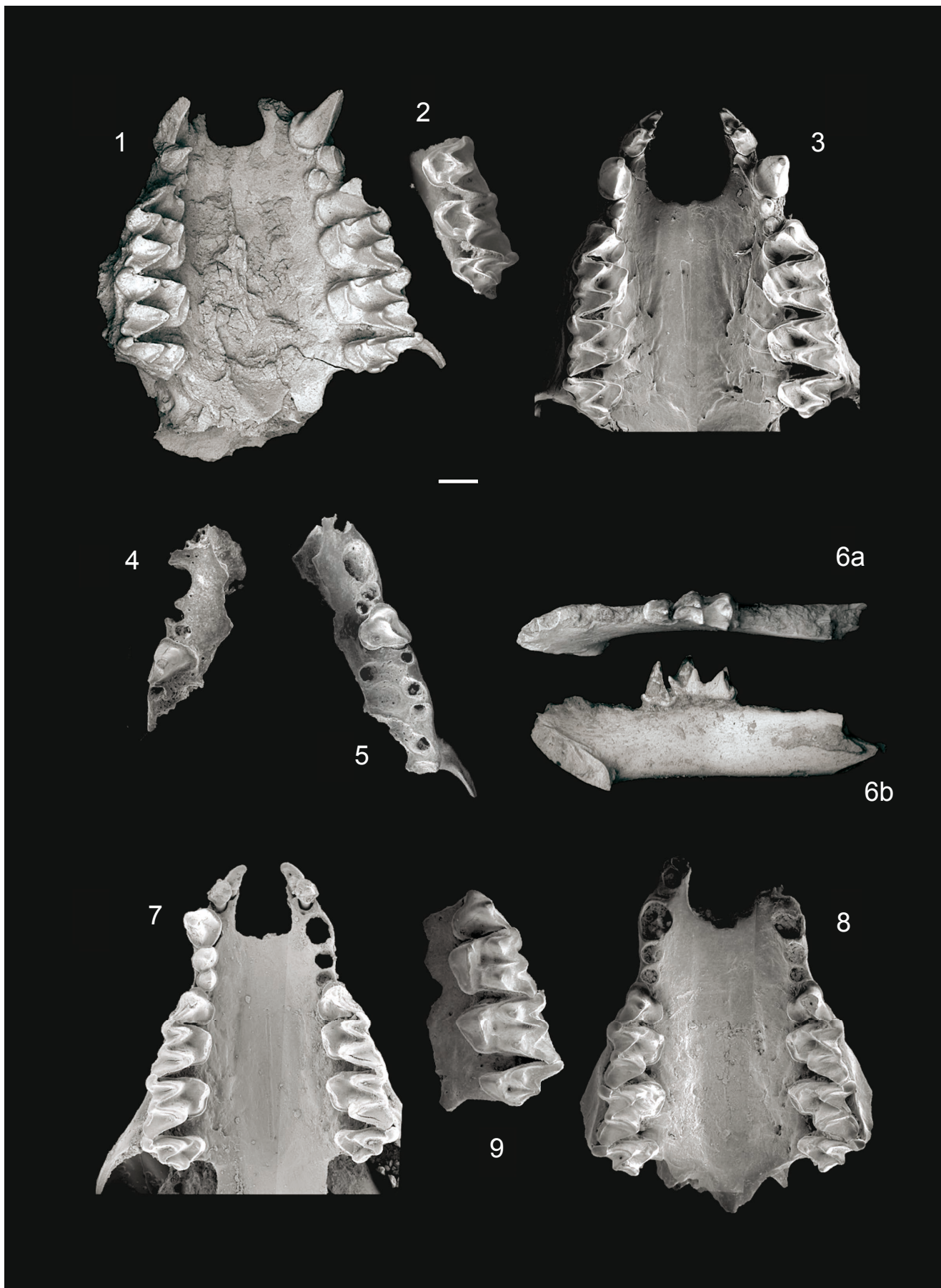
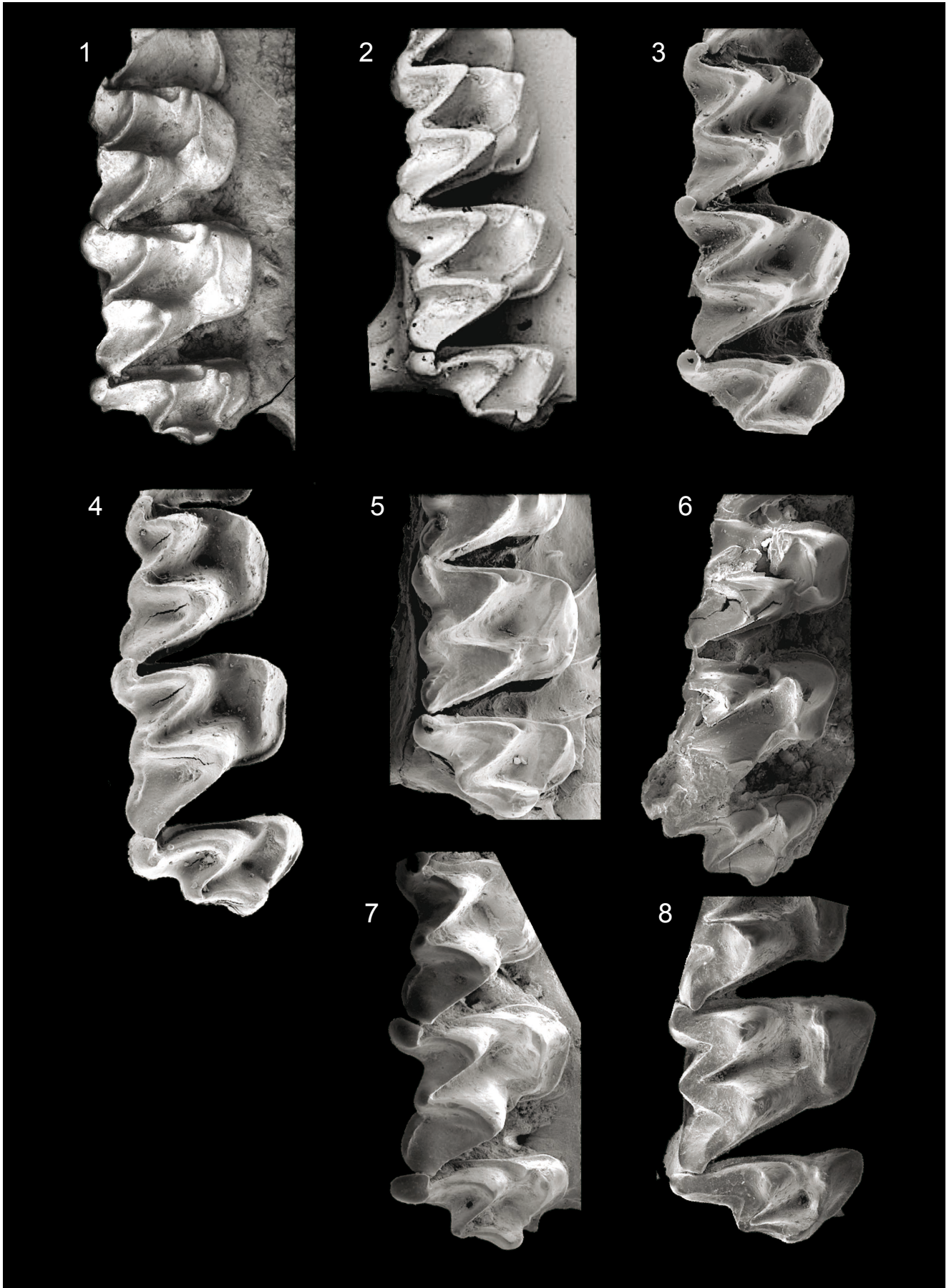


PLATE 3



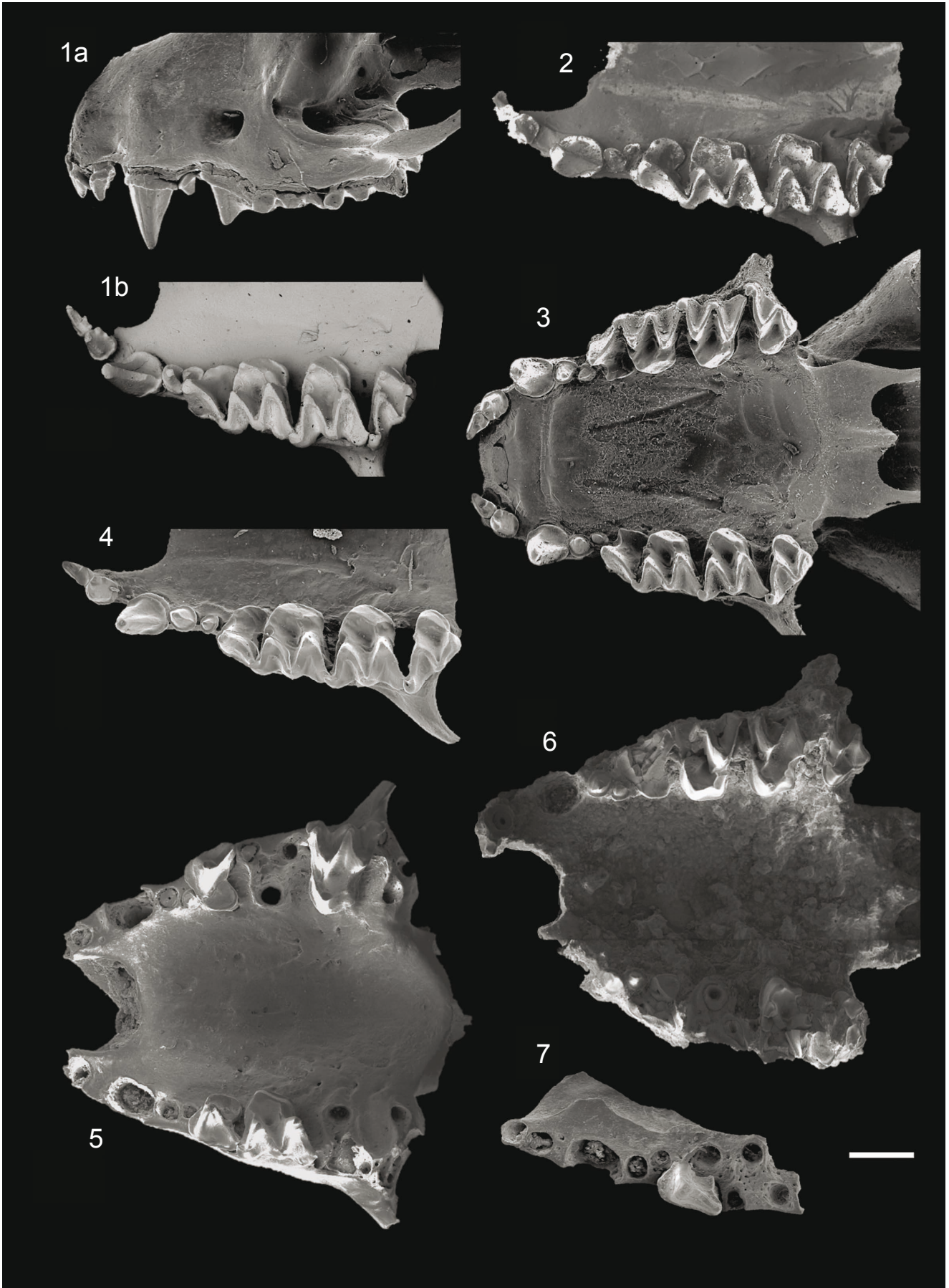
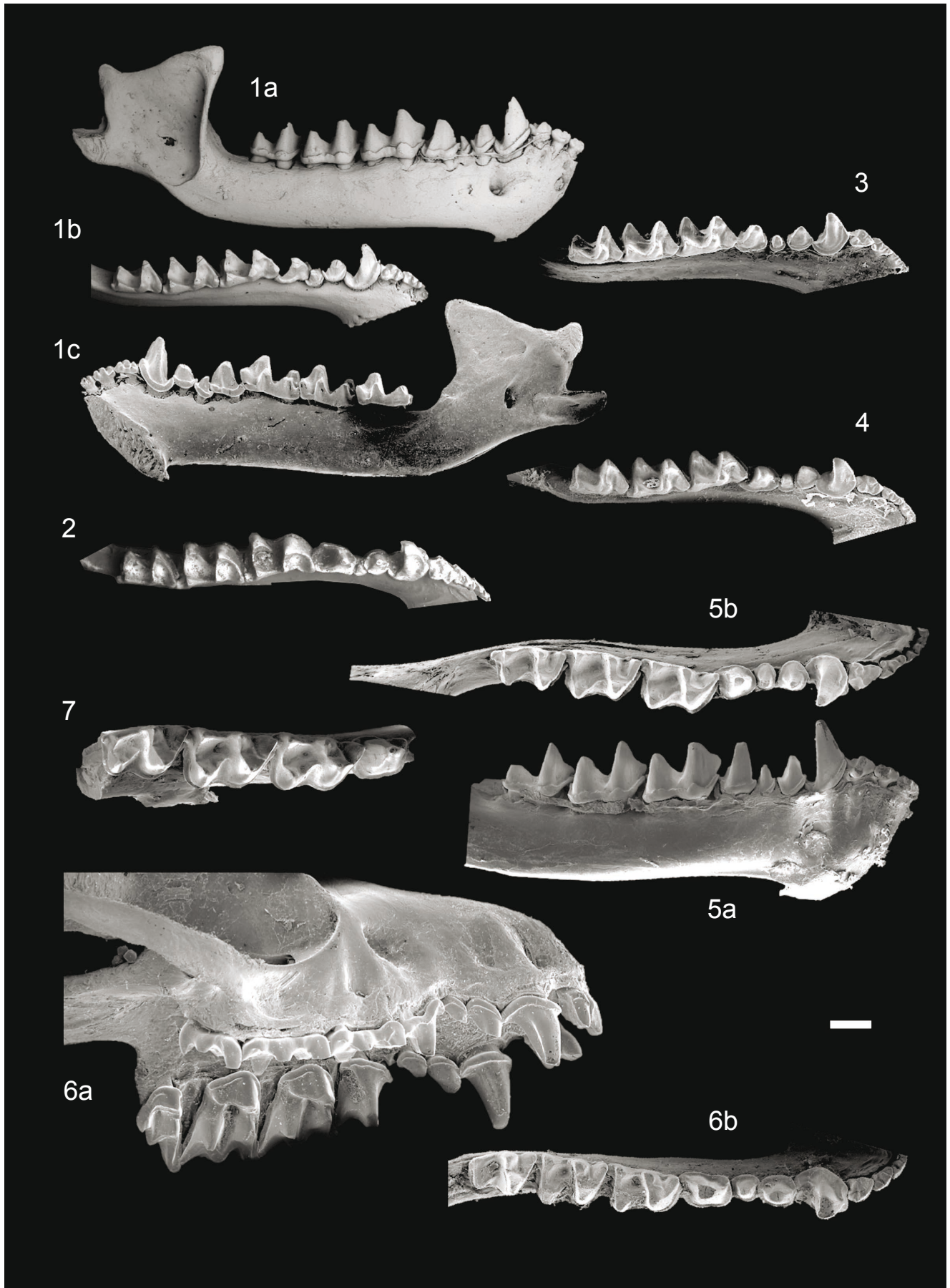
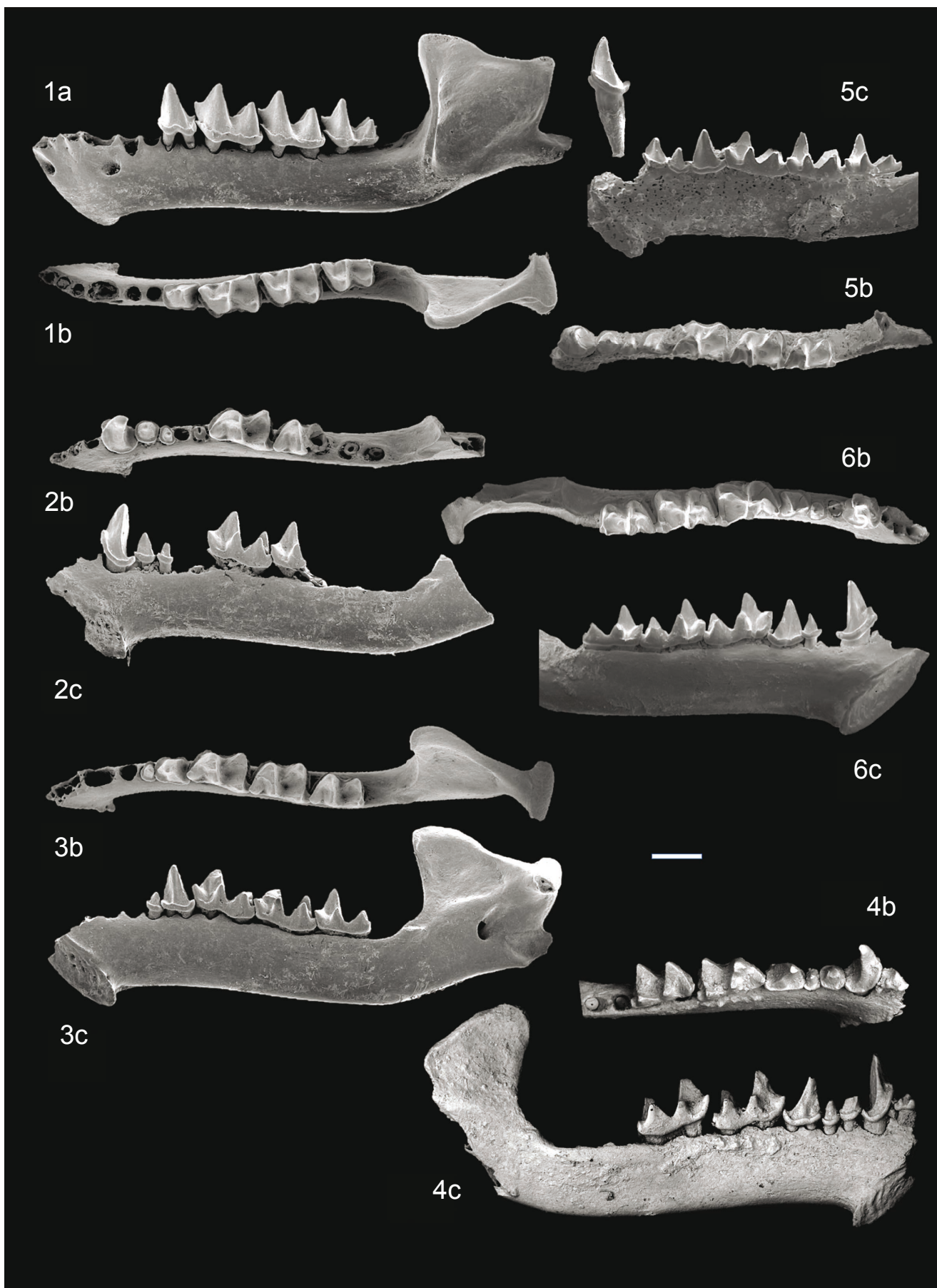
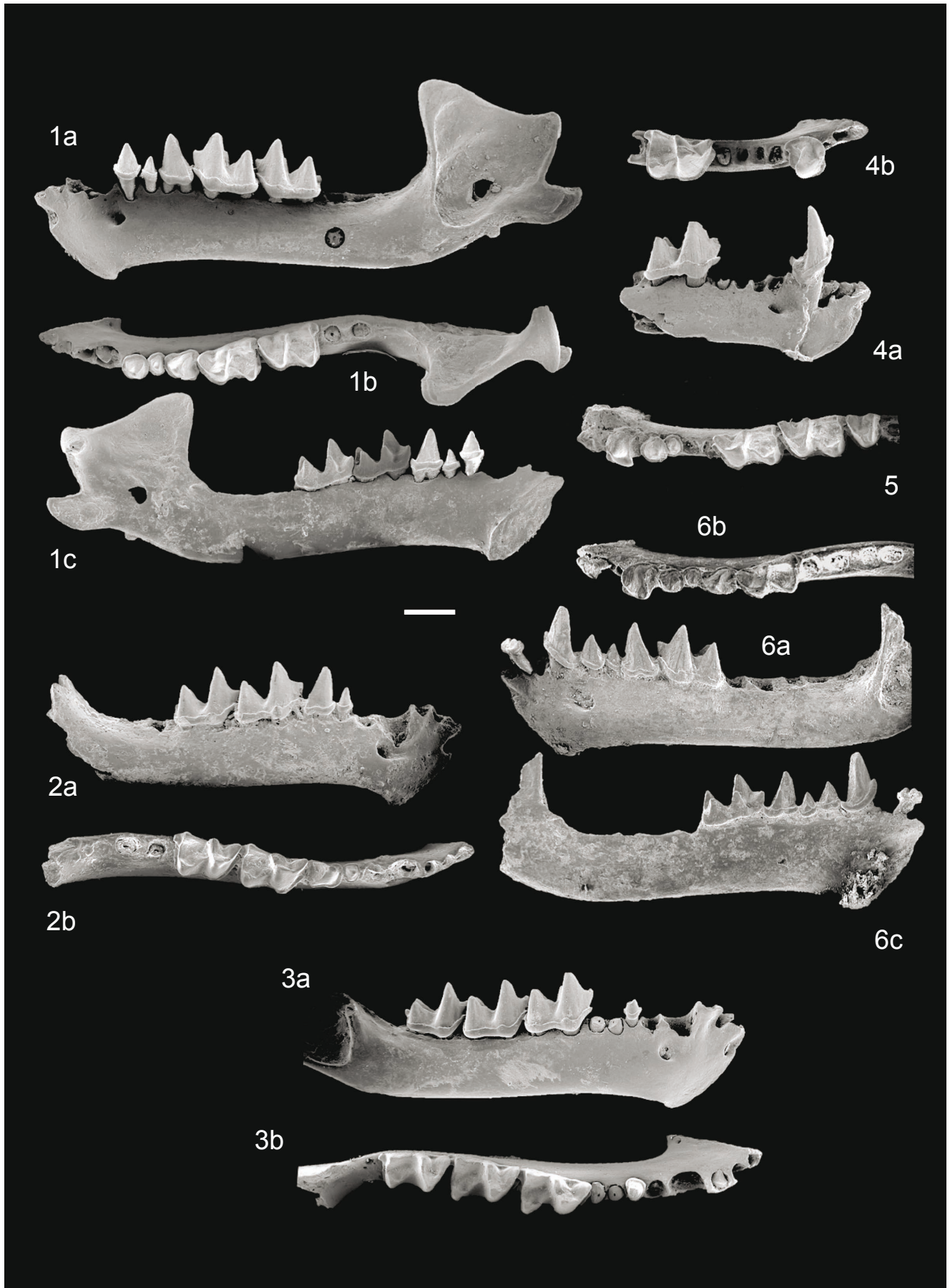




PLATE 5







## Appendix I

### Annotated list of fossil sites yielding remains of *M. frater* group

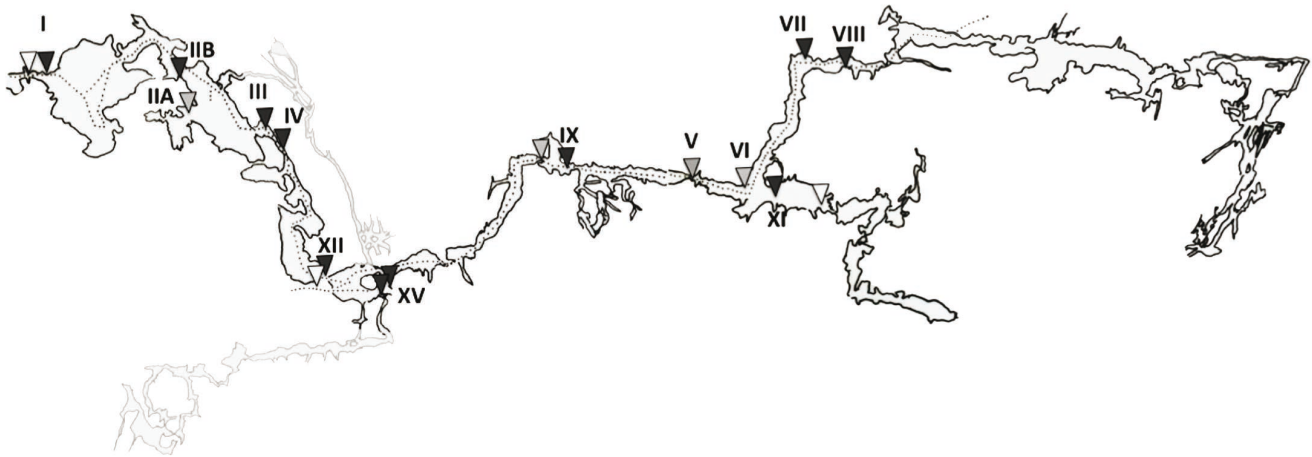
#### Beremend 26

Spacious cave completely fossilized by reddish clay and flowstone deposits in the western wall of a large limestone quarry near village Beremend, Villány Mts., Siklós distr., S Hungary (45°47' N, 18°26' E). Extensive sampling of the sediments and collection of fossils were performed from ca. 2000 to 2010 by László Pongrác (Hárkány), vast majority of the material is deposited in his private collection. For basic information on the site and the abundant fossil fauna dated to MN 15b see Császár and Kordos (2004), Čermák (2007) and Pazonyi (2011). Abundant bird remains from Beremend 26 were surveyed by Kessler (2014).

extensive sampling of fossiliferous deposits in four sites (and 5 successive layer in site I) quite rich in excellently preserved bat remains, unfortunately without other groups. A tentative assessment of age is MN 15 to early MN 17.

#### Sovinec 4

A fossilized cave denoted Sovinec cave 4 (not accessible now), ca. 20 m deep shaft with a fissure opening at bench of a small quarry near castle Sovinec in northern Moravia (49°50' N, 17°15' E). The cave was discovered and investigated in 1980 – 1982, thin debris deposits with mass accumulation of bat bones near the base of the shaft (ca. 17 m below entrance) were sampled on several occasions. The material includes about 1,500 cranial and dental fragments of bats (at least 11 spp.) and ca. 50 fragments of small ground mammals demonstrating the Early Pleistocene (Q 1) age of the assemblages (see Horáček and Ložek 1988 for a list).



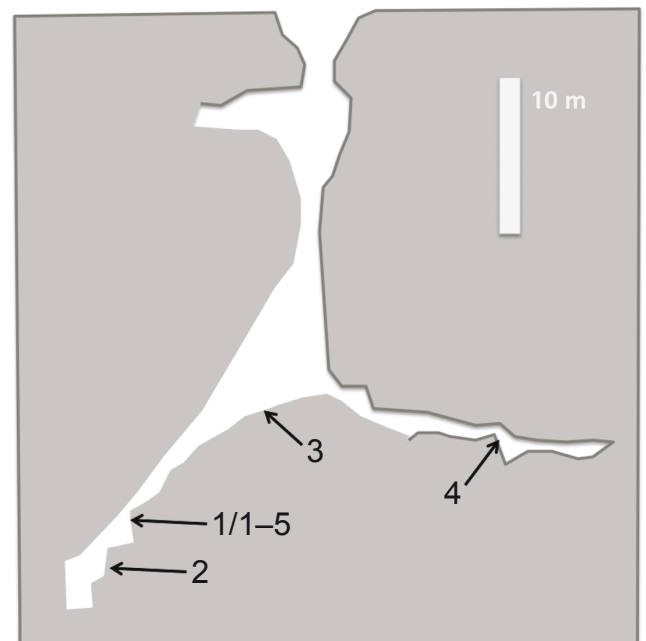
Tex-fig. A1. A map of Javoříčské caves (north Moravia, the Czech Republic) with position of particular fossiliferous sites.

#### Javoříčko

A spacious cave complex (more than 6 km long) near village Javoříčko in northern Moravia (41°50' N 16°54' E), in some part almost completely infilled by thick sequences of laminated flowstone deposits containing lens of unconsolidated sediments, some rich in bone remains of bats. During intensive investigations from 1978 up to now we discovered 15 fossiliferous sites (Text-fig. 7), some enormously rich particularly in bat remains (*Rhinolophus* cf. *kowalskii*, *R. lissiensis*, *R. variabilis*, *Myotis* cf. *kormosi*, *M. gundersheimensis*, *M. nattereri*, *M. schaubii*, *M.* cf. *exilis*, *M. emarginatus*, *Miniopterus schreibersii* etc.). About 2 % of the assemblages are composed of the allochthonous elements, mostly insectivores and rodents, which enable its biostratigraphic dating. Here we deal with site III, dated to early MN 17, and XI and VII, which due to presence of *Mimomys stehlini* are preliminary dated to MN 15b.

#### Urwista

A vertical shaft 37 m deep near Olsztyn, Jura Krakowsko-Czechstochowska, S Poland (50°43' N, 19°17' E), with a series of laminar flowstone infill altered with thin clayed horizons at the bottom. The site was investigated in 1980 by A. Bednarczyk, P. Bosák and I. Horáček, including



Tex-fig. A2. A vertical section of Urwista caves (Poland; after Szelerewicz and Górny 1986) with position of source sections of fossil material sampled by Horáček and Bosák in 1980.

## Včeláre 4D/12

A separate side cavity within a sedimentary infill of a spacious cave opened and soon destroyed in autumn 1979 by mining in quarry Včeláre in Slovakian karst ca. 100 m from the Slovakia/Hungary state border (48°33' N 20°49' E). The sedimentary sequence of the site covers the period of transition between biozones Q 1 and Q 2, i.e. ca. 1.2 My BP. For more details including a sketch of the deposits and list of fauna see e.g. Fejfar and Horáček (1983).

## Appendix II

### List of material surveyed in this paper

#### Institutional abbreviations

NMP	National Museum, Prague, the Czech Republic
ISZ	coll. numbers of Dept. of Zoology, Charles University, Prague, the Czech Republic (as “/ISZ” it refers to our handling numbers for the specimens of other collections)
PEU	Department of Paleontology, Friedrich-Alexander-Universität Erlangen-Nürnberg, Germany
HNHM	Hungarian Natural History Museum, Budapest, Hungary
PAN	Institute of Systematic and Evolution of Animals PAN, Krakow, Poland
BM(NH)	British Museum (Natural History), London, UK

#### Fossil specimens

*Myotis gerhardstorchi* sp. n.: NMP/ISZ: two rostra – Ber26/C1 (holotype) and Ber26/C2 (paratype); a fragment of maxilla – Ber26/C4 (paratype)

*Myotis cf. gerhardstorchi* sp. n.: NMP/ISZ: two fragments of maxilla – JavXI/547 and JavVII/226; one fragment of mandible – Ber26/C3

*Myotis frater* group: NMP/ISZ: three rostra – Sov4/1, Sov4/16, Sov353/3; eight fragments of maxilla – Sov353/2, JavIII/6, JavIII/11, UrwI/1/19, UrwI/1/21, UrwIII/113, UrwIII/114, UrwIII/129; 38 mandibles and mandibular fragments – Sov4/2–15, Sov4/18–20, Sov4/22, Sov353/1, Sov353/4–9, Sov9/8/1–4, UrwIh/166, UrwI/1/22–23, UrwI/2/39, JavIII/116, JavIII/2/223, JavVII/39, Vcel4D/12/1–2

*Myotis cf. capaccinii*: NMP/ISZ: a single mandible – Sov4/21

*Myotis dasycneme*: NMP/ISZ: a single fragment of maxilla – Sov4/25; 14 mandibles and mandibular fragments – Sov4/23–24, StudS2/2–3, JavIII/2/1–6, Karl2/3/1–4 (Q 4 Karlukovo 4, Bulgaria)

*Myotis gundersheimensis*: PEU/ISZ: 28 mandibles – GFIII/holotype, GFV/1–2, GFI/66–90

*Myotis cf. gundersheimensis*: a rostrum – Ber26/C30

*Myotis cf. baranensis*: NMP/ISZ: a single fragment of maxilla – Ber26/C18; one fragment of mandible – Ber26/C25

*Myotis delicatus*: PEU/ISZ: two mandibles – GFI/holotype, GFI/20

*Myotis cf. delicatus*: PAN/ISZ: three fragments of maxilla – Podl5/2–4; 7 mandibles – Podl5/1, JavIII/1, JavVII/52–56

*Myotis dasycneme subtilis*: PAN/ISZ: one mandible – Podl/paratype

*Myotis kormosi*: PEU/ISZ: 13 mandibles – GFIIa/holotype, GFV/45–47, GFI/1–9

*Myotis aemulus*: PEU/ISZ: 6 mandibles – GFI/holotype, GFI/1–3, GFII/4, GFIIa/5

*Myotis cf. podlesicensis*: PEU/ISZ: 5 mandibles, 2 rostra – GFV/48–52

*Myotis rapax*: PEU/ISZ: two mandibles – GFI/holotype, GFI/ra2

*Myotis exilis*: PEU/ISZ: 15 mandibles – GFI/holotype, GFI/32–35, 91–100

*Myotis helleri*: PEU/ISZ: 6 mandibles – GFIII/holotype, GFI/ins1–4, GFIII/ins2

*Myotis praeivius*: PEU/ISZ: 4 mandibles – GFI/holotype, GFI/paratype, GFI/pr3–4

*Myotis danutae*: PAN/HMNH: 5 mandibles, 2 rostra – Podl/holotype, Podl/1, Podl/6, Podl/92, Podl/244

*Myotis blythii*: NMP/ISZ: one fragment of maxilla – Ber26/bly1

#### Recent specimens

*Myotis frater kagyuae*: Japan – NMP/ISZ: N-101

*Myotis bucharensis*: Uzbekistan – NMP/ISZ: BB 7, 8, 9, SA223

*Myotis sicarius*: Nepal – BM(NH): 23.1.9.5.

*Myotis daubentonii*: Czech Rep. and Slovakia – NMP/ISZ: 14/63, 35/66, 66/75, 67/75, 68/75, 72/75, 73/75, 75/75, 76/75, 77/75, 83/62, 136/62, 137/62, 151/65, 348/64, 352/64, 359/64, Voz2019/1

*Myotis daubentonii nathalinae*: France – NMP/ISZ: F76/02

*Myotis capaccinii*: Bulgaria – NMP/ISZ: 921.24, 49193, 49208, 49209, 49210, 49211, 49223, 49224, 49340, 49344, 49442, 49668, 49669, 49670, 49671, 49672, 49673, 49742, 50098, 50100

*Myotis longipes*: Afghanistan – NMP/ISZ: AF433

*Myotis dasycneme*: Czech Rep. and Slovakia – NMP/ISZ: 230/58, 128/63, 151/64; 14 rostra – Dobš/0–5, Dobš/9–16

*Myotis bechsteinii*: Czech Rep., Slovakia, Bulgaria – NMP/ISZ: 10351, 49018, 49651, 49743, 49759, 49764, 49772, 49773, 49774, 49775, 49776, 49787, P6d-2/2007 II, P6d-2/2007 III, B71/C21

*Myotis mystacinus*: Czech Rep. and Slovakia – NMP/ISZ: 49300, 49311, 49339, 49463, 49475, 49496, 49499, 49503, 49507, 49519, 49524, 49525, 49533, 49541, 49542, 49566, 49636

*Myotis nattererii*: Czech Rep. and Slovakia – NMP/ISZ: 2/62, 12/75, 54/63, 163/59, 341/64, 357/64, B-0235, B-0475, B-0477, B-0479, B-0662, B-0768, B-0772, MN-3, MN-4

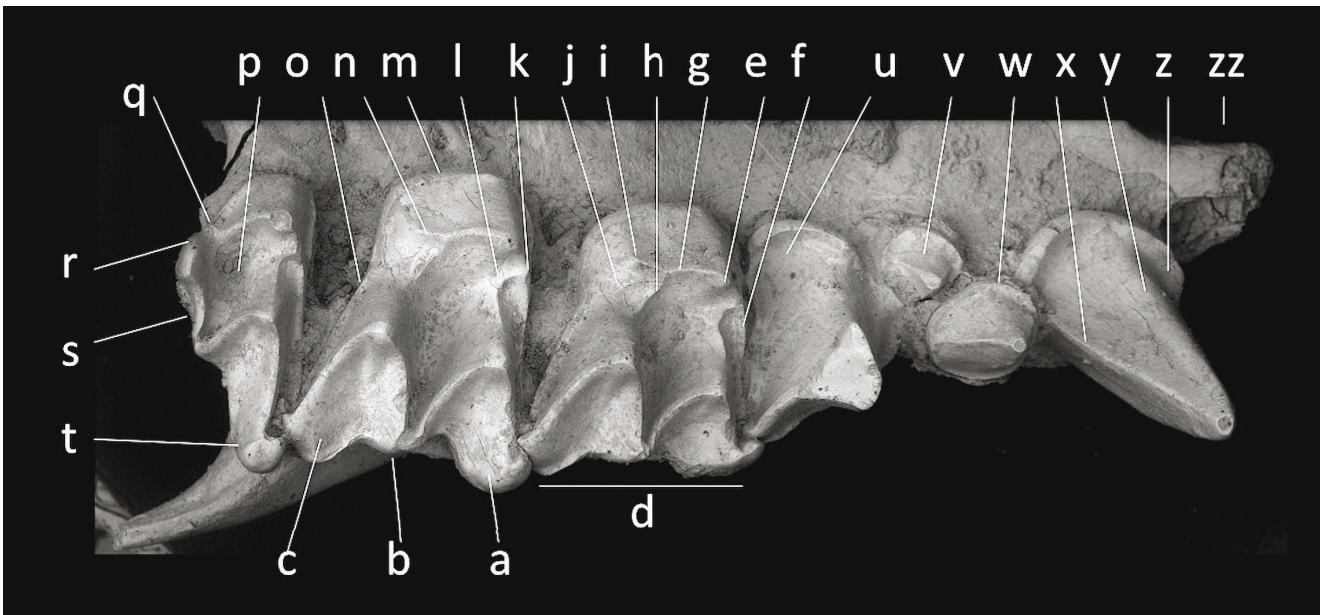
*Myotis emarginatus*: Czech Rep. and Slovakia – NMP/ISZ: 61/59, 158/62, 160/62, 162/62, 171/58, 183/65, 190/65, 191/65, 193/65, 194/65, 195/65, 201/65, 228/59, 229/59, 831/59, 833/59, 837/59, J-4, v 12 151, ZN-22

*Myotis brandtii*: Czech Rep. and Slovakia – NMP/ISZ: 49274, 49275, 49276, 49277, 49280, 49282, 49295, 49297, 49301, 49304, 49310, 49312, 49313, 49327, 49333, 49448, 49462, 49474, 49476, 49540

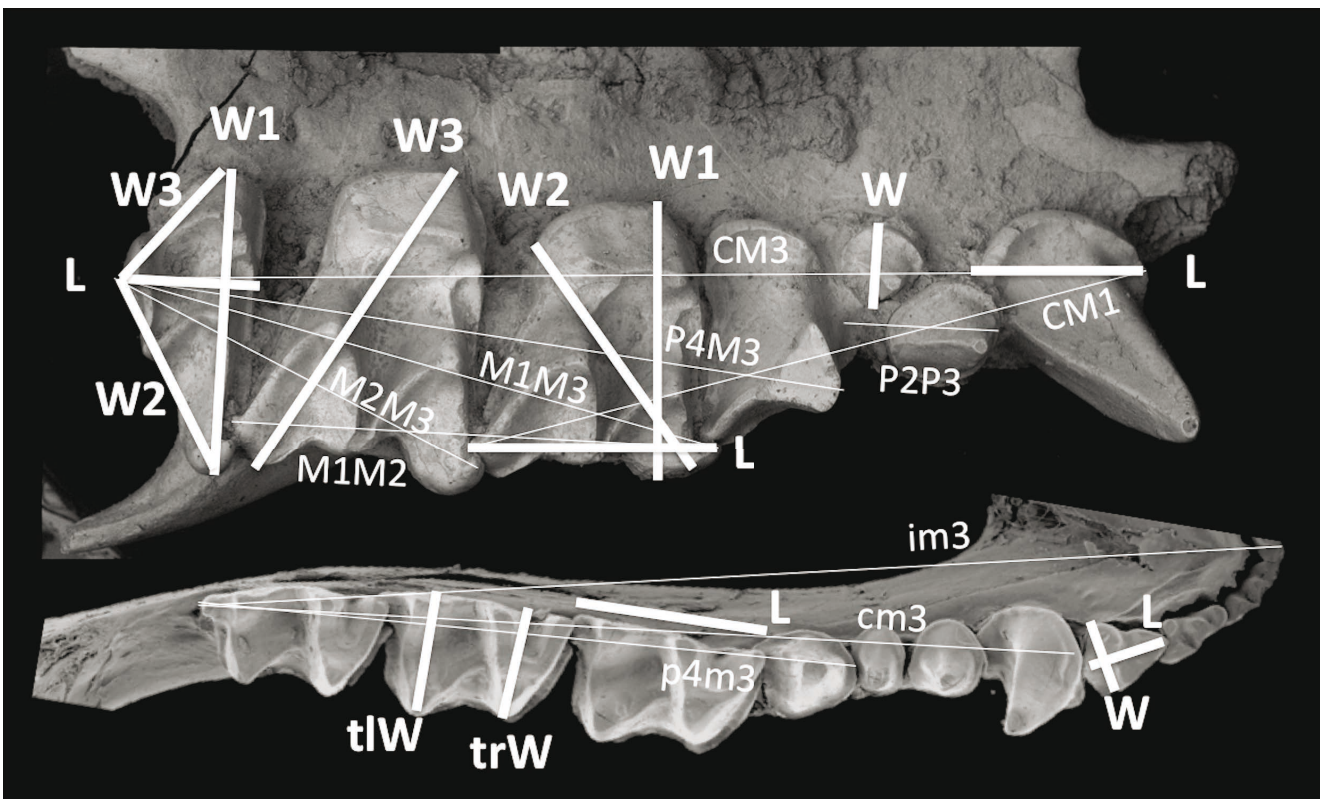
*Myotis blythii*: Czech Rep. and Slovakia – NMP/ISZ: 96/61, 121/61, 124/61, 150/61, 160/58, 178/58, 180/58, 184/58, 274/61, 798/58, 803/58, 858/58, 861/58, 864/58, 865/58, 866/58, 867/58, B-124, J-11

## Appendix III

### Odontological terms and measurement



Tex-fig. A3. A brief list of odontological terms used in this paper. a – paraconal fovea and parastyle wing of ectoflexus, b – mesostyle, c – metaconal fovea and metastyle wing of ectoflexus, d – ectoflexus, e – protocone, f – preprotocrista, g – postprotocrista, h – distal turn of the postprotocrista, i – hypoconal extension of protocone wall (= “metaconulus”), j – metalophus, k – protoconulus, l – paralophus, m – palatal cingulum of protoconal complex, n – transcrista (here rudimental), o – distal crown base, p – fossa (= “profossa”), q – transcrista of M3 (here particularly pronounced), r – metacone, s – premetacrista, t – parastyle and retained paraconal fovea, u – talonal heel of P4, v – P3, w – P2, x – distal crest of canine crown, y – thickened mesio-palatal ridge of the canine crown, z – prominent mesial cingulum without cingular cuspsules, zz – anterior palatal vacuity.



Tex-fig. A4. A scheme of measurements of maxillary and mandibular dentition and individual teeth (in bold). Further measurements not explained here (e.g. in Tabs A1, A2) are e.g. Lmd – total length of mandible, symL, symW – length and width of symphysis, Hmd1 and Hmd2 – height of mandible under m1 and m2 respectively, CrH – height of the coronoid process.

Table A1. Maxillary measurements of compared fossil and recent materials of *Myotis* (for further details on particular specimens see Appendix ID). Part 1: Dentition.

	Species	Site	IIM3	CM3	P4M3	MIM3	M2M3	M1M2	P4M1	CM1	P2P3	CC	P4P4	M3M3
FOSSIL	<i>M. gerhardstorchi</i> sp. n.	Beremend 26/C1	7.89	7.11	5.05	4.26	2.79	3.42	2.74	4.84	1.17	4.92	6.24	7.55
	<i>M. gerhardstorchi</i> sp. n.	Beremend 26/C2	7.95	7	4.97	4.14	2.6	3.3	2.8	4.8	1.28	4.8	6.35	
	<i>M. gerhardstorchi</i> sp. n.	Beremend 26/C4				4.04	2.7	3.12						
	<i>M. frater</i> group	Sovinesc/1		5.45	4.08	3.18	2.13	2.56	2.13	3.59	0.73	2.13	5.31	6.35
	<i>M. frater</i> group	Sovinesc/16	7	5.68	4.47	3.57	2.49	2.74	2.24	3.57	0.78	3.57	5.26	6.34
	<i>M. frater</i> group	Sovinesc/2	6.15	5.22	3.98	3.31	2.13	2.54	2.11	3.42	0.72	3.42		
	<i>M. frater</i> group	Sovinesc/3		5.19	3.85	3.15	2.18	2.36	2	3.37	0.71	3.37	5.08	5.63
	<i>M. cf. gerhardstorchi</i> sp. n.	Javoféko VII/226					2.88	2.88	2.82	4.61	0.71	4.61		
	<i>M. frater</i> group	Urweista I/1/19							2.82	2.82	0.88	2.82		
	<i>M. frater</i> group	Urweista I/1/21							2.47	2.47	0.69	2.47		
	<i>M. frater</i> group	Urweista III/113		7.14	4.9	3.97	2.59	3.29	2.81	5.04	0.8	5.04		
	<i>M. frater</i> group	Urweista III/114						3.4	2.77	4.4	0.71	4.4		
	<i>M. frater</i> group	Urweista III/129						3.08	2.6	4.4	0.85	4.4		
	<i>M. cf. gerhardstorchi</i> sp. n.	Javoféko XI/547		5.53	4.13	3.36	2.18	2.63	2.38	3.89	0.7	3.89		
	<i>M. frater</i> group	Javoféko III/6							2.37	3.85	0.7	3.85		
	<i>M. frater</i> group	Javoféko III/11		8.9	7.6	5.58	4.34	3.75	3.37	5.51	0.95	5.51	6.63	7.5
<i>Myotis sicarius</i>	Nepal		6.03	5	3.76	3.09	2.05	2.37	2.01	3.32	0.66	4.04	5.03	5.73
<i>Myotis frater kagiyae</i>	N-101													
<i>Myotis bucharensis</i>	C-Asia	Valid N Mean Minimum Maximum Std.Dev.	4 6.705 6.66 6.75 0.039	4 5.603 6.31 5.76 0.124	4 4.26 4.15 4.31 0.074	4 3.555 3.51 3.62 0.048	4 2.32 2.28 2.35 0.029	4 2.718 2.67 2.77 0.041	4 2.323 2.33 2.35 0.022	4 3.718 3.65 3.82 0.074	4 0.678 0.59 0.72 0.060	4 4.248 4.19 4.33 0.060	4 5.278 5.18 5.37 0.079	4 6.103 6.05 6.18 0.064
<i>Myotis dasycneme</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	17 7.592 7.32 7.89 0.185	19 6.331 6.16 6.63 0.125	19 4.872 4.71 5.08 0.095	19 3.991 3.74 4.22 0.111	19 2.618 2.43 2.78 0.091	19 3.024 2.77 3.2 0.104	19 2.571 2.44 2.73 0.073	19 4.122 3.89 4.44 0.136	19 0.816 0.65 0.96 0.092	17 4.685 4.47 4.85 0.100	16 6.016 6.25 6.25 0.110	15 6.999 6.83 7.36 0.134
<i>Myotis boechsteinii</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	14 8.215 7.93 8.49 0.167	14 6.981 6.73 7.24 0.143	14 4.799 4.59 4.91 0.093	14 3.261 3.77 4.03 0.071	14 3.139 3 3.28 0.077	14 2.653 2.53 2.76 0.068	14 4.511 3.28 5.09 0.641	14 1.244 1.19 1.39 0.060	14 0.908 0.82 0.96 0.060	14 4.091 3.92 4.28 0.116	14 6.915 5.06 5.46 0.139	15 14 14 14 14
<i>Myotis emarginatus</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	19 7.319 7.1 7.71 0.155	20 6.231 5.97 6.53 0.147	20 4.288 4.08 4.48 0.113	20 3.472 3.3 3.68 0.097	20 2.231 2.11 2.45 0.069	20 2.772 2.61 2.9 0.074	20 2.448 2.32 2.59 0.066	20 4.425 4.23 4.59 0.103	20 1.051 0.98 1.14 0.050	20 3.892 3.57 4.13 0.144	20 4.931 4.7 5.1 0.127	20 5.996 6.25 6.25 0.167
<i>Myotis nattereri</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	15 7.266 7.14 7.48 0.120	15 6.027 5.93 6.2 0.075	15 4.335 4.2 4.5 0.084	15 3.567 3.45 3.74 0.089	15 2.814 2.26 2.45 0.066	15 2.443 2.32 2.57 0.077	15 4.165 4.06 4.36 0.078	15 0.908 0.82 1.01 0.055	15 0.908 0.82 1.01 0.055	15 3.917 3.82 4.05 0.086	15 5.078 4.88 5.25 0.109	15 6.307 6.08 6.61 0.161
<i>Myotis capaccinii</i>	SE-Europe	Valid N Mean Minimum Maximum Std.Dev.	20 6.783 6.49 7.07 0.183	20 5.691 5.48 5.95 0.145	20 4.07 3.89 4.35 0.119	20 3.320 3.2 3.53 0.096	20 2.182 2.09 2.28 0.059	20 2.227 2.11 2.35 0.068	20 2.227 2.11 2.35 0.068	20 3.891 3.69 4.08 0.101	20 0.929 0.83 1.02 0.039	19 3.957 3.51 4.18 0.161	19 5.149 4.62 5.34 0.165	19 6.03 5.35 6.24 0.224
<i>Myotis daubentonii</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	17 6.275 5.89 6.66 0.217	17 5.255 4.94 5.63 0.185	17 3.805 3.63 4.11 0.134	17 2.052 1.91 2.25 0.088	17 2.413 2.24 2.57 0.094	17 2.052 1.91 2.19 0.084	17 3.539 3.33 3.74 0.133	17 0.805 0.7 0.88 0.050	17 0.805 0.7 0.88 0.050	17 3.698 3.39 4.44 0.245	17 4.732 4.35 5.67 0.302	17 5.622 5.1 6.75 0.384
<i>Myotis brandtii</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	19 6.51 6.19 6.77 0.147	20 5.364 5.07 5.56 0.132	20 3.866 3.61 4.08 0.113	20 3.213 3.04 3.41 0.093	20 2.111 1.98 2.27 0.075	20 2.47 2.34 2.65 0.083	20 2.099 1.98 2.26 0.087	20 3.606 3.4 3.84 0.241	20 0.829 0.74 0.9 0.049	19 3.503 3.34 3.74 0.111	20 4.630 4.38 4.89 0.128	20 5.434 5.08 5.78 0.165
<i>Myotis mystacinus</i>	C-Europe	Valid N Mean Minimum Maximum Std.Dev.	17 6.134 5.97 6.36 0.124	17 5.116 4.96 5.31 0.090	17 3.705 3.59 3.93 0.082	17 3.032 2.9 3.16 0.082	17 2.55 2.21 2.45 0.056	17 2.35 2.21 2.45 0.062	17 2.068 1.97 2.23 0.067	17 3.526 3.29 3.65 0.068	17 0.744 0.67 0.81 0.040	17 9.045 8.39 10.1 0.040	17 10.064 9.39 10.1 0.040	17 10.743 9.39 10.1 0.040
<i>Myotis longipes</i>	Afghanistan		6.11	5.15	3.98	3.33	2.23	2.47	2.08	3.37	0.67	3.59	4.58	5.53

RECENT

Table A1. Part 2: Individual teeth.

Species	FOSSIL																RECENT															
	I1L	I1W	I2L	I2W	CH	CL	CWP	P2L	P2W	P3L	P3W	P4L	P4W1	P4W2	P4W3	M1L	M1W1	M1W2	M1W3	M2L	M2W1	M2W2	M2W3	M3L	M3W1	M3W2	M3W3					
<i>M. gerhardstorchi</i> sp. n.	2.42	1.31	1.15	0.81	0.76	0.57	0.52	1.33	1.34	1.23	1.21	1.13	1.27	1.45	1.48	1.81	1.82	1.91	2.01	1.78	2.01	2.12	2.16	0.95	1.87	1.65	1.06	1.85	1.5	0.83		
<i>M. gerhardstorchi</i> sp. n.		1.22	0.95	0.84	0.72			1.23	1.21	1.13			1.27	1.45	1.48	1.65	1.75	1.82	2.05	1.68	1.98	1.89	2.25	0.87	1.85	1.5	0.83	1.86	1.54	1.17		
<i>M. frater</i> group						0.3	0.34	1.02	1.05	1.02	1.12		1.04	1.3	1.36	1.61	1.62	1.72	1.91	1.41	1.48	1.58	1.73	0.83	1.41	1.25	0.89	1.38	1.31	0.95		
<i>M. frater</i> group				0.5	0.44	0.4	0.33	0.92	0.93	0.89	1		1.04	1.09	1.33	1.57	1.7	1.73	2.02	1.58	2.01	1.96	2.24	0.98	1.92	1.49	1.19	1.44	1.34	0.92		
<i>M. frater</i> group								1.36	1.24	1.24	1.42		1.11	1.11	1.36	1.4	1.4	1.5	1.7	1.31	1.61	1.67	1.81	0.73	1.43	1.23	0.86	1.24	1.12	0.81		
<i>M. cf. gerhardstorchi</i> sp. n.								1.26	1.19	1.31	1.41		1.17	1.26	1.23	1.51	1.47	1.54	1.74	1.74	2.11	2.01	2.41	0.92	1.92	1.49	1.19	1.44	1.34	0.92		
<i>M. frater</i> group						0.53	0.48	1.11	1.17	1.26	1.23		1.17	1.26	1.23	1.77	1.72	1.77	2.14	1.74	2.11	2.01	2.46	0.98	1.92	1.49	1.19	1.44	1.34	0.92		
<i>M. frater</i> group				0.6	0.51	0.35	0.36	1.16	1.14	1.09	1.33		1.14	1.09	1.33	1.57	1.7	1.73	2.02	1.58	2.01	1.96	2.24	0.98	1.92	1.49	1.19	1.44	1.34	0.92		
<i>M. frater</i> group								1.3	1.12	1.11	1.36		1.12	1.11	1.36	1.4	1.4	1.5	1.7	1.31	1.61	1.67	1.81	0.73	1.43	1.23	0.86	1.24	1.12	0.81		
<i>M. cf. gerhardstorchi</i> sp. n.								1.07	1.1	0.96	1.24		1.07	1.1	0.96	1.37	1.37	1.43	1.59	1.85	2.28	2.2	2.75	0.92	1.95	1.47	1.01	1.13	0.83			
<i>M. frater</i> group	1.26	0.85	1.12	0.72	0.47	1.31	0.86	0.73	0.44	0.43	0.38	0.32	0.95	0.91	0.99	1.04	1.3	1.25	1.32	1.45	1.43	1.43	1.63	0.75	1.31	1.13	0.83	1.13	0.83			
<i>M. stearius</i>	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4		
<i>M. frater</i> group	0.415	0.4	0.55	0.545	1.755	0.97	0.773	0.433	0.43	0.295	0.278	1.028	0.97	1.015	1.123	1.405	1.308	1.46	1.608	1.4	1.55	1.565	1.745	0.8	1.455	1.273	0.883	1.455	1.273	0.883		
<i>M. dasyneume</i>	0.38	0.35	0.51	0.53	1.68	0.94	0.76	0.39	0.42	0.28	0.27	0.98	0.95	0.95	1.09	1.39	1.26	1.42	1.56	1.38	1.45	1.52	1.72	0.76	1.39	1.24	0.83	1.39	1.24	0.83		
<i>M. becksteinii</i>	0.48	0.48	0.59	0.55	1.81	1.02	0.78	0.47	0.44	0.31	0.28	1.11	0.99	1.09	1.15	1.44	1.36	1.5	1.69	1.42	1.61	1.61	1.77	0.86	1.53	1.31	0.95	1.31	0.95	1.31		
<i>M. emarginatus</i>	0.045	0.056	0.037	0.01	0.058	0.036	0.010	0.033	0.012	0.017	0.005	0.057	0.023	0.058	0.028	0.024	0.041	0.034	0.059	0.018	0.070	0.037	0.021	0.042	0.058	0.029	0.054	0.029	0.054	0.029		
<i>M. nattervi</i>	2	2	2	2	3	3	3	7	7	8	8	19	19	19	19	18	18	18	18	18	18	18	18	17	17	17	17	17	17	17		
<i>M. capaccinii</i>	0.63	0.495	0.63	0.575	1.73	1.067	0.9	0.539	0.494	0.405	0.433	1.112	1.168	1.183	1.306	1.554	1.558	1.646	1.822	1.583	1.722	1.788	1.981	0.981	1.68	1.433	1.092	1.68	1.433	1.092		
<i>M. daubentonii</i>	0.62	0.47	0.58	0.57	1.16	1.05	0.83	0.49	0.46	0.36	0.36	1.02	1.04	1.05	1.18	1.46	1.39	1.43	1.69	1.52	1.54	1.56	1.79	0.92	1.52	1.32	0.98	1.52	1.32	0.98		
<i>M. brandtii</i>	0.64	0.52	0.68	0.58	2.14	1.1	0.94	0.59	0.55	0.49	0.49	1.21	1.29	1.31	1.43	1.6	1.68	1.74	1.95	1.7	1.86	1.91	2.16	1.04	1.81	1.5	1.17	1.81	1.5	1.17		
<i>M. mystacinus</i>	0.014	0.035	0.071	0.007	0.509	0.029	0.061	0.038	0.036	0.045	0.047	0.049	0.066	0.069	0.075	0.035	0.081	0.083	0.067	0.048	0.098	0.101	0.096	0.021	0.039	0.089	0.051	0.060	0.051	0.060		
<i>M. longipes</i>	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14		
<i>M. emarginatus</i>	0.657	0.401	0.645	0.564	1.694	1.063	0.873	0.708	0.661	0.591	0.545	1.209	1.024	1.068	1.241	1.634	1.462	1.512	1.864	1.638	1.726	1.709	2.055	0.88	1.712	1.384	0.989	1.712	1.384	0.989		
<i>M. nattervi</i>	0.41	0.35	0.57	0.51	1.35	1	0.78	0.65	0.61	0.53	0.48	1.14	0.97	0.98	1.14	1.54	1.36	1.43	1.77	1.52	1.63	1.95	1.82	1.62	1.62	1.32	0.9	1.62	1.32	0.9		
<i>M. capaccinii</i>	0.72	0.49	0.73	0.63	1.93	1.18	0.96	0.77	0.73	0.65	0.59	1.29	1.1	1.13	1.34	1.72	1.59	1.61	1.97	1.79	1.81	1.79	2.14	0.92	1.89	1.47	1.11	1.89	1.47	1.11		
<i>M. brandtii</i>	0.035	0.041	0.041	0.041	0.168	0.047	0.048	0.039	0.032	0.030	0.032	0.046	0.041	0.039	0.061	0.059	0.064	0.052	0.056	0.067	0.059	0.053	0.063	0.027	0.073	0.042	0.052	0.042	0.052	0.042		
<i>M. daubentonii</i>	19	19	19	19	19	19	19	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20		
<i>M. brandtii</i>	0.519	0.391	0.446	0.52	1.957	1.078	0.787	0.653	0.659	0.479	0.464	1.137	0.924	0.986	1.095	1.472	1.372	1.465	1.708	1.414	1.636	1.668	1.928	0.774	1.564	1.203	0.919	1.564	1.203	0.919		
<i>M. nattervi</i>	0.49	0.34	0.37	0.48	1.69	0.98	0.74	0.6	0.62	0.42	0.38	1.06	0.83	0.88	1	1.37	1.29	1.37	1.59	1.52	1.56	1.76	2.06	0.71	1.48	1.13	0.82	1.48	1.13	0.82		
<i>M. capaccinii</i>	0.57	0.45	0.52	0.57	2.09	1.16	0.85	0.74	0.7	0.56	0.53	1.22	1	1.13	1.16	1.58	1.44	1.54	1.82	1.51	1.73	1.76	2.06	0.82	1.65	1.24	1	1.65	1.24	1		
<i>M. brandtii</i>	0.023	0.031	0.044	0.029	0.093	0.045	0.036	0.032	0.020	0.035	0.039	0.045	0.043	0.056	0.043	0.052	0.046	0.049	0.060	0.053	0.044	0.052	0.060	0.033	0.053	0.030	0.047	0.030	0.047	0.030		
<i>M. nattervi</i>	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15		
<i>M. capaccinii</i>	0.551	0.385	0.493	0.562	1.429	0.953	0.709	0.525	0.511	0.453	0.446	1.107	0.917	0.932	1.093	1.457	1.448	1.499	1.773	1.446	1.737	1.729	2.01	0.819	1.371	1.371	1.371	1.371	1.371	1.371		
<i>M. brandtii</i>	0.48	0.32	0.45	0.53	1.02	0.59	0.63	0.44	0.45	0.39	0.38	1.03	0.85	0.82	0.92	1.36	1.33	1.38	1.66	1.37	1.63	1.61	1.91	1.6	1.6	1.3	0.89	1.6	1.3	0.89		
<i>M. nattervi</i>	0.63	0.45	0.55	0.62	1.64	1.01	0.82	0.61	0.55	0.53	0.52	1.21	0.98	1.1	1.17	1.54	1.61	1.62	1.92	1.53	1.84	1.83	2.1	0.87	1.86	1.46	1.06	1.86	1.46	1.06		
<i>M. capaccinii</i>	0.041	0.039	0.029	0.029	0.161	0.035	0.051	0.050	0.031	0.037	0.036	0.051	0.036	0.065	0.057	0.054	0.075	0.057	0.072	0.054	0.065	0.065	0.061	0.035	0.074	0.051	0.044	0.051	0.044	0.044		
<i>M. brandtii</i>	19	19	19	19	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20		
<i>M. nattervi</i>	0.519	0.363	0.495	0.475	1.256	0.897	0.755	0.532	0.486	0.425	0.4	1.038	0.976	0.953	1.112	1.311	1.347	1.421	1.564	1.309	1.510	1.505	1.754	0.834	1.45	1.2	0.890	1.45	1.2	0.890		
<i>M. capaccinii</i>	0.35	0.31	0.4	0.4	0.96	0.81	0.7	0.46	0.4	0.36	0.34	0.95	0.91	0.87	0.99	1.26	1.22	1.3	1.43	1.24	1.39	1.36	1.59	0.78	1.2							



Table A2. Mandibular measurements of compared fossil and recent materials of *Myotis* (for further details on particular specimens see Appendix II), Part 1: Dentition.

Species	Site	Lmd	im3	cm3	p4m3	m1m3	cp4	p4m1	m1m2	m2m3	p2p3	symL	symW	Hmd1	Hmd2	Cr-H	CrL
<i>M. cf. gervillatorchi</i>	Berezniki 26/C3	6	16	20	22	23	26	26	25	24	28	18	22	29	26	15	12
<i>M. frater</i> group	Sovinec 4	10.968	6.955	5.916	4.461	3.727	2.282	2.037	2.585	2.481	0.829	2.376	0.762	1.546	1.529	3.21	2.952
		10.27	6.39	5.48	4.05	3.38	2.09	1.8	2.29	2.3	0.74	2.13	0.66	1.29	1.21	2.92	2.51
		11.25	7.34	6.51	4.91	4.22	2.91	2.21	2.9	2.81	1.11	2.61	0.9	1.78	3.4	3.54	3.33
<i>M. frater</i> group	Urwista	1	3	3	3	3	4	4	3	3	4	4	4	3	3	3	1
		12.25	7.427	6.443	4.84	4.23	2.27	2.073	2.917	2.787	0.89	2.375	0.838	1.673	1.6	3.7	3.21
		12.25	7.36	6.42	4.8	4.16	2.11	1.97	2.91	2.72	0.81	2.07	0.71	1.62	1.53	3.7	3.21
		12.25	7.55	6.49	4.9	4.27	2.43	2.15	2.92	2.83	1.04	2.64	0.92	1.76	1.66	3.7	3.21
<i>M. frater</i> group	Javorföko VII	6.85	6.85	6.06	4.4	3.71	2.44	2.12	2.54	2.19	0.93	2.38	0.8	1.61			
<i>M. frater</i> group	Javorföko III																
<i>M. frater</i> group	Javorföko III	6.57	6.57	5.75	4.35	3.83	2.37	2.13	2.59	2.54	0.84	2.21	0.68	1.36	1.47		
<i>M. cf. mystacinus</i>	Věcláre 4D/12	12.12	8	6.82	3.98	3.28	2.19	1.79	2.25	2.14	0.9	2.4	0.66	1.21	1.21		
<i>M. cf. mystacinus</i>	Věcláre 4D/12	12.7	8.05	6.85	5.07	4.27	2.62	2.38	2.88	2.86	0.4	2.7	0.77	1.8	1.85		
<i>M. cf. mystacinus</i>	Gundersheim	10.85	7.81	6.52	4.39	4.05	2.25	2.27	2.77	2.77	1.15	2.69	0.9	1.56			
<i>M. cf. mystacinus</i>	Podlesice	0	0	1	2	2	4	5	2	2	5	1	3	6	2	1	1
<i>M. cf. delicatus</i>	Javorföko III	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	10.58	6.98	6.02	4.45	3.6	2.54	2.03	2.5	2.6	1.02	2.5	0.81	1.42	1.4		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336	4.626	3.778	2.7	2.14	2.7	2.735	1.03	2.55	0.88	1.455	1.495		
<i>M. cf. delicatus</i>	Podlesice	11.25	7.6	6.48	4.91	3.96	2.82	2.25	3	2.87	1.04	2.6	0.95	1.5	1.6		
<i>M. cf. delicatus</i>	Gundersheim	12.1	8.3	7.03	5.09	4.11	2.98	2.3	2.7	2.74	1.1	2.8	0.92	1.68	1.7		
<i>M. cf. delicatus</i>	Gundersheim	3	4	5	5	5	3	4	4	2	2	2	2	4	4	1	0
<i>M. cf. delicatus</i>	Podlesice	10.97	7.315	6.336													

Table A2. Part 1: continued.

Species	Site	BM(NH) 23.1.9.5 N101	Lmd	im3	cm3	p4m3	m1m3	cp4	p4m1	m1m2	m2m3	p2p3	symL	symW	Hmd1	Hmd2	CrH	CrL
<i>M. sicarius</i>	Nepal	9.71	10.25	6.49	8	6.25	5	3.15	2.95	3.15	2.23	0.86	2.33	0.67	1.41	1.34	3.03	2.69
<i>M. frater kagayae</i>	Japan																	
<i>M. bucharensis</i>	C-Asia	4	10.92	7.288	6.06	4.623	3.978	2.168	2.08	2.768	2.593	4	2.41	0.74	1.295	1.24	3.04	3.02
		4	10.7	7.26	5.97	4.55	3.91	2.07	1.97	2.72	2.51	4	2.41	0.74	1.26	1.2	3.04	3.02
		4	0.147	0.043	0.108	0.066	0.050	0.068	0.080	0.050	0.057	0.029	2.41	0.74	1.33	1.28	3.13	3.02
															0.049	0.057	0.061	
<i>M. dasyneume</i>	C-Europe	7	13.09	8.084	6.804	5.056	4.313	2.594	2.09	2.939	2.859	9	5	0.882	7	6	5	5
		6	12.5	7.51	6.37	4.81	4.01	2.36	2.06	2.66	2.59	4	2.56	0.882	1.663	1.658	3.828	3.508
		6	0.317	0.380	0.244	0.136	0.166	0.118	0.082	0.169	0.131	0.104	0.129	0.083	0.162	0.169	0.156	0.161
<i>M. bechsteinii</i>	C-Europe	14	13.144	8.57	7.426	5.234	4.329	3.238	2.451	3.021	2.886	14	3	0.99	3	5	4	14
		12.65	12.65	8.2	7.11	5.1	4.25	3.03	2.39	2.96	2.79	1.23	2.85	0.83	1.6	1.44	3.81	3.23
		13.59	13.59	8.88	7.7	5.39	4.43	3.4	2.38	3.09	3.01	1.44	3.07	1.16	1.66	1.7	4.61	3.82
		0.266	0.266	0.175	0.153	0.092	0.062	0.099	0.058	0.038	0.065	0.064	0.112	0.165	0.031	0.095	0.212	0.153
<i>M. amarginatus</i>	C-Europe	16	11.726	7.645	6.636	4.693	3.874	2.863	2.236	2.713	2.53	20	0	0	0	0	19	19
		11.29	11.29	7.38	6.39	4.44	3.61	2.7	2.14	2.5	2.36	1.12	2.28	0.9	1.25	1.25	3.425	3.114
		12.23	12.23	8.03	7	4.95	4.07	3.02	2.36	2.84	2.69	1.29	2.28	0.9	1.28	1.25	3.16	2.84
		0.231	0.231	0.169	0.155	0.132	0.113	0.078	0.066	0.081	0.084	0.042	0.111	0.111	0.035	0	3.81	3.35
<i>M. nattereri</i>	C-Europe	15	11.698	7.652	6.399	4.644	3.886	2.614	2.122	2.714	2.582	15	1	1	2	2	14	14
		11.2	11.2	7.46	6.26	4.51	3.73	2.5	2	2.64	2.43	1.033	2.28	0.9	1.25	1.25	3.264	2.994
		12.09	12.09	7.86	6.55	4.76	3.99	2.73	2.17	2.77	2.71	0.97	2.28	0.9	1.28	1.25	3.11	2.77
		0.292	0.292	0.116	0.093	0.081	0.066	0.068	0.046	0.038	0.064	0.049	2.28	0.9	0.035	0	3.47	3.17
<i>M. capaccinii</i>	SE-Europe	17	11.174	7.086	5.952	4.290	3.630	2.416	1.954	2.514	2.408	19	0	0	3	5	18	18
		10.76	10.76	6.88	5.73	4.1	3.46	2.31	1.89	2.4	2.28	0.93	2.28	0.9	1.36	1.33	2.958	2.856
		11.64	11.64	7.27	6.11	4.46	3.79	2.52	2.01	2.64	2.51	1.07	2.28	0.9	1.3	1.26	2.63	2.63
		0.313	0.313	0.131	0.127	0.105	0.102	0.066	0.039	0.073	0.072	0.039	2.28	0.9	0.06	0.066	3.23	3.17
<i>M. daubentonii</i>	C-Europe	16	10.383	6.641	5.58	4.059	3.472	2.196	1.832	2.398	2.299	17	1	1	2	2	16	16
		10	10	6.25	5.25	3.83	3.29	2.01	1.66	2.29	2.14	0.81	2.37	0.78	1.35	1.305	2.888	2.787
		11.07	11.07	7	5.89	4.3	3.62	2.37	1.93	2.49	2.44	0.96	2.37	0.78	1.22	1.2	2.68	2.66
		0.293	0.293	0.180	0.179	0.118	0.088	0.107	0.066	0.061	0.068	0.043	2.37	0.78	1.48	1.41	3.15	3.01
<i>M. brandtii</i>	C-Europe	17	10.283	6.831	5.788	4.163	3.534	2.335	1.912	2.479	2.314	20	2	2	3	4	19	19
		9.91	9.91	6.61	5.51	3.94	3.38	2.2	1.81	2.35	2.18	0.82	2.165	0.73	1.187	1.125	2.794	2.694
		10.58	10.58	7.07	6.01	4.39	3.73	2.45	2.04	2.62	2.46	1	2.3	0.74	1.29	1.23	2.59	2.35
		0.214	0.214	0.142	0.137	0.115	0.106	0.073	0.056	0.070	0.081	0.043	0.191	0.014	0.091	0.072	3.05	2.83
<i>M. mystacinus</i>	C-Europe	13	9.849	6.472	5.451	3.981	3.358	2.177	1.843	2.359	2.195	17	2	2	4	4	16	16
		9.38	9.38	6.33	5.31	3.86	3.28	2.05	1.76	2.48	2.13	0.885	2.17	0.685	1.155	1.115	2.681	2.471
		10.2	10.2	6.66	5.6	4.08	3.48	2.27	1.91	2.46	2.26	0.95	2.25	0.72	1.06	1	2.43	2.2
		0.242	0.242	0.100	0.090	0.067	0.060	0.068	0.046	0.057	0.045	0.041	0.113	0.049	0.089	0.106	2.87	2.68
<i>M. longipes</i>	Afghanistan	10.28	10.28	6.83	5.61	4.28	3.63	2.05	1.93	2.52	2.41	0.78	0.113	0.049	1.14	1.14	2.55	2.48

RECENT



Table A2. Part 2. continued.

Species	i1L	i1W	i2L	i2W	i3L	i3W	cH	cL	cW	p2L	p2W	p3L	p3W	p4L	p4W2	m1L	m1tL	m1trW	m1tW	m2L	m2tL	m2trW	m2tW	m3L	m3tL	m3trW	m3tW				
<i>M. sticticus</i>	0.72	0.36	0.58	0.4	0.89	0.75	1.05	1.14	0.72	0.6	0.5	0.43	0.41	0.41	0.72	0.95	1.7	1.25	1.35	1.66	0.57	1.18	0.64	1.18	0.71	1.18	0.6	1.18	0.51	0.59	
<i>M. frater kagayae</i>	0.38	0.17	0.48	0.19	0.53	0.34	1.14	0.72	0.6	0.5	0.43	0.41	0.41	0.72	0.95	1.7	1.25	1.35	1.66	0.57	1.18	0.64	1.18	0.71	1.18	0.6	1.18	0.51	0.59	0.52	
<i>M. bucharensis</i>	3	3	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
Valid N	0.507	0.16	0.567	0.25	0.64	0.42	1.41	0.77	0.603	0.52	0.47	0.323	0.33	0.33	0.72	1.407	0.627	0.76	0.867	1.38	0.633	0.803	0.76	1.283	0.893	1.283	0.557	0.76	0.66	3	
Mean	0.44	0.13	0.56	0.23	0.63	0.39	1.41	0.76	0.57	0.51	0.43	0.32	0.32	0.72	1.29	0.627	0.57	0.7	0.82	1.36	0.58	0.76	0.85	1.283	0.893	1.283	0.557	0.76	0.66	3	
Minimum	0.57	0.19	0.57	0.26	0.66	0.45	1.41	0.78	0.62	0.53	0.5	0.34	0.34	0.74	1.48	0.69	0.69	0.84	0.92	1.41	0.67	0.89	0.96	1.3	0.96	1.3	0.59	0.8	0.68	3	
Maximum	0.065	0.03	0.006	0.017	0.017	0.03	0.01	0.0229	0.01	0.036	0.021	0.01	0.01	0.01	0.047	0.102	0.110	0.072	0.050	0.026	0.047	0.075	0.059	0.015	0.035	0.035	0.035	0.035	0.026	0.026	
Std.Dev.	3	3	3	3	3	3	4	4	4	5	5	5	5	6	6	7	7	7	7	6	6	6	6	5	5	5	5	5	5	5	
<i>M. dasyneume</i>	0.623	0.217	0.583	0.305	0.69	0.53	1.488	0.885	0.778	0.586	0.584	0.446	0.522	0.81	0.663	1.49	0.657	0.857	0.976	1.522	0.68	0.885	0.97	1.426	0.662	1.426	0.662	0.826	0.736	5	
Valid N	0.6	0.21	0.52	0.28	0.64	0.49	1.34	0.84	0.71	0.49	0.48	0.41	0.41	0.64	0.58	1.31	0.57	0.75	1.13	1.28	0.55	0.78	0.84	1.28	0.6	1.28	0.6	0.73	0.63	5	
Mean	0.65	0.23	0.64	0.33	0.73	0.57	1.56	0.91	0.81	0.66	0.63	0.48	0.58	0.94	0.73	1.64	0.75	1	1.13	1.63	0.73	0.96	1.09	1.53	0.73	1.53	0.73	0.88	0.73	5	
Minimum	0.025	0.012	0.051	0.024	0.037	0.034	0.100	0.033	0.046	0.066	0.060	0.033	0.068	0.102	0.053	0.120	0.054	0.080	0.085	0.127	0.068	0.072	0.083	0.114	0.048	0.114	0.048	0.062	0.060	0.060	
Maximum	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	
Std.Dev.	0.539	0.22	0.601	0.243	0.639	0.472	1.487	1.017	0.719	0.772	0.617	0.592	0.556	1.022	0.694	1.526	0.654	0.815	0.943	1.574	0.676	0.915	1.012	1.417	0.566	1.417	0.566	0.897	0.678	14	
<i>M. hechstetini</i>	0.49	0.17	0.55	0.21	0.56	0.42	1.22	0.9	0.59	0.73	0.58	0.53	0.51	0.95	0.63	1.46	0.61	0.75	0.86	1.33	0.55	0.62	0.85	0.92	1.33	0.48	1.33	0.48	0.83	0.59	14
Mean	0.62	0.28	0.66	0.28	0.69	0.53	1.62	1.09	0.85	0.8	0.69	0.66	0.62	1.11	0.77	1.59	0.69	0.91	1.03	1.61	0.74	1.02	1.1	1.51	0.61	1.51	0.61	1.01	0.77	14	
Minimum	0.038	0.026	0.036	0.021	0.038	0.030	0.116	0.055	0.079	0.021	0.030	0.042	0.030	0.044	0.045	0.036	0.026	0.057	0.054	0.029	0.033	0.047	0.049	0.051	0.038	0.051	0.038	0.049	0.043	0.043	
Maximum	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	
Std.Dev.	0.580	0.212	0.535	0.244	0.547	0.424	1.655	0.838	0.738	0.677	0.589	0.469	0.530	0.918	0.588	1.431	0.595	0.777	0.855	1.381	0.613	0.809	0.858	1.25	0.531	1.25	0.531	0.749	0.628	20	
<i>M. emarginatus</i>	0.49	0.14	0.18	0.18	0.18	0.37	1.51	0.41	0.67	0.59	0.54	0.48	0.47	0.82	0.53	1.32	0.55	0.69	0.81	1.3	0.56	0.75	0.81	1.15	0.47	1.15	0.47	0.69	0.69	20	
Mean	1.43	0.53	0.62	0.55	0.63	0.58	1.78	0.94	0.85	0.74	0.61	0.64	0.57	0.99	0.64	1.5	0.65	0.82	0.9	1.45	0.66	0.85	0.92	1.32	0.58	1.32	0.58	0.83	0.67	20	
Minimum	0.203	0.078	0.088	0.076	0.091	0.050	0.063	0.109	0.051	0.035	0.018	0.042	0.026	0.045	0.027	0.043	0.029	0.033	0.024	0.044	0.030	0.026	0.029	0.051	0.028	0.051	0.028	0.031	0.031	0.031	
Maximum	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	
Std.Dev.	0.038	0.019	0.022	0.030	0.034	0.041	0.062	0.026	0.030	0.034	0.021	0.039	0.019	0.037	0.034	0.029	0.024	0.037	0.040	0.032	0.030	0.038	0.037	0.037	0.034	0.037	0.034	0.030	0.030	0.030	
<i>M. nattereri</i>	17	17	17	17	17	17	18	18	18	19	19	19	19	19	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
Valid N	0.449	0.146	0.493	0.237	0.569	0.382	0.999	0.739	0.619	0.565	0.483	0.457	0.411	0.732	0.561	1.298	0.547	0.774	0.848	1.295	0.570	0.83	0.878	1.208	0.526	1.208	0.526	0.767	0.699	18	
Mean	0.4	0.12	0.44	0.18	0.46	0.35	0.84	0.66	0.57	0.52	0.42	0.4	0.37	0.68	0.52	1.22	0.5	0.69	0.79	1.24	0.53	0.72	0.79	1.09	0.43	1.09	0.43	0.72	0.58	18	
Minimum	0.5	0.18	0.53	0.3	0.64	0.42	1.09	0.8	0.67	0.61	0.55	0.5	0.46	0.78	0.61	1.39	0.6	0.86	0.93	1.39	0.64	0.91	0.96	1.29	0.61	1.29	0.61	0.86	0.71	18	
Maximum	0.034	0.018	0.026	0.034	0.045	0.021	0.080	0.035	0.031	0.027	0.039	0.026	0.025	0.029	0.026	0.042	0.026	0.044	0.036	0.043	0.033	0.045	0.043	0.054	0.037	0.054	0.037	0.035	0.035	0.045	
Std.Dev.	17	17	17	17	17	17	18	18	18	19	19	19	19	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	
<i>M. capaccinii</i>	0.464	0.171	0.477	0.211	0.546	0.374	0.988	0.722	0.596	0.53	0.467	0.344	0.391	0.674	0.525	1.262	0.535	0.711	0.768	1.236	0.539	0.741	0.792	1.166	0.519	1.166	0.519	0.71	0.609	17	
Mean	0.41	0.14	0.43	0.17	0.5	0.33	0.9	0.65	0.55	0.5	0.42	0.29	0.33	0.62	0.44	1.2	0.49	0.63	0.72	1.17	0.5	0.65	0.75	1.09	0.44	1.09	0.44	0.56	0.56	17	
Minimum	0.51	0.2	0.53	0.24	0.6	0.4	1.06	0.8	0.67	0.57	0.52	0.4	0.44	0.75	0.59	1.31	0.59	0.77	0.83	1.3	0.61	0.84	0.87	1.22	0.61	1.22	0.61	0.78	0.67	17	
Maximum	0.027	0.018	0.027	0.019	0.027	0.022	0.049	0.043	0.031	0.023	0.024	0.026	0.031	0.040	0.040	0.035	0.031	0.037	0.031	0.041	0.041	0.046	0.038	0.036	0.036	0.036	0.036	0.028	0.032	0.032	
Std.Dev.	20	20	20	20	20	20	18	18	18	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	
<i>M. brandtii</i>	0.432	0.157	0.475	0.212	0.569	0.436	1.159	0.765	0.604	0.509	0.439	0.419	0.395	0.694	0.562	1.293	0.557	0.699	0.784	1.250	0.543	0.725	0.79	1.142	0.492	1.142	0.492	0.668	0.589	19	
Mean	0.36	0.12	0.43	0.15	0.52	0.38	1.07	0.68	0.55	0.46	0.4	0.34	0.34	0.62	0.52	1.23	0.51	0.64	0.74	1.18	0.49	0.65	0.72	1.07	0.44	1.07	0.44	0.63	0.52	19	
Minimum	0.49	0.23	0.52	0.27	0.64	0.47	1.28	0.84	0.68	0.55	0.48	0.45	0.43	0.84	0.63	1.38	0.61	0.78	0.84	1.31	0.6	0.79	0.85	1.26	0.38	1.26	0.38	0.73	0.65	19	
Maximum	0.036	0.028	0.028	0.036	0.026	0.024	0.048	0.041	0.040	0.022	0.024	0.030	0.025	0.048	0.032	0.040	0.025	0.037	0.033	0.033	0.033	0.042	0.043	0.053	0.039</						