A PRIMITIVE EMBALLONURID BAT (CHIROPTERA, MAMMALIA) FROM THE EARLIEST EOCENE OF ENGLAND

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CONTENTS

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ABSTRACT

A new genus, *Eppsinycteris,* is erected for *Adapisorex? anglicus* COOPER, 1932, from the earliest Eocene Blackheath Beds of Abbey Wood, London, England. Various derived character states indicate that it belongs to the order Chiroptera (bats) rather than to the extinct "insectivore" family Adapisoricidae. Other derived character states are shared with fossil and modern members of the family Emballonuridae. Placement of the new genus in this family extends the record of the Emballonuridae back in time by about 10 million years. It is the earliest record of a modern bat family and one of the earliest bats. This implies that the differentiation of at least some modern bat families took place in the Palaeocene, where no authenticated records of bats yet exist. The primitive characters of the earliest bats make the family Nyctitheriidae an unlikely stem group for the order Chiroptera. A tentative plausible alternative exists in some unnamed upper molars from the Palaeocene of Walbeck, Germany.*Wyonycteris chalix*, described as a bat from the Late Palaeocene of Wyoming, U.S.A., fits better in the family Nyctitheriidae.

RESUME

Un nouveau genre, *Eppsinycteris,* est créé pour *Adapisorex? anglicus* COOPER, 1932 des Blackheath Beds d'âge Eocène le plus précoce d'Abbey Wood, Londres, Angleterre. Divers états dérivés de caractères indiquent qu'il appartient à l'ordre des Chiroptera (chauve-souris) et non à la famille éteinte "insectivore" des Adapisoricidae. D'autres états dérivés de caractères sont partagés avec des membres fossiles et modernes de la famille des Emballonuridae. L'attribution du nouveau genre à cette famille étend l'histoire des Emballonuridae dans le passé d'environ dix millions d'années. Ceci implique que la différentiation d'au moins quelques familles modernes de chauve-souris ait eu lieu pendant le Paléocène, où elles n'ont pas été trouvées jusqu'à présent. Les caractères primitifs des chauve-souris les plus anciennes montrent que la famille des Nyctitheriidae est un groupe souche improbable pour l'ordre Chiroptera. Quelques molaires supérieures du Paléocène de Walbeck fournissent une alternative plausible. *Wyonycteris chalix*, décrit comme une chauve-souris du Paléocène tardif du Wyoming, Etats-Unis, représenterait plutôt un Nyctitheriidae.

INTRODUCTION

The holotype and only known specimen of *Adapisorex? anglicus* COOPER, 1932 has had a checkered history. The specimen is a nearly complete lower jaw which was collected and presented to the Natural History Museum, London (BMNH) in 1931 by an amateur palaeontologist, Mr F.J. Epps, who with Mr St.J. Marriott made the first excavations at the site of Abbey Wood in the 1920's (Marriott, 1925). Russell (1964: 63-64) was unable to see the specimen while preparing this publication, but from the original photographs produced for Cooper's paper, recognised that it differed drastically from typical species of *Adapisorex* and required a new generic name. He suggested that it might belong to the subfamily Geolabidinae, which at that time was included in the family Erinaceidae (see McKenna 1960). A combination of dental and osteological characters argues for placement in the order Chiroptera.

SYSTEMATICS

Order **CHIROPTERA** BLUMENBACH, 1779
Family **EMBALLONURIDAE** DOBSON, 1875

Genus *EPPSINYCTERIS* nov.

Type and only species: *Adapisorex? anglicus* COOPER, 1932.

Etymology: After F.J. Epps and nycteris - Greek for bat. Feminine.

Diagnosis: Small emballonurid, M_1 length 1.55mm (see Table 1 for other measurements). Dental formula: ? 1? 3? 3?
? 1 3 3 .

P_2 as large as P_4 according to its single alveolus.

P_3 three-rooted, only slightly smaller than P_4 with a single main cusp.

P_4 trenchant with mesiodistally orientated paracristid without differentiated paraconid; small metaconid situated high on crown distolingual to the tip of the protoconid; buccal outline in occlusal view gently biconvex; buccal side of crown extended basally (exodaenodont) with bilobed ventral edge; talonid basin absent.

Lower molars with: transverse protocristid; trigonid broadly open lingually, with large mesially projected paraconid, and slightly elongated mesially in a gradient increasing from M_3 to M_1; protoconid and metaconid of M_{2-3} diverge occlusally; metaconid slender; entoconid very low, crestiform and rather mesially located on M_{1-2}, missing on M_3; hypoconulid distinctly lingual of midpoint of unbroken postcristid; on M_{1-2}, hypoconid slightly lower than protoconid; additionally, talonid downstepped ventrally with respect to trigonid.

Horizontal ramus straight in dorsal view as far forward as P_2. Coronoid process high and expanded anteroposteriorly. Anterior slope of ascending ramus relatively shallow (70° to the base of the tooth row). Angular process slender and only very slightly deflected laterally.

Tooth	l	w1	w	w2
P_3	1.00		0.65	
P_4	1.05		0.75	
M_1	1.55	0.85+		0.95+
M_2	1.60	0.85+		0.95+
M_3	1.60	0.85		0.75

Table 1.— Length (l) and width (w) measurements in millimetres at crown base of *Eppsinycteris anglica*. w1 and w2 are widths of trigonid and talonid where differentiated.

Eppsinycteris anglica (COOPER, 1932) comb. nov.

(Plates 1-2; Fig. 1a)

v* 1932 *Adapisorex? anglicus* Cooper, pp. 460-461, pl. 11, fig. 1, pl. 12, fig. 1.
v. 1964 *"Adapisorex" anglicus* COOPER; Russell, pp. 63-64.
v. *1980 "Adapisorex" anglicus* COOPER; Hooker, p. 102.
v. *1980 "Adapisorex" anglicus* COOPER; Hooker & Insole, p. 38.
v. *1987 "Adapisorex" anglicus* COOPER; Collinson & Hooker, p. 290.

Diagnosis: As for genus.

Holotype: Natural History Museum, London, Palaeontology Department (BMNH) M13776: right dentary with P_3–M_3 and nearly complete ascending ramus, from the Lessness Shell Bed (presumed), Blackheath Beds, earliest Eocene, early Ypresian, of Abbey Wood, London.

Description

The molars are fairly heavily naturally worn, suggesting quite an old individual. Associated full ossification has probably been influential in the survival of such an unusually intact jaw in the nearshore semimarine high energy setting of the shelly and pebbly Blackheath Beds. Postmortem abrasion has damaged the condyle and removed the tip of the angular process. Another postmortem effect is major loss of tooth enamel: completely from P_3, from the entire buccal walls of P_4 and M_1; from the lingual side of the P_4 and M_1 paraconid, protoconid and metaconid tips; and from a patch on the protoconid and the buccal cingulum of M_2. The localised nature of this enamel loss is more consistent with dissolution by a predator's or scavenger's stomach juices than from mechanical attrition during water transport (e.g. cf. Andrews 1990, fig. 3.18J-L), although it could also have been caused by partial exposure to scour on the sediment surface.

When figured by Cooper (1932), the dentary had, in addition to the two premolars and three molars, a complete large oval alveolus in front of P_3 and the backwall of an apparently slightly larger alveolus in front of that. These were interpreted by Russell (1964: 63) to represent respectively a single rooted P_2 and a canine, P_1 being missing. This interpretation is followed here as it seems slightly more likely than that they represent P_2 and P_1. Beneath the mesial half of the P_2 alveolus was a mental foramen. A second mental foramen mentioned by Cooper as existing below M_1 is in fact only a dimple in the bone surface, not a foramen. At some time in the following three decades, the specimen was damaged and is now truncated anteriorly through the P_2 alveolus and the part with the mental foramen is lost.

What remains of the crown of P_3 is a shallow dome with a pit mesial of the centre. As all enamel is missing, it is probable that the pit indicates proximity to the pulp cavity and that in life the single-cusped tooth had a much taller crown. In occlusal view, it tapers slightly mesially. There appears to have been a distolingual cingulum rather as on P_4. In addition to the mesial and distal roots, there is a third root on the lingual side, unusual for such a crown morphology. There is no other evidence of abnormality, but as the specimen is unique and the crown so damaged it is impossible to judge the significance of this third root.

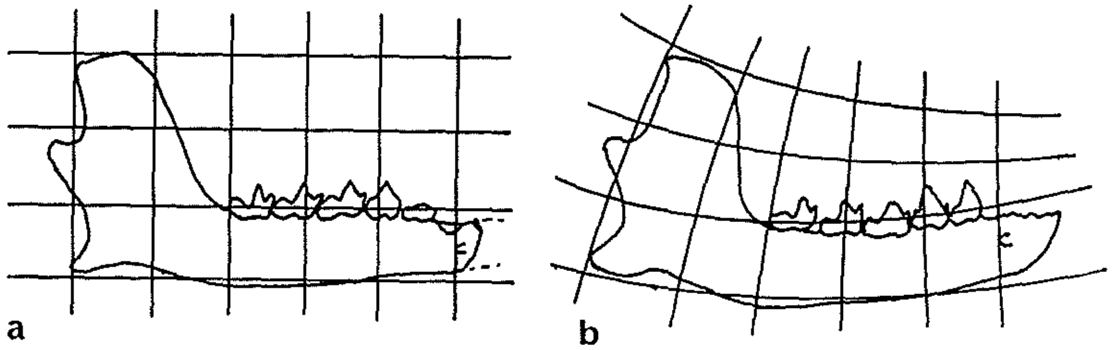

Figure 1.— Grid transformations applied manually to the dentaries of: a, *Eppsinycteris anglica* (COOPER); and b, *Archaeonycteris trigonodon* REVILLIOD, to show shape changes in the ascending ramus (after Cooper, 1932, pl. 11, fig. 1 and Habersetzer & Storch, 1989, fig. 5A).

P_4 has a very distinctive morphology, with its bilobed buccal exodaenodonty and high vertical mesial and distal walls in buccal view (Pl. 2, fig. 2). It is a simple nonmolariform tooth with paracristid and protocristid subtending a very obtuse angle lingually. A high crest, presumably homologous with the cristid obliqua trends distally and slightly buccally from the small metaconid to the distal tooth margin. There is no talonid basin, only a cingulum lingually adjacent to the cristid obliqua. The bilobation of the lingually extended crown on the buccal side delineates two shallow vertically elongate concave areas on either side of the protoconid. The more distal is the more extensive and would have occluded with a tall P^4 paracone.

All three molars are approximately equal in size apart from the slight reduction in height and width of the M_3 talonid. The downstepping of the talonid relative to the trigonid is more marked on M_1 than M_2. The hypoconulid projects slightly distally on M_3. Because of loss of buccal enamel on $M_{1\text{–}2}$, the nature of the buccal cingulum can only be fully appreciated on M_3 where the enamel covering is essentially complete. Even here it is truncated distal to the protoconid by wear produced by the M^3 paracone. It would originally have continued as far as the mesial side of the hypoconid. Ghosts of complete buccal cingula are preserved in the profile of the exposed dentine of $M_{1\text{–}2}$ and are most readily seen in occlusal view (Pl. 2, fig. 1). The cristid obliqua of the molars descends steeply to a notch near its mesial end, rising again only very slightly and not ascending the distal wall of the trigonid. The latter is smooth for occlusion with aligned upper molar preparacrista, preparaconule crista and preprotocrista without offsetting by a paraconule (Pl. 2, fig. 4). The trigonid attachment point of the cristid obliqua is relatively buccal, behind the protoconid, but it retreats very slightly lingually from M_1 to M_3. The mesial elongation of the trigonid, which increases from M_3 to M_1 is less obvious in occlusal view on $M_{2\text{–}3,}$ because of the occlusal divergence of the protoconid and metaconid on these teeth (Pl. 1, fig. 5) and because of the considerable wear on the tips of their protoconids. For these reasons, the ratio of the distance between the paraconid and metaconid versus metaconid and protoconid is less than on M_1. The elongation is nevertheless clearly shown in lingual view (Pl. 2, fig. 3).

The ascending ramus has a sloping anterior edge with a distinct anteroposteriorly extended coronoid process which is rounded at the anterior corner and angled at c. 90° posteriorly. Little can be said of the condyle as it is abraded posteriorly and medially, but the dorsal remnant of the articulation is curved about a transverse axis. The condyle is situated fairly high above the tooth row and intermediate between the coronoid tip and the narrow, slightly laterally deflected angular process. The latter terminates slightly anterior of the vertical plane of the condyle. More derived bats have a steeper anterior edge to the ascending ramus and either a tapering or truncated coronoid process (Pl. 1, figs. 1-4). *Archaeonycteris* from Messel, next to *Eppsinycteris*, has probably the most primitive ascending ramus structure for bats (e.g. Habersetzer & Storch 1989, fig. 5A - SMF ME 963). Simple forward tilting of the ascending ramus apparently initiated the shape changes (Fig. 1).

COMPARISONS AND AFFINITIES

ADAPISOREX

Cooper (1932) referred his new species *anglicus* to this genus with some doubt. Other than having broadly "insectivore"-like teeth, there is very little similarity between *Eppsinycteris anglica* and either *Adapisorex gaudryi* LEMOINE, 1883, from the Late Palaeocene of Cernay, France, or *A. abundans* RUSSELL, 1964, from the Late Palaeocene of Walbeck, Germany. The latter two species have bunodont cheek teeth with low trigonid, low crestiform paraconid, high entoconid, median hypoconulid, reduced M_3, near molariform P_4 and mental foramina below P_2 and P_4 (see Russell 1964). In fact Cooper made his comparisons with *"A". dolloi* TEILHARD, 1927, which is now referred to *Paschatherium* RUSSELL, 1964, but this genus is no closer in morphology to *E. anglica* than is *Adapisorex*.

GEOLABIDIDAE

The subfamily Geolabidinae, to which Russell (1964) tentatively referred *E. anglica*, is now usually given family rank following Butler (1972). Butler (1988) related *Centetodon,* the best known member of the family, to the soricomorph lipotyphlans *Nesophontes* and *Solenodon*. *Centetodon* is similar to *Eppsinycteris* in having lower molars with a buccal cristid obliqua, low entoconid and a slightly lingual hypoconulid. In contrast, however, the trigonid is tall and the talonid low; the paraconid is not so large or procumbent; and the cingulum development is restricted to a precingulid. P_4 has somewhat similar buccal exodaenodonty and lacks a talonid basin, but the metaconid is tall and distinct. P_2 is two-rooted. There are two mental foramina: below P_{1-2} and P_{3-4}; the angular process is straight, projecting beyond the low level condyle; and the coronoid process tapers dorsally (see Lillegraven *et al.*1981). Most of these differences from *Eppsinycteris* appear to be primitive, but the degree of difference is such as to suggest that the relationship is distant.

Character	*Eppsinycteris anglica*	*Icaronyct? menui*	*Archaeon. brailloni*	*Honrovits tsuwape*
M entoconid	low	**high**	low	low
M hypoconulid	slightly lingual	**nyctalodont**	slightly lingual	slightly lingual
M_3 hypoconulid	**small**	**small**	**small**	large
M talonid/trigonid level	downstepped	**same level**	**same level**	**same level**
M_{1-2} hypoconid	low	**high**	low	low
M trigonid backwall	transverse	transverse	**oblique**	**oblique**
M trigonid mesial elongation	**yes A**	no	no	no
M protoconid & metaconid	**divergent**	**divergent**	convergent	convergent
M metaconid	**slender**	broad	broad	**slender**
P_4 metaconid	*small*	large	large	**absent**
P_4 bilobed	**yes A**	no	no	no
P_4 buccally	**high A**	low	low	low
P_3	large	large	large	**small**
P_2	large	small	small	large
Jaw curvature begins at:	canine	P_3	?	$\mathbf{P_4}$

Table 2.— Comparative character table. Bold script indicates derived state or a more derived state. Italics indicate a less derived state. A = autapomorphy for *Eppsinycteris anglica*. Abbreviations: *Icaronyct?* = *Icaronycteris*; *Archaeon.*=*Archaeonycteris*. See Russell *et al.* (1973) and Beard *et al.* (1992) for details.

CHIROPTERA

The following characters of *Eppsinycteris* are all found in primitive bats and in combination occur in no other order:

- Only one mental foramen which is below P_2.
- Dentary angular process flexed slightly laterally.
- Lower molars with complete buccal cingulum.
- Molar cristid obliqua low and joins trigonid buccal of midline.
- Cristid obliqua does not ascend distal wall of trigonid.
- Large procumbent molar paraconid.
- Molar hypoconulid nearer to entoconid than to hypoconid.
- Nonmolariform P_4.

Table 2 compares *Eppsinycteris* with other Early Eocene bat genera: the European archaeonycteridids *Archaeonycteris* and *Icaronycteris* and the North American natalid *Honrovits* (see Russell *et al.* 1973, Beard *et al.* 1992, for detailed descriptions and illustrations). *Ageina* is poorly known and has been tentatively placed in the Natalidae (Beard *et al.* 1992), whilst *Hassianycteris joeli* SMITH & RUSSELL, 1992, described from a dentary with P_4–M_1, appears very similar to *Honrovits*. These two European taxa have therefore been omitted from Table 2. An attempt has been made to distinguish derived from primitive character states by outgroup comparison with a variety of non-bat groups with "insectivorous" teeth. The derived states shared between *Eppsinycteris* and the other genera are few and incongruent, giving no strong evidence of special relationship to any.

EMBALLONURIDAE

The characters of P_4 and the molar trigonids, labelled with an A in Table 2, indicating autapomorphic status, are found in the southern European Middle Eocene (MP13) to Oligocene emballonurid *Vespertiliavus* SCHLOSSER, 1887. The teeth have been figured in detail by Sigé (1988). In the case of P_4, the specialisations are less marked, in particular the height of the mesial and distal walls and the tiny or absent metaconid, but the overall pattern and the bilobate exodaenodonty are very similar. P_2 is large as in *Eppsinycteris*, but the polarity of this character is uncertain. Even if derived its importance is diminished by being shared with *Honrovits*.

The main differences from *Eppsinycteris* are: the relationships of the $M_{2\text{-}3}$ protoconid and metaconid, which are convergent instead of divergent occlusally; the P_3 is tiny although often retains two roots (Sigé 1988); the molar talonids are much better developed with higher hypoconid and entoconid and are at the nyctalodont, verging on myotodont grade; the coronoid process is tall but tapers to a point and the anterior edge of the ascending ramus is steep. Apart from the cusp convergence character, most other differences from *Eppsinycteris* are interpretable as typical bat advancements of increased dilambdodonty, or related to shortening of the face and expansion of the braincase.

It is significant that the P_4 bilobation occurs in varying degrees in several modern genera of emballonurids: *Diclidurus, Saccopteryx, Rhynchonycteris, Peropteryx* and *Taphozous*. The classification of these genera in different subfamilies and the fact that *Taphozous* has weaker P_4 bilobation than its close relative*Vespertiliavus* suggest that this character is primitive for the Emballonuridae.

It is interesting that *Vespertiliavus* and modern *Diclidurus* and *Taphozous* have horizontal rami that are straight as far anteriorly as the P_2 as in *Eppsinycteris*. This is a primitive character which cannot be used to indicate relationship, but nevertheless points to a primitive state within the family Emballonuridae. It suggests that the derived state of facial shortening as marked by strong curvature of the dentary evolved within the Emballonuridae independently of other bat families.

Nearly all emballonurids have the progressive M_3 to M_1 mesial trigonid elongation, some greatly exaggerated (whilst retaining the primitive transverse orientation of the trigonid backwall, except in *Taphozous*) and it thus seems to be a reliable family autapomorphy. The Recent rhinopomatid *Rhinopoma* (also in the superfamily Emballonuroidea) has similar elongation of the trigonid, but this does not increase from M_3 to M_1 and the P_4 is not bilobed. Some modern phyllostomatids (e.g. *Crotopterus, Mimon, Macrotus*) have trenchant exodaenodont bilobed distal premolars. However, the pattern is different in detail from *Eppsinycteris* and the lower molar trigonids lack the mesial elongation character, instead specialising in other ways. A relationship with the family Phyllostomatidae is thus not envisaged for *Eppsinycteris*.

The only difficulty with placement of *Eppsinycteris* in the Emballonuridae comes from the degree of phenetic difference from known genera and the considerable primitiveness of some of the characters. The latter imply parallel evolution of certain characters that unite other very early bats: viz. vertical ascending ramus and level positioning of bases of lower molar trigonid and talonid. Nevertheless, in the light of the evidence from other characters presented here, there is no real reason for regarding these as bat synapomorphies. Hopefully, upper teeth of *Eppsinycteris* will be discovered in due course and will further clarify its relationships.

The previous earliest record of the family Emballonuridae is *Vespertiliavus* from MP14 in the Middle Eocene (Lutetian) of Laprade, Quercy, France (Sudre *et al.* 1990). *Eppsinycteris* therefore extends the record of the family earlier in time by about ten million years.

EVIDENCE FOR BAT ORIGINS

The following characters of *Eppsinycteris* are considered primitive for bats and some might be expected to provide some indication of their nearest relatives:

- Nearly straight dentary.
- Ascending ramus with sloping anterior edge.
- Coronoid process high and anteroposteriorly long at dorsal extremity.
- Distal wall of lower molar trigonid transverse.
- Lower molar hypoconulid lingual of postcristid midpoint, but linked to entoconid by crest.
- Lower molar entoconid very low.
- $M_{1\text{-}2}$ hypoconid low.
- $M_{1\text{-}2}$ talonid downstepped with respect to trigonid.
- P_4 with metaconid.
- P_3 relatively large.

The question of bat origins is plagued by the lack of any postcranials remotely like those of bats prior to the articulated skeleton of *Icaronycteris index* JEPSEN, 1966, from the North American late Early Eocene, and by the small scale of the differences between

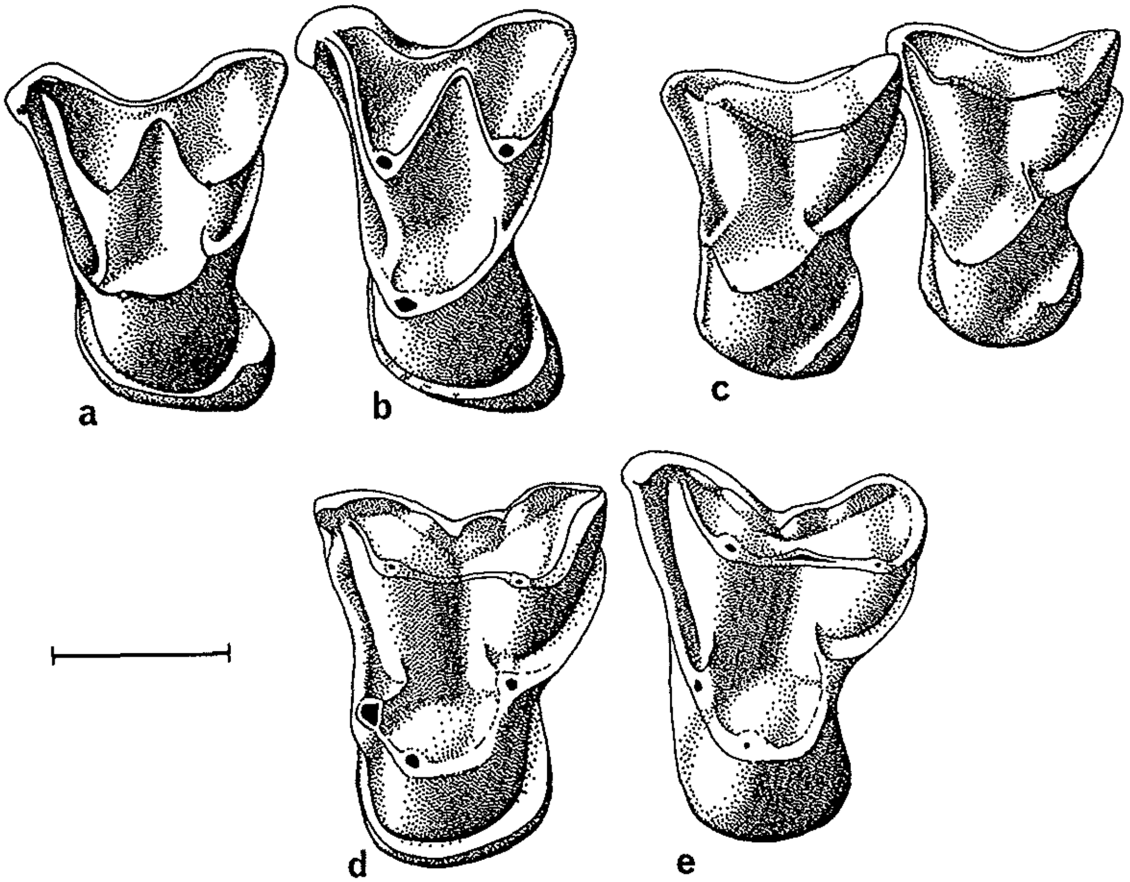

Figure 2.— Occlusal views (drawn from epoxy casts) of upper left first and second molars of: a,b, *Icaronycteris? menui* RUSSELL, LOUIS & SAVAGE (Muséum National d'Histoire Naturelle, Paris, nos Mu-236-L, Mu-426-L); c, *Leptacodon catulus* KRISHTALKA (American Museum of Natural History, New York no. 48173, composite of left and right sides); and d,e, unnamed taxon from Walbeck (Geiseltalmuseum, Halle, both no. Wa/416, the M^2 reversed from the right). Scale bar = 1mm.

the teeth of the earliest bats and those of other groups of Palaeogene insectivorous eutherians.

The idea that the extinct family Nyctitheriidae might include the ancestors of bats or even be bats has recently regained favour (e.g. Gingerich 1987, Van Valen 1979) following the original suggestion by Matthew (1918). An alternative view of the relationships of the Nyctitheriidae is that they are primitive soricomorph Lipotyphla (e.g. Butler 1988). The primitive nyctithere *Leptacodon munusculum* SIMPSON, 1935, from the Palaeocene of Wyoming and Montana, U.S.A., shares an overall similarity in its lower molars with *Eppsinycteris*, including the derived states of slightly lingual hypoconulid and complete M$_3$ buccal cingulum. It differs in having a more prominent M$_3$ hypoconulid, taller molar entoconid, less buccal although weak molar cristid obliqua that ascends the distal trigonid wall, a more molariform P$_4$ and mental foramen below P$_3$ (see Krishtalka 1976, fig. 2). Most of these may be primitive characters; a similarly prominent M_3 hypoconulid exists in *Honrovits*, uniquely for bats (Beard *et al.* 1992); moreover, the P_4 is less molariform than in other species of *Leptacodon* and it could be argued that *L. munusculum* is already showing a trend in reduction in the direction of bats. In contrast, the higher entoconid suggests an advancement with enhanced late buccal phase occlusion associated with a larger upper molar protocone lobe.

The upper molars of primitive bats are more different from nyctitheres than are the lower molars. The preparacrista is transverse and tends to join a stylocone, whereas it is more oblique and joins the parastyle tip in *Leptacodon* (N.B. uppers unknown for *L. munusculum*); the paraconule is close to the protocone and the metaconule is close to the metacone, whereas the two are more nearly central in *Leptacodon*; and the ectoflexus is deep, whereas it is shallow in *Leptacodon* (Fig. 2a-c; McKenna 1968, fig. 5; Krishtalka 1976, fig. 5B). By using primitive tribosphenic therians as outgroup, the bat states for all three characters are deduced to be primitive and the nyctithere states derived. The shift in orientation of the preparacrista follows narrowing of the stylar shelf and a shift in emphasis of buccal phase shear to more lingual crests (see Crompton & Kielan-Jaworowska 1978, Butler 1990). This suggests that the Nyctitheriidae are more specialised in their dental groundplan than the Chiroptera and do not provide a likely stem group for this order.

Nyctitherium, type genus of the Nyctitheriidae, is rather enigmatic in having upper molars with transverse preparacrista joining a stylocone (see Robinson 1968). However, it differs from bats in having a deeply notched upper molar centrocrista and consequently a very shallow buccal phase trajectory for the lower molar hypoconid. It also has a reduced postparaconule crista yet no paraconule reduction; in primitive bats the reverse occurs. It appears likely that the transverse preparacrista in *Nyctitherium*, in contrast to bats, represents a reversal to the primitive state, to allow passage of the lower molar protoconid between the metacone and paracone of adjacent upper molars in a shallower trajectory than in other nyctitheres. It does not therefore represent a trend towards bats.

Four $M^{1/2}$'s from the Palaeocene of Walbeck, of which two have been described and illustrated but not named by Russell (1964: 57, pl. 16, fig. 3a), share with primitive bats the three primitive states described above (Fig. 2d-e). They also share with them two apparently derived states: a distolingually flexed postprotocrista and in some individuals a complete lingual cingulum. They are more primitive in having a virtually straight centrocrista with only very slight buccal flexing, no sign of a hypocone and prominent paraconule and metaconule. Moreover, the buccal position of the metaconule together with the absence of dilambdodonty suggests that the lower molar hypoconulid could have been central rather than lingual in position. This suggests that the lingual position of the hypoconulid in nyctithere lower molars is due to a more lingual upper molar metaconule rather than to progressive dilambdodonty as in bats. The hypoconulid position would thus not be homologous in the two groups. These Walbeck teeth thus differ from primitive bats only in primitive characters and present a plausible alternative to the Nyctitheriidae as sister taxon to known bats. This hypothesis can be tested if lower molars and premolars can be found.

Wyonycteris chalix GINGERICH, 1987 was described as a Late Palaeocene bat and the earliest discovered. It has a more or less premolariform P_4 and a dentary curvature suggesting some facial shortening. However, it lacks a complete lower molar buccal cingulum (as noted by Hand *et al.* 1994); has a mental foramen below P_4; is nyctalodont; and has centrally placed paraconule and metaconule and oblique preparacrista joining the parastyle tip on the upper molars. These characters are thus more consistent with attribution to the Nyctitheriidae.

CONCLUSIONS

There are now two modern families of bats, the Emballonuridae (*Eppsinycteris*) and Natalidae (*Honrovits* and possibly *Ageina*)(see Beard *et al.* 1992), and additionally one modern superfamily, the Rhinolophoidea (see Sigé 1991), recorded from the Early Eocene. *Ageina* and *Eppsinycteris* are from MP8-9, the latter from early in that biochronologic unit, which appears to be very early in the Eocene (Hooker 1991). This implies either extremely rapid differentiation of the order Chiroptera at the beginning of the Eocene, or more likely a considerable history extending back into the Palaeocene, of which we have as yet no record, except possibly the Walbeck teeth.

What is most likely in the future to advance our knowledge of the relationships of bats with other mammalian orders is the discovery of a Palaeocene site yielding articulated skeletons. Such conditions existed at Menat in southern France, where a plesiadapid, a carnivore and a leptictid were discovered (Gingerich 1976: 35). Unfortunately, however, the site is no longer available for collecting.

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LEGENDS OF PLATES

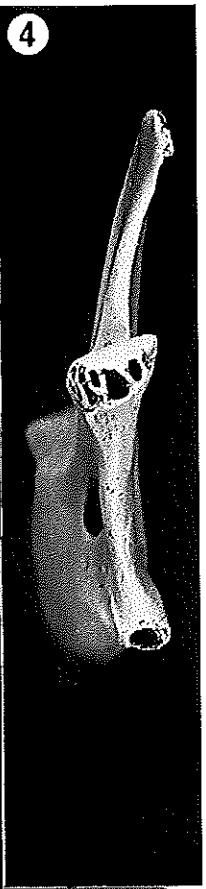
PLATE 1

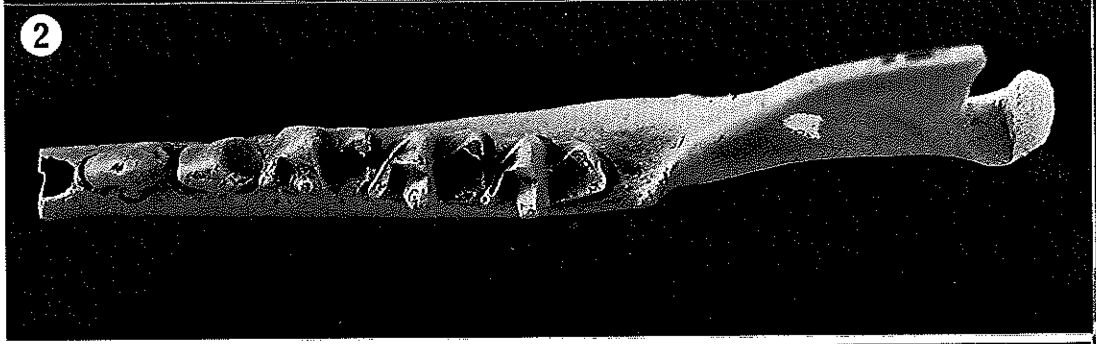
Holotype of *Eppsinycteris anglica* (COOPER) from the Blackheath Beds, Abbey Wood; figs. 1-4, light micrographs of right dentary, coated with ammonium chloride, in lateral (1), dorsal (2), medial (3) and posterior (4) views; Fig. 5, SEM of tooth row (epoxy cast) in disto-occlusal view. Scale bars = 1mm.

PLATE 2

Holotype of *Eppsinycteris anglica* (COOPER) from the Blackheath Beds, Abbey Wood; SEM's of epoxy casts of tooth row in occusal (1), buccal (2), lingual (3) and occlusolingual (4) views. Scale bar = 1mm.

PLATE 1





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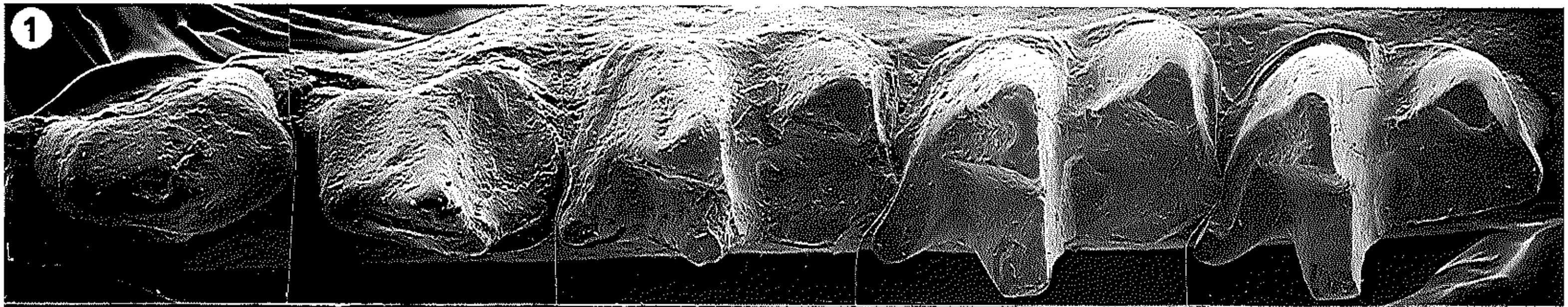
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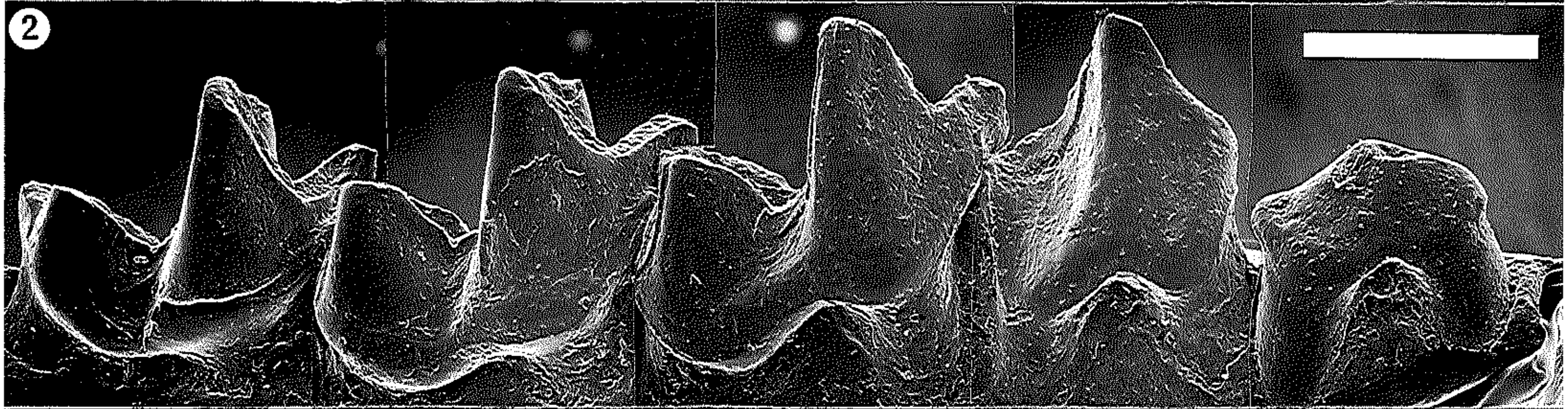
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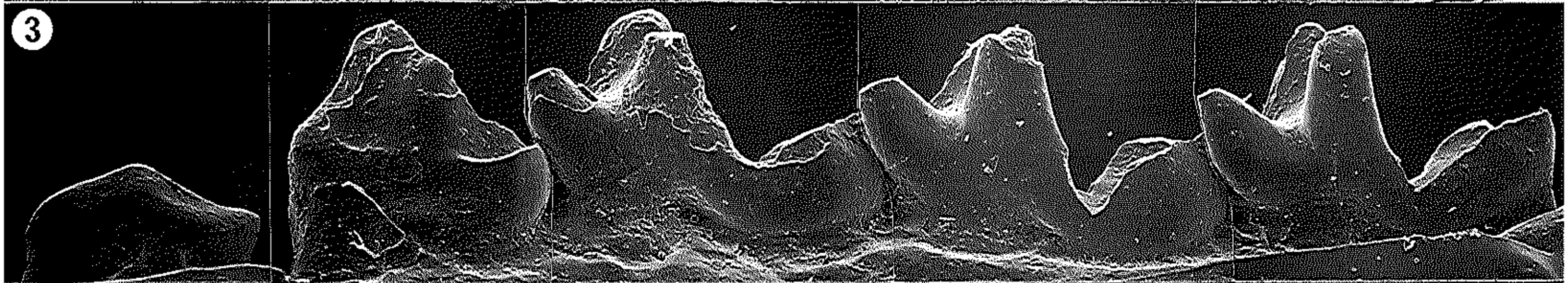
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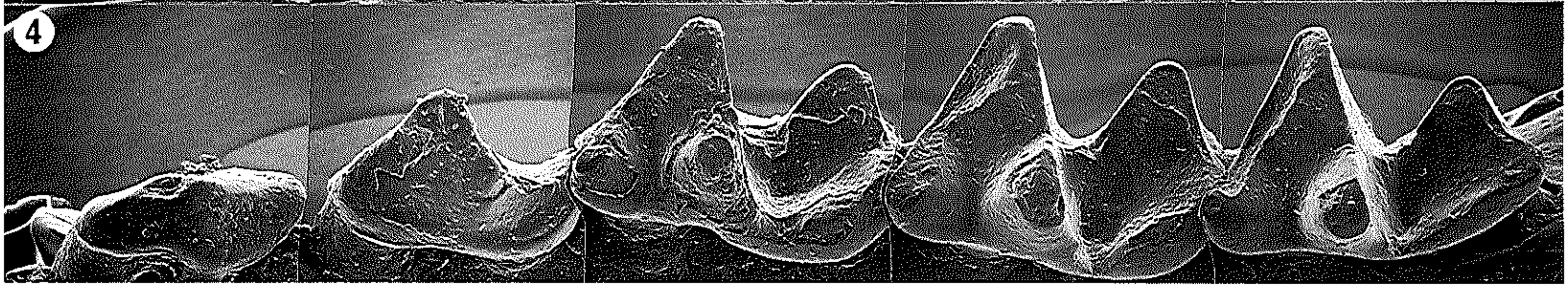
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