



THE NEW EARLY MIOCENE BAT RECORDS FROM THE MOLASSE SITES OF SOUTH GERMANY

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Abstract: Fossil bats are described from deposits of the Upper Freshwater Molasse of the Forsthart and Rembach sites in East Bavaria of South Germany (MN 4). The material comprises 13 fragments, representing at least six different species, all belonging to Vespertilionidae. A fossil form from Rembach, close to the Oriental clade of *Hesperoptenus*, represents the first and oldest fossil record of this clade in Europe. The assignment of bat records to extant Oriental clades *Hesperoptenus* and *Submyotodon* in Rembach, as well as different forms of *Miostrellus* in Forsthart indicate considerable diversity in Early Miocene vespertilionid bats, and have exciting palaeobiogeographic implications. Fossils are discussed in regards to taxonomic, stratigraphic and palaeoecological significance.

Key words: Chiroptera, Vespertilionidae, Early Miocene, Molasse, Southern Germany, *Hesperoptenus*, *Submyotodon*, *Miostrellus*, *Vespertilio*, *Myotis*

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Introduction

Miocene mammal faunas with fossil bats are well known from South German localities. Rich bat assemblages, including some peculiar genera and species were described from the Middle Miocene sites of Petersbuch, near Eichstätt (Bavaria; Ziegler 2003). Other Middle Miocene mammalian faunas from the Freshwater travertine of the Goldberg and Steinberg localities in the southeastern part of the Nördlinger Ries (Bavaria) include even richer assemblages of molossid and vespertilionid bats (Rachl 1983). A few single bat fragments are known from the Early Turolian site of Dorn-Dürkheim 1 (MN 11, Rheinhessen, Southwest Germany; Storch 1978). Early Miocene sites with bats are also well-presented in South Germany. Thus, the Early Miocene sites of Wintershof-West (Bavaria; Ziegler 1993) and Stubersheim 3 (Baden-Württemberg; Ziegler 1994) have yielded very diverse and abundant bat faunas. Some hundreds of well-preserved bat bones and jaws were described from other Early Miocene sites of Petersbuch 28 and 62, including the description of several new species (Rosina and Rummel 2012). However, most of these sites have a karstic genesis; many bat faunas were found in karstic fissure fillings. Bat records from fluvial localities are comparatively rare.

The numerous sites in southern Germany are associated with a detailed stratigraphic study of the Upper Freshwater Molasse, a formation which is of top significance for Early Miocene stratigraphy of Central Europe, and paleoenvironmental studies of that period. Some Freshwater Molasse sites have also yielded bat records; Late Orleanian fauna of the Sandelzhausen site (MN 5) includes two bat taxa (Ziegler 2000).

The presence of bat remains at the Forsthart and Rembach sites was reported earlier by Ziegler and Fahlbusch (1986), who provided detailed descriptions of these sites and their mammalian fauna. According to Ziegler et al. (2005), the Forsthart site is a former marl pit, located 1 km west-north-west of the church of Forsthart, 12 km west of Vilshofen, East Bavaria, South Germany (N 48°38'21.420" E 13°00'57.247"); the Rembach site is also a former marl pit, exposed 350 m south-east of Rembach, 20 km east of Vilshofen, East Bavaria, South Germany (N 48°36'13.116" E 12°54'39.721"). Stratigraphically, both sites belong to "Limnische Süßwasserschichten", a transitional between the "Oncophora-Schichten" and the Upper Freshwater Molasse, Otnangian/Karpatian, Middle Orleanian (Cícha et al. 1972, Ziegler et al. 2005). Their biostratigraphic correlation (Cícha et al. 1972, Fejfar 1974) places them in the *Megacricetodon* aff. *bavaricus-Eumyarion bifidus* zone, prior to FAD

Megaacricetodon minor and *M. lappi*. They belong to the basal stage of the Upper Freshwater Molasse (OSM) units C + D (Heissig 1997, Aziz et al. 2008), corresponding to the MN 4 zone of the mammalian biochronological scale for the European Neogene (Steininger 1999). The bat remains supplementing a rich fauna of small mammals from Rembach and Forsthart were listed as Chiroptera indet. by Ziegler and Fahlbusch (1986). The present paper provides a detailed analysis of those remains, and discusses their possible meaning and significance for further study of the early history of European bat fauna.

Material and methods

The fossil bat material is represented only by dentary fragments and isolated teeth. The dental terminology follows Miller (1907); for the upper canines, we follow the terminology used by Rosina (2015).

Measurements are given in millimeters, with 0.01 mm precision. Lengths of the individual teeth and tooth-rows were taken as the maximal distances between posterior and anterior crown edges of the respective teeth. Tooth widths were taken as the maximal distances between the lingual and buccal crown edges. The following measurements were taken: length (L) × maximal width (W) of M1, M2, M3; length (L) × width (W) × height of C sup.; length × width of the molar trigonid (Wtr) × width of the molar talonid (Wtl) of m1 and m3; and Hmdm3 – height of a mandibular corpus measured from the lingual side below m3. All fossil material is stored in the Bavarian State Collection for Paleontology and Geology, Munich. The photographs were taken on a SEM (scanning electron microscope) of the AMU (Applied Materials Laboratory, University of Augsburg, Germany).

Abbreviations

BSP – The Bavarian State Collection for Paleontology and Geology (Munich, Germany)
coll. – collection
NMA – The Natural Museum of city of Augsburg (Augsburg, Germany)
SMF – The Senckenberg Research Institute (Frankfurt-am-Main, Germany)
SMNS – The State Museum of Natural History Stuttgart (Stuttgart, Germany)
CoMR – Private collections of Dr. Michael Rummel (Augsburg, Germany)
sup. – superior

Systematic palaeontology

Order Chiroptera BLUMENBACH, 1779
Superfamily Vespertilionoidea GRAY, 1821
Family Vespertilionidae GRAY, 1821
Genus *Hesperoptenus* PETERS, 1868

cf. *Hesperoptenus* (sp. n.)

Text-fig. 1a

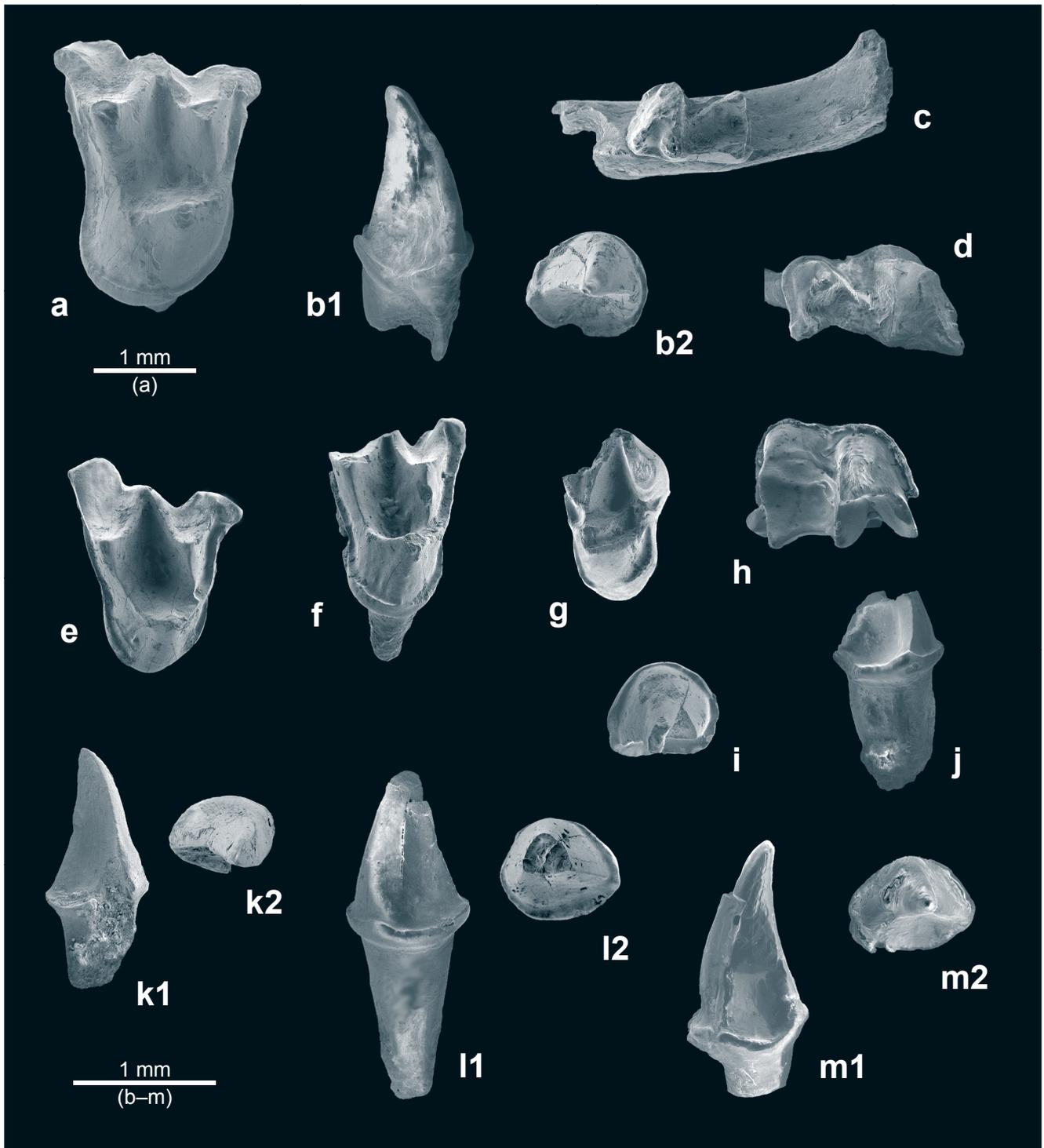
Material and measurements. Rembach, BSP 1959 XXVIII630-1, right M1 2.23 × 2.70.

Description. The M1 is very massive and compacted, with a regular W-shaped ectoloph. It has a short paracrista and a large protocone. The preprotocrista connects with the paracingulum and extends to the parastyle. The regions of the stylocone and mesostyle are damaged, but they seem to be well developed. The crown is without conules or para- or metalophs, and is shaped by a well-developed cingulum. The postprotocrista extends to the lingual base of the metacone without either the hypocone or posterolingual talon, thus, the trigon basin is closed.

Comparison. In view of all the above characters, the fossil specimen belongs to the family Vespertilionidae. The molar from Rembach is very close in size to those of *Otonycteris*, *Ia* and some large species of *Eptesicus*. However, it differs from both recent and fossil species of these genera in having a closed trigon basin, and a high posterolingual slope of the protocone, lacking any trace of the hypoconal undulation and/or talonal extension (Text-fig. 1a; compare with Menu 1985: 115, figs 30–31, Mein and Ginsburg 2002: 24, fig. 38). In these characters, it differs also from *Ia lanna* MEIN et GINSBURG, 1997 (MN 4 site Li Mae Long of Thailand; Mein and Ginsburg 1997: 801, fig. 11B), and from the European *Eptesicus campanensis*, which is similar to our fossil in having a closed trigon basin (compare with Rosina and Rummel 2012: 469, fig. 4H).

The shape of the fossil molar crown from Rembach corresponds most to type C of Menu (1985: 115, fig. 32). Indeed, the fossil is similar to the *Scotophilus* in general appearance of the first upper molar crown, but it is noticeably different from *Scotophilus* in having a regular W-shaped ectoloph, and by the lack of the posterolingual talon. Precisely in these morphological features the large recent species of *Hesperoptenus* (*tickelii* and *tomesii*) differs from *Scotophilus* (Hill 1976: 25). The Rembach fossil specimen is morphologically most similar in size and in the general appearance of the M1 crown to the large species of *Hesperoptenus* (Text-fig. 2; see also Hill 1976: pl. 3 figs d–f). In particular, it is much closer to *H. tomesii*, which is however somewhat larger than the Rembach specimen (M1 2.28 × 3.08 in the specimen SMF 69325 of *H. tomesii*). Furthermore, the first upper molar of *H. tomesii* differs from the Rembach specimen in having a small but distinct depression of the lingual cingulum separating the protoconal and hypoconal parts of the crown (Text-fig. 2). Therefore, we regard the Rembach specimen as a form close to *Hesperoptenus* (supposedly belonging to that genus), though obviously not identical with the extant species distributed in the Oriental region. In our opinion, the morphological peculiarities of the Rembach fossil convincingly support its independent taxonomical status. On the other hand, description of a new taxon on the basis of only a single tooth could be inaccurate. In any case, if our interpretations are correct, and the Rembach bat represents the first fossil record of *Hesperoptenus*, it is the first record of that clade beyond realm of the Oriental region.

For a definite taxonomic conclusion, more material is needed, as well as more detailed information on dental variation in early clades of vespertilionine bats, including the fossil bats, for which no data on maxillary dentition are available. Such a situation exists with *Scotophilus libycus*



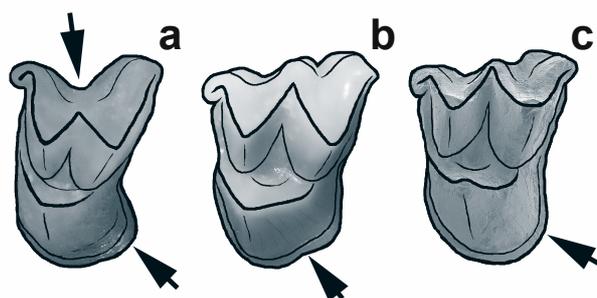
Text-fig. 1. a – cf. *Hesperoptenus* (sp. n.), right M1, BSP 1959 XXVIII630-1, Rembach, occlusal view; b – cf. *Vespertilio* (sp. n.), right C sup., BSP 1959XXVIII630-2, Rembach; c – *Submyotodon petersbuchensis*, fragment of right dentary with m3, BSP 1959 XXVIII630-3, Rembach, occlusal view; d – *Miostrellus* (sp. n.), left m3, BSP 1959 XXVII-Ch10, Forsthart, occlusal view; e – *Miostrellus* (sp. n.), right M1, BSP 1959 XXVII-Ch1, Forsthart, occlusal view; f – *Miostrellus* cf. *risgoviensis*, right M2, BSP 1959 XXVII-Ch2, Forsthart, occlusal view; g – *Miostrellus* (sp. n.), left M3, BSP 1959 XXVII-Ch3, Forsthart, occlusal view; h – *Myotis* sp., left m1, BSP 1959 XXVII-Ch9, Forsthart, occlusal view; i – *Miostrellus* cf. *risgoviensis*, right C sup., BSP 1959 XXVII-Ch8, Forsthart; j – *M. cf. risgoviensis*, right C sup., BSP 1959 XXVII-Ch7, Forsthart; k – cf. *Miostrellus* sp., right C sup., BSP 1959XXVII-Ch4, Forsthart; l – *Myotis* sp., left C sup., BSP 1959 XXVII-Ch5, Forsthart; m – *Miostrellus* (sp. n.), right C sup., BSP 1959 XXVII-Ch6, Forsthart; 1 – lingual view, 2 – occlusal view.

HORÁČEK et al., 2006 from the MN 4–5 site Jebel Zelten (Libya), and with an articulated skull of *Samonycteris majori* REVILLIOD, 1922 (Horáček et al. 2006: 139, fig. 4) from the Late Miocene site of Mytilini (Samos, Greece).

The upper molar from Rembach is somewhat similar to the upper molars of the Late Paleogene African genus *Philisis* (Sige 1985: 165, fig. 3), which probably belongs to the same phylogenetic clade as *Scotophilisis* (Horáček et al. 2006).

Naturally, though, the Oligocene *Philisis* shows many distinct trends distinguishing it from the cf. *Hesperoptenus* from Rembach.

Remarks. From the Middle Miocene site of Anwil (MN 7/8, Switzerland), a single upper second molar (specimen Al. 198) was identified by Engesser (1972) as “Vespertilionidae, *Scotophilus?*”. This specimen is very similar in the general appearance of the crown to the Rembach specimen (compare with Engesser 1972: 130, fig. 38), and it is assumed that it could also be classified as *Hesperoptenus*. If so, the *Hesperoptenus* from Rembach might not be the sole record of this Oriental genus in Europe.



Text-fig. 2. a – left M1 of recent *Scotophilus dingari*, SMF 2515; b – left M1 of recent *Hesperoptenus tomesi*, SMF 69325; c – right M1 of cf. *Hesperoptenus* (sp. n.), BSP1959 XXVIII630-1, Rembach, occlusal view (mirror image). Black arrows mark sites of differences between the crowns.

Genus *Vespertilio* LINNAEUS, 1758

cf. *Vespertilio* (sp. n.)

Text-fig. 1b

Material and measurements. Rembach, BSP 1959 XXVIII630-2, the right C sup. $0.93 \times 0.78 \times 1.60$.

Description. The upper canine is small and slender; triangular in cross-section with a damaged lingual cingulum. The crown has a well-developed concave disto-lingual face, and only the lingual and distal crests. The anterolingual cingulum is well developed and forms a narrow lingual talon.

Comparison. It exhibits all features typical for vespertilionid bats, and shares the most typical features of upper canines of *Vespertilio* and *Nyctalus* species: 1) triangular cross-section; 2) a wide concave distolingual face; 3) appearance of the lingual and distal crests only; 4) an expansion of the anterolingual part of the cingulum, which forms a narrow thickening. Unfortunately, part of the lingual cingulum of the Rembach fossil is damaged, so the presence of small cuspid on its anterolingual part, as in *Vespertilio*, is obscured. The Rembach upper canine differs from those of *Miostrellus*, due to the presence of a visible expansion of the lingual cingulum, and in a more concave lingual face of the crown (e.g., compare with Rachl 1983: 229, fig. 70c).

The upper canine of *Nyctalus* shows a more developed anterolingual thickening of the cingulum, and frequently tends to have a second tip on the cutting edge of its crown. The fossil upper canine of Rembach does not share these morphological traits, but shows most of the above-listed morphological features of *Vespertilio*. If this Rembach specimen would indeed belong to that clade, then it would represent by far the oldest record of the genus. The few other fossil records of *Vespertilio* s. str. are much younger. Besides the Pliocene records (*V. villanyiensis* HORÁČEK, 1997, Villány 3, Hungary, MN 17; Horáček 1997) and China (*V. sinensis* (PETERS, 1880), Bilike, Inner Mongolia, China, ~MN 14; Qiu and Storch 2000), a single dentary fragment of *V. cf. villanyiensis* was described from the Late Turolian of Russia (MN 12–13, Morskaya 2; Rossina et al. 2006), and several isolated teeth (Rosina and Sinita 2014: 156, fig. 3) from the Late Turolian of Ukraine (MN 12, Egorovka 1, Palievo) were reported. All these fossil forms are considerably larger than the fossil from Rembach (compare with Rosina and Sinita 2014: 154, tab. 2).

Genus *Submyotodon* ZIEGLER, 2003

Submyotodon petersbuchensis ZIEGLER, 2003

Text-fig. 1c

Material and measurements. Rembach, BSP 1959 XXVIII630-3, the right dentary fragment with m3 $0.95 \times 0.6 \times 0.55$; Hmdm3 = 1.05.

Description. A delicate and very small dentary fragment, broken behind the m3 and at the alveolar margin of m2. The trigonid part of the crown is partly damaged. The postcristid is very low, and the hypoconulid is very tiny. However, it can be seen that the postcristid joins the entoconid, thus, the m3 is myotodont. The paralophid is slightly curved. The cristid obliqua and the postcristid both show visible grooves.

Comparison. The myotodont crown with a well-developed cingulid suggests that the fossil represents a member of the family of Vespertilionidae. This very tiny specimen shares the following features with *S. petersbuchensis* (MN 6, Petersbuch, Germany; Ziegler 2003): a very small size, a visibly compressed trigonid, almost unreduced talonid, curved lophids and cristids, and the appearance of visible grooves in cristids. The last trait is very typical of *Submyotodon*, which differentiates this taxon from the *Myotis*-species. Direct comparison of the fossil under study with *M. cf. helleri* KOWALSKI, 1962 from the Middle Miocene site of Petersbuch (CoMR P10-00594.2; see also Ziegler 2003) shows that the Rembach fossil is smaller ($1.14 \times 0.70 \times 0.57$ for the m3 of the specimen of P10-00594.2; Ziegler 2003: 476). It further differs from *M. cf. helleri* from Petersbuch in a less reduced talonid. According to all of the morphological features listed above, this Rembach specimen can be associated with *S. petersbuchensis*.

Remarks. Morphology of the talonids of the m3s of *S. petersbuchensis* is variable: most of them exhibit the myotodont condition, as in the specimen under study, and only some of them are submyotodont (Ziegler 2003: 479).

Genus *Miostrellus* RACHL, 1983

Miostrellus cf. *risgoviensis* RACHL, 1983

Text-fig. 1f, i–j

Material and measurements. Forsthart, BSP 1959XXVII-Ch2 (Text-fig. 1f), the right M2 ca. $1.15 \times$ ca. 1.55 ; BSP 1959 XXVII-Ch7 (Text-fig. 1j), the right C sup. ca. 0.83×0.65 ; BSP 1959 XXVII-Ch8 (Text-fig. 1i), the right C sup. 0.80×0.70 .

Description. The meso- and metastyle of the upper molar (Text-fig. 1f) are broken, and the area of the paraconule and preprotocrista is also damaged. The preprotocrista connects with the paracingulum; the postprotocrista extends to the lingual base of the metacone, and thus the trigon basin is closed. The crown has neither a hypocone nor a posterolingual talon.

The upper canines (Text-fig. 1i–j) are small and slender; the apexes are broken. The crowns are triangular in cross-section, shaped by a well-developed cingulum and show distinct posterior and lingual crests. The buccal crest and the anterior ridge are weak, so the anterolingual face and the anterobuccal ridge are seamlessly joined together into a single convex surface. The posterobuccal face is slightly concave. The posterolingual concavity is wide, but without the lingual talon.

Comparison. The shape of the M2 crown with a well-developed cingulum and the lack of the hypocone suggest that the tooth belongs to the vespertilionid bat. This specimen from Forsthart is almost identical with M2 of the holotype of *M. risgoviensis* (BSP 1966 XXXIV703; Rachl 1983: 226, 229, tab. 52, fig. 70a).

Due to the damage of the canine teeth, it is difficult to accurately judge the shape of their crowns. However, they undoubtedly belong to the vespertilionid bats. According to the triangular shapes in cross-section, and because of the lack of the lingual talons, the upper canines from Forsthart are most similar to those of *M. risgoviensis* (see, e.g., BSP 1966 XXXIV705; see also Rachl 1983: 229, fig. 70c). On the other hand, the Forsthart canines are similar to the upper canine from Rembach (cf. *Vespertilio* sp., BSP 1959 XXVIII630-2; Text-fig. 1b) in having some expansion of the lingual cingulum. Nevertheless, due to the absence of the lingual talons in the canines from Forsthart, and the sharing of most of the above-listed morphological traits with *M. risgoviensis*, they are assigned to *M. cf. risgoviensis*. Moreover, they also correspond to it in size (Rachl 1983: 226, tab. 52).

cf. *Miostrellus* sp.

Text-fig. 1k

Material and measurements. Forsthart, BSP 1959 XXVII-Ch4, the right C sup. $0.78 \times 0.63 \times 1.30$.

Description. A tiny upper canine with damaged anterolingual part. The crown is evidently triangular in cross-section, shaped by a well-developed cingulum, and shows distinct posterior and lingual crests. The buccal crest is weak, but visible. The posterobuccal face is slightly concave. The posterolingual concavity is wide; the lingual cingulum forms a weak but noticeable lingual talon.

Comparison. It is obviously a canine of a vespertilionid bat, exhibiting both in size and morphology characters of the genus *Miostrellus* (triangular occlusal outline, concave posterobuccal face). It is smaller than *M. risgoviensis* (Rachl 1983: 226, tab. 52) and smaller than specimens BSP 1959 XXVII-Ch7-8, but falls into the variation range of *M. risgoviensis*.

Miostrellus (sp. n.)

Text-fig. 1d, e, g, m

Material and measurements. Forsthart, BSP 1959 XXVII-Ch6 (Text-fig. 1m), the right C sup. $0.98 \times 0.73 \times 1.60$; BSP 1959 XXVII-Ch1 (Text-fig. 1e), the right M1 1.30×1.50 ; BSP 1959 XXVII-Ch3 (Text-fig. 1g), the left M3, LM3 = ca. 0.85 ; BSP 1959 XXVII-Ch10 (Text-fig. 1d), the left m3 $1.30 \times$ ca. $0.75 \times$ ca. 0.65 .

Description. The M1 (Text-fig. 1e) has no conules, but shows a distinct paraloph. The postprotocrista extends posteriorly to the base of the metacone, thus the trigon basin is closed. The crown has neither the hypocone nor the posterolingual talon. The considerable expansion of the posterobuccal part of the ectoflexus cingulum forms a wide and flat posterobuccal shelf.

The M3 (Text-fig. 1g) is much damaged: the stylocone and the most part of paracrista are broken, a small part of paracone, the metacone and the protocone are preserved. The metacone is somewhat reduced, thus, the tooth crown is slightly compressed.

The crowns of both the upper canine and the m3 (Text-fig. 1d) were broken, but were later restored by being glued together. The upper canine (Text-fig. 1m) is slender and triangular in cross-section. It is shaped by a well-developed cingulum, and shows distinct posterior and lingual crests. The buccal crest is weak, but also visible. The posterobuccal face is slightly concave. The posterolingual concavity is wide.

The lingual part of the talonid of m3, including the entoconid, is broken (Text-fig. 1d). However, some parts of the hypoconilid and entoconid, as well as the postcristid and the hypoconid are preserved. The trigonid is also damaged: the tips of the paraconid and protoconid are broken, and the metaconid is heavily damaged. Nevertheless, the lower molar is evidently myotodont, with a slightly reduced talonid.

Comparison. According to the general appearance of the crowns, all fossils evidently belong to vespertilionid bats.

The M1 from Forsthart is similar to the *Miostrellus* in general appearance of the first upper molar crown, which has a distinct paraloph, but neither paraconule nor hypocone. This fossil is most similar to the M1 of *M. risgoviensis* (e.g., BSP 1966 XXXIV705; see also Rachl 1983: 229, fig. 70c), but the Forsthart fossil is appreciably larger in size (compare with Rachl 1983: 226, tab. 52). It is close in size to the Early Miocene *M. petersbuchensis* (Rosina and Rummel 2012: tab. S7, supplementary data). However, the Forsthart fossil is effectively distinguishable from *M. petersbuchensis* in having a high postprotocrista, which extends to the base of the metacone without any metaloph, and a weaker protocone area (compare with Rosina and Rummel 2012: 471, fig. 5A).

The M1 from Forsthart shares these traits with M1 of *M. risgoviensis*, which is much smaller. The Middle Miocene *M. noctuloides* from Sansan (e.g., specimens Sa. 13.617-618, MN 6, France; Baudelot 1972) and *M. aff. noctuloides* from Sandelzhausen (MN 5, Germany; Ziegler 2000) are very close in size to the *Miostrellus* sp. from Forsthart (Baudelot 1972: 53). However, the latter differs from both the *M. noctuloides* from Sansan and the *M. aff. noctuloides* from Sandelzhausen in the lack of a hypocone (compare with Baudelot 1972: 57, 369, fig. 21, pl. II, figs 10–11, Ziegler 2003: 462, fig. 3.3, Ziegler 2000: 127, pl. 10, fig. 120). Due to this feature, the *Miostrellus* from Forsthart is also separated from the Early Miocene *Eptesicus aurelianensis* ZIEGLER, 1993 (Wintershof-West, Stubersheim 3, Germany, MN 3; Ziegler 1993, 1994), the M1 of which have a distinct hypocone and something like a metaloph (specimens BSP 1980 XXX II 641, SMNS 45744 H1; Ziegler 1994: 113, pl. 5, figs 5–6).

The M3 is similar to the Early Miocene *M. petersbuchensis* from Petersbuch (Rosina and Rummel 2012: 471, fig. 5A) and *M. aff. noctuloides* from Sandelzhausen (Ziegler 2000: 127, pl. 10, fig. 122) in the somewhat compressed shape of the crown, due to a less developed metacone, and in having a well-developed cingulum. However, the Forsthart fossil is somewhat larger (compare with Rosina and Rummel 2012: tab. S7, supplementary data, Ziegler 2000: 101, tab. 7). Moreover, it corresponds in size to specimen BSP 1959 XXVII-Ch1.

Despite the damage, the upper canine crown can be seen to be triangular in cross-section, its posterobuccal face is slightly concave, and the lingual talon is absent. All these features of the upper canine from Forsthart are shared with those of *Miostrellus risgoviensis* (e.g., BSP 1966 XXXIV705; see also Rachl 1983: 229, fig. 70c), but the Forsthart canine is somewhat larger (Rachl 1983: 226, tab. 52). It is close in size to specimen BSP 1959 XXVIII630-2 of cf. *Vespertilio* sp. from Rembach, but differs from it primarily in the lack of the lingual talon and in having a slightly concaved posterobuccal face (Text-fig. 1m2). On the other hand, the Forsthart canine is very similar in size to the upper canines of *M. aff. noctuloides* from Sandelzhausen (Ziegler 2000: 101, tab. 7), and appears to correspond in size to other specimen of *Miostrellus* from Forsthart (BSP 1959 XXVII-Ch1).

The m3 from Forsthart is similar to *Miostrellus* in appearing to have a somewhat reduced talonid. In addition, it has a somewhat elongated paralophid, as in *Miostrellus petersbuchensis*, and is very similar to the latter in size (Rosina and Rummel 2012: tab. S7, supplementary data). The m3 from Forsthart differs from the *M. aff. noctuloides* from Sandelzhausen in being larger (Ziegler 2000: 101, tab. 7). Nevertheless, according to all the above listed morphological features, we assign all these specimens from Forsthart to the genus *Miostrellus*.

Genus *Myotis* KAUP, 1829

Myotis sp.

Text-fig. 1h, 1

Material and measurements. Forsthart, BSP 1959 XXVII-Ch9 (Text-fig. 1h), the left m1 $1.30 \times 0.67 \times 0.80$; BSP 1959 XXVII-Ch5 (Text-fig. 1l), the left C sup. 0.93×0.78 .

Description. The upper canine (Text-fig. 1l) is oval in cross-section, and has a well-developed cingulum. The lingual and buccal crests are very weak, and only the posterior crest is well developed. The posterolingual concavity is wide, but only slightly concave. The lingual talon is absent.

The first lower molar (Text-fig. 1h) is myotodont; the hypoconulid is well developed. The para- and metalophid are only somewhat curved. The metalophid is convex in the posterior direction, so that the tip of the metaconid is directed forward. The talonid is wider than the trigonid.

Comparison. The shape of the crown of the fossil upper canine from Forsthart corresponds most closely to type A of Menu (1985: 92, fig. 7). The posterolingual concavity of the crown is visibly developed; the area of the anterolingual face, the anterobuccal ridge and the posterobuccal face are seamlessly joined together into a single convex surface. These are the typical features of an upper canine of *Myotis*.

The upper canine from Forsthart is smaller than that of the Middle Miocene *M. bavaricus* from Petersbuch (MN 7–8, Germany; Ziegler 2003: 467, tab. 4), but slightly larger than that of the Middle Miocene *M. murinoides* from Sansan (MN 6, France; Baudelot 1972: 24), and further differs from it due to the lack of a strong buccal and lingual cingulum and the posterobuccal protuberances (Baudelot 1972: 35, fig. 13). At the same time, the upper canine from Forsthart is appreciably smaller than those of *M. aff. murinoides* from Sandelzhausen (MN 5, specimen BSP 1959 II 7776: $1.11 \times 0.94 \times 1.70$; Ziegler 2000: 102). The fossil canine from Forsthart is most similar in size to some of the specimens of *M. aff. murinoides* (e.g., SMNS 45742.8; Ziegler 1994) from Stubersheim 3 (MN 3, Germany; Ziegler 1994: 104).

The para- and metalophids of the first lower molar from Forsthart are only somewhat curved, which is typical for the species of *Myotis* and *Vespertilio*. However, the metalophid of the Forsthart molar is convex in the posterior direction, so that the tip of the metaconid is directed forward instead of backwards, as with *Vespertilio*. In addition, the m1 from Forsthart is more slender than those of *Miostrellus*. On the basis of these morphological traits, the fossil m1 from Forsthart is also assigned to *Myotis* sp. The m1 from Forsthart is evidently smaller than those of the Middle Miocene *M. bavaricus* from Petersbuch (MN 7–8, Germany; Ziegler 2003: 467, tab. 4), as well as those of the Middle Miocene *M. reductus* from Petersbuch 6 (Ziegler 2003: 474, tab. 6) and the Early Miocene *M. cf. sanctialbani* from Petersbuch 28 (MN 3, Germany; Rosina and Rummel 2012: tab. S1, supplementary data). At the same time, the m1 from Forsthart is appreciably larger than both those of the Middle Miocene *M. ziegleri* (Baudelot 1972: 48) and the nominative species *M. murinoides* from Sansan (Baudelot 1972: 24). It compares well in size with some specimens of *M. aff. murinoides* (e.g., SMNS 45742.1; Ziegler 1994: 104) from Stubersheim 3 and the Early Miocene *M. aff. reductus* from Petersbuch 28 and 62 (Rosina and Rummel 2012: tab. S5, supplementary data).

Remarks. Both the Early Miocene *M. aff. murinoides* from Stubersheim 3 and Wintershof-West (specimen BSP 1937 II 20417, = *Vespertilionidae* gen. et sp. indet.; Ziegler 1993, 1994: 106) and the *M. aff. reductus* from Petersbuch 28

Table 1. Comparison of *Myotis* specimens from the Forsthart site with the most similar Miocene *Myotis* species of Europa; maximum and minimum values and arithmetic mean (in parentheses) are given; all measurements in mm.

species	locality	age	specimen number	LC sup.	WC sup.	Lm1	Wtrm1	Wtlm1	reference
<i>Myotis</i> sp.	Forsthart (Germany)	MN 4	BSP 1959 XXVII-Ch5	0.93	0.78	–	–	–	own data
<i>Myotis</i> sp.	Forsthart (Germany)	MN 4	BSP 1959 XXVII-Ch9	–	–	1.30	0.68	0.80	own data
<i>M. aff. murinoides</i>	Stubersheim 3 (Germany)	MN 3	SMNS 45742.1	–	–	1.31	–	0.78	Ziegler 1994
<i>M. aff. murinoides</i>	Stubersheim 3 (Germany)	MN 3	SMNS 45742.8	0.89	0.77	–	–	–	Ziegler 1994
<i>M. aff. murinoides</i>	Stubersheim 3 (Germany)	MN 3	stub3/17.2 (coll. Wannemacher)	0.77	0.67	–	–	–	Ziegler 1994
<i>M. aff. murinoides</i>	Stubersheim 3 (Germany)	MN 3	SMNS 45742.3	–	–	1.23	–	0.74	Ziegler 1994
<i>M. aff. murinoides</i> *	Wintershof-West (Germany)	MN 3	BSP 1937 II 20417	–	–	1.23	–	0.78	Ziegler 1993
<i>M. murinoides</i>	Sansan (France)	MN 6	Sa. 13.657 neotype	–	–	1.25	–	0.80	Baudelot 1972
<i>M. murinoides</i>	Sansan (France)	MN 6	hypodigm	0.72–0.85 (0.78)	0.60–0.70 (0.65)	1.14–1.31 (1.23)	0.65–0.79 (0.72)	0.68–0.84 (0.76)	Baudelot 1972
<i>M. aff. murinoides</i>	Sandelzhausen (Germany)	MN 5	BSP 1959 II 7776	1.11	0.94	–	–	–	Ziegler 2000

* Vespertilionidae gen. et sp. indet. (Ziegler 1994: 106)

are morphologically very close to each other (Tab. 1; Ziegler 1993: 154, pl. 5, fig. 7, 1994: 107, pl. 3, figs 1–3, Rosina and Rummel 2012: 474, fig. 6 D–E). Both fossil forms are somewhat larger than the nominative *M. murinoides* from Sansan (Tab. 1). It seems probable that the Early Miocene *Myotis* forms from Germany belong to the same taxon, which apparently differs from the *M. murinoides* from France. However, further morphological studies are needed for definitive conclusions that are beyond the scope of this paper.

Discussion

Biostratigraphic considerations and palaeobiogeographic remarks

It is worth mentioning that all six taxa of fossil bats found in both the Rembach and Forsthart sites belong to the vespertilionid bats. Neither rhinolophids nor megadermatids were found in Rembach and Forsthart, although these bat remains are very common and abundant in fossil assemblages of other Early Miocene sites in Germany, such as Wintershof-West (Ziegler 1993), and Petersbuch 28 and 62 (Rosina and Rummel 2012). The situation is the same with the Early Turolian sites from lacustrine and fluviatile deposits in the Ukraine, where all five sites yielded remains of only vespertilionid bats (Rosina and Sinitsa 2014). Rare remains of vespertilionids were also found in non-karstic sites of France (Bernardière and Lobrieu, MN 11; Mein 1999), Spain (Valdeganga 2, MN 16; Mein et al. 1978), the Southern European area of Russia (Morskaya 2, MN 12; Rossina et al. 2006) and the Czech Republic (Merkur-North, MN 3 and Citice, MN 5; Horáček 2001). Bat assemblages from other non-karstic sites of Sansan (MN 6, France; Baudelot 1972), Schaffhausen 1 (MN 1, Harburg, Germany; Dehm 1978),

Oberdorf (MN 4, Western Styrian Basin, Austria; Ziegler 1998), Dolnice 1 (MN 4, the Czech Republic; Horáček 2001) and Merkur-North (MN 3, the Czech Republic; Horáček 2001) are almost entirely composed of vespertilionids, and include only scanty remains of megadermatids, rhinolophids or molossids (Ziegler 1998, Horáček 2001). Such a difference in bat fauna composition between karstic and non-karstic fossil assemblages is evidently caused by taphonomical reasons, including refuge preferences of different bat species.

There are many vertebrate fossil-bearing sites that are associated with the Freshwater Molasse deposits (Ziegler et al. 2005). However, only a few of these sites have produced fossil bat remains. Besides the Early Miocene sites of Rembach and Forsthart, in the area of Southern Germany they are the Middle Miocene sites of Burg-Balzhausen (MN 5; Seehuber 2008), Kirrberg-Sandgrube (MN 6; *ibid.*) and Sandelzhausen (MN 5; Ziegler 2000). From the site of Kirrberg-Sandgrube, the dentary fragment with p4 – m3 belonging to *Megaderma lugdunensis* was only described (Seehuber 2008: 287, pl. 5, figs 7–9). A single left m2 of Chiroptera indet. was mentioned from the site of Burg-Balzhausen (Seehuber 2008: 62). Our examinations of this latter specimen (NMA 2005-777/1927) allow relating this fossil to the genus *Eptesicus*, due to the presence of a curved paralophid, a metalophid which is convex in the anterior direction and because of the myotodonty of the molar crown. In any case, both the sites of Burg-Balzhausen and Kirrberg-Sandgrube are much younger than the Rembach and Forsthart sites. The bat association from the Freshwater Molasse site of Sandelzhausen includes numerous remains of *Miostrellus* aff. *noctuloides*, and a few records of *Myotis* aff. *murinoides* (Ziegler 2000), which might suggest certain similarities with the Forsthart assemblage. From the Bohemian Early Miocene sites of Dolnice 1, Citice, and Merkur-North, the bat association from the latter includes

rare fossils in the Neogene of Europe of *Nyctalus* and cf. *Vespertilio* (Horáček 2001), which might indicate some resemblance to the Rembach assemblage.

The fossil bat assemblage from Rembach include records of *Hesperoptenus* and *Submyotodon* genera, modern representatives of which are currently distributed through South and Central Asia, and the Indomalayan region (Borissenko and Kruskop 2003, Benda and Gaisler 2015, Ruedi et al. 2015). Fossil records of *Submyotodon* are recorded from the Early Miocene site of Petersbuch 28 (Germany; Rosina and Rummel 2012), from the late Middle Miocene site of Petersbuch 6 (Germany; Ziegler 2003), and from the Late Miocene site of Gritsev (Ukraine, MN 9; Rosina pers. obs.). As mentioned above, we proposed also a discovery of *Hesperoptenus* genus (= *Scotophilus*?) from the Middle Miocene site of Anwil (Switzerland; Engesser 1972). If it is valid, the new fossils of *Hesperoptenus* and *Submyotodon* in the Early Miocene sites of Rembach suggest that from at least the Early Miocene, the range of their distribution had spread apparently to the whole of Central Europe. That such a situation could have continued during the Middle Miocene and the entire Late Miocene is proved by the finds of *Submyotodon* in the Ukraine, and *Hesperoptenus* in Switzerland. On the assumption that climatic requirements for the ancient *Submyotodon* and *Hesperoptenus* were as restrictive as they are today for recent species, we can propose a tropical or subtropical climate in Europe in the Early Miocene, which lends even more support to the conventional models of Neogene climate reconstructions (Utescher et al. 2000, Zachos et al. 2001, Mosbrugger et al. 2005).

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