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Cochlea Size in Extant Chiroptera and Middle Eocene Microchiropterans from Messel

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The question of mono- or diphyletic origin of bats and the systematic status of the oldest known bats from the Eocene of Europe and North America has been the subject of controversy [1 – 6]. It is now generally accepted that all of these Eocene bats are microchiropterans and not ancestors of either Micro- or Megachiroptera as formerly proposed [2]. For the species *Icaronycteris index* Jepsen 1966, Early Eocene of Wyoming, and *Palaeochiropteryx tupaiodon* Revilliod 1917, early Middle Eocene of Germany, it was reported that the size of the cochlea is as large as in extant Microchiroptera, and it was concluded that the echolocation system of these Eocene species was already very sophisticated [4, 7]. This was considered as one argument (among various others) for a diphyletic origin of Micro- and Megachiroptera [6]. It was, however, not clear whether the data base was sufficient for these conclusions. The aim of the present study is to establish the relations of cochlea size of six fossil species of three families from Messel and 298 extant chiropterans of all major higher taxa.

A relationship between cochlea size and echolocation performance has been suggested for some selected extant species [8], but a systematic study has not been undertaken so far. Thus, an evaluation of the relative size of the cochlea for Early Tertiary bats may be achieved by comparison with taxa of extant bats with known echolocation and foraging behavior [9 – 11]. We provide in this paper a representative sample of 147 species of 28 genera of extant Vespertilionidae bats as the most generalized group. The sample of extant Megachiroptera includes 71 species with a skull width less than 21 mm, including all genera. Only a few examples of carnivorous, sanguivorous, and frugivorous Microchiroptera are considered. The six bat species from Messel have been shown from their preserved stomach contents to have been exclusively insect feeders [14].

In this study high-resolution radiographic measuring procedures improved the reliability of the compared data of extant and fossil materials. Examples of radiographs are given in Figs. 1 and 2 for two extant bat species and in Fig. 3 for two Messel bats. Skulls were individually microradiographed with Microx (Nicolet) and Faxitron (Hewlett Packard) X-ray apparatus after an exact orientation of the neurocranium to the center beam. The accuracy of centering for the dorsoventral exposure was within an angle of ± 3 ° (compare the asymmetrical projection of crista sagitalis on the lower radiograph in Fig. 2 with the ideal centering on the upper picture as extremes). Original radiographs were directly enlarged and measured with a resolution of 0.04 mm. By this procedure more details were visible compared to any kind of reproduction on prints, especially in regions of superimposed morphological structures. The length and the width of the skulls were measured. The length of the skull also depends on variations in dentition and types of food resources (e.g., elongation of the rostrum in nectar feeders) and thus was rejected as a suitable comparative measure. From the various measures of the skull width the distance between the outermost bony margin of the semicircular canals proved to be best suited. This measure of the basicranial width is rather unaffected by ecological constraints and can be easily depicted from radiographs. The oblique diameter of the cochlea was measured from the end of the first half turn of the cochlea to the end of the second half turn [12] at the clear outline of the cochlea visible in the radiographs (Fig. 1). Thus, no parts of the promontorium of the cochlea and no parts of the vestibular organ are included. The same radiological methods can be applied to fossil material. However, due to the position of the fossil in the oil shale and in the resin matrix (Fig. 3) a more skillful procedure is required, and it is necessary to rotate and tilt the specimen in different spacial planes with respect to the X-ray beam.

Fig. 1. Enlarged radiograph of the cochlea of *Rhinopoma hardwickei*. Cross symbols connected by a straight line indicate the width of the cochlea measured across the second half turn

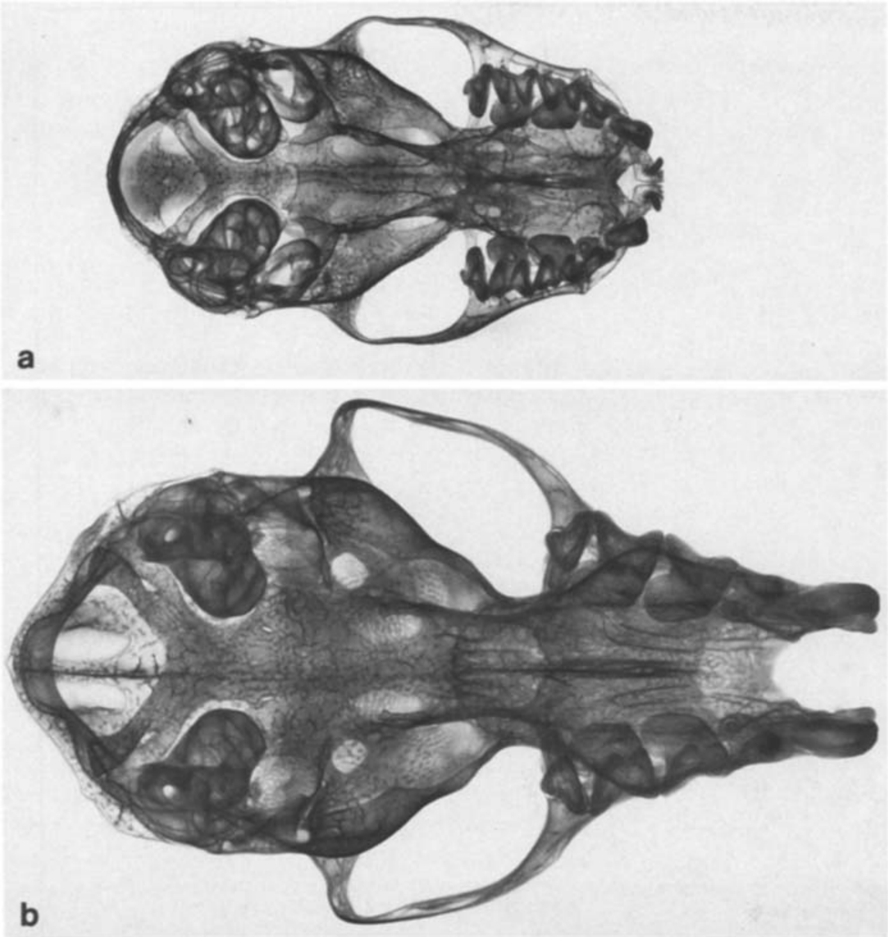

Fig. 2. Radiographs of the skulls of two extant bats. a) *Rhinopoma hardwickei* is an insectivorous bat which emits constant frequency (30 – 35 kHz) and frequency-modulated sounds as well [27]. The cochlea is medium-sized and compares with the vast majority of echolocating vespertilionid bats (see also the regression line for vespertilionids in Fig. 4 and *R. hardwickei* indicated by No. *10*). b) *Megaderma lyra* is a carnivorous and insectivorous bat, which echolocates with faint, simply structured, broad-band sounds. It hunts successfully without echolocation by passive acoustic location [28, 29]. The cochlea is small (see also Fig. 4, indicated by No. *5*), and skulls with similarly proportioned basicranial and occipital regions are also found in many Megachiroptera

This is possible by means of a specially developed remote-controlled specimen manipulator and the application of a particular microfocus technique [15]. This technique allows spatial separation of fossil and film without loss of resolution.

Radiographic investigation of the otic region discloses clear-cut correlations between the diameter of the cochlea and the width of the skull. These are markedly different for various taxonomic groups and even diagnostic for some families. However, the fan-like distribution pattern of these correlations (Fig. 4) reflects not only taxonomic units but also different stages of acoustical specialization in extant Chiroptera, which can be classified as follows:

1. Bats with a very small cochlea (as compared to basicranial width): The

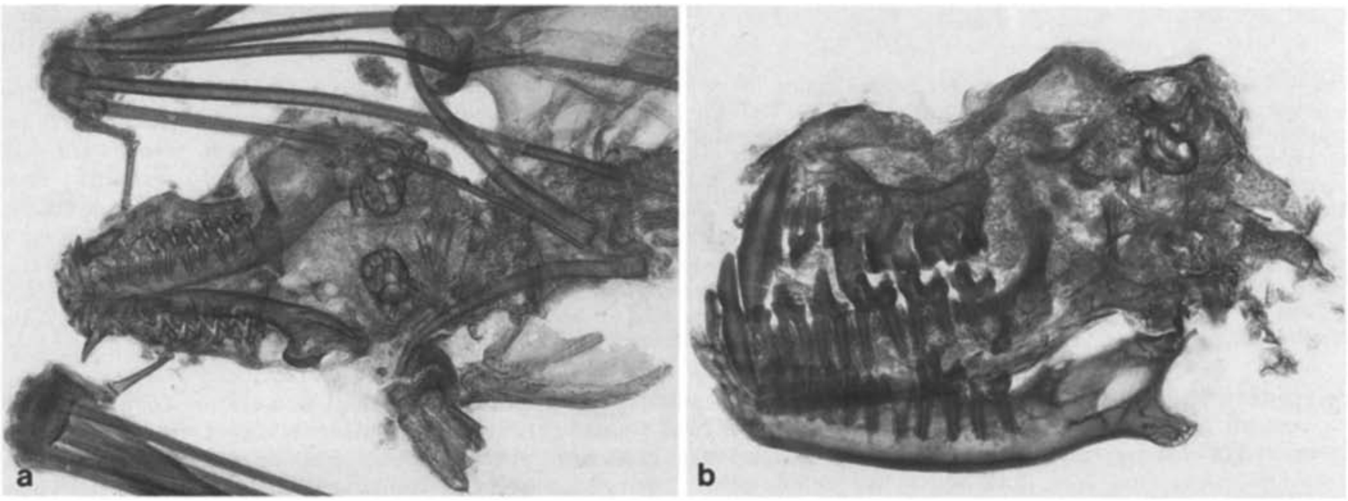

Fig. 3. Radiographs of two Eocene bats from Messel. a) *Palaeochiropteryx tupaiodon* is the smallest of the six investigated species. The figure is a composite of two radiographs of a single specimen which was split into two halves while excavating, and transferred later to two artifical resin plates. The lateral outlines of the semicircular canals are clearly visible, and the inner ears are completely preserved with 2.5 turns. The skull is partly crushed (for size of the cochlea, compare *P.t.* in Fig. 4). b) *Hassianycteris messelensis* is the most advanced Messel bat in dental and skeletal features [3, 30], and it is considered a rapid- and high-flying bat. Only the left cochlea is completely preserved (for size of the cochlea, see *H.m.* in Fig. 4); the basicranial width cannot be measured on this specimen

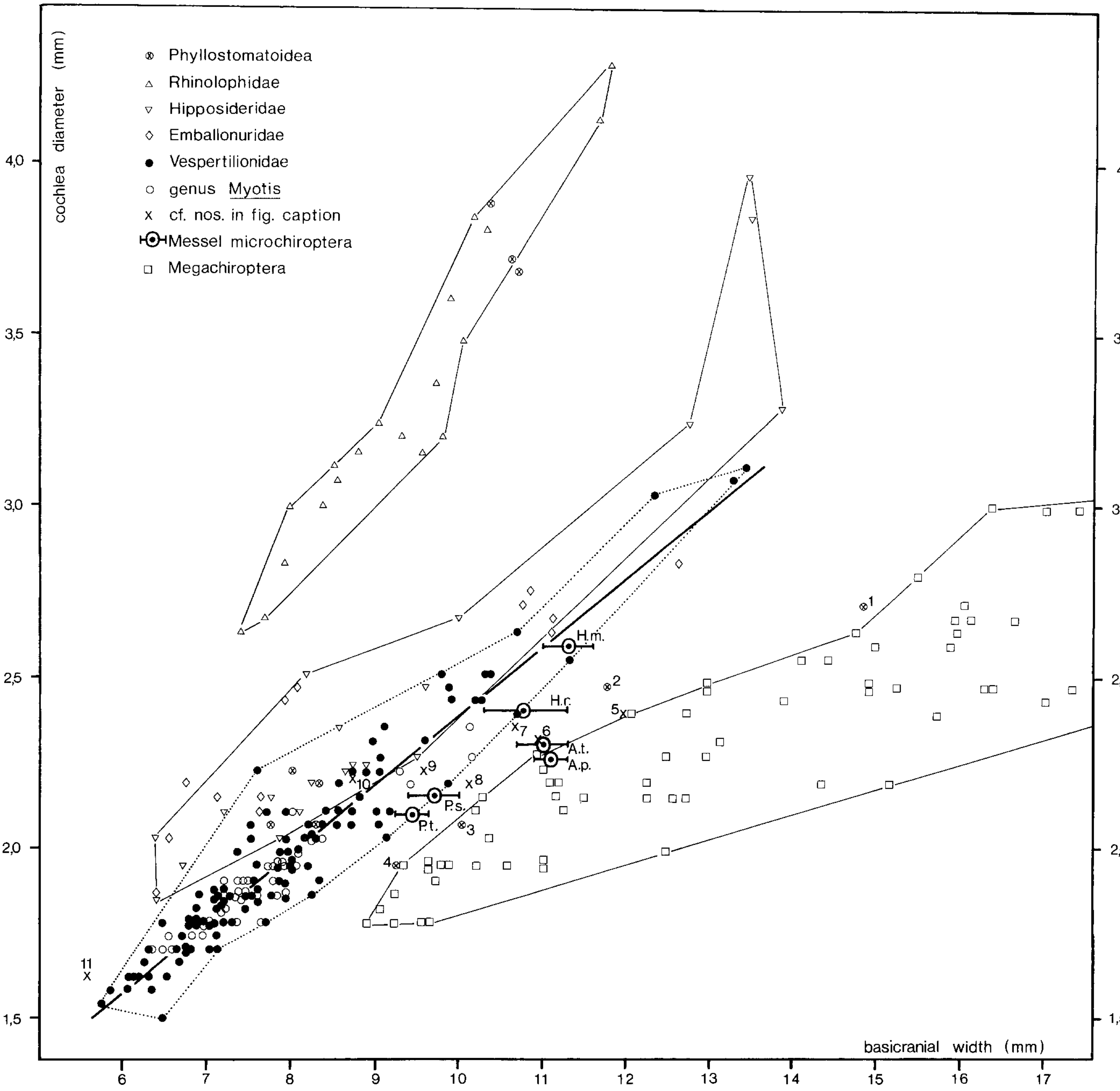

Fig. 4. Plot of the oblique diameter of the cochlea against the basicranial width of extant Chiroptera and Eocene microchiropterans from Messel. The regression line is calculated only for vespertilionids. It is significant that this line also divides the total range of variation for extant Chiroptera into two subequal parts. Note the position of Messel Microchiroptera, overlapping with vespertilionids and nonecholocating Megachiroptera. Abbreviations for Messel bats: *Hassianycteris messelensis* (*H.m.*, $n = 3$), *H. revilliodi* (*H.r.*, $n = 1$), *Palaeochiropteryx spiegeli* (*P.s.*, $n = 3$), *P. tupaiodon* (*P.t.*, $n = 4$), *Archaeonycteris trigonodon* (*A.t.*, $n = 2$), *A. pollex* [31] (*A.p.*, $n = 2$). Extant Microchiroptera indicated by Nos.: *1 Phyllostomus hastatus, 2 Trachops cirrhosus, 3 Leptonycteris nivalis, 4 Carollia perspicillata, 5 Megaderma lyra, 6 M. spasma, 7 Nycteris grandis, 8 Desmodus rotundus, 9 Rhinopoma microphyllum, 10 R. hardwickei, 11 Craseonycteris thonglongyai*

polygone with the lowest slope (Fig. 4) includes all genera of the Megachiroptera, which mainly rely on vision. Very few species emit short ultrasonic clicks to avoid obstacles but not for the echolocation of food sources [11, 16]. These exceptional cases of primitive echolocators among the genus *Rousettus* show no peculiarity of the cochlea size as compared to other flying foxes (e.g., *R. leschenaulti* with a cochlea width of 2.31 mm and a basicranial width of 13.12 mm and *R. aegyptiacus* with 2.59 and 14.98 mm, respectively).

2. Microchiroptera with a small cochlea: These bats, belonging to a wide systematic spectrum (Nos. 1–8, Fig. 4), are characterized by rather diverse foraging strategies. They are not typical aerial insect feeders. Various species feed on nectar, pollen, small vertebrates, or blood [17]. Their

orientation does not depend exclusively on echolocation, but also on thermoreception, passive acoustic location, vision, or olfactory sense. It is of interest that some of these bats have a relatively small cochlea, similar to Megachiroptera.

3. Microchiroptera with a medium-sized cochlea: This group includes all of the Vespertilionidae. The variation in the size of the inner ears for vespertilionid genera is closely centered along the regression line in Fig. 4 ($r = 0.957$, $n = 147$). This is also evident within the larges genus, *Myotis* (Fig. 4, open circles). The regression line was calculated only for vespertilionids and conveniently serves as a general reference for classifying bats, whether they have small or large inner ears. The overall variation in bats, including megabats, exhibits a symmetrical fan-like distribution pattern with respect to vespertilionids.

Vespertilionids are distributed worldwide, and this largest family among extant Microchiroptera can be considered as a typical representative of bats feeding on insects on the wing. There are, however, some exceptions, such as highly specialized fishing bats. The majority of vespertilionids echolocate with ultrasonic frequency-modulated (FM) sounds. Large Emballonuridae of the Old World, Rhinopomatidae, and Molossidae (molossids are not shown in Fig. 4) are also comparable in medium cochlea sizes to vespertilionids which results in a broad overlap of measurements (Fig. 4).

4. Microchiroptera with an enlarged cochlea: The polygone of Old World Hipposideridae shows generally larger inner ears than vespertilionids (regression line in Fig. 4) and overlaps only with relatively few vespertilionid taxa. Hipposiderids echolocate with short constant frequency sounds terminated by a brief frequency-modulated part (CF/FM sounds). It is noteworthy that the only species which was found to have an inner ear size below the mean (Fig. 4, regression line) is *Hipposideros speoris* Schneider 1800, a bat which occasionally stops using CF/FM sounds and echolocates with FM sounds [18]. New World emballonurids with a small cranial width also show a large cochlea (Fig. 4, open rhombus). This is also true for the tiny *Craseonycteris thonglongyai* Hill 1974 (Fig. 4, No. 11), which emits short CF/FM sounds.

5. Bats with an extremely enlarged cochlea: Rhinolophidae have the largest cochleae among extant bats. They are considered to be acoustically the most specialized extant bats for hunting within dense vegetation by their long CF/FM sounds, a constant Doppler compensation, many particularities in the cochlea's construction, and neurophysiological specializations [10, 19]. The New World *Pteronotus parnellii parnellii* (Gray 1843), (Mormoopidae, Phyllostomatoidea) is comparable to rhinolophids due to its consistent Doppler compensation, similar CF/FM sounds, and similar foraging behavior within dense vegetation. Although *Rhinolophus* and *Pteronotus* show considerable differences in the details of peripheral [20] and central processing [21] of the echolocation sounds, the morphometrical relations of the enlarged cochleae are identical. Figure 4 shows the data for *P. p. parnellii* at the upper margin of the rhinolophid polygone and the measurements for *P. p. rubiginosus* (Wagner 1843) and *P. p. fuscus* (J. A. Allen 1904) at the lower margin. Closely related mormoopid bats, e.g., *P. personatus* (Wagner 1843), *P. davyi* (Gray 1838), and *P. suapurensis* (J. A. Allen 1904) [22, 23], without the above-mentioned physiological and ecological specializations, are characterized by much smaller inner ears (Fig. 4, crossed circles within the hipposiderid polygone and slightly below). This again indicates a high degree of adaptability of the cochlea size to environmental constraints.

The fossil Microchiroptera from Messel (families Archaeonycterididae, Palaeochiropterigidae, Hassianycterididae [3]) represent a rather isolated group of insect-feeding bats, compared to the spectrum of acoustic specializations described so far. Typical extant insect-feeding bats in Fig. 4 range from vespertilionids to rhinolophids. They are obviously characterized by the larger size of the cochlea. *Hassianycteris* and *Palaeochiropteryx*, representing extinct families with various plesiomorphic characters, only overlap in cochlea width with the lower extreme of vespertilionids. The even more plesiomorphic family to which *Archaeonycteris* belongs even overlaps in cochlea width with Megachiroptera. This supports our idea of a continuous enlargement of the cochlea from Megachiroptera through Rhinolophidae which mirrors the functional significance of the acoustic sense.

The results shown in Fig. 4 are in contradiction to previous studies [4, 7, 13], which suggested a highly specialized echolocation system in Early Tertiary Microchiroptera ("Eochiroptera"). The consistent use of the total skull length in these studies must have masked functional correlations between the size of the cochlea and the peculiarities of echolocation. Obviously, this has caused the misleading statement that these functional correlations are not available [13]. The smaller cochlea of the Messel bats, on the other hand, provides evidence that the echolocation performance was less advanced. We suppose that this was one of the possible reasons for the extinction of these microchiropteran families ("Eochiroptera") during the Eocene and their replacement by modern families. The latter supposedly had evolved on southern continents and immigrated to Europe successively [24]. The flight apparatus was functionally already perfectly developed in Early Tertiary bats [3, 12]. This suggests that sophisticated echolocation was evolved only in modern families after full adaptation to aerial insectivory.

The data presented here diminish one argument for the diphyletic origin of bats. The size of the cochlea does not separate Micro- from Megachiroptera [6, 7]. Rather, it connects both groups, especially due to the extinct Microchiroptera described here. Although the acoustic organ is highly adaptable to environmental constraints, the morphology of the cochlea supports the view of monophyly of Chiroptera. The close relationship between Micro- and Megachiroptera is also shown by the convergence of polygones in Fig. 4. The functional meaning of this fan-like distribution pattern is not clear to us. Therefore, we undertook a comparison, using the same methods, of lipothyphlan insectivores, rodents, and primates. As far as we can determine from these current outgroup studies, all these taxa show no overlap with Microchiroptera but they do overlap with Megachiroptera. However, the variation in insectivores and rodents includes even much smaller sizes of the cochlea. *Sorex cinereus* Kerr 1792 (basicranial width 5.26 mm) is the smallest insectivore ($n = 83$), and *Mus minutoides* Smith 1834 (basicranial width 7.13 mm) is the smallest rodent ($n = 45$) considered. The width of the cochlea is 0.89 and 1.29 mm, respectively, and this is far below the measures for chiropterans (Fig. 4). Both species represent the minimum tip of their taxon polygone and clearly demonstrate the small size of the inner ears as compared the echolocating microchiropterans. Primates are generally much larger and are thus also difficult to include in our study. However, it is possible to include primates using the species forming the minimum tip of the polygone ($n = 27$), *Microcebus murinus* (J. F. Miller 1777). This very small primate has a basicranial width of 13.04 mm, a measurement shared whith many Micro- and Megachiroptera. The diameter of the cochlea is only 2.14 mm, which is comparable to the lower extreme of Megachiroptera. This again suggests that the corridor between Megachiroptera and vespertilionid bats occupied by Early Tertiary Microchiroptera characterizes a moderate advance in acoustic evolution.

The five stages of acoustic specialization derived from the size of the inner ears further suggest a polarity from echolocation with short multiharmonic sounds to echolocation with long CF/FM sounds. This agrees with basic features in earlier concepts for the evolution of echolocation [25, 26]. For the Eocene Messel bats we would propose: rather short, multiharmonic pulses for Archaeonycterididae, echolocation sounds within a frequency band of 30–90 kHz for Palaeochiropterigidae, and intense sound frequencies below 30 kHz for Hassianycterididae. However, this working hypothesis derived from extant Microchiroptera [9–12] needs more detailed comparison with extant species having small cochlea size.

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The Hydrazinium Ion Coordinating Trivalent Rhenium in $(NH_4)_{0.5}(H_2O)_{0.5}[Re_3Cl_{10}(N_2H_5)Cl_{0.5}(H_2O)_{0.5}] \cdot 3H_2O$

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An increasing number of ternary ammonium halides containing anions with the double-bonded triangular core of trivalent rhenium have recently been synthesized and structurally characterized. $(NH_4)_3[Re_3Cl_{12}]$ [1] and $NH_4[Re_3Br_{10}]$ [2] are prominent examples. During attempts to synthesize analogous hydrazinium halides, we have now obtained dark red single crystals of a compound in which the $(N_2H_5)^+$ cation enters the inner coordination sphere of the Re_3^{9+} core as a monodentate out of plane-terminal ligand. For mononuclear complexes such as $(N_2H_5)_2MCl_4(H_2O)_2$ with M = Pt, Pd [3], but not in $(N_2H_5)_2[PtI_6]$ [4], such a behavior had already been established by X-ray structure determination or suggested through vibrational spectroscopy.

$(NH_4)_{0.5}(H_2O)_{0.5}[Re_3Cl_{10}(N_2H_5)Cl_{0.5}(H_2O)_{0.5}] \cdot 3H_2O$ (*1*) is obtained from the hot-saturated hydrochloric acid solution of $ReCl_3$ to which hydrazinium hydrochloride, $N_2H_6Cl_2$,