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Auditory Features and Affinities of the Eocene Bats *Icaronycteris* and *Palaeochiropteryx* (Microchiroptera, incertae sedis)

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ABSTRACT

The earliest known bats are skeletons of *Icaronycteris index* from the early Eocene of western Wyoming and a few less well-represented species from the early Eocene of France. Also known are *Palaeochiropteryx tupaiodon* and several other species from the middle Eocene of western Germany. These taxa have been regarded as primitive forms, either “ancestral” to echolocating microchiropterans or “ancestral” to both micro- and megachiropterans. Details of basicranial structure suggest that these Eocene forms were, however, specialized echolocators comparable to Recent microchiropterans. Moreover, quantitative analysis reveals that the Eocene bats have a more pronounced expansion of the cochlea than many Recent microchiropteran species. There is clear justification for reference of *Icaronycteris* and *Palaeochiropteryx* to the Microchiroptera. Converse-

ly, there is no reason to recognize a “primitive-ancestral” group, Eochiroptera, that is excluded from Microchiroptera or Megachiroptera. The relationships of *Icaronycteris* and *Palaeochiropteryx* within Microchiroptera remain uncertain. Association of these taxa and several other Eocene forms within the microchiropteran superfamily Palaeochiropterygoidea fails to clarify these relationships. Palaeochiropterygoidea has not been defined by derived characters, and *Icaronycteris* and *Palaeochiropteryx* are more accurately designated Microchiroptera incertae sedis. Several primitive features shown by *Icaronycteris* suggest that the development of a sophisticated system for echolocation within Microchiroptera occurred earlier than certain modifications of the postcranial skeleton.

INTRODUCTION

The oldest bats in the fossil record are early Eocene in age. *Icaronycteris index* was de-

scribed by Jepsen (1966) from an exquisite, nearly complete skeleton found in the Green

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River Formation of Fossil Lake, Wyoming. Later found were two other skeletons of this genus (Novacek, 1985a). Also known from early Eocene faunas are *Icaronycteris? menui*, *Archaeonycteris brailloni*, and *Ageina tobieni*, all described by Russell et al. (1973) from the Mutigny and Avenay quarries in northeast Epernay, Marne, France. These latter three species are known only from partial dentitions.

The middle Eocene bat *Palaeochiropteryx tupaiodon* was first described by Revilliod (1917) from the famous "Grube Messel" near Darmstadt, Hessen, West Germany. A large number of skeletons (more than 54 individuals) of this bat have been recovered from the site (see Smith and Storch, 1981). Other bats from the Messel pit include *Archeonycteris trigonodon* Revilliod, 1917; "*Archaeonycteris*" *revilliodi* Russell and Sigé, 1970; *Hassianycteris messelensis* Smith and Storch, 1981; and *Hassianycteris magna* Smith and Storch, 1981. All of these forms are represented by nearly complete skeletons. In addition, several species of middle Eocene bats (*Cecilionycteris prisca* Heller, 1935; *Matthesia germanica* Sigé and Russell, 1980; and *Matthesia? insolita* Sigé and Russell, 1980) are known from the "Grube Cecilie," Geiseltal, near Halle a. S., East Germany.

The affinities of these fossil forms are problematic. Winge (1923, p. 304) regarded *Palaeochiropteryx* as essentially a primitive vespertilionid of the suborder Microchiroptera. In a recent review, Smith and Storch (1981) endorsed some of Winge's views, but did not refer *Palaeochiropteryx* to the Vespertilionidae. They grouped the above-cited species (except for *Hassianycteris* which they loosely allied with emballonurids or rhinolophids and recognized as Microchiroptera incertae sedis) within the Palaeochiropterygoidea Revilliod 1917, suborder Microchiroptera. From this group they removed *Archaeopteropus transiens* Meschinelli, 1903 (locality: Monteviele, northeast Italy, early Oligocene), and referred this species to the Megachiroptera. In this action they claimed that Palaeochiropterygoidea was "... less paraphyletic" (Smith and Storch, 1981, p. 163). Their grouping also endorses Jepsen's (1966) original description of *Icaronycteris*, wherein this taxon was assigned in the Microchiroptera.

The above classification is, however, in conflict with certain other studies. Segall (1971) argued that *Icaronycteris index* shared a more general basicranial structure with erinaceid insectivorans and megachiropterans, and lacked many of the morphological correlates with ultrasonic echolocation found in microchiropterans. Furthermore, Jepsen (1966, 1970) had also emphasized the large number of primitive traits in the skeleton of *Icaronycteris*. Accordingly, Van Valen (1979) recognized *Icaronycteris* and other palaeochiropterygoideans as members of the suborder Echioptera, a group either more remotely divergent than or "ancestral" to the Microchiroptera and Megachiroptera (Van Valen, 1979, fig. 1).

Study of described and undescribed material representing *Icaronycteris* contradicts Segall's (1971) description of the auditory system of this bat as "non-microchiropteran." *Icaronycteris* and *Palaeochiropteryx* both clearly show several features that correlate with the presence of ultrasonic echolocation in Recent microchiropterans. This point was the subject of a brief report (Novacek, 1985a). The purpose of this paper is to provide a more thorough description of these traits, better reproductions of the relevant illustrations, and a discussion on the systematic implications of the auditory morphology and other cranioskeletal features in these fossil bats.

ACKNOWLEDGMENTS

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Figures 1, 3, 7, 8, and 9 are stereophotos, radiographs, and drawings from G. L. Jepsen.

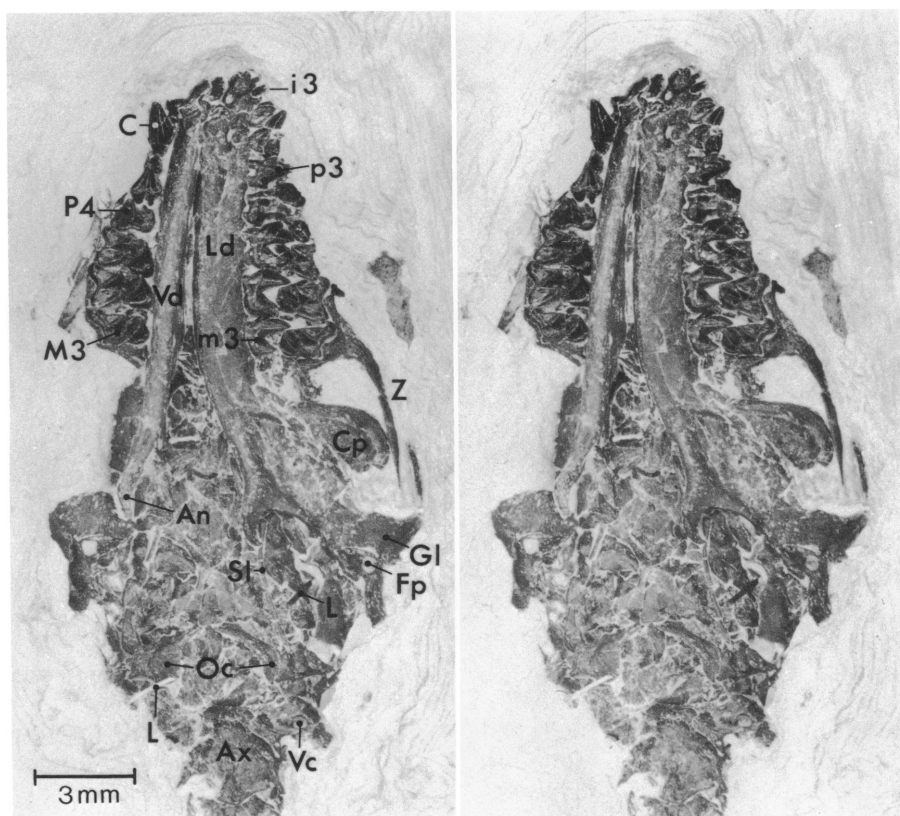


Fig. 1. Stereophotograph of ventral skull of *Icaronycteris index*; type, PU (Princeton University) 18150. Note this specimen is now deposited in the Yale Peabody Museum Collection. Figure from Jepsen (1970). Symbols are: An, angular process of dentary; Ax, axis; C, upper right canine; Cp, coronoid process of left dentary; Fp, postglenoid foramen; Gl, glenoid fossa; i3, third lower left incisor; L, locator bristles; Ld, labial surface of left dentary; M3, third upper right molar; m3, third lower left molar; Oc, occipital condyles; P4, fourth upper right premolar; p3, third lower left premolar; Sl, left stylohyal; Vc, vertebroarterial canal of atlas; Vd, ventral border of right dentary; Z, zygomatic arch.

sen's collection of figures of *Icaronycteris index*. These were loaned by D. Baird at Princeton and are now maintained, along with the type specimen, by the Yale Peabody Museum. Dr. H. Tuengerthal made the radiographs shown in figure 4; Chester Tarka prepared figure 2; Barbara Pilarzk made figure 5; and Lisa Lomauro prepared figures 6 and 10 as well as the final layouts for all figures. This paper was supported by the Frick Laboratory Endowment Fund in Vertebrate Paleontology at the American Museum of Natural History.

AUDITORY STRUCTURES

COCHLEA: Segall (1971) remarked that the type of *Icaronycteris index* (PU [Princeton

University] 18150) did not show marked enlargement of the cochlea, although he acknowledged that only a small part of this structure was preserved. He based his assessment on the observation that in *Icaronycteris* the basioccipital is rather broad and straight along its boundaries with the tympanic cavity and diverges only in its posterior region. Segall (1971) contrasted this condition, which is characteristic of many mammals including megachiropterans, with the typically narrow, strongly biconcave basioccipital of microchiropterans. Whereas some microchiropterans do show a very reduced, biconcave basioccipital (particularly natalids, some rhinolophids, and vespertilionids), in several other microchiropterans (many

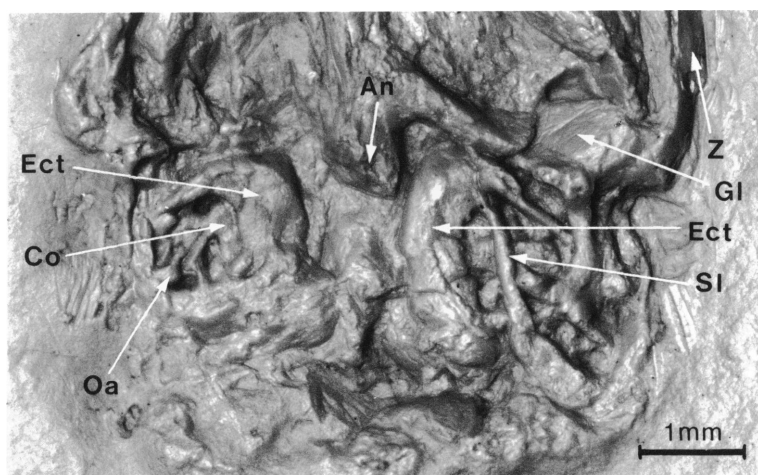


Fig. 2. Ventral view of basicranium and jaws of *Icaronycteris* cf. *index*; UW (University of Wyoming) 2244. Modified from Novacek (1985a). Symbols are: Co, cochlea; Ect, ectotympanic; Oa, orbicular apophysis of the malleus. For other symbols, see fig. 1.

phyllostomids, some mormoopids [e.g., *Pteronotus macleayii*] and some emballonurids) the basioccipital is nearly as broad between the cochleae as is typically found in megachiropterans. Nevertheless, the basioccipital is generally narrower and more strongly biconcave in microchiropterans than in megachiropterans. This condition is not only a function of the large cochlea, but is also due to the presence of a distinct basicochlear fissure medial to the cochlea, an opening less developed in megachiropterans, and altogether absent in most mammal groups (Novacek, 1980). Unfortunately the condition in *Icaronycteris* for the basioccipital is very difficult to determine. Given the distortion and damage to this element, which is even more severe in the type, PU 18150 (fig. 1) than in UW (University of Wyoming) 2244 (fig. 2), it is difficult to appreciate the basis for Segall's observation on the original specimen. However, a radiograph of the type specimen (fig. 3) is more revealing. It suggests, contrary to Segall's (1971) assessment, that *Icaronycteris* does have a distinct biconcave basioccipital similar to that in many microchiropterans.

The problem remains to establish the degree of the development of the cochlea in *Icaronycteris*, for this structure is clearly much

larger in modern microchiropterans than in megachiropterans (Pye, 1966; Henson, 1970; Novacek, 1980, 1985a). In *Icaronycteris* only a rough estimate of cochlear dimensions can be made by measuring distances between auditory structures adjacent to the cochlea. For example, the location of the medial border of the ectotympanic annulus (slightly shifted during preservation to lie in a more horizontal position) gives an indication of the medial edge of the promontorium cochlea. The recessed area (the facial canal and the epitympanic recess) below the malleus give some indication of the lateral edge of the promontorium cochlea (figs. 1–3). These relationships can be appreciated in the better preserved basicrania of *Palaeochiropteryx* (fig. 4).

The maximum width of the cochlea is a useful parameter because it is a function of the expansion of the basal turn (fig. 5B), the region of the cochlea particularly sensitive to high-frequency vibrations in adult mammals (Dallos, 1973; Henson, 1970; Bruns, 1979; Bruns et al., 1983–84; Harris and Dallos, 1984). The large cochlea in microchiropterans is dominated by the basal turn which lends to the structure the appearance of a snail shell strongly tapered toward its apex

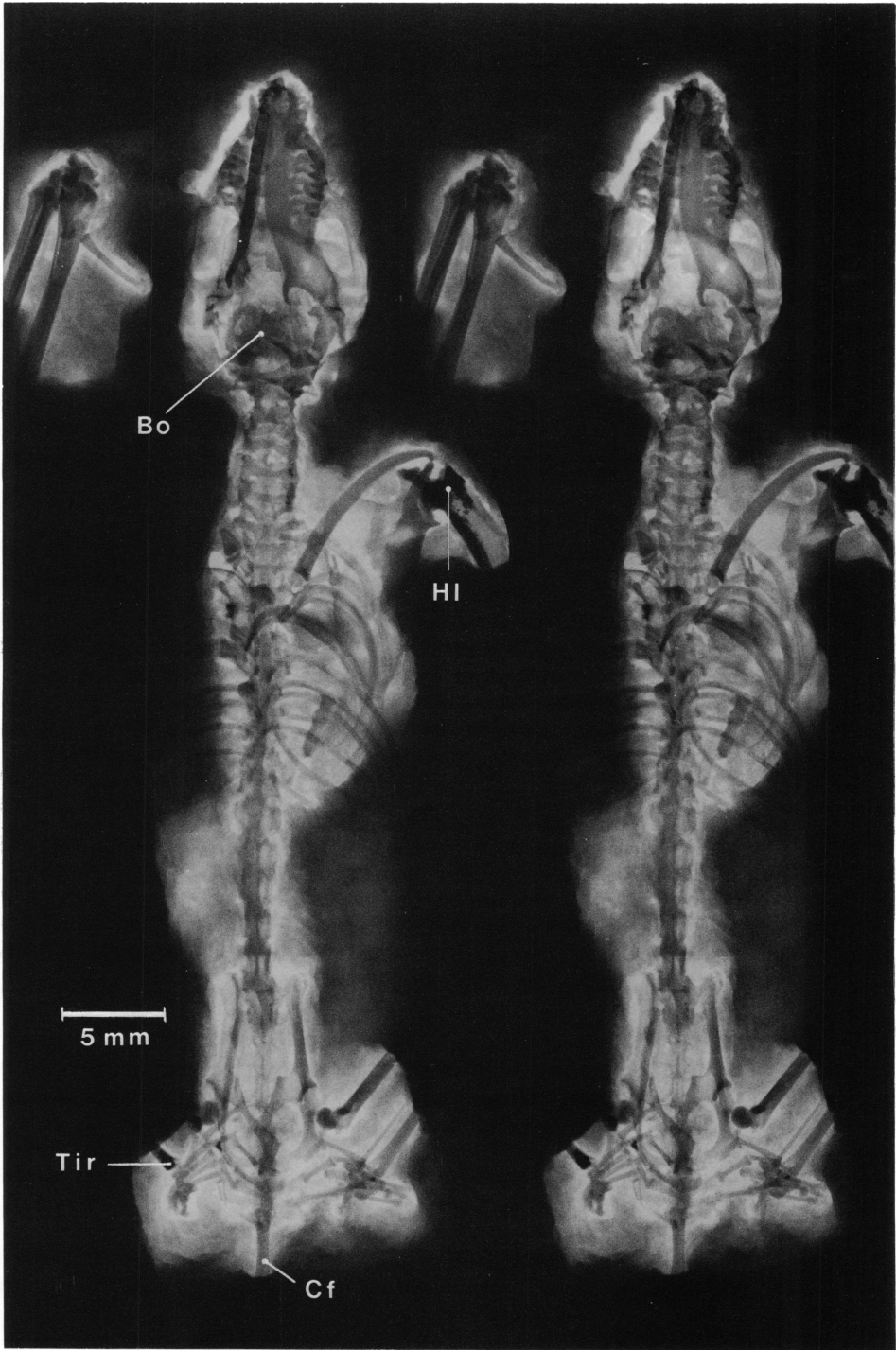


Fig. 3. Stereophoto-radiographs of ventral skeleton of *Icaronycteris index*; PU 18150. From Jepsen (1970). Symbols are: Bo, basioccipital; Cf, fourth caudal vertebra; HI, left humerus; Tir, right tibia.

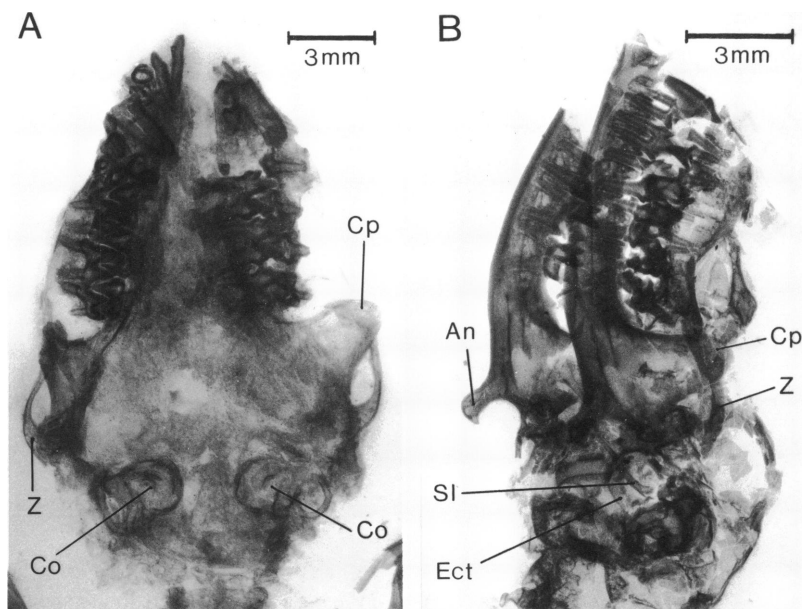


Fig. 4. *Palaeochiropteryx tupaiodon*. Positive prints of radiographs of (A) dorsoventral view of SMF-ME (Senckenberg Naturmuseum und Forschungsinstitut) 788-B and (B) lateral view of SMF-ME 1127. Modified from Novacek (1985a). For symbols see figs. 1 and 2.

(fig. 5B). By contrast, most other mammals have cochleae that are not so strongly tapered, due to the smaller basal turn and a significantly smaller width relative to other skull elements.

The fact that maximum cochlear width can only be estimated in *Icaronycteris* is irrelevant to broad-based comparisons among both megachiropteran and microchiropteran species. Figure 6, a plot of maximum cochlear width against skull length for 96 bat species, clearly shows that despite a very liberal range of error in measurement, the estimated allometric width of the cochlea in *Icaronycteris* is well within the polygon defining microchiropterans. In support of the above-cited observations, the cochlear width is relatively much greater in microchiropterans than in megachiropterans. Note that the polygons for the two suborders do not overlap. Also, the cochlear width in microchiropterans shows a weaker correlation and more positive allometry with skull length ($r = 0.64$, slope = 0.8) than in the case of megachiropterans ($r = 0.92$, slope = 0.30). These parameters in microchiropterans are highly unusual, whereas

megachiropterans show allometric relationships typical of many groups of small to medium-size mammals, a contrast with interesting implications (Graybeal and Novacek, in prep.).

Palaeochiropteryx is more accessible to quantitative analysis. Radiographs of specimens from the Senckenberg Museum collections show beautifully preserved cochlea (fig. 4A). These readily yield large cochlear widths that lie well within the microchiropteran polygon (fig. 6). Note that both *Icaronycteris* (by estimate) and *Palaeochiropteryx* show relatively more expanded cochlea than many microchiropteran species (explicit treatment of cochlear size variation within the bat suborders is provided by Graybeal and Novacek, in prep.).

Although cochlear size might seem a direct function of the degree of emphasis of echolocation, the relationship is by no means clear-cut. This is due to the problem of quantifying in a meaningful way the degree to which a species has refined echolocation pulses. It has been noted that the cochlea, especially the basal turn, seems best developed in species

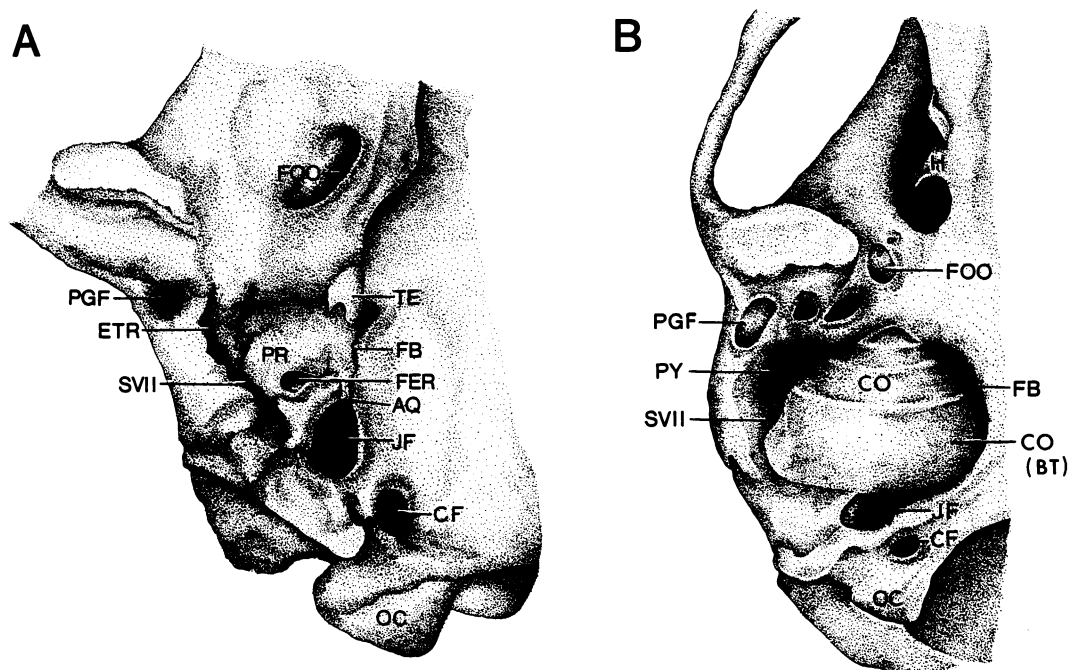


Fig. 5. Right basicrania of (A) *Pteropus policephalus*, SDSU (San Diego State University) 1152 and (B) *Rhinolophus* sp., SDSU 1215. Both specimens with bulla and ectotympanic removed. Not to scale. Symbols are: AQ, aqueductus cochleae; CF, condyloid foramen; CO, cochlea; CO(BT) basal turn of cochlea; ETR, epitympanic recess; FB, basicochlear fissure; FER, fenestra rotundum; FOO, foramen ovale; H, hamular process; JF, jugular foramen; OC, occipital condyle; PGF, postglenoid foramen; PR, promontorium cochlea; PY, pyriform fenestra; SVII, sulcus for facial (VII) nerve; TE, flange for eustachian tube.

(e.g., *Rhinolophus hipposideros*, *Pteronotus parnellii*) that emit a long, constant frequency (CF), pure tone terminated by a brief "flick" of an FM (frequency modulated) sweep (Henson, 1970). These long CF-short FM bats have a region of the basilar membrane within the basal turn of the cochlear labyrinth (an "acoustic fovea") that is highly sensitive to the long pure tone of the bat's vocalization (Bruns, 1979). Unfortunately, such refined analyses do not pertain to most species. Hence, it is virtually impossible to attribute, through analogy with living species, any particular "adaptive mode" to cochlear development in *Icaronycteris* or *Palaeochiropteryx*. There is, however, no indication that these fossil bats were any more conservative in refinement of the echolocation system than are most living species of Microchiroptera. The apparent expansion of the cochlea in *Icaronycteris* and *Palaeochiropteryx* is important in suggesting a close relationship be-

tween these taxa and the echolocating microchiropterans.

MALLEUS: The ear ossicles are not clearly preserved in any of the specimens of *Palaeochiropteryx* that I have studied. Likewise, the type (PU 1850) of *Icaronycteris* fails to show evidence of these elements. A partial malleus is, however, apparently preserved in the University of Wyoming specimen of *Icaronycteris* (fig. 2) and this bone shows at least one feature of interest. The orbicular apophysis at the base of the manubrium of the malleus is unusually large, a condition common to microchiropterans, many small insectivorous, such as soricids, and many rodents (Fleischer, 1978, p. 73). By contrast, this process is weakly developed in megachiropterans and most other mammals.

Because of the widespread occurrence of this structure it is difficult to attribute a particular mode of auditory sensitivity to the presence of the orbicular apophysis. Never-

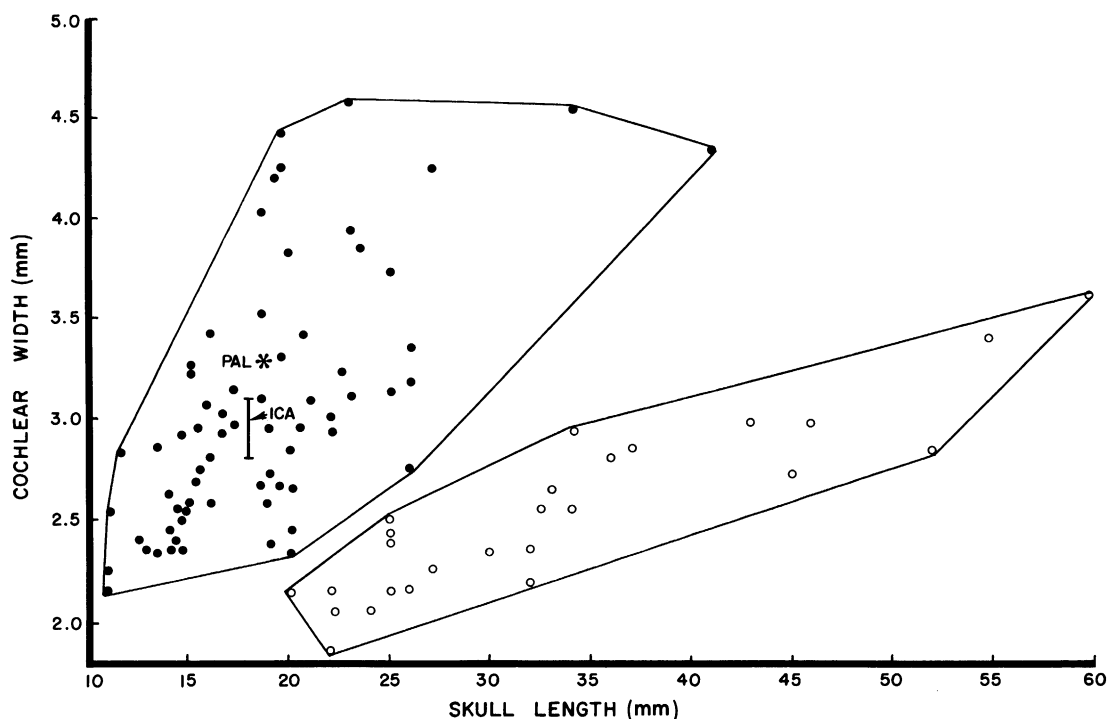


Fig. 6. Plot of maximum width of cochlea (ordinate) against skull length (abscissa) for 96 species of Microchiroptera (●), Megachiroptera (○), *Palaeochiropteryx* (*), and *Icaronycteris* (vertical line represents range of error in estimate of maximum cochlear width). From Novacek (1985a). Points represent 17 of 19 Recent bat families (two monotypic families of microchiropterans, the Myzopodidae, and Craseonycteridae, are omitted). Convex polygons define the outer boundaries of values for each of the two suborders. Cochlear width has a weaker correlation and more positive allometry with skull length in microchiropterans ($r = 0.64$, slope = 0.80) than in megachiropterans ($r = 0.92$, slope = 0.30).

theless, the presence of this feature in *Icaronycteris* corroborates the argument that the auditory system of this fossil bat shared the specialized auditory condition seen in microchiropterans. Moreover, it is of interest that the orbicular apophysis is particularly prominent in groups (e.g., soricids, certain rodents, see Fleischer, 1973, 1978) that display some, albeit less refined, mode of high-frequency echolocation (Fenton, 1984).

Taking these facts into account, Fleischer (1978) hypothesized that the malleus-incus complex in microchiropterans represents a strong departure from the primitive condition. In the latter, the center of mass lies near the axis of rotation of the ossicle system. In the "microtype" exhibited by microchiropterans and the above noted groups, the center of mass is shifted away from this axis, largely

because of the relatively enormous orbicular apophysis. Fleischer (1978, p. 33) further argues "... thus starting from the ancestral type, two radically different lines of evolutionary adaptation evidently occurred: in one, the center of mass is shifted toward and finally into the rotational axis, resulting in the freely mobile type. In the other, the center of mass is shifted further away from the axis by the development of the orbicular apophysis, resulting in the microtype. That the microtype is a highly functional ear is easily apparent because it is found in bats, which have a sophisticated sonar system."

This explanation encounters difficulty, as the large orbicular apophysis acts to increase the moment of inertia of the system, lowering its natural resonant frequency. Hence, the apophysis may seem an odd feature in ani-

mals particularly sensitive to ultra high-frequency sounds. Addressing this apparent contradiction, Fleischer (1978, p. 34) considered echolocating bats with the following argument:

"But these animals also have great problems perceiving low frequencies since their middle ear is tuned to extremely high frequencies. Predominately, this is the result of the minute size and the rigid fusion between the gonial and tympanic. Without the orbicular apophysis, the natural frequency of the malleus-incus complex might simply be too high, even for the bats. These relations hold true for the other mammals with a microtype ear as well, because the middle ear in bats does not really differ from theirs."

Fleischer's arguments seem reasonable, though a bit ad hoc. I leave it to others to scrutinize their validity with experimentation. In the context of this study, the presence of the large orbicular apophysis (1) is shared by *Icaronycteris* and microchiropterans, (2) is probably a derived mammalian feature, and (3) seems to be a consistent component in forms that exhibit some mode of ultrasonic audition.

STYLOHYAL: The stylohyal element is preserved in both the Princeton University (figs. 1, 3) and University of Wyoming (fig. 2) specimens of *Icaronycteris* and in at least a few specimens (fig. 4B) of *Palaeochiropteryx*. This observation by itself is hardly noteworthy. The stylohyal, a component of the laryngeal-hyoid apparatus, is common in mammals, including megachiropterans, and is clearly a primitive feature. Nevertheless, in megachiropterans, as in many mammals, the stylohyal is usually a weak, filamentous structure easily lost from macerated skulls (Klaauw, 1931). That this element does remain in most macerated skulls of microchiropterans is due to its more robust development and its strong attachment to other elements of the hyoid-laryngeal apparatus.

As is shown in the excellent study by Griffiths (1983), the stylohyal is the site of attachment for muscles that constrict the pharynx and brace the hyoid apparatus. The hyoid stabilizers allow the extrinsic laryngeal muscles to pull from the hyoid and move the larynx forward, an action that precedes the

emission of a series of high-frequency pulses during vocalization (Suthers and Fattu, 1973). The well-developed stylohyal is then an intrinsic component of the specialized laryngeal-hyoid system in echolocating bats. Its similarly strong development in *Icaronycteris* and *Palaeochiropteryx* offers additional support for the argument that these taxa as well were accomplished echolocators. It should be noted that certain other mammal groups (e.g., canid and felid carnivores) have a well-developed stylohyal and hyoid apparatus, but these conditions seem to relate to the rapid tongue movement (through action of the stylohyoideus muscle) associated with feeding. Presumably, this specialization was acquired independently of that in microchiropterans.

In reviewing this manuscript, T. A. Griffiths mentioned his own observations of features of the hyoid apparatus in *Icaronycteris* (based on Jepsen's 1970 stereophoto) that corroborate those given above. In addition to the stylohyal, he noted the robust proportions of other elements of the hyoid apparatus. He also pointed out that the stylohyal's posterolateral end is expanded into a paddle-shaped moiety, a feature found throughout microchiropterans but not in megachiropterans (Sprague, 1943). I thank Dr. Griffiths for sharing this unpublished information with me.

OTHER BASICRANIAL FEATURES: In his description of the basicranium of *Icaronycteris*, Segall (1971) mentioned a few features in which this taxon resembled either microchiropterans or megachiropterans. These features are not easily connected with a particular function of the auditory system, but are of phylogenetic interest.

Based on PU 1850, Segall (1971) observed that the ectotympanic in *Icaronycteris* was annular (a complete ring with a dorsal malleolar plate) rather than horseshoe-shaped (open dorsally without a well-developed malleolar plate). However, the annular morphology of this element, though probable, is not absolutely certain in either the Princeton specimen (figs. 1, 3) or the University of Wyoming specimen (fig. 2). Moreover, it is not clear in specimens of *Palaeochiropteryx* that I have studied whether the ectotympanic is

annular or horseshoe-shaped. This ambiguity is unfortunate because the "horseshoe-shaped" ectotympanic is characteristic of megachiropterans, the annular form, of microchiropterans (Segall, 1971). It is generally argued that the dorsally open ectotympanic is the primitive mammalian condition (Klaauw, 1931; Segall, 1971; Archibald, 1977; Novacek, 1980).

Perhaps another aspect of the ectotympanic is of greater interest. In microchiropterans this element is anteromedially expanded to form a large tapered styliiform process whose dorsal surface is distinctly concave. Thus, the styliiform process forms a cradle for both the auditory (eustachian) tube and the tensor tympani muscle (Staněk, 1933; Henson, 1970). The process is present in the ectotympanics of many other mammals, including some megachiropterans, but does not approach the expanded form seen in microchiropterans, where the tensor tympani muscles are unusually large (Staněk, 1933; Henson, 1961, 1970; Novacek, 1980). In *Icaronycteris* the styliiform process is not clearly preserved, but the ectotympanic does show marked expansion in its anteromedial region (figs. 1–3). This suggests that the apex of this process may have been present but was damaged during fossilization. More definite identification is not possible. Specimens of *Palaeochiropteryx* do not clearly show such details of the ectotympanic.

Segall (1971) noted several basicranial features of *Icaronycteris* which resembled echinosoricine hedgehogs and megachiropterans in their generalized, or primitive, status. These are: (1) the more oblique orientation of the anterior edge of the glenoid fossa (in microchiropterans this border is usually oriented transversely or even recedes medially), (2) the relatively more lateral position of the postglenoid foramen with respect to the anterolateral corner of the tympanic cavity, and (3) the well-developed horizontal lamella of the superior external meatus. These features in *Icaronycteris* are not easily recognized. The anterior edge of the glenoid region is not so oblique in the University of Wyoming specimen (fig. 2). In fact, the orientation of this border seems more transverse (and more microchiropteran-like) in the type specimen than Segall (1971) suggested. This edge is ante-

riorly directed only in its most medial region (fig. 1). By contrast, megachiropterans and insectivorans show an oblique orientation for most of the length of this border (Segall, 1971, fig. 1G, H). Moreover, the oblique medial portion of this border in *Icaronycteris* illustrated by Segall (1971, fig. 1J₁) may simply be an artifact, due to the compression of the alisphenoid against the anterior edge of the glenoid (fig. 1). In *Palaeochiropteryx* the morphology in this region is not clearly preserved (fig. 4).

The position of the postglenoid foramen relative to the tympanic cavity in *Icaronycteris* is also problematic. The type seems to preserve the relationship Segall (1971, fig. 1J₁) reconstructed. However, comparison of this specimen (figs. 1, 3) with UW 2244 (fig. 2) shows that the tympanic region has been shifted somewhat medially in the type, as there is clearly a gap between this area and the postglenoid region. Reconstruction would yield a condition where the postglenoid foramen is like that in microchiropterans in being situated adjacent to the anterolateral corner of the tympanic cavity.

Segall's (1971) description of the lamellar suprameatal bridge in *Icaronycteris* seems correct. However, this lamella does not appear so horizontal as it does dorsoventral in its orientation (note the perspective shown by the stereophotograph in fig. 1). The large superior meatal lamella in this form is probably, as Segall (1971) suggested, a more conservative condition typically modified to a very narrow bridge in most microchiropterans. I have not been able to identify the morphology of this region in specimens of *Palaeochiropteryx* available to me.

Finally, it should be noted that both *Icaronycteris* (figs. 1–3) and *Palaeochiropteryx* (fig. 4) resemble microchiropterans in having a very well-defined, hooklike angular process. As Segall (1971) observed, the angular process is much less spurlike in megachiropterans. The significance of this difference is moot, as the hooklike angular process is found in many other mammals, including lipotyphlan insectivorans. However, it seems probable that the angular process in megachiropterans, which is of a form common in both eutherians and metatherians, represents the more conservative condition.

AFFINITIES OF *ICARONYCTERIS* AND *PALAEOCHIROPTERYX*

In the introduction of this paper I outlined some of the contradictory views regarding the affinities of earliest bats. Two hypotheses seem likely: either these bats are bona fide microchiropterans or they are members of a group that if not "ancestral," is more remotely divergent than the modern bat suborders. (The third possibility, that the fossil taxa are most closely related to megachiropterans is unpopular and unlikely, but will be given its due in the analysis to follow.)

In this context, *Icaronycteris* poses the most interesting problem. The genus was described and illustrated in some detail by Jepsen (1966, 1970), who showed that it retained a number of very primitive features either modified or poorly documented in *Palaeochiropteryx*. It stands to reason then that the latter will certainly fall in with the Microchiroptera if *Icaronycteris* does. The converse may not be true, because *Palaeochiropteryx* appears to have a slightly "more derived skeleton" than *Icaronycteris*—cf. Revilliod (1917) and Richter and Storch (1980) with Jepsen (1966, 1970).

Jepsen (1966, 1970) noted the following characters in which *Icaronycteris* would be regarded as "primitive" or "generalized" or as lacking specializations seen in other bats: (1) large number of teeth, (2) "insectivorous" shapes of teeth, (3) uncoalesced ribs, vertebrae, and sternal elements, (4) shapes of centra and neural arches on cervical vertebrae, (5) lack of a prominent keel on the mesosternum, (6) long tail, (7) shape of the scapula, (8) relatively short radius, (9) index claw (i.e., clawed terminal phalanx on digit 2 of wing), (10) complete phalangeal formula, (11) head and neck of the femur at angle to shaft, (12) big toe (digit 1) shorter than others, (13) no calcar, and (14) low aspect ratio of wings (estimated to have been between 2.75 and 2.84).

It is clear that several of these features, though primitive, are not confined to *Icaronycteris*. Many bats have the dental count of 38 (character 1, above) seen in *Icaronycteris* (Natalidae, Thyropteridae, Myzopodidae, and Vespertilionidae including the nearly worldwide genus *Myotis*—see Vaughan, 1970a). The "insectivorous" (i.e., dilambdodont)

form of the cheek teeth (2 above) in *Icaronycteris* is either a primitive bat trait overwhelmingly prevalent in Microchiroptera or a derived trait that distinguishes this suborder (see below). The long tail (6) seen in *Icaronycteris* is present in a few other groups (e.g., vespertilionids, natalids, rhinopomatids). The cervical vertebrae (4) may actually indicate a special feature shared with microchiropterans (see below). The index claw is undoubtedly a primitive bat character retained in most megachiropterans but lost in all living microchiropterans and *Palaeochiropteryx*. Although in most living bats the digits of the hindfoot are of relatively equal length, digit 1 (12) is relatively shorter in various species of pteropodids, emballonurids, and vespertilionids, as well as in *Icaronycteris*. Finally, the calcar, while present in most groups, is also absent (13) in most Phyllostomidae and some Pteropodidae and in Rhinopomatidae and Craseonycteridae (Hill, 1974).

Remaining then are a few traits which potentially document a more primitive condition in *Icaronycteris* than in Recent bat suborders. These are:

Uncoalesced ribs, vertebrae, and sternal elements (fig. 7): In many bats, particularly in older individuals, there is a tendency toward ankylosed fusion of the elements of the costal-sternal thoracic region (Walton and Walton, 1970). Variation in this condition is not well documented, but the sternal elements in modern bats are, according to Vaughan (1970a, p. 110), "invariably fused." Hence, *Icaronycteris* appears to retain a more primitive condition for the sternal elements than in living bat suborders. It should be added that the degree of fusion of these elements is very difficult to determine in the Princeton specimen. There also remains the possibility that this specimen represents a juvenile individual where fusion of bony elements is incipient.

Lack of a prominent keel on the mesosternum (fig. 7): The mesosternal keel is well developed in many bats (Vaughan, 1970a; Walton and Walton, 1970) and, superficially, *Icaronycteris* appears to be more conservative in lacking this feature. However, the mesosternum in *Icaronycteris* hardly differs from those of several species (*Taphozous peli*, *Tadarida media*, *Myotis lucifugus*, *Rousettus*

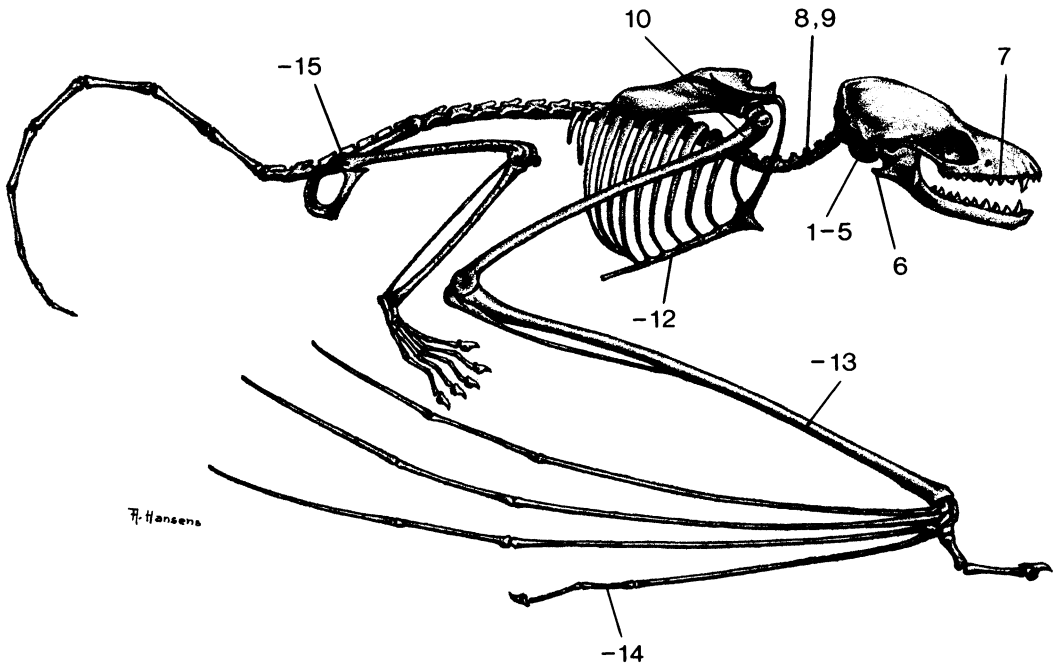


Fig. 7. Lateral view of right side of skeleton of *Icaronycteris index* (PU 18150) $\times 1.4$. Reconstruction originally published as figure 2 in Jepsen, 1970. Numbers correspond to characters listed and explained in figure 10. A minus sign indicates that the corresponding character is lacking in *Icaronycteris* but is present in the Recent Mega- and Microchiroptera.

aegyptiacus, and others—see Walton and Walton, 1968, 1970; Vaughan, 1970a; Norberg, 1972; Kingdon, 1974) where the median ridge of the mesosternum fails to develop into a prominent keel. *Icaronycteris*, like other bats, has a well-developed ventral keel on the manubrium, a feature which varies considerably in form and size within the order (Vaughan, 1970a).

Shape of the scapula (fig. 7): Modern bats are distinctive in having a scapula with a much larger infrapinnous fossa than suprapinnous fossa. The infrapinnous fossa is the site of attachment for important flight muscles (Vaughan, 1970a, p. 128). In *Icaronycteris* the suprapinnous fossa is relatively larger, but hardly more so than in pteropodids (cf. Jepsen, 1970, figs. 1, 9; Vaughan, 1970a, fig. 22a). It is therefore highly uncertain that the scapula has a more derived form in all living chiropterans relative to that in *Icaronycteris*.

Relatively short radius (fig. 7): The short length of this element in relation to total wing span, length of the humerus, and length of

the metacarpals III–V seems to differentiate *Icaronycteris* from most living species, although quantitative data for this comparison have not been reviewed. Based on this and lengths of other elements, the wings of *Icaronycteris* were thought by Jepsen (1970) to be very short and broad with a low aspect ratio, although his estimate of wing proportions seems doubtful (see below).

Complete phalangeal formula (fig. 7): In *Icaronycteris* the terminal phalanges of digits III, IV, and V in the wing are nubbins of small bones, and there is even a tiny ossified clawlet on the terminal phalanx of digit V (Jepsen 1970, fig. 14). In *Rhinopoma* the distal phalanges of digits II, III, IV, and V carry small claw-shaped cartilages that fail to ossify in the adult (Wassif and Madkour, 1963). The usual number of ossified phalanges in digits III, IV, and V is only two in Megachiroptera, Rhinopomatidae, Emballonuridae, Noctilionidae, Nycteridae, Megadermatidae, Rhinolophidae, Hipposideridae, Natalidae, and Furipteridae (Walton and Walton, 1970).

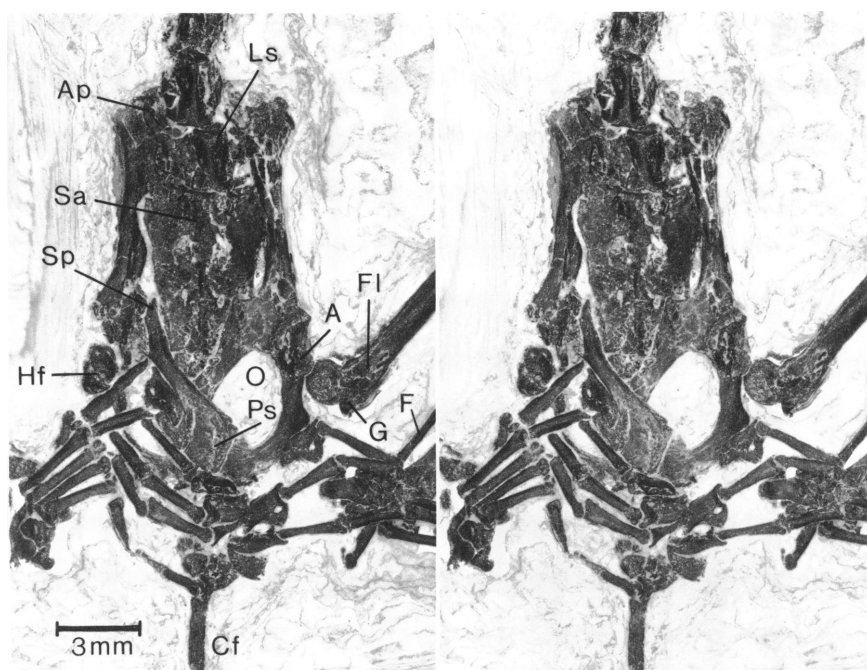


Fig. 8. Stereophotographs of ventral view of pelvic region of *Icaronycteris index* PU 18150. From Jepsen (1970). Symbols are: A, acetabulum; Ap, anterolateral process of seventh lumbar vertebra; Cf, fourth caudal vertebra; F, fibula; Fl, lesser trochanter of femur; G, greater trochanter of femur; Hf, head of femur; Ls, seventh lumbar vertebra; O, obturator foramen; Ps, pubic symphysis; Sa, sacrum; Sp, spine of pubis.

Three bony phalanges are retained, however, in at least the third digit of the Phyllostomidae, Thyropteridae, Myzopodidae, Mormoopidae, and Mystacinidae (Hill, 1974). Miller (1907) presented evidence that the third phalanx of digit III might be represented by cartilage in those microchiropterans that have only two phalanges. The homology of these cartilaginous elements with the terminal phalanges has been questioned (see discussion in Walton and Walton, 1970), although it is generally accepted that in bats the distal phalanx of the third and fourth digits, if present, is always cartilaginous. Thus, the significance of the condition in *Icaronycteris* is that the complete phalangeal formula of the wing (2-3-3-3-3) is represented entirely by ossified elements. By contrast, modern bats either variously reduce this phalangeal formula in one or more of digits II-V or have only cartilaginous terminal phalanges. The complete phalangeal formula (2-3-3-3-3) of the pes in *Icaronycteris* is also found

in most modern bat groups except Hipposideridae, Thyropteridae, and Myzopodidae (Miller, 1907).

Head and neck of femur at angle to the shaft (fig. 8): The head of the femur is offset craniomedial to the shaft in *Icaronycteris* but not to the extent seen in terrestrial mammals. In this trait, *Icaronycteris* is clearly more conservative than living mega- and microchiropterans, where the head is nearly aligned with the shaft and the neck is very short or absent (Vaughan, 1970; Walton and Walton, 1970).

Low aspect ratio: The relatively short length of the radius indicates that *Icaronycteris* had rather short and broad wings. However, Jepsen's (1970) estimate of aspect ratio (the ratio of wing length over wing width) of between 2.75 and 2.84 seems extraordinarily low, as these ratios generally range between 5.6 and 10 (Vaughan, 1970b; Norberg, 1972). The standard formula of calculating aspect ratios is wing span²/wing area, due to the irregular

shape of the wing. A precise calculation is virtually impossible in *Icaronycteris*, although from reconstruction of approximate wing shape (Jepsen, 1966, cover illustration) and measurements of limb elements (Jepsen, 1970), I estimate an approximate aspect ratio of 5.0. Hence, the aspect ratio for the wings in *Icaronycteris* may have been low but not significantly lower than in certain living bats (e.g., *Artibeus*, *Rousettus*, see Vaughan, 1970b; Norberg, 1972).

These considerations shorten the list of primitive features found in *Icaronycteris* that are lost or modified in the Recent mega- and microchiropterans. I would only recognize four such features: the unfused sternal elements, the relatively short radius (although this character has not been quantitatively assessed), the complete phalangeal formula for the wing (2-3-3-3-3) represented entirely by ossified elements, and the canted head and neck of the femur.

By themselves, then, these features suggest that all modern bats form a group that excludes *Icaronycteris* in fusion of the sternal elements, lengthening of the radius, loss of phalanges or retention of (embryonic) cartilaginous phalanges in some digits of the wing, and reduction of the femoral neck and alignment of the head near the axis of the shaft.

Contradicting this argument are a number of specializations shared by *Icaronycteris* and microchiropterans, but lacking in megachiropterans. These include the basicranial features noted above, namely (1) enlarged cochlea, (2) the biconcave basioccipital ?, (3) the large orbicular apophysis of the malleus, (4) the well-developed, ossified stylohyal, (5) the annular ectotympanic ?, (6) the hooklike angular process of the mandible, and (7) the development of ultrasonic echolocation that is inferred from the presence of features 1, 2, 3, and 4.

In addition to these, *Icaronycteris* shares with microchiropterans several other potential synapomorphies.

Dilambdodont upper molars (fig. 1): The dilambdodont crown pattern—wherein the labial cusps are linked by a high, sharp W-shaped ectoloph—is probably a specialization that evolved several times within Eutheria. Dilambdodonty is found in soricid and

talpid insectivorans, didelphid marsupials, and a variety of other extant and fossil groups. The origin of the peculiar molar crown pattern in megachiropterans is highly uncertain. There is no evidence for or against the supposition that this pattern derived from dilambdodonty (Koopman and MacIntyre, 1980). Within Microchiroptera, however, the highly specialized molars of desmodontines and nectar-feeding bats are probably a derivative of the dilambdodont condition (Phillips, 1971; Griffiths, 1985). The latter construction, particularly well suited for mastication of hard insect parts, is undoubtedly the primitive crown morphology for microchiropterans, yet it cannot be taken as the primitive state for all bats and the morphotypical condition for the order remains ambiguous. An additional feature shared by *Icaronycteris* and microchiropterans is nyctalodonty (where the hypoconulid of the lower molars is situated far lingual and a well-defined postcristid runs to the hypoconulid—see Menu and Sigé, 1971). It is not clear that nyctalodonty is primitive for Microchiroptera as it is absent in some bats (Van Valen, 1979).

Interlocking accessory processes on the medial-ventral section of cervical vertebrae: These processes are developed on cervical vertebrae 2 and 3 in *Icaronycteris*, but in some living microchiropterans they are found on vertebrae 2–5. These structures appear to confer stability to the vertebral column during strong backward flexion of the neck. As a result, microchiropterans are able to thrust their heads down and backwards (away from the chest) during roosting so that the head is actually right side up. Such modifications in structure and behavior are not shared by megachiropterans (see discussion in Jepsen, 1970). Apparently, *Icaronycteris* shared the unusual cervical condition with living microchiropterans.

Narrow neural arches on cervical vertebrae separated by gaps equal to or greater than the width of the arches: This modification also promotes extreme flexion of the neck. In megachiropterans the cervical neural arches are of a more general design, being developed as broader lamellae.

Pectoral and deltoid ridges of humerus united as a single flange (fig. 9): This feature

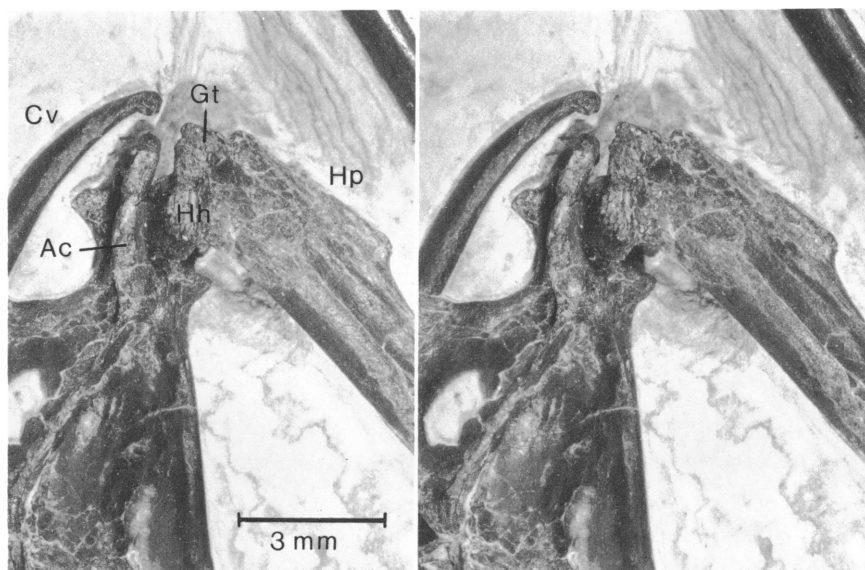


Fig. 9. Stereophotographs of right shoulder girdle of *Icaronycteris index*. From Jepsen (1970). Symbols are: Ac, acromion process; Cv, clavicle; Gt, greater tuberosity (trochiter) of humerus; Hh, head of humerus; Hp, pectoral ridge of humerus.

is found in microchiropterans, *Icaronycteris*, *Palaeochiropteryx*, and other Eocene chiropterans known from skeletal features, but is lacking in *Archaeopterus* and Recent Megachiroptera (Van Valen, 1979). The “deltoid-pectoral crest” is also lacking in Craseonycteridae but the condition in that taxon seems divergently specialized (Hill, 1974). The crest is the site of insertion for the deltoid and pectoralis muscles, which are extremely important for control of the wing-beat cycle (Vaughan, 1970a).

The addition of these features to the basicranial traits noted above muster a strong case for the close relationship of *Icaronycteris* with microchiropterans (fig. 10). If this hypothesis is accepted, the question of relationships of *Palaeochiropteryx* is easily settled, for it shares with *Icaronycteris* and microchiropterans the specializations noted above (where known) and does not retain some of the primitive traits (e.g., index claw, relatively short radius) found in the North American fossil (see Revilliod, 1917; Richter and Storch, 1980).

Jepsen (1966, 1970) noted several characters in which *Icaronycteris* resembled megachiropterans but not microchiropterans. These are: premaxillaries not united at

midline, long nasal bones, and coronoid process of mandible with rounded superior border and claw on index finger (digit II). The presence of united or separate premaxillaries varies within both bat suborders, and other characters are doubtlessly primitive. Hence, none of these features provide clear evidence for the close affinities of *Icaronycteris* with megachiropterans, and this hypothesis can be regarded as unsubstantiated.

The argument favored here, then, is that both *Icaronycteris* and *Palaeochiropteryx* are close relatives of living microchiropterans, and (at least the former genus) retain(s) a few primitive skeletal traits independently modified in megachiropterans and other microchiropterans, as shown in figure 10. This scheme favors the idea that the Eocene bats (at least *Icaronycteris*) while a member of Microchiroptera, are an outgroup to all of the Recent families of this suborder. However, the possibility that these Eocene taxa have special affinities within Microchiroptera (i.e., are related to one or another microchiropteran family) cannot, at present, be dismissed. In the meantime, the Palaeochiropterygoidea seems merely an artificial convention to group several early microchiropterans whose relationships with modern

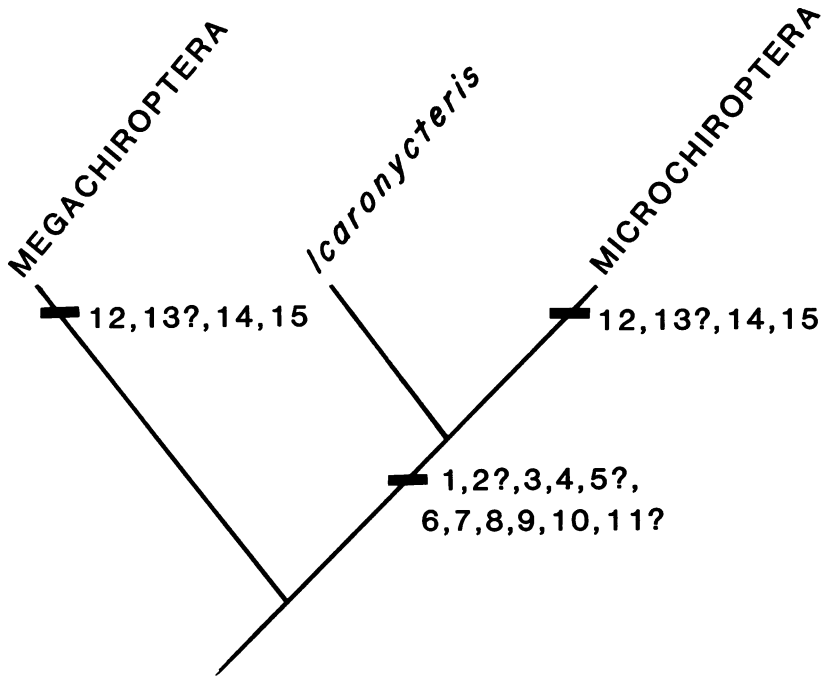


Fig. 10. Cladogram favoring close relationship between *Icaronycteris* and Recent Microchiroptera showing both supportive and contradictory characters. ? indicates an incompletely documented character or a condition inferred from the morphological evidence. Numbers refer to the following characters: (1) enlarged cochlea, (2) biconcave basioccipital, (3) large orbicular apophysis of malleus, (4) well-developed ossified stylohyal, (5) annular ectotympanic, (6) hooklike angular process of the mandible, (7) dilambdodont upper molars, (8) interlocking accessory process on cervical vertebrae, (9) narrow, biconcave neural arches on cervical vertebrae, (10) pectoral and deltoid ridges of humerus united as single flange, (11) ultrasonic echolocation as inferred from characters 1, 2, 3, and 4, (12) fusion of sternal elements, (13) lengthening of radius, (14) complete phalangeal formula (2-3-3-3-3) reduced or terminal phalanges unossified, (15) neck of femur reduced or lost and head aligned with long axis of shaft.

families of this suborder remain poorly known (see Smith and Storch, 1981). Hence, *Icaronycteris* and *Palaeochiropteryx* are more accurately designated as Microchiroptera incertae sedis. Moreover, there seems no justification for a formal designation of an "ancestral" group (e.g., Eochiroptera sensu Van Valen, 1979) to distinguish *Icaronycteris*, *Palaeochiropteryx*, and other Eocene bats from the Recent chiropteran suborders.

It is noted in passing that the scheme shown in figure 10 might be construed by advocates of the diphyletic origin of bats (e.g., Pettigrew, 1986) as supportive evidence. It is important, however, to remind such advocates that the postcranial features thought to evolve independently in modern mega- and micro-

chiropteran (fig. 10) are insignificant in comparison to the complex of skeletal features (primarily relating to wing structure) shared by these groups and found in no other mammals. Neither this paper nor any other presents crucial evidence that refutes the concept of bat monophyly.

In conclusion, the foregoing analysis is consistent with the view that a sophisticated echolocating system was present in the earliest known bats, and was acquired before some modifications of the postcranial skeleton. That the earliest bats can be allied with a particular bat suborder suggests that the order arose much earlier than their first appearance in the fossil record. How much earlier is anybody's guess.

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