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SHORT COMMUNICATION

High bat (Chiroptera) diversity in the Early Eocene of India

Thierry Smith · Rajendra S. Rana · Pieter Missiaen · Kenneth D. Rose · Ashok Sahni · Hukam Singh · Lachham Singh

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Abstract The geographic origin of bats is still unknown, and fossils of earliest bats are rare and poorly diversified, with, maybe, the exception of Europe. The earliest bats are recorded from the Early Eocene of North America, Europe, North Africa and Australia where they seem to appear suddenly and simultaneously. Until now, the oldest record in Asia was from the Middle Eocene. In this paper, we report the discovery of the oldest bat fauna of Asia dating from the Early Eocene of the Cambay Formation at Vastan Lignite Mine in Western India. The fossil taxa are described on the basis of well-preserved fragments of dentaries and lower teeth. The fauna is highly diversified and is represented by seven species belonging to seven genera and at least four families. Two genera and five species are new. Three species exhibit very primitive dental characters, whereas four others indicate more advanced states. Unexpectedly, this fauna presents strong affinities with the European faunas from the French Paris Basin and the German Messel locality. This could result from the limited fossil record of bats in Asia, but could also suggest new palaeobiogeographic scenarios involving the relative position of India during the Early Eocene.

Keywords Chiroptera · Mammalia · Early Eocene · Vastan · India

T. Smith (✉)
Department of Palaeontology,
Royal Belgian Institute of Natural Sciences,
rue Vautier 29,
1000 Brussels, Belgium
e-mail: Thierry.Smith@naturalsciences.be

R. S. Rana · L. Singh
Department of Geology, H.N.B. Garhwal University,
Srinagar 246175 Uttaranchal, India

P. Missiaen
Aspirant FWO Vlaanderen, Research Unit of Palaeontology,
University of Ghent,
Krijgslaan 281-S8,
9000 Ghent, Belgium

K. D. Rose
Center for Functional Anatomy and Evolution,
Johns Hopkins University School of Medicine,
Baltimore, MD 21205, USA

A. Sahni
Centre of Advanced Study in Geology, Panjab University,
Chandigarh 160014, India

H. Singh
Birbal Sahni Institute of Palaeobotany,
53 University Road,
Lucknow 226007, India

Introduction

The earliest known bats are from the Early Eocene of the Paris Basin in France (Russell et al. 1973), the Green River Basin in Wyoming (Jepsen 1966), Chambi in Tunisia (Sigé 1991), and Queensland, Australia (Hand et al. 1994). Until now, the oldest record of bats in Asia was based on one tooth discovered in the early Middle Eocene of Pakistan (Russell and Gingerich 1981), and the first real bat fauna was described from the late Middle Eocene of Yuanqu Basin, China (Tong 1997).

The recent discovery of a few isolated bat teeth in the Early Eocene of western India at Vastan Mine, Gujarat (Rana et al. 2005) prompted us to make new excavations at the locality. Vastan Lignite Mine northeast of Surat exposes the Cambay Formation, which is of middle-late Ypresian age based on the presence of *Nummulites burdigalensis*. The mammal fauna is composed of typical endemic groups, such as anthracobunids, as well as the first modern mammals of India, including primates, artiodactyls, and rodents (Bajpai et al. 2005a; Rose et al. 2006). The most abundant and diversified mammals discovered are the bats, which are represented by jaws, isolated teeth, and bones. The Vastan bats are the oldest bats of Asia and represent, together with the European bats, the oldest bat faunas ever found. This paper discusses the systematics of the bats, based on the lower dentition, to highlight the extraordinary diversity observed of these earliest bats. The upper dentition and bones that confirm this diversity will be described in a second more detailed paper with a phylogenetic analysis of the early bats, including analysis of characters. The material here described and figured is sufficient to distinguish the taxa and necessary for their systematic attribution.

Abbreviations of institutes housed material from Vastan: GU/RSR/VAS—Garhwal University, Srinigar; IITR/SB/VLM—Indian Institute of Technology, Roorkee.

Systematic palaeontology

Order Chiroptera Blumenbach 1779

Sub-order Microchiropteramorpha Simmons and Geisler 1998

Family Icaronycteridae Jepsen 1966

Genus *Icaronycteris* Jepsen 1966

Icaronycteris sigei sp. nov.

Etymology For French palaeontologist Bernard Sigé, in recognition of his contributions to knowledge of early European and African bats.

Holotype GU/RSR/VAS 137 (Fig. 1a), nearly complete left dentary with P_3-M_2.

Referred specimens GU/RSR/VAS 136 (Fig. 1b), left dentary with $M_{1–3}$; GU/RSR/VAS 139, left dentary with P_4-M_3; GU/RSR/VAS 194, left dentary with P_4-M_3 (Table 1).

Diagnosis Dentary shallow with narrow symphysial surface and two mental foramina, below $I_{2–3}$ and below P_2. P_4-M_3 with well-developed paraconids and P_4 with very prominent metaconid; P_4 lacks partial lingual cingulum, unlike *I. menui*. Hypoconulid of $M_{1–3}$ lingually displaced and connected to entoconid by a crest. Larger (12–20%) than *I. index* and *I. menui*; dentary behind M_3 more elevated at base of ascending ramus than in *I. index*.

Discussion *Icaronycteris* has been considered to be the most plesiomorphic bat (Simmons and Geisler 1998). Its anatomy is known from exceptionally well-preserved skeletons of *I. index* from the Green River Formation, Wyoming

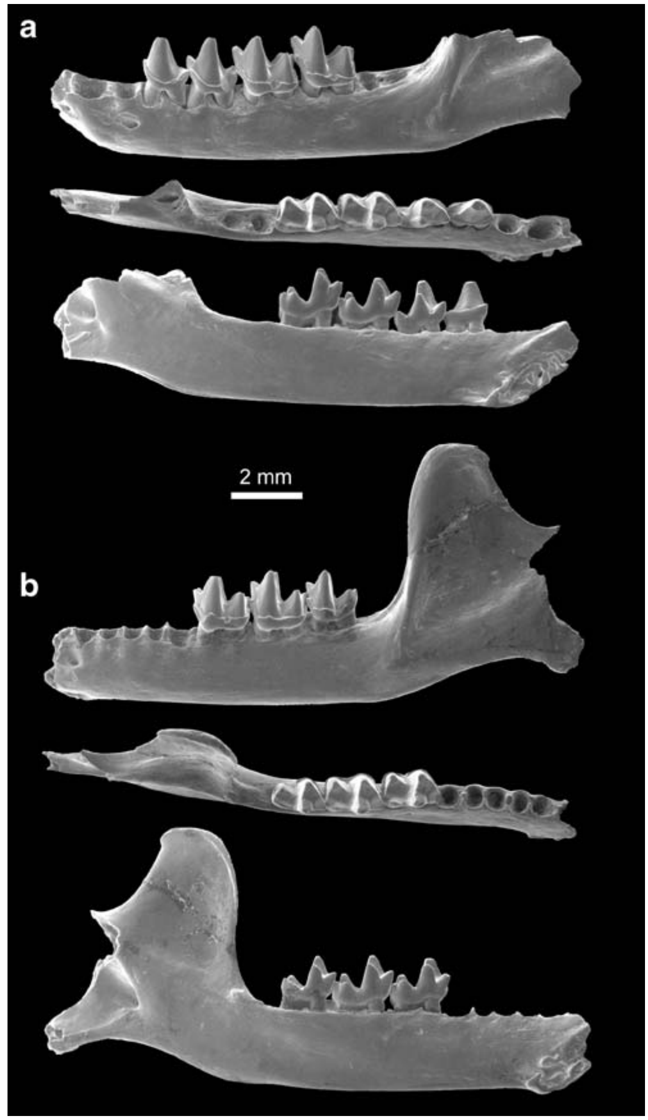

Fig. 1 *Icaronycteris sigei* sp. nov. **a** dentary with P_3-M_2 (GU/RSR/VAS 137), **b** dentary with $M_{1–3}$ (GU/RSR/VAS 136) in labial, occlusal, and lingual views

(Jepsen 1966; Simmons and Geisler 1998) and from isolated teeth of *I.? menui* from Mutigny and Avenay, France (Russell et al. 1973). We confirm here that the holotype and most of the teeth referred to *I.? menui* from Mutigny belong to the genus *Icaronycteris*. However, the material from Avenay is probably represented by a mix of two taxa. One of them appears to represent *Icaronycteris*, whereas the second indicates another genus more derived by the postcristid joining hypoconid to hypoconulid, with a notch between the entoconid and the hypoconulid (nyctalodonty).

Family Archaeonycteridae Revilliod 1917

Protonycteris gunnelli gen. et sp. nov.

Etymology The generic name refers to the primitive molar morphology of this bat; the species' name is for American

Table 1 Measurements of the figured specimens (in mm)

Specimen number	Description	Position		Measurements	
		Length		Width	
				Trigonid	Talonid
Icaronycteris sigei sp. nov.					
GU/RSR/VAS 137	Left dentary with P_3-M_2 (holotype)	P_3	1.30	0.80	
		P_4	1.50	0.90	
		M_1	1.80	1.15	1.10
		M_2	1.80	1.20	1.10
GU/RSR/VAS 136	Left dentary with M_{1-3}	M_1	1.70	1.15	1.10
		M_2	1.75	1.20	1.10
		M_3	1.55	1.05	0.75
Protonycteris gunnelli gen. et sp. nov.					
GU/RSR/VAS 436	Left dentary with P_3-M_3 (holotype)	P_3	1.65	1.05	
		P_4	1.75	1.15	
		M_1	2.00	1.40	1.40
		M_2	2.10	1.50	1.40
		M_3	1.90	1.35	1.05
Archaeonycteris storchi sp. nov.					
GU/RSR/VAS 140	Right dentary fragment with P_4-M_2 (holotype)	P_4	1.35	0.85	
		M_1	1.50	0.95	1.00
		M_2	1.55	1.05	1.00
Hassianycteris kumari sp. nov.					
GU/RSR/VAS 59	Left P_4		1.80	1.15	
GU/RSR/VAS 61	Right lower canine		1.65	1.35	
GU/RSR/VAS 56	Right M_1 or M_2		2.35	1.40	1.65
GU/RSR/VAS 561	Left M_1 or M_2		2.30	–	1.40
Cambaya complexus Bajpai et al. 2005a					
GU/RSR/VAS 435	Right dentary with P_4-M_3	P_4	1.35	0.80	
		M_1	1.75	1.00	1.05
		M_2	1.75	1.15	1.10
		M_3	1.60	1.10	0.80
Microchiropteryx folieae gen. et sp. nov.					
GU/RSR/VAS 96	Left dentary frag. with M_3	M_3	1.00	0.60	0.50
GU/RSR/VAS 459	Right dentary frag. with M_1 and M_3	M_1	1.20	0.60	0.70
		M_3	1.10	0.60	0.55
Jaegeria cambayensis Bajpai et al. 2005b					
GU/RSR/VAS 458	Left dentary frag. with P_4-M_1	P_4	1.00	0.70	
		M_1	1.35	0.90	0.95
GU/RSR/VAS 100	Left dentary frag. with M_{2-3}	M_2	1.35	0.95	0.90
		M_3	1.25	0.85	0.70

GU/RSR/VAS Garhwal University/Rajendra Singh Rana/Vastan

palaeontologist Gregg Gunnell for his contributions on early bat phylogeny.

Holotype and only known specimen GU/RSR/VAS 436 (Fig. 2a), nearly complete left dentary with P_3-M_3.

Diagnosis Lower molars short, wide, with posterolabially incomplete ectocingulum, strong hypoconid, relatively weak entoconid, slightly lingually shifted hypoconulid, short and weak oblique crest. P_4 with small, low paraconid, and prominent metaconid with long posterior crest. Two mental foramina present, below I_3 and below front of P_2; narrow symphysis. About the size of *Archaeonycteris trigonodon* but differs from it in having wider lower molars, incomplete labial cingulum, and more central hypoconulid.

Discussion Protonycteris is referred to archaeonycterid bats because of the weak entoconid, relatively labial oblique crest on the lower molars, and well-developed metaconid on P_4. *Protonycteris* is plesiomorphic in the position of the hypoconulid. However, P_4 appears to be derived relative to *Icaronycteris* in having less well-developed paraconid, metaconid, and talonid.

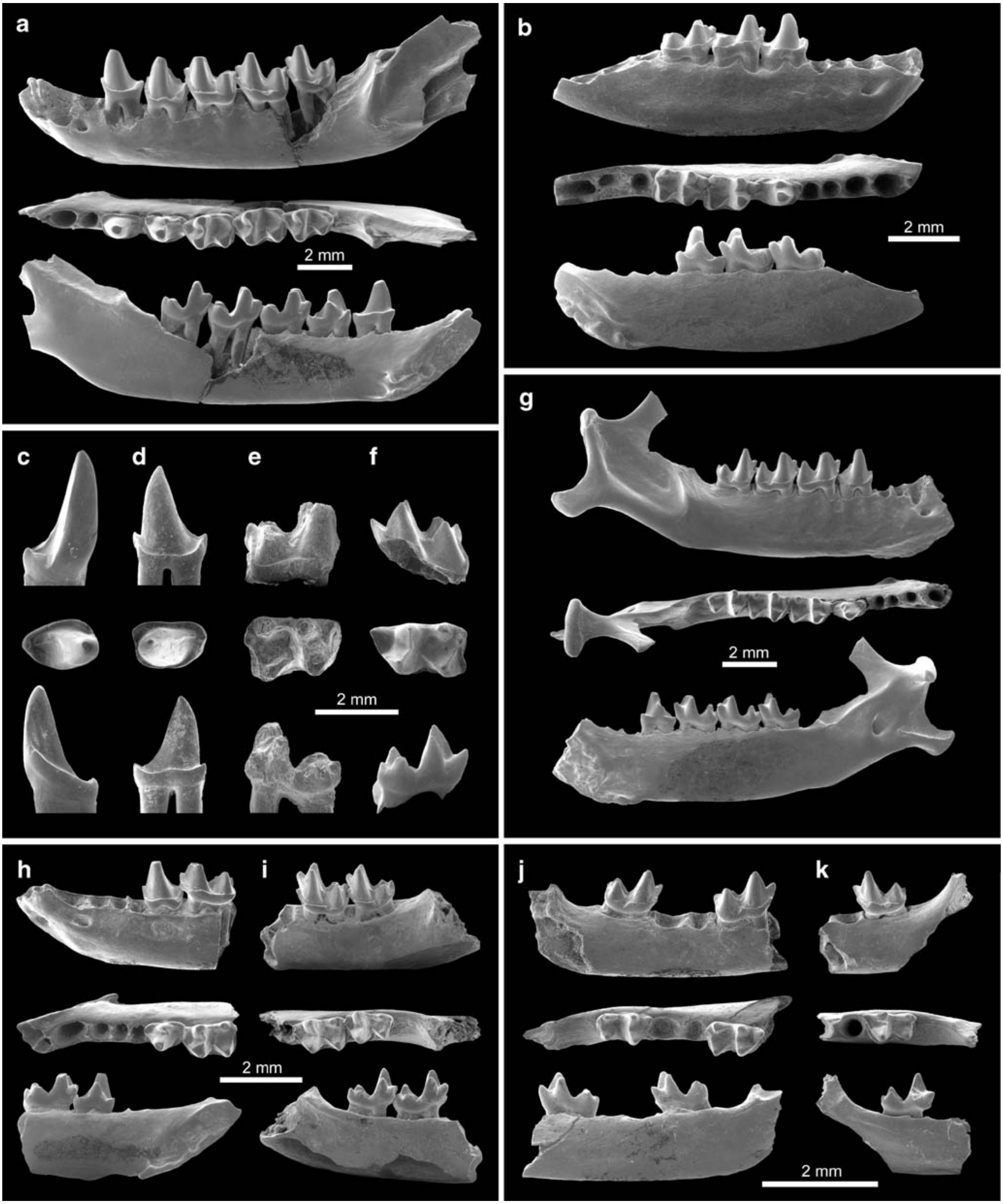

Fig. 2 **a** *Protonycteris gunnelli* gen. et sp. nov., dentary with P_3-M_3 (GU/RSR/VAS 436); **b** *Archaeonycteris*? *storchi* sp. nov., dentary fragment with P_4-M_2 (GU/RSR/VAS 140); **c**–**f** *Hassianycteris kumari* sp. nov. **c** lower canine (GU/RSR/VAS 61), **d** P_4 (GU/RSR/VAS 59), **e** M_1 or M_2 (GU/RSR/VAS 56), **f** M_1 or M_2 (GU/RSR/VAS 561); **g** *Cambaya complexus*, dentary with P_4-M_3 (GU/RSR/VAS 435); **h**–**i** *Jaegeria cambayensis* **h** dentary fragment with P_4-M_1 (GU/RSR/VAS 458), **i** dentary fragment with M_{2-3} (GU/RSR/VAS 100); **j**–**k** *Microchiropteryx folieae* gen. et sp. nov. **j** dentary fragment with M_1 and M_3 (GU/RSR/VAS 459), **k** dentary fragment with M_3 (GU/RSR/VAS 96)

Archaeonycteris? Revilliod 1917
Archaeonycteris? *storchi* sp. nov.

Etymology For German palaeontologist Gerhard Storch, in recognition of his contributions to the knowledge of early European bats.

Holotype GU/RSR/VAS 140 (Fig. 2b), right dentary fragment with P_4-M_2.

Referred specimen GU/RSR/VAS 135, left dentary fragment with M_{1-3}.

Diagnosis 35% smaller than *Archaeonycteris brailloni*, and 20–25% smaller than *A. trigonodon* and *Protonycteris gunnelli*. Differs from *A. brailloni* by the absence of a paracristid on P_4 and from *P. gunnelli* in having a somewhat deeper dentary, lower paraconid and metaconid on P_4, higher length/width ratio on lower molars, and more distinct and relatively stronger entoconid and hypoconulid with a deeper talonid basin.

Discussion This species is referred to archaeonycterid bats for the same reasons noted above for *Protonycteris gunnelli*, but it shares most of the characters with the genus *Archaeonycteris*. However, the absence in *A.? storchi* of a paracristid on P_4, which is present on P_4 of *A. brailloni* from Avenay (Russell et al. 1973), represents a more advanced state. A detailed analysis of the dental characters of *Archaeonycteris* should help to ascertain the generic attribution of *A*? *storchi*.

Family Hassianycterididae Habersetzer and Storch 1987
Genus *Hassianycteris* Smith and Storch 1981
Hassianycteris kumari sp. nov.

Etymology For Indian palaeontologist Kishor Kumar, for his contributions to the knowledge of Indian Eocene mammal faunas.

Holotype GU/RSR/VAS 59 (Fig. 2d), a left P_4.

Referred specimens GU/RSR/VAS 60, left P_4; GU/RSR/VAS 132, right P_4; GU/RSR/VAS 61 (Fig. 2c), right lower canine; GU/RSR/VAS 56 (Fig. 2e), right M_1 or M_2; GU/RSR/VAS 561 (Fig. 2f), left M_1 or M_2.

Diagnosis Canine tall, P_4 tall and premolariform, molars nyctalodont with wide talonid on M_{1-2} and strong entoconid. About the size of *H. magna*, 12–15% larger than *H. messelensis* and *H. revilliodi*, and 35% larger than "*Hassianycteris*" *joeli*. Differs from those species in having straighter ectocingulum on P_4 and from *H. revilliodi* in having taller canine and P_4.

Discussion This is the largest bat from Vastan. It is most similar to *H. magna* from the early Lutetian of Messel (Germany) and presents the typical derived characters for the genus *Hassianycteris*, including tall premolariform P_4, tall and straight lower canine, nyctalodont lower molars with wide talonid and well-developed entoconid. *H. joeli* from the late Ypresian of Belgium (Smith and Russell 1992) differs from other species of *Hassianycteris* by its small size, reduced P_4, narrow M_1, relatively central hypoconulid, and weak development of nyctalodonty. These characters are shared with *Honrovits tsuwape*, the oldest natalid bat from the late Early Eocene of Wyoming (Beard et al. 1992).

Family Hassianycterididae? Habersetzer and Storch 1987
Genus *Cambaya* Bajpai et al. 2005a
Cambaya complexus Bajpai et al. 2005a

Holotype IITR/SB/VLM 508, isolated left P_4.

Referred specimen GU/RSR/VAS 435 (Fig. 2g), nearly complete right dentary with P_4-M_3.

Emended diagnosis Dentary relatively deep, with wide, anteroventrally expanded symphysis and large mental foramen situated between C and P_2. P_4 with very low paraconid, long crest at back of prominent metaconid, short talonid, and incomplete lingual cingulum. Molars narrow and nyctalodont with long cristid obliqua, relatively low hypoconulid, high entoconid on M_{1-2}, and complete ectocingulum.

Discussion Bajpai et al. (2005a) described a P_4 from Vastan that they attributed to the first nyctitheriid insectivore from India. Although the tooth resembles P_4 of the Asian nyctitheriid *Bumbanius*, it more closely conforms to typical bat morphology, with a complete ectocingulum and a partial lingual cingulum mirroring those of P_4 in GU/RSR/VAS 435. Unfortunately, the holotype is a single tooth, but the more complete specimen described here eliminates any doubt that *Cambaya* is chiropteran, not nyctitheriid. *Cambaya complexus* presents several derived features such as the reduced paraconid and talonid on P_4, the development of the nyctalodonty on the lower molars, and a deeper dentary than in all other Vastan bats except perhaps *Hassianycteris*. These derived characters exclude allocation to Icaronycteridae or Archaeonycteridae. In some features, *Cambaya* resembles Palaeochiropterygidae, but the morphology of M_3 and the deep dentary with expanded symphysis are not typical of that family. The derived characters of *C. complexus* are present in Hassianycterididae, whereas the semi-molariform morphology of P_4 distinguishes *C. complexus* from *Hassianycteris*. *C. complexus* may represent a more primitive state than *Hassianycteris*.

Family Palaeochiropterygidae Revilliod 1917
Microchiropteryx folieae gen. et sp. nov.

Etymology The generic name refers to the very small size of this bat; the species name is for Belgian palaeontologist Annelise Folie for her contribution to the Indian Eocene vertebrate project.

Holotype GU/RSR/VAS 96 (Fig. 2k), left dentary fragment with M_3.

Referred specimens GU/RSR/VAS 459 (Fig. 2j), right dentary fragment with M_1 and M_3.

Diagnosis Lower molars very small, long and narrow, and strongly nyctalodont. M_3 with well-basined, square talonid, entocristid parallel to the long axis of the tooth, and postcristid perpendicular to the long axis of the tooth. Differs from *Palaeochiropteryx tupaiodon* and *P. spiegeli* in having narrower lower molars and more labial cristid obliqua.

Discussion This very small bat is rare in Vastan. It is referred to Palaeochiropterygidae because of its small size, narrow, nyctalodont lower molars, well-developed anteroposteriorly elongated entoconid, and the orientation of the M_3 entocristid and postcristid. These last two characters result in the square shape of the talonid similar to that of M_3 in *Palaeochiropteryx*, *Cecilionycteris*, and *Lapichiropteryx*. *Microchiropteryx*, however, is much smaller than the other genera.

Family indet.
Genus *Jaegeria* Bajpai et al. 2005b
Jaegeria cambayensis Bajpai et al. 2005b

Holotype IITR/SB/VLM/585, left M_1 or M_2.

Referred specimens GU/RSR/VAS 458 (Fig. 2h), left dentary fragment with P_4-M_1; GU/RSR/VAS 100 (Fig. 2i), left dentary fragment with $M_{2–3}$.

Emended diagnosis Dentary shallow with two mental foramina, below I_3 and below the back of the *C. alveolus*. P_4 with low paraconid, well-developed metaconid, and short, rounded talonid. $M_{1–3}$ nyctalodont with very lingual hypoconulid just posterior to entoconid and long cristid obliqua forming an acute angle with the posterior crest. M_3 with somewhat reduced talonid basin.

Discussion Bajpai et al. (2005b) described a few lower teeth from Vastan as the first fossil marsupials of India, including one lower molar attributed to peradectines and one lower molar and three tooth fragments attributed to herpetotheriines. However, comparisons with the bats described here indicate that the holotype and only complete tooth of the purported herpetotheriine *Jaegeria cambayensis* is a left M_1 or M_2 of a nyctalodont bat; additionally, more complete specimens are referred to the species here. The diagnostic characters of *J. cambayensis* indicate that it is not referable to Icaronycteridae, Archaeonycteridae, or Hassianycterididae. It might belong to a primitive palaeochiropterygid, a new family, or perhaps an extant family.

Diversity and affinities of Early Eocene Indian bats

The bat fauna from Vastan is the earliest known from both India and Asia. Surprisingly, it also represents the most diverse known Early Eocene bat fauna. However, none of the seven Vastan bats seems to belong to an extant family, with the possible exception of *J. cambayensis*, which has not been definitively identified at the family level.

Where known, all these bats seem to have a lower jaw with three incisors, three premolars, and an elongate angular process (Simmons and Geisler 1998). Of the seven species, three are particularly primitive (*Icaronycteris sigei*, *Protonycteris gunnelli*, and *Archaeonycteris*? *storchi*) based on having an unreduced metaconid on P_4 and tribosphenic molars that are not yet nyctalodont (Russell and Sigé 1970). The new genus *Protonycteris* is phylogenetically significant because it has an incomplete ectocingulum and a nearly central hypoconulid on the talonid basin. The presence of an ectocingulum and lingual displacement of the hypoconulid has been considered important synapomorphies of bat molars, and their incipient development in *Protonycteris* indicates its very plesiomorphic position.

The four other species (*Hassianycteris kumari*, *Cambaya complexus*, *Jaegeria cambayensis*, and *Microchiropteryx folieae*) are more derived in having nyctalodont teeth. *J. cambayensis* and *M. folieae* are well advanced in nyctalodonty and could represent precursors to myotodonty (in which the postcristid runs to the entoconid) based on the hypoconulid being almost fully lingual and just posterior to the entoconid. This last condition is especially evident on the M_3 of *M. folieae*.

The resemblance of the Indian bat fauna from Vastan to Eocene European bat faunas is astonishing. This is especially the case with the bats from the late Early Eocene of the Paris Basin (Russell et al. 1973) and the early Middle

Eocene of the German Messel locality (Habersetzer and Storch 1987; Storch et al. 2002). The similarity could simply result from the fact that most Eocene bats are European and early Eocene Asian bat faunas are unknown (Gunnell and Simmons 2005). The only Asian genus close to the Indian taxa is *Lapichiropteryx* from the late Middle Eocene of Yuanqu Basin, China (Tong 1997). This palaeochiropterygid bat shares several characters with *Microchiropteryx*, but comparison below the family level is difficult because *Microchiropteryx* is insufficiently known. The poorly diversified North American bat faunas and the absence of bats in Early Eocene Central Asian faunas may also suggest new palaeobiogeographic scenarios implicating the relative position of India and connections with Europe during the Early Eocene.

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