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**LIPOTYPHLA, PROTEUTHERIA(?), AND CHIROPTERA (MAMMALIA)  
FROM THE EARLY-MIDDLE EOCENE  
KULDANA FORMATION OF KOHAT (PAKISTAN)**

By

Donald E. Russell<sup>1</sup> and Philip D. Gingerich<sup>2</sup>

*Abstract.*—Two new genera and species of insectivores, *Seia shahi* and *Pakilestes lathrius*, and an unnamed chiropteran are described from the early-middle Eocene Kuldana Formation at Chorlakki, Kohat District, North-West Frontier Province, Pakistan. These are the first insectivores and bats to be described from the Eocene of the Indo-Pakistan subcontinent. *Seia* appears to be an erinaceomorph lipotyphlan, but the affinities of *Pakilestes* are less certain. The unnamed bat could be a representative of either Eochiroptera or Microchiroptera.

INTRODUCTION

Ten orders of mammals are represented in the early-middle Eocene collections described to date from India and Pakistan: Primates, Condylarthra(?), Creodonta, Cetacea, Sirenia(?), Rodentia, Tillodontia, Artiodactyla, Perissodactyla, and Proboscidea (West, 1980; Gingerich and Russell, 1981). Hussain et al. (1978) described a collection of rodent teeth obtained by screen washing and we have described a small primate (Russell and Gingerich, 1980), but with these exceptions all of the remains found to date are mammals of medium to large size. In this paper we describe two new insectivores and an unnamed bat from Chorlakki, Kohat District, North-West Frontier Province, Pakistan. These are the first representatives of the orders Lipotyphla, Proteutheria(?), and Chiroptera to be described from the early-middle Eocene of India and Pakistan. They bring to thirteen the total number of mammalian orders represented in the early Cenozoic of Indo-Pakistan.

Coordinates of the Chorlakki locality are 33°37'20" N latitude, 71°55'20" E. longitude; it is situated in the easternmost exposure of Kuldana Formation in Panoba Dome about 4 km NNW of the village of Chorlakki. Most fossils, including those described here, come from a 10–30 cm thick bed of hard calcareous conglomerate. Bone is common in this bed, which has produced a diverse mammalian fauna. The teeth described here were recovered by processing blocks of the calcareous Chorlakki bone bed in 10% formic acid and then screen washing the residue. This process is very time consuming, but it appears to be the only way to recover the smaller component of the mammalian fauna represented at Chorlakki.

Specimen numbers prefaced by GSP-UM refer to specimens to be deposited in the Pakistan National Museum of Natural History, Islamabad, or with the Geological Survey of Pakistan (GSP), Islamabad and Quetta. Sharp epoxy casts of these specimens are also being deposited

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permanently in the University of Michigan Museum of Paleontology (UM), Ann Arbor, and the Muséum National d'Histoire Naturelle, Paris. Specimen numbers prefaced by GH are in the Geiseltalmuseum, Halle (German Democratic Republic). Those prefaced by Louis are in the private collection of M. Pierre Louis, Cormicy (France).

## SYSTEMATIC PALEONTOLOGY

### Order LIPOTYPHLA

#### Suborder ?ERINACEOMORPHA

#### Family undetermined, probably new

#### *Seia*, new genus

*Type species*.—*Seia shahi*, new species.

*Included species*.—Type species only.

*Diagnosis*.—Differs from all previously known lipotyphlans in that upper molars lack a hypocone, and the anterior and posterior cingula are joined by a prominent lingual cingulum.

*Etymology*.—*Seia*, Urdu (pronounced say-ee-ah, masculine), porcupine or, occasionally, hedgehog; in reference to the probable erinaceomorph relationships of this genus.

#### *Seia shahi*, new species

Pl. 1, figs. 1-5

*Holotype*.—GSP-UM 121, a right upper second molar ( $M^2$ ).

*Referred specimen*.—GSP-UM 120, a right  $M^1$ .

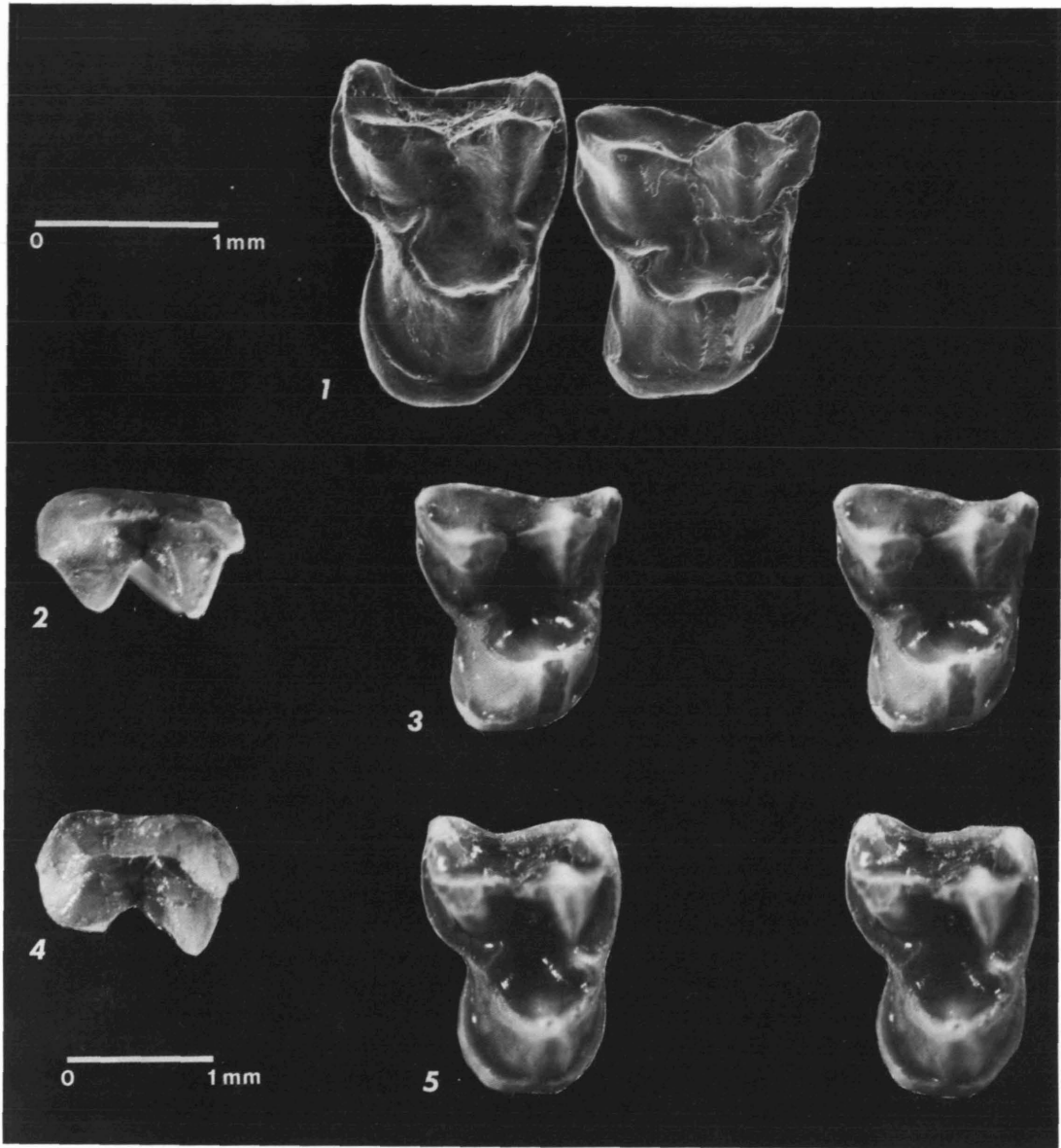
*Type locality*.—4 km NNW of Chorlakki village, Kohat District, North-West Frontier Province, Pakistan.

*Age and distribution*.—Late early Eocene or early middle Eocene of the Kuldana Formation, Kohat District, Pakistan.

*Diagnosis*.—As for the genus, see above.

*Etymology*.—*shahi*, named for Dr. S. M. Ibrahim Shah, Director, Paleontology and Stratigraphy Branch, Geological Survey of Pakistan, in appreciation of his substantial contributions to the success of our paleontological expeditions.

*Description*.—The holotype  $M^2$ , GSP-UM 121, is moderately broad transversely with respect to its anteroposterior length. The parastylar and metastylar crests are both directed labially, parallel to the transverse axis of the tooth, and they do not protrude anteriorly or posteriorly beyond the general outline of the crown. A narrow but distinct stylar shelf is created by the sloping labial sides of the paracone and metacone together with the well developed labial cingulum connecting the stylar crests. The paracone and metacone are sharply pointed cusps of but moderate height; the paracone is traversed by a vertical crest on its lingual side that is absent on the metacone. Both cusps possess crests that connect their summits to their respective styles and, curiously, the cusps are joined by median crests united up to about half the height of the cusps. The paracone and metacone are not fused however, as is seen, for example, in palaeoryctids; they remain distinct and separated at their bases. Conules are present, subequal in



## EXPLANATION OF PLATE 1

- Figure 1 — *Seia shahi*, composite right M<sup>1</sup> (GSP-UM 120) and M<sup>2</sup> (GSP-UM 121, holotype) in occlusal view, scanning electron micrograph, x 25.
- Figure 2 — *Seia shahi*, right M<sup>1</sup> (GSP-UM 120) in labial view, x 20.
- Figure 3 — *Seia shahi*, right M<sup>1</sup> (GSP-UM 120) in occlusal view, stereophotograph, x 20.
- Figure 4 — *Seia shahi*, right M<sup>2</sup> (GSP-UM 121, holotype) in labial view, x 20.
- Figure 5 — *Seia shahi*, right M<sup>2</sup> (GSP-UM 121, holotype) in occlusal view, stereophotograph, x 20.

size, with the paraconule being slightly more lingually situated. Each is connected to its respective labial style by a strong, rather flaring cingulum. This feature, in addition to the anteroposterior length of the trigon basin, particularly suggests lipotyphlan relationships. The presence of short "internal" conule crests (postparaconule and premetaconule cristae) could also

support a lipotyphlan relationship (although they also occur in a number of non-lipotyphlan families). The fact that lingually the tooth is not narrow or pointed tends to suggest erinaceomorph affinity. The basal cingulum that extends from the level of the conules uninterrupted around the lingual side of the tooth is slightly enlarged in the area where a hypocone is normally situated, but no cusp development is perceptible.

GSP-UM 120, an  $M^1$ , differs from the holotype in having styles that protrude anteriorly and posteriorly, and the tooth is less broad transversely. Lingually the trigon basin is relatively longer and the paraconule is situated labially with respect to the metaconule. The basal cingulum is weaker lingually, but in the hypoconal region it is enlarged more than that of  $M^2$ , and there exists a faint suggestion of a crestiform cuspule. This tooth is slightly damaged at its base dorsal to the parastyle.

It must be emphasized that these two specimens were recovered as isolated teeth during the sorting of acid-treated sediment residues, and their association is not assured. They are considered to represent the same taxon because of their similar morphology.

*Measurements.*—GSP-UM 121 (holotype),  $M^2$ : anteroposterior length, 1.4 mm; labiolingual breadth, 1.8 mm. GSP-UM, 120  $M^1$ : anteroposterior length, 1.45 mm; labiolingual breadth, 1.6 mm.

*Discussion.*—As mentioned above, the general outline of the upper molars of *Seia* is suggestive of erinaceomorph affinities, but the absence of a hypocone is difficult to reconcile with the morphology of typical members of this group. The lingual part of the molars is reminiscent, on the contrary, of that seen in the early to middle Eocene bat *Archaeonycteris*, as well as in some living vespertilionids, but the labial cusp arrangement of chiropteran upper teeth is very different from that in *Seia*. The same sort of similarity and extreme difference is also found in the upper molars of *Tupaia*. Special relationship to Paroxyclaenidae (including the formerly referred *Dulcidon*) can also be eliminated, as can any affinity with early omomyid primates, Paleocene apatemyids, didelphid marsupials, and palaeoryctoid insectivores. Pentacondontids present some intriguing features in common with *Seia*, and resemblances can be seen to *Pantomimus learyi*, *Coriphagus montanus*, and, to a lesser degree, *Coriphagus encinensis*. However, these are North American middle Paleocene forms distant in time and space from the Chorlakk specimens and they are more than twice as large as *Seia* in linear dimensions. The late Paleocene form "*Diacodon*" *minutus* has weakly developed hypocones on the upper  $M^1$ – $M^2$  and shows a similarity to *Seia* in cusp arrangement, but, compared to those of *Seia*, these teeth are notably more transversely elongate.

A small collection of teeth from late Eocene localities of San Diego County, California, referred to *Aethomylos*, are characterized by the absence of a hypocone on the upper molars and, like the taxon described here, by the extreme difficulty encountered in trying to determine their relationships (see Novacek, 1976). Apart from these two features, *Aethomylos* bears little resemblance to *Seia*.

Comparison with Adapisoricidae appears to hold more promise; *Neomatronella*, Russell et al. (1975, p. 177) in particular, shares a number of characters with *Seia*. Distinctive features of the latter, however, include higher, more developed crests between the paracone and the metacone that form a barrier (in  $M^2$ ) closing off the trigon basin from the labial shelf (this is less marked in  $M^1$ ); also, the posterior wall of the trigon basin (between the metaconule and the protocone) is more vertical than in *Neomatronella*. The greatest difference between the French and Pakistan forms is the presence of a distinct hypocone in the former and its absence in the latter. The suggestion of a small swelling in the position of the hypocone on  $M^1$  in *Seia* diminishes this difference from *Neomatronella* and Adapisoricidae slightly, and *Seia* may possibly be an adapisoricid. Of the two adapisoricids described from Asia, no upper teeth have been described from the late Eocene or middle Oligocene *Ictopidium*, and upper molars of *Tupaiodon* from the middle Oligocene are quite different.

One other taxon bears some resemblance to *Seia*. This is an unnamed form from the middle or late Paleocene locality of Walbeck (German Democratic Republic) represented by a single upper molar, probably  $M^2$ , GH-Wa/416, the tooth figured on the right side of figure 3a, Plate XVI, in Russell, 1964). This specimen from Walbeck shows many of the same basic traits as those seen in *Seia*, with relatively minor differences that could be primitive within the limits of the same group. Unfortunately, the broader affinities of the Walbeck tooth are no more clear than those of *Seia*.

In summary, *Seia*, is regarded with some uncertainty as an erinaceomorph lipotyphlan. The labial parts of the upper teeth (from the conules labiad) are the principal evidence suggesting this relationship, and the great anteroposterior lengths of the lingual parts of  $M^1$  and  $M^2$  support this assignment, making distant any affinity with palaeoryctoids and many other groups of insectivores or proteutherians. Despite the difficulty in placing *Seia* within the existing classification of insectivores, the Walbeck tooth GH-Wa/416 cited above suggests that the Pakistan form is possibly part of a more widely distributed, if poorly known, group of early Cenozoic mammals.

### Order PROTEUTHERIA(?)

#### Family *Incertae sedis*

#### **Pakilestes**, new genus

*Type species*.—*Pakilestes lathrius*, new species.

*Included species*.—Type species only.

*Diagnosis*.—Lower molars ( $M_1$  or  $M_2$ ) are distinguished by a low, large, anteriorly extended paraconid, with an angle between the paracristid and protocristid of about  $40^\circ$ . The protoconid is considerably higher than the metaconid. A short and narrow talonid is set off by a deep labial indentation from the trigonid, and it is closed lingually. Talonid cusps are low, approximately of equal height, and little developed. *Pakilestes* differs from *Seia* in having lower molar talonids proportionately much too small to occlude with the broad protocones characteristic of the latter.

*Etymology*.—*Pak*, abbreviation for Pakistan, with reference to the country of origin; and *lestes*, Gr. (masc.), robber, a common root for names of insectivore genera, in reference to the presumed predatory habits of this genus.

#### **Pakilestes lathrius**, new species

Pl. 2, fig. 1–6

*Holotype*.—GSP-UM 122, a right lower molar, presumably  $M_1$ .

*Referred material*.—GSP-UM 123, trigonid of a left ? $M_2$ ; and, questionably, GSP-UM 146, a left ? $P_4$ .

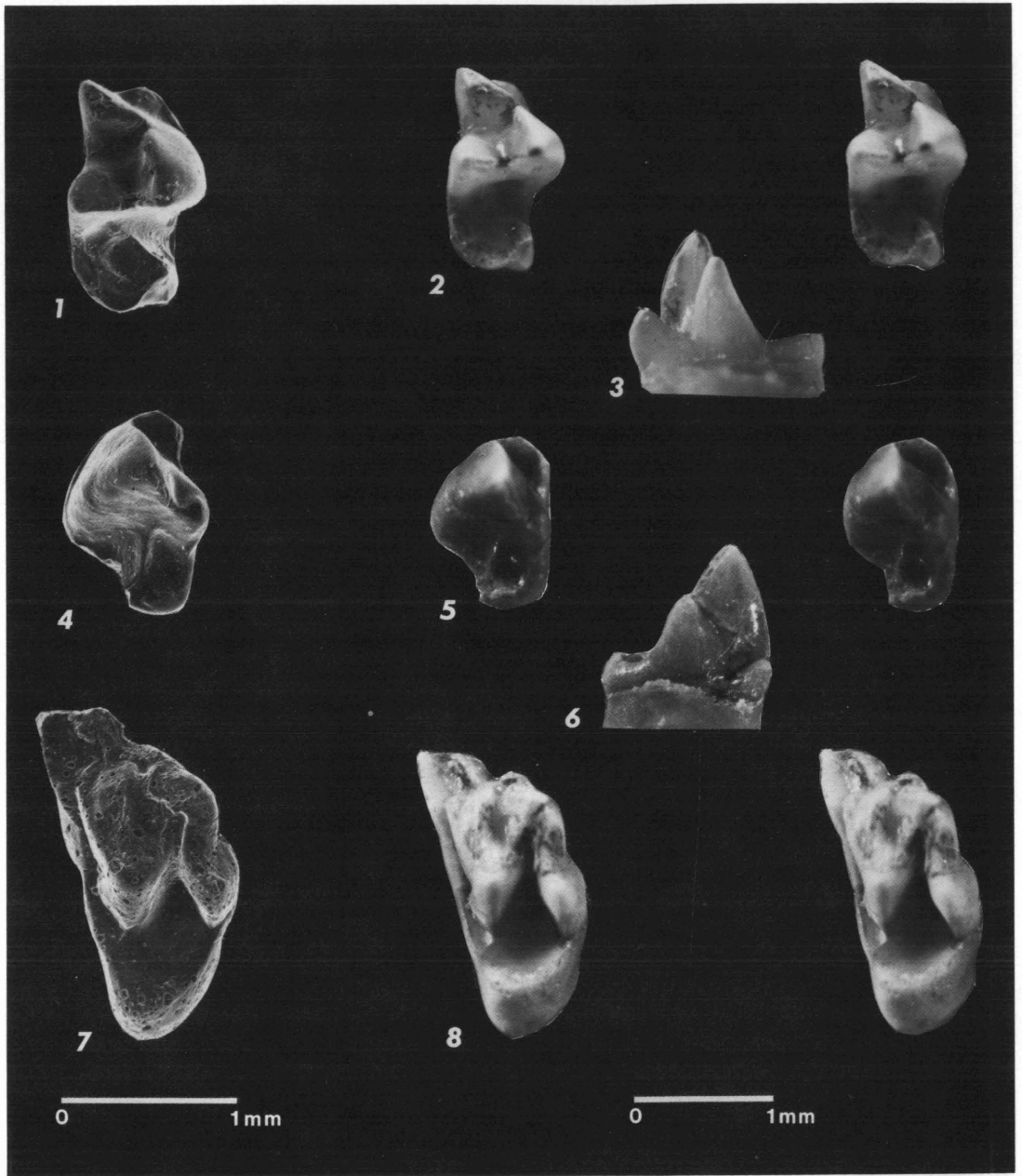
*Type locality*.—4 km NNW of Chorlakki village, Kohat District, North-West Frontier Province, Pakistan.

*Age and distribution*.—Late early Eocene or early middle Eocene of the Kuldana Formation, Kohat District, Pakistan.

*Diagnosis*.—As for the genus, see above.

*Etymology*.—*lathrios* (Gr.), hidden or secret; with reference to the relative inaccessibility of the Chorlakki locality.

*Description*.—The type specimen, GSP-UM 122, probably an  $M_1$ , belonged to an animal that was adaptively insectivorous. It has strong prevallid and postvallid shearing surfaces on the



## EXPLANATION OF PLATE 2

- Figure 1 — *Pakilestes lathrius*, right ?M<sub>1</sub> (GSP-UM 122, holotype) in occlusal view, scanning electron micrograph, x 25.  
 Figure 2 — *Pakilestes lathrius*, right ?M<sub>1</sub> (GSP-UM 122, holotype) in occlusal view, stereophotograph, x 20.  
 Figure 3 — *Pakilestes lathrius*, right ?M<sub>1</sub> (GSP-UM 122, holotype) in lingual view, x 20.  
 Figure 4 — *Pakilestes lathrius*(?), left ?P<sub>4</sub> (GSP-UM 146) in occlusal view, scanning electron micrograph, x 25.  
 Figure 5 — *Pakilestes lathrius*(?), left ?P<sub>4</sub> (GSP-UM 146) in occlusal view, stereophotograph, x 20.  
 Figure 6 — *Pakilestes lathrius*(?), left ?P<sub>4</sub> (GSP-UM 146) in lingual view, x 20.  
 Figure 7 — Chiropteran indet. A, left M<sup>3</sup> (GSP-UM 118) in occlusal view, scanning electron micrograph, x 25.  
 Figure 8 — Chiropteran indet. A, left M<sup>3</sup> (GSP-UM 118) in occlusal view, stereophotograph, x 20.



trigonid. The paraconid is strongly developed but low, and the high protoconid is the most prominent cusp. The trigonid is relatively broad, basined, and widely open lingually. Below the paralophid a heavy cingular shelf is present, which rapidly attenuates on the anterolabial base of the protoconid. Labially, along the vertical axis of the tooth, the trigonid is noticeably convex. The talonid is shorter and narrower than the trigonid; it is well basined and closed lingually. Neither an entoconid nor a hypoconulid is evident on the slightly worn crest encircling the talonid and, if formerly present, they could have been only weakly developed. A modest hypoconid rises slightly above the talonid rim, and the cristid obliqua connecting it and the posterior wall of the trigonid is concave and extends up on the trigonid to a point below and midway between the metaconid and the protoconid-metaconid notch. It is unusual to have the cristid obliqua join the metaconid so far lingually.

GSP-UM 123 is identified as the trigonid of a left ?M<sub>2</sub> because it is identical in preserved parts to GSP-UM 122 but slightly larger.

GSP-UM 146, tentatively identified as a left P<sub>4</sub>, is thought to represent *Pakilestes lathrius* because of its morphological similarity to the holotype, but the two were not found in association. As in the holotype, the protoconid of GSP-UM 146 is triangular in horizontal cross section and it is the dominant cusp on the trigonid. The paraconid is situated very low on the crown, and the metaconid is intermediate in height between the paraconid and protoconid. Labially (and vertically), the protoconid is markedly convex and a weak basal cingulum is present on the anterolabial surface of the trigonid. The metaconid is small, but distinct, and it is situated posterolingually from the protoconid. The talonid is particularly short and narrow, being restricted to an area behind the lingual half of the trigonid. Despite its small size, it is distinctly basined and closed lingually. It is possible that a small hypoconid was present but this area of the talonid is damaged; no other talonid cusps are developed. The cristid obliqua extends up rather high on the posterior trigonid wall to a level just below the protoconid-metaconid notch.

*Measurements.*—GSP-UM 122 (holotype), M<sub>1</sub>: anteroposterior length, 1.3 mm; labiolingual breadth, 0.9 mm. GSP-UM 146, ?P<sub>4</sub>: anteroposterior length, 1.15 mm; labiolingual breadth, 0.8 mm.

*Discussion.*—The holotype M<sub>1</sub>, GSP-UM 122, is striking because of two characteristics: its apparent carnassial adaptation and the narrowness of the talonid, particularly where this joins the trigonid. These features are seen in the early Eocene miacid species *Xinyuictis tenuis* from Yuanshui in Jiangxi and in *Miacis jepseni* from Wyoming. However, the molar indicates that *Pakilestes* was a much smaller form. The morphology of P<sub>4</sub>, if it is correctly referred to *Pakilestes*, is quite different from that seen in any Miacidae.

A more pertinent comparison can be made with the Gashato (late Paleocene or early Eocene of Mongolia) genera *Hyracolestes* and *Sarcodon*. Szalay and McKenna (1971) restudied these genera and considered them to be descendants of an early palaeoryctoid source whose earliest known member was *Deltatheridium* from the Late Cretaceous of Mongolia. They added *Sarcodon* (=“*Opisthopsalis*”) and *Hyracolestes* to the family Deltatheridiidae. Kielan-Jawarowska (1975) presented a thorough analysis of *Deltatheridium*, based on new well-preserved material, noting that its relationships to both eutherian and metatherian mammals are uncertain and that descendants of Deltatheridiidae are not known. This places *Sarcodon* and *Hyracolestes* back into the limbo they have so often frequented.

Van Valen (1966) was of the opinion that *Hyracolestes* and “*Opisthopsalis*” (not yet recognized as a synonym of *Sarcodon*) were barely separable generically, and he provisionally referred them to the Erinaceoidea. The type specimen of *Sarcodon*, however, is an upper molar with possible palaeoryctoid affinities (as seen also by Van Valen) and its synonymy with

"*Opisthopsalis*" by Szalay and McKenna (1971) is the principal justification for classification of these forms in Palaeoryctoidea. Their familial status remains even less certain. As noted by Van Valen,  $P_4$ - $M_1$  of *Sarcodon* (= "*Opisthopsalis*") and *Hyracolestes* are quite similar. But other features of the snout and anterior dentition described by Szalay and McKenna show the two genera to be distinct. All of this illustrates the pitfall inherent in attempting to fit fragmentary material (including that described here) into an as yet poorly understood classification of insectivores. With this in mind, we suggest that *Pakilestes* may be related at a family level to *Hyracolestes* and *Sarcodon*.

There is also some resemblance between *Pakilestes* and *Butselia*, a lipotyphlan from the early Oligocene of Hoogbutsel (Belgium). The resemblance of  $P_4$  and  $M_1$  in these two forms is too great to be ignored, although we can do little more than cite it until upper molars of *Pakilestes* are found for comparison with the distinctive upper teeth of *Butselia*. In the lower dentition the angle between the prevallid and postvallid shearing planes (i.e., between the paracristid and protocristid) of  $M_1$  is about  $40^\circ$  in *Pakilestes*, compared with  $44^\circ$  in *Butselia*,  $57^\circ$  in *Hyracolestes*, and  $50$ - $55^\circ$  in *Sarcodon*. This angle on  $P_4$  is about  $98^\circ$  in *Pakilestes*, compared with  $42^\circ$  in *Butselia*,  $23^\circ$  in *Hyracolestes*, and  $26^\circ$  in *Sarcodon*.

In summary, about all we can say about the relationships of *Pakilestes* is that it is an "insectivore", either a palaeoryctoid proteutherian, a soricomorph lipotyphlan, or perhaps a third as yet unrecognized group. The material presently available is inadequate to permit a more precise determination.

## Order CHIROPTERA

### Chiropteran indet. A

*Material*.—GSP-UM 118, left upper  $M^3$  (Pl. 2, fig. 7-8).

*Description*.—This specimen differs from  $M^3$  in all other chiropterans by a combination of features including possession of a long parastyle, a large prominent mesostyle with a strong labial indentation between it and the metacone, a metacone situated lingually with respect to the paracone, a V-shaped paracone that is labially wide but not very extended labiolingually, a postparaconule crista that is straight, faint, and short, a metacone confluent with the post-protocrista and lacking any premetaconule crista, and the absence of a basal lingual cingulum. In proportions, GSP-UM 118 is broader transversely and shorter anteroposteriorly than nearly all chiropteran third upper molars.

*Measurements*.—GSP-UM 118,  $M^3$ : anteroposterior length, 1.0 mm; labiolingual breadth, 1.9 mm. The parastyle is broken, and labiolingual breadth was measured from the labial notch between the parastyle and the mesostyle to the lingual edge of the tooth along an axis parallel to the anterior, nearly rectilinear, border. The anteroposterior length was measured perpendicular to the labiolingual breadth.

*Discussion*.—Compared to the earliest known bats (Eochiroptera of Van Valen, 1979, not the Paleochiroptera of Smith, 1976) GSP-UM 118 displays a distinct morphology. Its maximum anteroposterior diameter relative to labiolingual diameter is less than that found in *Icaronycteris*, *Ageina*, *Archaeonycteris*, and *Cecilionycteris*. However, it is closely approached by one of three specimens referred to *Icaronycteris? menui* (a species that is perhaps generically distinct from *Icaronycteris index*) and by a specimen of *Palaeochiropteryx*.

In addition to its more slender proportions, the  $M^3$  described here differs from that of *Icaronycteris* from the early Eocene of Wyoming in having a much longer parastyle (discernable even in its broken condition), a much larger mesostyle, a greater indentation between the mesostyle and metacone, a metacone situated lingually with respect to the paracone, a paracone

less extended transversely and wider labially, a postparaconule crista that is weaker and shorter, and by lacking both a short premetaconule crista and a basal lingual cingulum.

GSP-UM 118 differs from the  $M^3$  of *Ageina* (early Eocene of France) in its more slender proportions, possession of a (probably) longer parastyle, oblique posterolabial border with a prominent mesostyle, and metacone situated more lingually with respect to the paracone, and in lacking a basal lingual cingulum. The paracone of *Ageina* is short transversely, as in GSP-UM 118, but it is not as wide labially. The preparaconule crista is curved, short, and moderately strong, and the postmetaconule crista is absent.

Of the three (or four) species known of *Archaeonycteris*,  $M^3$  is known only in *A. brailioni* from the early Eocene of France and *A. revillodi* from the middle Eocene of Germany (in which the specimen lacks the parastyle through breakage). No mesostyle is present on these teeth, and GSP-UM 118 differs markedly in possessing a large cusp at this position. Moreover, the Pakistan tooth is more slender, with the metacone more lingually situated relative to the paracone. The paracone is less extended in transverse diameter. The Pakistan tooth lacks a basal cingulum, as does *A. revillodi*, but this cingulum is present anteriorly and posteriorly in *A. brailioni*. The postparaconule crista is poorly developed in *A. revillodi* and this crest is short and curved; the premetaconule crista is confluent with the postprotocrista. In *A. brailioni* the postparaconule crista is worn or incomplete, not touching the preprotocrista, while the premetaconule crista is absent (not confluent).

Compared with  $M^3$  of *Cecilonycteris prisca* from the middle Eocene of Germany (GH 2884), the Pakistan tooth displays a considerably more slender outline, a much longer parastyle, a mesostyle even more prominent than that in GH 2884, and a less sharply pointed and crestiform paracone and metacone. The metacone in GH 2884, as in GSP-UM 118, is situated lingually with respect to the paracone and the basal cingulum is absent lingually, although it is present anteriorly and posteriorly. *Cecilonycteris* differs from the Pakistan tooth in having an incomplete postparaconule crista, not touching the preprotocrista, and the premetaconule crista is absent.

The  $M^3$  of *Icaronycteris? menui* (Russell et al., 1973) from the early Eocene of France resembles GSP-UM 118 in proportions and in the presence of a long parastyle, but differs in lacking a prominent mesostyle. The paracone in the Pakistan tooth contrasts with that in two of the three  $M^3$ 's referred to the French species in being less extended transversely and wider labially, but a similar condition is seen in Louis-392 Mu, where the basal cingulum is also weak or lacking; the latter is strongly developed in the other two specimens. In GSP-UM 118 the metacone is situated more lingually than in *Icaronycteris?*. In the latter the postparaconule crista is slightly curved, stronger, and longer; the premetaconule crista is present but very short.

In *Palaeochiropteryx tupaiodon*,  $M^3$  is a slender tooth, approaching GSP-UM 118 in proportions (Russell and Sigé, 1970). As only a labial fragment of  $M^3$  is available for *P. speigeli* (both species from the Lutetian of Germany), its transverse diameter is unknown. *P. tupaiodon* has a long parastyle, a rather strong mesostyle, and a lingually positioned metacone, all of which resemble GSP-UM 118. Moreover, the basal cingulum is lacking lingually, although this is likely to be of minor importance since it is present anteriorly and posteriorly and it is probably variable. The postparaconule and premetaconule cristae are similarly developed. GSP-UM 118 differs, however, in the greater development of its mesostyle, which is concomitant with a marked posterolabial indentation in the posterior border of the crown labial to the metacone. Both the paracone and the metacone are more massive, and the small crestiform paraconule, present occasionally in *P. tupaiodon*, is absent.

A review of such early European microchiropteran genera or subgenera as *Vespertiliavus*, *Necromantis*, *Pseudorhinolophus*, *Paleophyllophora*, and *Rhinolophus* reveals a basic similarity in their  $M^3$  to the Pakistan tooth described here, although these differ considerably in

details. A closer approach to the morphology of GSP-UM 118 is seen in some specimens of *Stehlinia* (=“*PaleunycTERIS*”, “*Revillodia*”, and “*Nycterobius*”) and *Tadarida* (=“*Nyctinomus*”). In view, however, of the inconclusive nature of the single isolated tooth from Pakistan and the dental variation so prevalent in living bats, no special affinity can be proposed. If GSP-UM 118 is not an eochiropteran, it seems most similar to members of the Vespertilionoidea.

The primitive morphology of GSP-UM 118 permits its attribution to either suborder, Eochiroptera or Microchiroptera. This morphology is typical of that seen most commonly in chiropteran dentitions, indicating adaptation to a diet of insects. With the exception of Pteropodidae, Phyllostomatidae, and Desmodontidae, this dentition occurs with only minor variation in members of all remaining families of bats. Consequently, resolution of the ordinal and familial affinities of the Pakistan specimen is at present unfeasible.

#### Chiropteran indet. B

A fragment of a right lower chiropteran molar ( $M_1$  or  $M_2$ , GSP-UM 154, seems significantly larger than the  $M^3$  described above. Whereas the latter, GSP-UM 118, is about 10% larger than  $M^3$  in *Palaeochiropteryx tupaiodon*, comparable measurements of GSP-UM 154 and the lower  $M_1$  or  $M_2$  of *P. tupaiodon* indicate a size difference of about 35%. On this basis we postulate the presence of two bats in the Chorlakkii fauna. Since GSP-UM 154 represents the posterior part of a lower molar, it is possible to observe what Menu and Sigé (1971) called nyctalodonty, that is, a linkage of the hypoconulid and the hypoconid by the posterior crest of the tooth with isolation of the entoconid. It is of interest to note that the same condition exists in *Palaeochiropteryx*, although it is also the most prevalent state found in living microchiropterans. An isolated hypoconid, GSP-UM 119, from a left lower molar is also referable to Chiroptera. This specimen further substantiates the existence of a relatively large bat at Chorlakkii.

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