

Early Eocene rodents (Mammalia) from the Subathu Formation of type area (Himachal Pradesh), NW sub-Himalaya, India: Palaeobiogeographic implications

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Based on isolated upper cheek teeth, two new early Eocene rodents (*Subathumys solanorius* gen. et sp. nov. and *Subathumys globulus* gen. et sp. nov.) and three others (*Birbalomys* cf. *sondaari*, *Birbalomys* sp., cf. *Chapattimys* sp.) are recorded from the lower–middle part of the Subathu Formation of the type area in Himachal Pradesh, northwestern sub-Himalaya (India). The new rodents exhibit morphological features most similar to the unified ctenodactyloid family Chapattimyidae (including Yuomyidae), which is also represented in the assemblage from the upper part (middle Eocene) of the Subathu Formation. The associated lower cheek teeth are provisionally described as three indeterminate chapattimyd taxa. The new Subathu rodents are somewhat younger than the previously documented early Eocene assemblages from the Indian subcontinent, and are chronologically intermediate between the early Eocene ailuravines from Gujarat in the western peninsular India and the middle Eocene chapattimyids from northwestern India and Pakistan. They suggest that chapattimyids originated in the sub-Himalayan region during the Ypresian, which is earlier than previously believed. The absence of ailuravines in this as well as younger rodent assemblages from the subcontinent seems to suggest that ailuravines (Ischyromyidae), within a relatively short time after their appearance in the peninsular India in the early Eocene, may have been replaced by the indigenous chapattimyids. The co-occurrence in the early Eocene Subathu assemblage of three or more chapattimyids indicates their early radiation and dominance during the early and middle Eocene. This record of rodents opens the possibility of recovery of other small mammal remains in older levels of the Subathu Formation, which will be important for understanding linkage with early Eocene faunas from peninsular India, Europe and North America.

1. Introduction

Until about a decade ago, the Eocene terrestrial mammals in India were known only from a middle Eocene level of the late Paleocene–middle Eocene Subathu Formation in the northwestern sub-Himalaya (Ranga Rao 1971; Sahni and Khare 1973; Kumar and Sahni 1985; Kumar 1991, 1992; Kumar *et al.* 1997a, b). Recently, however, a variety of small and small–medium sized mammals has been

documented from the early Eocene (~54–53 Ma) Cambay Shale Formation in Vastan (Gujarat), peninsular India (Rana *et al.* 2004, 2008; Bajpai *et al.* 2005; Rose *et al.* 2009a, b, 2013; Kumar *et al.* 2010). In the Vastan mammal fauna, several taxa have closer affinities with European than with Asian relatives, suggesting a terrestrial faunal link between India and Eurasia close to the Paleocene–Eocene transition (Smith *et al.* 2007; Rana *et al.* 2008; Rose *et al.* 2009a, b, 2013; Kumar *et al.* 2010). This

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revelation and the need to probe further the palaeobiogeographic scenarios with respect to India–Asia convergence and land mammal faunas of the critical late Paleocene–early Eocene interval prompted us to revisit the Subathu horizons in the sub-Himalayan region and focus on its older part. Our initial work on the early Eocene Subathu beds has yielded fossils of rodents, which bear significantly on the early radiation of Rodentia on the subcontinent, and form the basis of this contribution (figure 1).

The earliest known fossil rodents come from the late Paleocene of Asia and North America (Rose 1981; Li *et al.* 1987; Dawson and Beard 1996; Meng and Li 2010), but the group began to diversify only in the early Eocene. In South Asia, Eocene rodents were first recorded from the middle Eocene horizons (Lutetian) – the Subathu Formation in India and the Kuldana Formation in Pakistan. From India, a diverse assemblage of Eocene rodents has been known from the uppermost part of the Subathu Formation of Himachal Pradesh as well as Jammu and Kashmir (Sahni and Khare 1973; Sahni and Srivastava 1976; Kumar *et al.* 1997a, b). Most of the rodents from this stratigraphic level have been referred to a rather diverse family Chapattimyidae (Ctenodactyloidea), which was then restricted in the Indo-Pakistan region, and a few to a closely similar Eastern and Central Asiatic family Yuomyidae (Kumar *et al.* 1997a, b). Across the border in Pakistan, a coeval terrestrial mammal yielding horizon in the Kuldana Formation of Kala Chitta Range (Punjab) yields a nearly identical assemblage of middle Eocene chapattimyids and yuomyids (Hussain *et al.* 1978; Hartenberger

1982; Dawson *et al.* 1984; Thewissen *et al.* 2001). In contrast to fairly diverse assemblages from the middle Eocene horizons, the record of early Eocene rodents from the Indian subcontinent is rather limited both in terms of number of specimens as well as species diversity even though it is considered crucial for understanding the early radiation of Eocene rodents in the south Asian region (De Bruijn *et al.* 1982; Bajpai *et al.* 2007; Rana *et al.* 2008).

Herein we describe a new early Eocene rodent assemblage from a significantly older stratigraphic level in the lower-middle part of the Subathu Formation of the stratotype area in the Solan District of Himachal Pradesh – the fossiliferous level falls in Mathur and Juyal's (2000) faunal zone IV (*Cordiopsis subathooensis*–*Turritella subathooensis* zone), which is considered to be of an early Eocene (late Ypresian) age based on foraminiferal biostratigraphy. Prior to this report, early Eocene rodents in the Indian subcontinent were known only from the subsurface beds of the Cambay Shale Formation 'exposed' in the Vastan open cast lignite mine near Surat (Gujarat) in peninsular India (Bajpai *et al.* 2007; Rana *et al.* 2008) and from the Mami Khel Clay in Barbara Banda, Kohat District, northern Pakistan (De Bruijn *et al.* 1982).

The early Eocene rodents recorded here from Subathu represent two species of a new rodent genus *Subathumys* and three other taxa (*Birbalomys* cf. *sondaari*, *Birbalomys* sp. and cf. *Chapattimys* sp.), all having clear affinities with the ctenodactyloid families Chapattimyidae and Yuomyidae, which are also represented in the middle Eocene assemblage from the Subathu Formation. It may be mentioned here that both *Birbalomys* and *Chapattimys*, particularly the former, are dominant in the middle Eocene (Lutetian) assemblage from the Indo-Pakistan region (Hussain *et al.* 1978; Kumar *et al.* 1997a, b). The European ailuravine (Ischyromyidae) *Meldimys* recorded from the early Ypresian of peninsular India or any other ailuravine seems to be absent in the Subathu Formation. Similarly, cocomyids present in the early Eocene of Pakistan have not been found in the Subathu fauna so far. The record of early Eocene rodents from Subathu has multi-fold significance:

- it is the first report of rodent fossils from the early Eocene horizons of the Subathu Formation,
- the familial affinities of this assemblage are distinct from those of the previously known early Eocene rodent assemblages from India and Pakistan,
- it extends the antiquity of chapattimyids and yuomyids to the early Eocene, and
- age-wise this assemblage is intermediate, i.e., older than the one from the middle Eocene horizons (Lutetian) of the Subathu and Kuldana

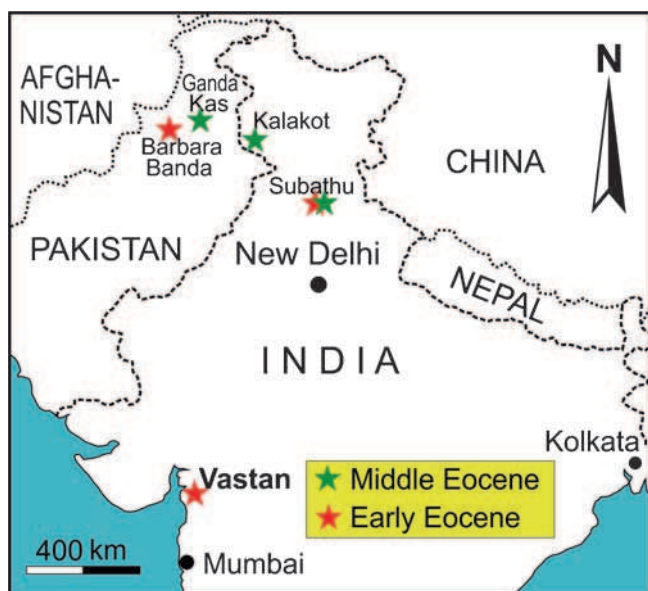


Figure 1. Map of the Indian subcontinent showing the early and middle Eocene rodent sites.

formations and younger than that from the early Eocene (~54–53 Ma, early Ypresian) Cambay Shale Formation of peninsular India and probably also younger than that from the early Eocene Mami Khel Clay of northern Pakistan.

The new fossils have implications on palaeobiogeography and early radiation of rodents in south Asia.

2. Geological setting

The rodent material described in this paper was recovered from the red beds in the lower-middle part of the late Paleocene–middle Eocene Subathu Formation exposed in a tributary of the Kuthar River near the cantonment town of Subathu (30°57'50"N; 76°58'33"E) in the Solan District of Himachal Pradesh, northwestern India (figure 2). The Subathu Formation represents the last phase of the Tethys Sea in the northwest sub-Himalayan

region and is exposed from Jammu and Kashmir in the northwest through the states of Himachal Pradesh (stratotype area) and Uttarakhand to Nepal in the southeast (Singh 1980; Nanda and Kumar 1999; Kumar and Loyal 2006). It overlies the Precambrian Simla Slates in Himachal Pradesh and Sirban Limestone in Jammu and Kashmir and is overlain by the continental deposits of the Murree Group (=Dagshai and Kasauli formations/Dharamsala Formation). It is richly fossiliferous and yields foraminifers, mollusks and fish remains, etc., almost throughout its thickness (Kumar and Loyal 1987; Kumar 1989; Mathur and Juyal 2000). The marine mammal remains occur mostly in the lower-middle part (Sahni and Kumar 1980; Sahni *et al.* 1980a, b; Bajpai and Gingerich 1998) and land mammals mostly in the upper part of the Subathu Formation (Ranga Rao 1971; Sahni and Khare 1973; Sahni *et al.* 1980a, b; Ranga Rao and Mishra 1981; Kumar and Sahni 1985; Kumar

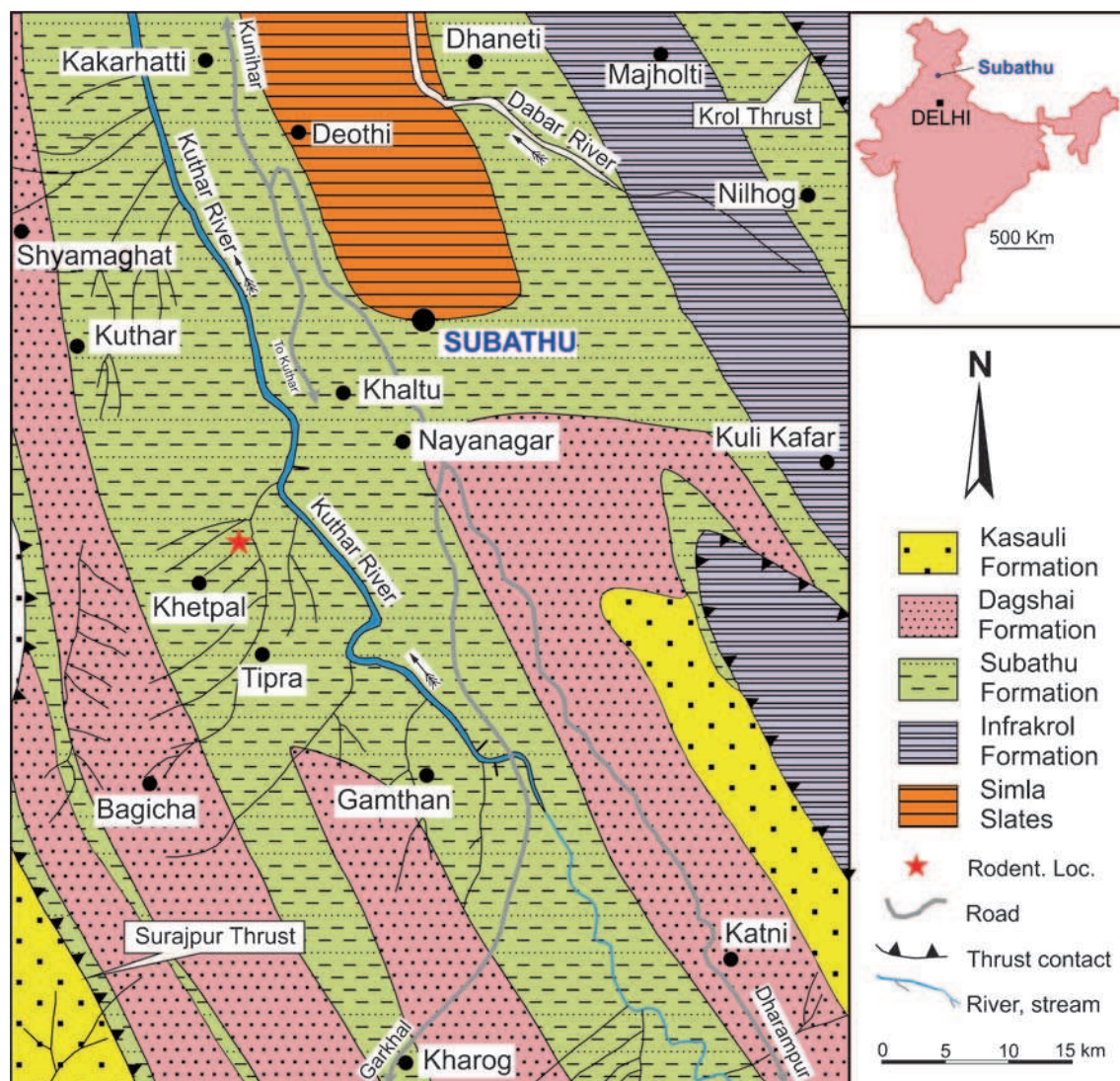


Figure 2. Geological and location map of the Subathu town in the Solan District of Himachal Pradesh showing the early Eocene rodent-yielding site; inset shows the position of Subathu in the map of India (after Kumar and Loyal 2006).

and Jolly 1986; Kumar 1991, 1992, 2000; Srivastava and Kumar 1996; Kumar *et al.* 1997a, b). The land mammal remains, prior to this work, were documented only from the red beds occurring in the terminal part of the Subathu Formation, which is equivalent to Mathur and Juyal's (2000) faunal zone VIII (*Musculus nuttalli*–*Parinomya blanfordiana* zone). A generalized lithological log of the Subathu Formation showing foraminiferal zones and land mammal yielding horizons is shown in figure 3.

The Subathu Formation is largely a shallow marine grey–green shale–limestone succession with

subordinate siltstone and sandstone, having continental red beds in its terminal part, which yield a variety of land vertebrates, including rodents of middle Eocene age (Kumar and Sahni 1985; Kumar *et al.* 1997a, b). However, in its stratotype area (Subathu, Himachal Pradesh) the red beds are also present in the lower–middle part of the Subathu Formation, indicating a short episode of sea regression (Mathur and Juyal 2000; Kumar and Loyal 2006). These red beds, here referred as the older Subathu red beds, yielded the rodents described herein. They are not present in the Subathu

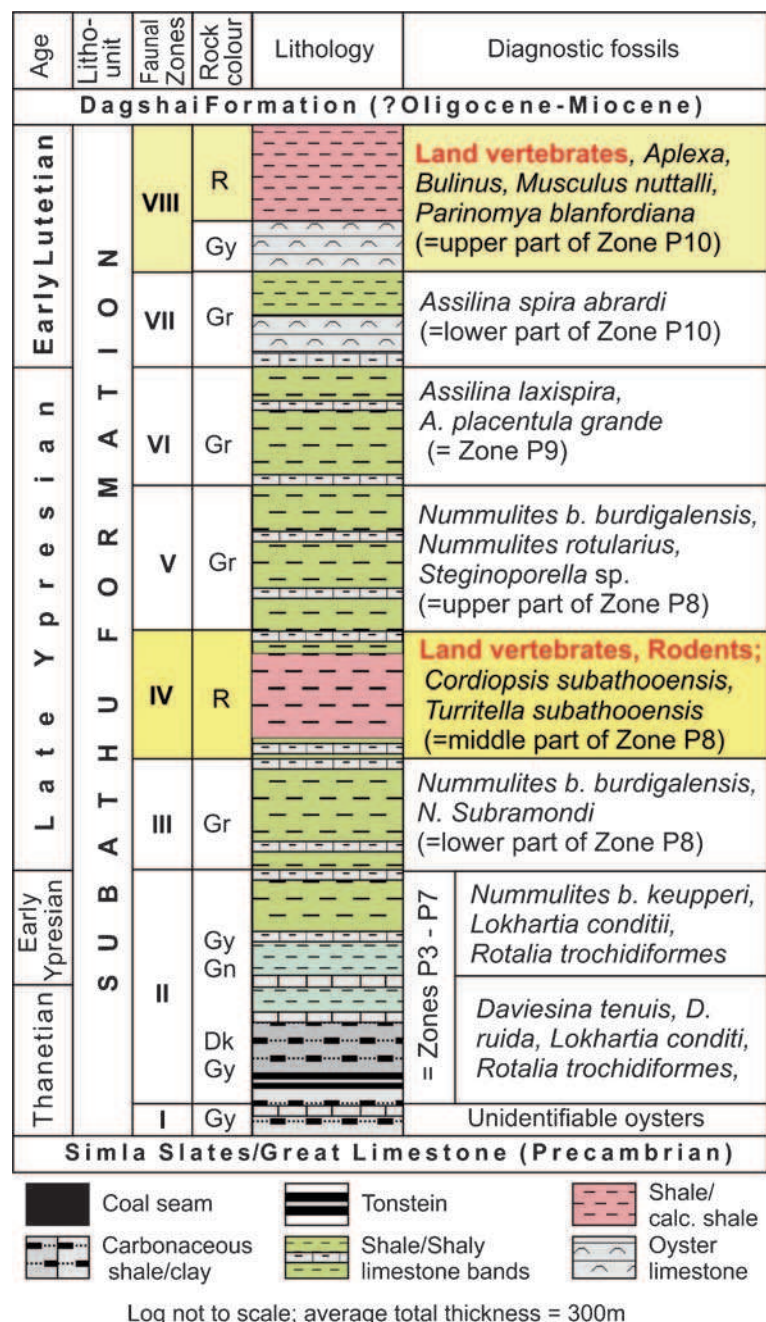


Figure 3. Generalized lithological log of the Subathu Formation showing the foraminiferal zonation (after Mathur and Juyal 2000) and the position of older and younger Subathu red beds.

succession of other well known vertebrate rich areas, such as Kalakot, Metka and Mohgala in Jammu and Kashmir (Singh 1980; Kumar and Sahni 1985).

The older Subathu red beds comprise a ~30 m thick zone of brownish red shales that occur as a distinct lithological unit within the shallow marine grey-green shale–limestone unit (figure 4). They correspond to Mathur and Juyal's (2000) faunal zone IV (*Cordiopsis subathoensis*–*Turritella subathoensis* zone) and are considered to be of late Ypresian age based on foraminiferal biostratigraphy. They are generally poorly fossiliferous – gastropods and rodent remains have so far been recovered from just a couple of sites along the Kuthar River that flows by the side of Subathu town. The rodent yielding fossiliferous shale is lensoidal with a maximum thickness

of ~20 cm. The fossiliferous shale at times has clayey granules and is very similar to the middle Eocene rodent bearing granule stone in the terminal part of the Subathu Formation (=younger Subathu red beds). In thin sections of the fossiliferous shale, fragmentary bones and teeth and some gastropods can be seen (figure 5). The grey-green shale–limestone beds that underlie the older Subathu red beds are rich in turritellid gastropods.

3. Materials and methods

The new rodent material from the Subathu Formation comprises 17 isolated cheek teeth and several incisor fragments. Post-cranials, possibly of rodents

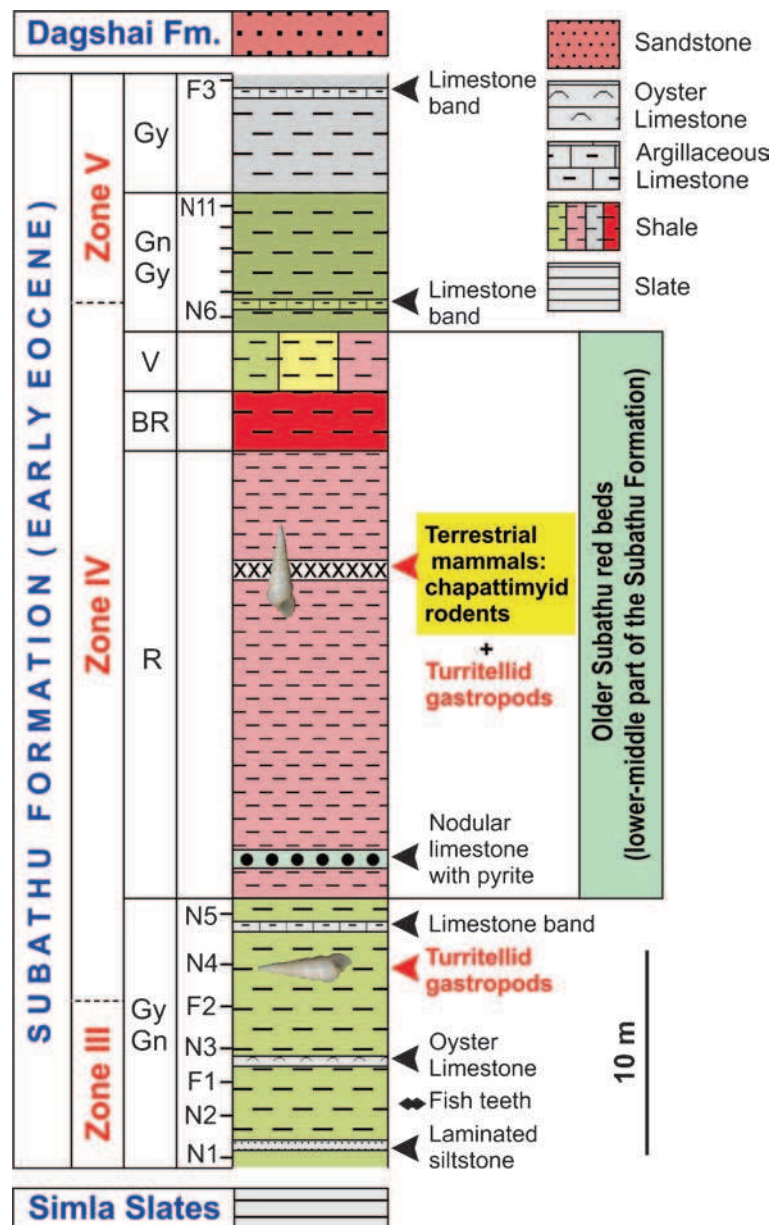


Figure 4. Lithological log of a part of the Subathu Formation showing the older Subathu red beds and the position of early Eocene rodent yielding level.

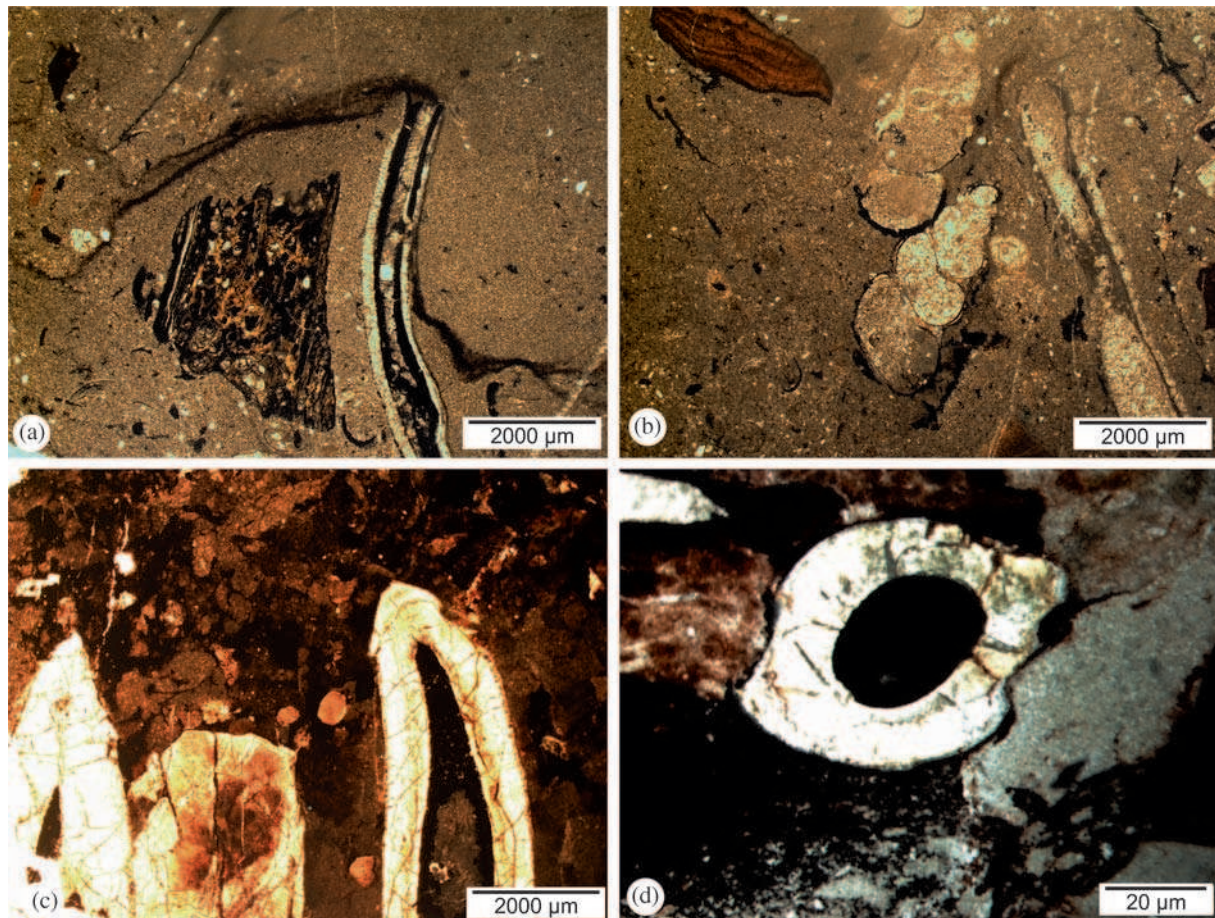


Figure 5. Photomicrographs of rodent-yielding fossiliferous sediments from the older Subathu red beds of the Subathu Formation showing bone and teeth fragments (a, c, d) and gastropods (b).

and/or other small mammals are too fragmentary and unidentifiable. Other vertebrate remains found associated with rodents include siluroid fish teeth, isolated teeth of ziphodont crocodilians, and a fragmentary tooth of an unidentified small mammal other than a rodent. Of the 17 teeth, eleven including a P3, are from the upper jaws and six from the lower. Morphologically, they exhibit clear affinities with chapattimyids and yuomyids (Ctenodactyloidea), which as already mentioned are also known from a younger level (Lutetian) of the Subathu Formation (Kumar *et al.* 1997a, b). Their chapattimyid–yuomyid affinity is corroborated by the two P4s in the collection, which are molariform thus precluding relationship with ctenodactylids and/or cocomyids, which have also been reported from the subcontinent (De Bruijn *et al.* 1982). Moreover, dominant middle Eocene chapattimyid *Birbalomys* is also represented in the collection. There are no lower premolars in the collection. The teeth are easily distinguishable from ailuravines (Ischyromyidae), which have recently been documented from the peninsular India (Rana *et al.* 2008) by following characters: larger hypocone, smaller parastyle and mesostyle and missing crest

that descends from the protocone in the talon on upper molars, and less isolated entoconid and missing or very reduced mesoconid (incorporated in the ectolophid) on lower molars (figure 6).

The upper teeth are referable to two species of a new rodent genus (*Subathumys*), and three other taxa closely related to middle Eocene forms. A few teeth currently described as indeterminate species may turn out to be distinct when additional material is collected and studied because in such a small collection of isolated teeth, intraspecific variations are difficult to account for. We have conscientiously refrained from attributing lower teeth to the newly erected or to other identified taxa as we found it difficult to ascertain as to which lower teeth will go with which upper and *vice versa*. Therefore, based on difference in size and morphology, the lower teeth are described separately under three categories, viz., Chapattimyidae indet. 1, Chapattimyidae indet. 2 and Chapattimyidae indet. 3 pending formal generic and specific assignments, when additional material is forthcoming.

All fossil materials treated herein were recovered from the same stratigraphic level and locality mostly by screen-washing of matrix using gasoline

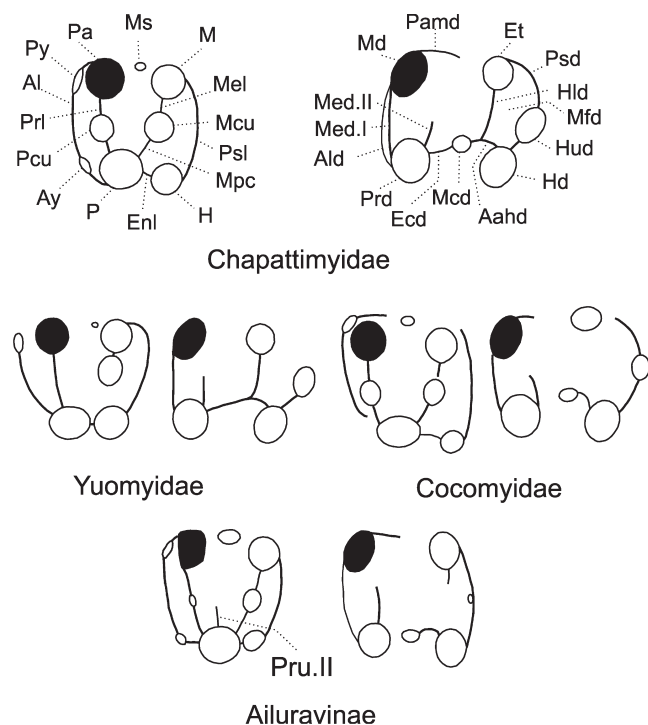


Figure 6. Schematic showing comparison of occlusal dental patterns of upper (left) and lower (right) molars for Chapattimyidae, Yuomyidae, Cocomyidae and Ailuravinae (modified after Marivaux *et al.* 2004). *Upper molars*: Al: anteroloph; Ay: anterostyle; Enl: endoloph; H: hypocone; M: metacone; Mcd: metaconule; Mel: metaloph; Mpc: metacone-protocone connection; Ms: mesostyle; P: protocone; Pa: paracone; Pcu: protoconule; Prl: protoloph; Pru.II: protolophule II; Psl: posteroloph; Py: parastyle. *Lower molars*: Aahd: anterior arm of hypoconid; Ald: anterolophid; Ecd: ectolophid; Et: entoconid; Hd: hypoconid; Hld: hypolophid; Hud: hypoconulid; Mcd: mesoconid; Md: metaconid; Med.I: metalophulid I; Med.II: metalophulid II (=protolophid or posterior arm of protoconid); Mfd: metafossettoid; Pamd: posterior arm of metaconid; Prd: protoconid; Psl: posterolophid.

and water. A couple of teeth were extracted directly from the exposure surface. The quality of preservation of isolated teeth is variable, but generally good. We found no evidence of any post-mortem deformation, though some teeth have suffered variable amount of damage, which is ascribed to post-depositional breakage. In this paper, the upper premolars and molars are indicated by P and M, respectively, and lower molars by m. The dental terminology adopted here follows Escarguel (1999) and is depicted in figure 7. The method of measurement of teeth adopted here follows Kumar *et al.* (1997b) and the measurements are given in table 1. All dimensions shown in table 1 against length and width represent maximum measured values rather than anterior/posterior and/or trigonid/talonid width, etc.

Repository: All fossils described and illustrated in this paper are catalogued as WIMF/A (Wadia

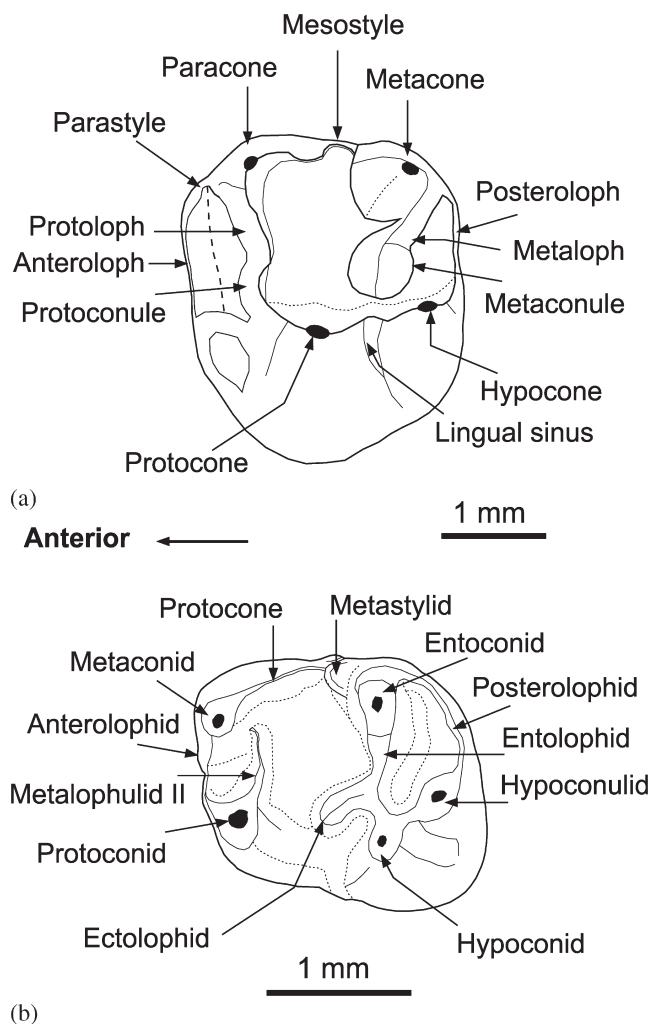


Figure 7. Dental terminology used for describing upper and lower molars. (a) *Subathumys solanorius* gen. et sp. nov., WIMF/A 1636 (holotype), LM2; (b) Chapattimyidae indet. 1, WIMF/A 1626, Lm1. Both specimens are from the older red beds (early Eocene) of the Subathu Formation.

Institute Microfossil Collection) numbers and stored in the repository of the Wadia Institute of Himalayan Geology at Dehradun (India).

4. Systematic palaeontology

Class: Mammalia Linnaeus 1758
Order: Rodentia Bowdich 1821
Superfamily: Ctenodactyloidea Tullberg 1899
Family: Chapattimyidae Hussain *et al.* 1978 (McKenna and Bell 1997)

Genus *Subathumys* nov.

Etymology: Named after 'Subathu', a cantonment town in the Solan District of Himachal Pradesh, near where the fossiliferous site is situated.

Type species: *Subathumys solanorius* sp. nov.

Table 1. Measurements (in mm) of isolated upper and lower cheek teeth of early Eocene rodents from the older red beds of the Subathu Formation, Solan District, Himachal Pradesh, northwestern sub-Himalaya, India.

Genus and species	Specimen no.	Tooth	Length	Width	Crown area (L × W)	Length-width ratio (L/W)
<i>Subathumys solanorius</i> gen. et sp. nov.	WIMF/A 1636	LM2	2.10	2.52	5.292	0.833
<i>S. solanorius</i> gen. et sp. nov.	WIMF/A 1620	RM1	2.00	2.24	4.480	0.892
<i>S. globulus</i> gen. et sp. nov.	WIMF/A 1635	RM2	2.20	2.32	5.104	0.948
<i>Birbalomys</i> cf. <i>sondaari</i>	WIMF/A 1625	RM1	2.04	2.32	4.733	0.879
<i>Birbalomys</i> sp.	WIMF/A 1622	RP4	1.82	1.80	3.276	1.011
<i>Birbalomys</i> sp.	WIMF/A 1628	LM1-2	1.56	1.84	2.870	0.847
<i>Birbalomys</i> sp.	WIMF/A 1621	RM1-2	2.14	2.24*	4.793	0.955
<i>Birbalomys</i> sp.	WIMF/A 1633	RM2	1.94	2.20	4.268	0.881
cf. <i>Chapattimys</i> sp.	WIMF/A 1623	LP4	1.58	2.20	3.476	0.718
cf. <i>Chapattimys</i> sp.	WIMF/A 1629	LM1	1.86	2.30	4.278	0.808
Chapattimyidae indet. 1	WIMF/A 1626	Lm1	1.96	1.78	3.488	1.101
Chapattimyidae indet. 1	WIMF/A 1631	Rm3	2.52	2.10	5.292	1.2
Chapattimyidae indet. 2	WIMF/A 1627	Lm1	2.08	1.74	3.619	1.195
Chapattimyidae indet. 2	WIMF/A 1634	Lm3	2.38	1.98	4.712	1.202
Chapattimyidae indet. 3	WIMF/A 1632	Lm2	1.48	1.52	2.249	0.973
Rodentia indet.	WIMF/A 1630	P3	1.06	1.24	1.314	0.854
Rodentia indet.	WIMF/A 1624	Rm2-3	2.08*	1.54*	3.203	1.350

*Estimate based on reconstruction.

Diagnosis: Differs from *Birbalomys* and *Chapattimys* in having anterior upper molars with hypocone substantially smaller than protocone and not shifted lingually in relation to protocone and also in having an interrupted metaloph that converges towards the protocone, but does not join it. Similar to *Meldimys musak* from peninsular India in having a reduced hypocone and an externally extended mesostyle, but differs in lacking a crest that descends from the protocone into the trigon basin, possessing a weaker parastyle, stronger protoconule and an interrupted metaloph (not joined to protocone).

***Subathumys solanorius* sp. nov.**
(Figure 8a, c; table 1)

Etymology: Solan+-orius, Latin, place (district of Solan) where the type locality is situated.

Holotype: WIMF/A 1636, an isolated left upper second molar (LM2).

Referred material: WIMF/A 1620, an isolated left upper first molar (RM1).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Diagnosis: Differs from *Subathumys globulus* in having anterior upper molars with normal rather than inflated lingual cusps, more reduced hypocone and in possessing a distinct mesostyle.

Description and remarks: M1-2 are characterized by their hypocone, which is substantially

smaller than the protocone and is not shifted lingually in relation to the protocone. In fact, in the holotype (LM2), the protocone lobe clearly protrudes more lingually than the hypocone. In M2, the protocone and hypocone are more widely separated than in M1. The protocone is massive and the largest cusp; the paracone is larger than the metacone. The protoconule is smaller than the metaconule and lies on the protoloph closer to the protocone than to the paracone. The protoloph is complete unlike the metaloph, which converges towards the protocone but terminates at the metaconule rather than joining the protocone. The metaloph converges towards the midpoint on the endoloph rather than towards the apex of the protocone, making the trigon 'U' shaped unlike in other chapattimyids in which it is rather 'V' shaped. The shelf between the anteroloph and protoloph is anteroposteriorly broad. The anteroloph terminates anterior to the apex of the protocone; the posteroloph is distinct and extends to the tip of the hypocone. The parastyle is weak, whereas the mesostyle is distinct and slightly lingually extended as in *Meldimys*. A pronounced sinus is situated between the protocone and the hypocone.

The ailuravine *Meldimys* and the yuomyid *Advenimus* are also known to have a reduced hypocone (smaller than the protocone). *Subathumys* differs clearly from *Meldimys* in lacking a crest that descends from the protocone into the trigon basin, in weaker parastyle, and in metaloph that does not join the protocone. In M1-2 referred to

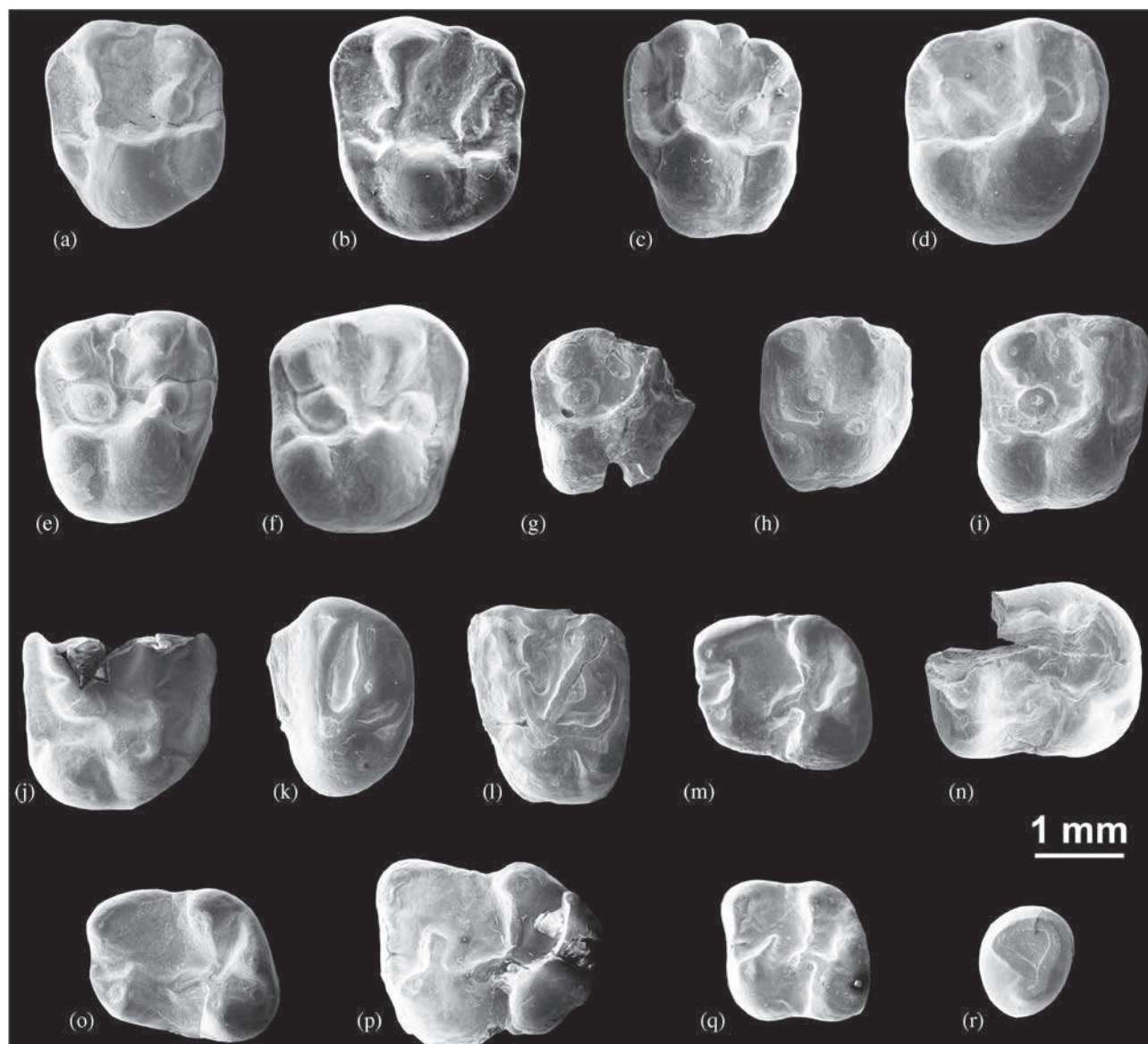


Figure 8. Isolated cheek teeth of chapattimyid rodents from the early Eocene older Subathu red beds, lower-middle part of the Subathu Formation, Subathu, Himachal Pradesh (India). Scale bars represent 1 mm. (a–c) *Subathumys solanorius* gen. et sp. nov. (a, c) compared with cf. *Petrokoslovia* sp. indet. 1 (b) from the younger Subathu red beds, (a) left M2 (WIMF/A 1636); (b) left M2 (WIMF/A 1210); (c) right M1, reversed (WIMF/A 1620); (d) *Subathumys globulus* gen. et sp. nov., right M2 (WIMF/A 1635); (e–f) *Birbalomys* cf. *sondaari* (e) compared with *Birbalomys sondaari* (f) from the younger Subathu red beds, (e) right M1 (WIMF/A 1625); (f) left M1-2, reversed (WIMF/A 1187); (g–j) *Birbalomys* sp. (g) right P4 (WIMF/A 1622); (h) left M1-2, reversed (WIMF/A 1628); (i) right M2 (WIMF/A 1633); (j) right M1-2 (WIMF/A 1621); (k, l) cf. *Chapattimyus* sp.; (k) left P4 (WIMF/A 1623); (l) left M1 (WIMF/A 1629); (m–n) Chapattimyidae indet. 1 (m) left m1 (WIMF/A 1626); (n) partly damaged right m3, reversed (WIMF/A 1631); (o–p) Chapattimyidae indet. 2 (o) left m1 (WIMF/A 1627); (p) left m3 (WIMF/A 1634); (q) Chapattimyidae indet. 3 left m2 (WIMF/A 1632); (r) Rodentia indet. P3 (WIMF/A 1630).

Advenimus cf. *burkei* by Averianov (1996), the metaconule is smaller than the metacone, and a distinct protoconule is present. It may be mentioned here that the attribution of some upper dentitions from the early Eocene of Kyrgyzstan to *Advenimus* by Averianov (1996) needs to be confirmed as opined by Dashzeveg and Meng (1998). The lower cheek teeth of *S. solanorius* gen. et sp. nov. are yet to be recognized.

The holotype M2 of *Subathumys solanorius* gen. et sp. nov. has a striking morphological and metrical resemblance with a tooth described as cf. *Petrokoslovia* sp. indet. 1 from the middle Eocene beds of the Subathu Formation of Kalakot area in Jammu and Kashmir, India (Kumar *et al.* 1997b; Plate 3, figure 31). However, the tooth from Kalakot (WIMF/A 1210, figure 8b) has a more pronounced anteroloph that extends lingually up to the base of

protocone rather than terminating anterior to the apex of protocone. Further, it has a small ledge-like lingual cingulum between protocone and hypocone, an anteroposteriorly broader shelf between the anteroloph and protoloph, a stronger parastyle, a smaller metacone, an interrupted endoloph and weaker protoconule–protocone connection. It is possible that the two specimens may turn out to be congeneric/conspecific when additional material is found and studied. *Petrokoslovia* (= *Petrokozlovia*) is a yuomyid known from the middle Eocene of Mongolia and Kazakhstan (Shevyreva 1972, 1976). *Petrokoslovia* is characterized by a weak hypocone which is at the same level as the protocone and not lingually or labially shifted, lack of metaconule–protocone connection, protoconule submerged in protoloph to absent, and a well-developed parastyle (Marivaux *et al.* 2004). In *Subathumys solanorius* gen. et sp. nov., the hypocone is not at the same level as the protocone but somewhat labially positioned and the parastyle is weaker.

***Subathumys globulus* sp. nov.**

(Figure 8d; table 1)

Etymology: Epithet ‘globulus’ refers to globular shape of tooth with inflated lingual cusps.

Holotype: WIMF/A 1635, an isolated right upper second molar (RM2).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Diagnosis: Differs from *Subathumys solanorius* in having globular anterior upper molars with inflated lingual cusps, less reduced hypocone and in lacking a mesostyle.

Description and remarks: M2 is globular with noticeably inflated (bunodont) protocone and hypocone, which are well separated from each other. The protocone is the largest and highest cusp; the hypocone is smaller than the protocone, but less than in *Subathumys solanorius*. The paracone is larger than metacone and the two cusps are more widely separated from each other than in *S. solanorius* (figure 8a, c) and *Birbalomys* sp. (figure 8g–j). A mesostyle is absent or indistinct. An apparently large protoconule is incorporated in the protoloph. The metaconule is larger than the protoconule; it is massive and somewhat transverse than the roundish and conical one in *S. solanorius*. The metaloph is directed towards the apex of the protocone, but it terminates at the metaconule and does not join the protocone. The valley between the protoloph and anteroloph is anteroposteriorly broad and nearly as deep as the trigon basin. The anteroloph does not join the apex of the protocone

but terminates much below and anterior to it. The lingual sinus between the protocone and the hypocone is shallower and more open than in *Subathumys solanorius* and *Birbalomys* sp. The lower cheek teeth of *S. globulus* gen. et sp. nov. are yet to be recognized.

Birbalomys* cf. *sondaari (Hussain *et al.* 1978) (Figure 8e; table 1)

Referred material: WIMF/A 1625, an isolated right upper first molar (RM1).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: WIMF/A 1625, an unworn M1 differs from all other anterior molars in the collection in possessing an interrupted protoloph and a large inflated protoconule, which is isolated from the paracone but connected to the protocone. Its metaconule is also inflated, nearly as large as the metacone and a little larger than the protoconule. The metaconule is slightly isolated from the metacone and widely isolated from the protocone. The protoloph is interrupted; its labial part after descending from the paracone lingually towards the protoconule, turns posteriorly, terminating into the trigon basin rather than joining the protoconule, which is connected to the protocone. This tooth has striking morphological and metrical resemblance with the anterior molars of the middle Eocene chapattimyid *Birbalomys sondaari* (Kumar *et al.* 1997b; Plate 2, figures 7–9) in the position and morphology of protoconule and protoloph, but teeth of the latter taxon differ in having (i) a hypocone clearly lingually shifted in relation to protocone, (ii) a metaconule, which is weakly connected to the protocone, (iii) a weaker parastyle, (iv) the shelf between the protoloph and anteroloph anteroposteriorly broader, and (v) an anteroloph, which extends lingually up to the base of the protocone rather than terminating on protocone (figure 8f).

The morphological differences between the anterior molars of *B. sondaari* and the tooth described here may just be representing intraspecific variation, but the same cannot be said conclusively until additional material is forthcoming.

***Birbalomys* sp.** (Sahni and Khare 1973) (Figure 8g–j; table 1)

Referred material: WIMF/A 1621, an isolated partly damaged right upper M1-2; WIMF/A 1622, an isolated right upper fourth premolar (RP4); WIMF/A 1628, an isolated left upper first or second molar (LM1-2); WIMF/A 1625 right upper

first molar (RM1); WIMF/A 1633, isolated right upper second molar (RM2).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: The cheek teeth have close morphological similarity with the teeth of various species of the middle Eocene rodent *Birbalomys*. However, they differ from the known species of *Birbalomys* mainly in possessing an interrupted metaloph as opposed to an uninterrupted one in the latter taxon. P4 is nearly as long as broad, whereas M1-2 are broader than long. P4 and M1-2 have subequal protocone and hypocone; hypocone is slightly shifted further lingually in relation to the protocone or is at the same level as the protocone. Metaloph converges towards the protocone, but does not join it; it is connected to the metacone. An indistinct protoconule is incorporated into the protoloph, which is complete. A mesostyle is present, but unlike the case in *Subathumys solanorius* it is not extended externally. The posteroloph is higher than the anteroloph and is connected to the hypocone without any sinus in between. The anteroloph joins the anterior arm of protocone. A parastyle is present.

WIMF/A 1621 (RM1-2) is squarish and lacks its labial part, including apices of paracone and metacone; metaconule is large; metaloph converges towards the protocone and appears weakly connected to it. The tooth is characterized by the presence of a distinct lingual sinus between the posteroloph and the hypocone unlike the situation in *Chapattimys* and *Subathumys*. In this respect as well as in general, this tooth is similar to M2 in the holotype of *Birbalomys woodi* (Kumar *et al.* 1997b; Plate 1, figure 1).

Teeth of *Birbalomys* sp. differ from those of *Subathumys solanorius* gen. et sp. nov. in having subequal hypocone and protocone on P4-M2, from *Subathumys globulus* gen. et sp. nov. in having rectangular rather than globular upper cheek teeth with normal rather than inflated lingual cusps and possessing a mesostyle, and from the known species of *Chapattimys* in having (i) an interrupted metaloph, which is not connected to the protocone, (ii) a hypocone, which is almost at the same level as the protocone rather than being markedly lingually shifted, and (iii) in being not so lophate. A definitive taxonomic (specific) assignment of fossils referred here to *Birbalomys* sp. will be attempted when more teeth are recovered.

cf. *Chapattimys* sp. (Hussain *et al.* 1978)
(Figure 8k, l; table 1)

Referred material: WIMF/A 1623, an isolated left upper P4; WIMF/A 1629, an isolated left upper M1.

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: Cheek teeth differ from those of *Subathumys*, *Birbalomys* cf. *sondaari* and *Birbalomys* sp. described here in possessing an uninterrupted metaloph and are similar to known species of *Birbalomys* and *Chapattimys* on this feature. Metaloph converges towards the protocone and is clearly connected to it. Protoconule is indistinct, probably incorporated in the protoloph. WIMF/A 1623 and 1629 are more transverse (broader than long) than the teeth of *Birbalomys*, but are similar to those of *Chapattimys* in being distinctly lophate. P4 is characterized by its roundish posterior margin and rather closely placed paracone and metacone making the trigon basin very narrow with a biconvex outline rather than 'V' shaped. It has some resemblance with the P4 of *Chapattimys wilsoni* described by Hussain *et al.* (1978; Plate 4, figure 1) from the middle Eocene of Pakistan, but differs in being over 20% larger, having more closely situated paracone and metacone and in possessing a larger metaconule, which is not incorporated in the metaloph. The M1 is quite worn with a somewhat lingually protruded hypocone, a large metaconule and distinct 'V' shaped and uninterrupted protoloph and metaloph giving the tooth a lophate appearance. Due to its much worn nature, it is difficult to compare it with the known species of *Chapattimys*. However, in size it compares well with *C. debruinji*.

***Chapattimyidae* indet. 1** (Hussain *et al.* 1978)
(Figure 8m, n; table 1)

Referred material: WIMF/A 1626, an isolated left lower first molar (Lm1); WIMF/A 1631, partly damaged right lower third molar (Rm3).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: The m1 shows a mix of chapattimyid and yuomyid characters: hypoconulid and hypoconid situated closer together and connected by a ridge; hypoconulid and entoconid situated wider apart, but connected by the posterolophid; entolophid nearly transverse and joins the ectolophid; mesoconid indistinct; ectolophid curved and incomplete, terminates at the posterior slope of protoconid; posterior arm of metaconid long and high; a small metastylid present between metaconid and entoconid; metalophulid II well developed, high

and straight/transverse (rather than directed towards entoconid) extending to the posterolabial slope of metaconid thus closing the trigonid basin from the talonid. Among the known chapattimyids, WIMF/A 1626 has considerable morphological resemblance with the m1 (WIMF/A 1148) of *Birbalomys vandermeuleni* from the middle Eocene of Kalakot (Kumar *et al.* 1997b; Plate 3, figure 2), in features like short ectolophid and long and high posterior arm of metaconid. However, the m1 of *B. vandermeuleni* is substantially smaller and also differs in possessing a prominent cingular ledge between the hypoconid and hypoconulid.

WIMF/A 1631, a rather large m3 is characterized by its rectangular shape and differs from the other m3 (WIMF/A 1634, Chapattimyidae indet. 2) in the collection in being posteriorly as wide as anteriorly, rather than narrower. Further, its hypoconulid and entoconid are connected by a high posterolophid, entolophid or hypolophid is very weak to absent, and the anterior arm of entoconid is characteristically higher and longer. A distinct hypoconulid is incorporated in the posterolophid. A small mesostylid is present. An ectolophid appears more complete than in other lower teeth and extends almost to the apex of the protoconid. A part of the tooth with metaconid is missing. WIMF/A 1631 has some morphological resemblance with m3 (WIMF/A 1146) of *B. vandermeuleni* from the middle Eocene of Kalakot (Kumar *et al.* 1997b; Plate 3, figure 4), particularly in features like overall shape of tooth, high posterolophid incorporating hypoconulid and high and long anterior arm of entoconid, however, the m3 of latter species is substantially smaller with a posteriorly protruded hypoconulid lobe.

Chapattimyidae indet. 2 (Hussain *et al.* 1978) (Figure 8o, p; table 1)

Referred material: WIMF/A 1627, an isolated left lower first molar (Lm1); WIMF/A 1634, an isolated left lower third molar (Lm3).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: WIMF/A 1627 is of the same size as another m1 in the collection (WIMF/A 1626, Chapattimyidae indet. 1) described above, but differs mainly in having (i) a hypoconulid almost equidistant from hypoconid as well as entoconid (=postero-centrally placed) rather than being closer to hypoconid, (ii) a hypoconulid that is connected neither to hypoconid nor to entoconid, i.e., posterolophid is absent, (iii) slightly posteriorly directed entolophid that does not join the ectolophid, (iv) a

rather straight ectolophid with a small mesostylid, and (v) a weaker and shorter metalophulid II that does not extend as far towards the metaconid leaving the trigonid open posteriorly. A metastylid is not discernible. WIMF/A 1627 shows considerable morphological and metrical resemblance with m1-2 (WIMF/A 1199) of *Birbalomys sondaari* from the middle Eocene of Kalakot (Kumar *et al.* 1997b; Plate 2, figure 3), especially in postero-centrally placed hypoconulid, however, the latter has more bunodont cusps. Differs from both *Birbalomys* and *Chapattimyids* in having shorter ectolophid and in lacking hypoconulid–entoconid connection (posterolophid).

The m3 is posteriorly narrower substantially as in *Birbalomys* and *Chapattimyids* with a massive protoconid, a large metaconid and a hypoconulid well separated from the hypoconid as well as the entoconid. It is somewhat larger to go with the two m1s in the collection and more so with the lone m2. Yet it has been provisionally associated with one of the two m1s (WIMF/A 1627) based on similarities like a transverse entolophid that joins the thicker ectolophid, well separated hypoconid and hypoconulid, and a similarly oriented but longer metalophulid II. The morphology and size of the present m3 is broadly similar to those of *Birbalomys*. It differs from m3 of *B. woodi* in being shorter and less narrower posteriorly, and in possessing a stronger entolophid and a nearly straight metalophulid II.

Chapattimyidae indet. 3 (Hussain *et al.* 1978) (Figure 8q; table 1)

Referred material: WIMF/A 1632, an isolated left lower second molar (Lm2).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: WIMF/A 1632 (m2) is considerably smaller than both the m1s (WIMF/A 1626 and WIMF/A 1627) and m3s (WIMF/A 1631 and WIMF/A 1634) as well as most upper teeth, except P3, in the collection and hence almost certainly represents a distinct taxon. Morphologically, it is more akin to WIMF/A 1626 (Chapattimyidae indet. 1, figure 8m) than to WIMF/A 1627 (Chapattimyidae indet. 2, figure 8o) except in possessing a shorter metalophulid II, which is directed towards the entoconid rather than towards the metaconid, a lower posterolophid between entolophid and hypoconulid, a shorter ectolophid, and in lacking a metastylid. A mesostylid is apparently absent.

Among the known chapattimyids, the present tooth is comparable, in size, only to the middle Eocene taxa *Birbalomys ijlsti* and to a lesser extent to *B. vandermeuleni*. However, morphologically, it displays closer resemblance to the m2 of *B. vandermeuleni* (Kumar *et al.* 1997b, Plate 3, figure 3), particularly in the development and orientation of entolophid and metalophulid II, hypoconid–hypoconulid connection and a shorter ectolophid, but differs in being almost squarish, lacking a mesostylid (on the ectolophid) possessing a cingular ledge between the protoconid and the hypoconid and in possessing a distinct cingular ledge below the hypoconid–hypoconulid.

Rodentia indet. (Bowdich 1821)
(Figure 8r; table 1)

Referred material: WIMF/A 1630, an isolated upper third premolar (P3).

Horizon and locality: Lower Eocene (Ypresian) older Subathu red beds of the Subathu Formation of stratotype area, Subathu (30°57'50"N; 76°58'33"E), Solan District, Himachal Pradesh.

Description and remarks: P3 is rather large and well preserved. Among the Eocene rodents from the Indo-Pakistan region, a P3 is known only for the middle Eocene chapattimyid *Birbalomys woodi*, in which it is preserved with other teeth in the holotype skull (Sahni and Khare 1973). Compared to P4, the present P3 is not as small as of *B. woodi*, which appears as a rudimentary peg-like tooth without evidence of any occlusion (Sahni and Khare 1973; Kumar *et al.* 1997b; Plate 1, figure 1). In contrast, the present P3 has a distinct occlusal morphology, indicating its functional nature (figure 8r). A P3 is present in all ctenodactyloid families (Cocomyidae, Chapattimyidae, Yuomyidae, Tamquamidae) except Ctenodactylidae (Wang 1994). Based on size, the present P3 could well go with either of the taxa described here except perhaps Chapattimyidae indet. 3, which is represented by a rather small m2.

5. Discussion

5.1 Composition of early Eocene rodent assemblages from South Asia

There are now three early Eocene rodent assemblages known from the Indian subcontinent: (i) Vastan assemblage from the Cambay Shale Formation, Gujarat, peninsular India (Bajpai *et al.* 2007; Rana *et al.* 2008), (ii) Subathu assemblage from the Subathu Formation, northwestern India (this work), and (iii) Barbara Banda assemblage from the Mami Khel Clay in northern Pakistan (De

Bruijn *et al.* 1982). The Vastan rodent assemblage is known by ~20 isolated cheek teeth mostly referable to an ailuravine ischyromyid, *Meldimys musak* (Rana *et al.* 2008).

Among the other rodent teeth documented from the Cambay Shale Formation of Vastan area, a rather large P4 was referred to a new ctenodactyloid, *Anthramys vastani* and a considerably smaller M1-2 to an indeterminate taxon having close affinity with the Chapattimyidae (Bajpai *et al.* 2007). The P4 of *A. vastani* is characterized by its globular and sub-molariform shape, an indistinct or missing hypocone, uninterrupted protoloph and metaloph with distinct protoconule and metaconule, and a transverse crest that originates from the protoloph and extends anteriorly to join the anteroloph dividing the valley between anteroloph and protoloph (Bajpai *et al.* 2007; figure 2a–c). It differs clearly from the P4s of ctenodactylids and cocomyids in being sub-molariform, from chapattimyid P4s in lacking a hypocone and from yuomyid P4s in possessing an uninterrupted metaloph. Size-wise, it is comparable to the P4 of *Meldimys musak* (Rana *et al.* 2008, figure 3b) though it is slightly more transverse (length/width=1.71/2.36 mm as against 1.7/2.0 in *M. musak*). In occlusal morphology as well, it has similarities with *M. musak*, particularly in reduced hypocone, and uninterrupted protoloph and metaloph with distinct protoconule and metaconule. Two other important features noted by Bajpai *et al.* (2007) on P4 of *A. vastani* are: somewhat closely placed metacone and paracone, and the presence of a short arcuate crest that descends labially from the metacone. While the labial crest mentioned by Bajpai *et al.* (2007) could be a part of the externally extended mesostyle, which is characteristically present in *M. musak*, the paracone and metacone do not appear to be particularly closely placed in the latter species. However, a right P4 of another ailuravine, *M. louisi* from the early Eocene of Avenay in the Paris Basin (Escarguel 1999; Plate 3e) is also globular and has similarly closely placed paracone and metacone like in the P4 of *A. vastani*. Therefore, although *A. vastani* sample is inadequate to determine its precise affinity, it is likely that *A. vastani* represents an ailuravine, possibly *M. musak*. The other tooth (M1-2) described by Bajpai *et al.* (2007) as cf. Chapattimyidae gen. et sp. indet. (Bajpai *et al.* 2007; figure 2f–h) is morphologically closely similar to M1s of *M. musak* (Rana *et al.* 2008, figure 3c–d) though metrically smaller. Its length/width, as recorded by Bajpai *et al.* (2007), are 1.41/1.38 mm as against 1.9/2.15 and 2.1/2.5 mm for two M1s of *M. musak*. This tooth certainly represents an ailuravine, most likely *M. musak*, or a smaller species of *Meldimys*. Thus no chapattimyid, or any rodent

other than ailuravines appears to be present in the collections known so far from the early Eocene beds of Vastan (Gujarat) in peninsular India.

The Barbara Banda rodent assemblage from the Mami Khel Clay of Kohat in Pakistan is represented by just three isolated teeth, of which two (P4 and M1-2) have been referred to distinct but unnamed cocomyids and the third (p4) to an indeterminate paramyine (Ischyromyidae) by De Bruijn *et al.* (1982). The attribution of a robust non-molariform P4 and a rather lophodont and smaller M1-2 to two distinct cocomyids appears to be justified. However, the attribution of a p4 (De Bruijn *et al.* 1982; figure 6) to an indeterminate paramyine is debatable as also opined by Rana *et al.* (2008), who compared it with p4s of known ischyromyids from Europe and North America and concluded that it represented neither a paramyine nor a reithroparamyine (inclusive of *Microparamys*). The morphology and metrics of this p4 suggest that it could actually represent an ailuravine, or more likely a pseudoparamyine, both of which probably shared the same biogeographical history.

The early Eocene Subathu rodent assemblage documented here from the older red beds of the Subathu Formation in the northwest sub-Himalaya is distinct and more diverse than the aforementioned assemblages from Vastan and Barbara Banda. It comprises 17 cheek teeth referable to two new and three other taxa showing clear affinities with chapattimyids and yuomyids. Interestingly, there are no ailuravines, cocomyids, paramyines or pseudoparamyines in the Subathu assemblage. One of the reasons for this difference in composition of the early Eocene rodent assemblages from Subathu, Vastan and Barbara Banda could be due to the difference in their respective ages (table 2).

Apart from the difference in age, the absence of ailuravines in the sub-Himalayan sections could also be attributed to (i) the early Eocene beds coeval to those of Vastan have not been sampled yet in the Himalayan region – this is likely because there appear to be no continental beds of an early Ypresian age in the sub-Himalayan region, (ii) for an unknown reason ailuravines failed to disperse to the Himalayan region even though other small mammals such as diacodexeid artiodactyls could do so, and (iii) ailuravines did not survive beyond early-early Eocene. Likewise, the absence of chapattimyids in the Vastan rodent assemblage could also be due to two reasons: (i) the chapattimyids, like raoellid artiodactyls and anthracobunid perisodactyls originated in the sub-Himalayan region in specific environmental conditions created by the shrinking and shallowing of Tethys Sea and did not disperse into other areas, including peninsular

India, and (ii) the chapattimyids appeared in the later part of the early Eocene (=late Ypresian), which is yet to be sampled in peninsular India. For further insights, it is important to investigate the late Paleocene, basal Eocene and younger early Eocene terrestrial horizons of the peninsular India as well as of the sub-Himalayan region.

The co-occurrence in the early Eocene rodent assemblage from Subathu of at least three or more chapattimyids of substantially different size and morphology indicates their early radiation in this fauna. Such diversity is clearly more compared to other coeval assemblages from the subcontinent and the reasons for this are presently hard to understand. Were there some islands in the close vicinity of India that may have supported diverse rodents in advance of the later invasions from Asia to India?

5.2 Chronology of early Eocene rodent assemblages from South Asia

The ages of the three early Eocene rodent assemblages from the Indian subcontinent are apparently distinct as also corroborated by their taxonomic composition. The likely chronology is depicted in table 2. The Vastan rodent assemblage is well constrained at ~54–53 Ma (early Ypresian) based on foraminiferal biostratigraphy and the occurrence of age-diagnostic dinoflagellate cyst assemblage (Sahni *et al.* 2006; Garg *et al.* 2008; Puneekar and Saraswati 2010). This is also corroborated by the mammalian fauna recorded thus far from the same stratigraphic level (Smith *et al.* 2007; Rose *et al.* 2009a, b, 2013, 2014; Kumar *et al.* 2010).

As regards to the age of the Barbara Banda assemblage, there is some ambiguity. It was originally considered as broadly of an early Eocene age (De Bruijn *et al.* 1982). Later studies, including a recent one, supported late-early Eocene or even early-middle Eocene ages (Gingerich *et al.* 1983; Thewissen *et al.* 1983; Pivnik and Wells 1996; Khan and Clyde 2013). However, Leinders *et al.* (1999) based on faunal associations in different Eocene localities of Pakistan and primitive nature of rodents and of the associated diacodexeid artiodactyl, *Diacodexis pakistanensis* from Barbara Banda determined early part of the early Eocene or the earliest Eocene age. The possibility of the so called ‘paramyine’ p4 from Barbara Banda actually being an ailuravine or more likely a pseudoparamyine as discussed earlier does not seem to reflect much on the precise age of the assemblage. However, it does indicate that Barbara Banda rodents are older than early-middle Eocene and likely also older than the early Eocene Subathu rodents. This is because ailuravines and pseudoparamyines are present neither in the

Table 2. *Chronology and taxonomic composition of Eocene rodent assemblages of the Indian subcontinent (composition follows classification by McKenna and Bell 1997).*

Age	Horizons and localities	Composition
Middle Eocene (Lutetian)	(i) Younger red beds, Subathu Formation, Kalakot, Rajauri District (Jammu and Kashmir) and Subathu, Solan District (Himachal Pradesh), NW sub-Himalaya, India (Sahni and Khare 1973; Sahni and Srivastava 1976; Kumar <i>et al.</i> 1997a, b) (ii) Kuldana Formation, Ganda Kas, Punjab, Pakistan (Hussain <i>et al.</i> 1978)	Chapattimyidae (=Chapattimyidae+Yuomyidae) Chapattimyinae <i>Birbalomys woodi</i> <i>B. sondaari</i> <i>B. vandermeuleni</i> <i>B. lavocati</i> <i>B. ijlsti</i> <i>Chapattimys debruijini</i> <i>C. ibrahimshahi</i> <i>C. wilsoni</i> <i>C. asifi</i> (<i>Gumbatomys asifi</i>) Yuomyinae cf. <i>Advenimus bohlini</i> cf. <i>Petrokoslovia</i> sp. indet. 1 cf. <i>Petrokoslovia</i> sp. indet. 2
Early Eocene (late Ypresian)	Older red beds, Subathu Formation, Subathu, Solan District (Himachal Pradesh), NW sub-Himalaya, India (Present work)	Chapattimyidae (=Chapattimyidae+Yuomyidae) <i>Subathumys solanorius</i> <i>S. globulus</i> <i>Birbalomys</i> cf. <i>sondaari</i> <i>Birbalomys</i> sp. cf. <i>Chapattimys</i> sp. Chapattimyidae indet.
Early Eocene (?early-middle Ypresian)	Mami Khel Clay, Barbara Banda, Kohat, Pakistan (De Bruijn <i>et al.</i> 1982)	Cocomyidae Genus A sp. I Genus A sp. II ?Pseudoparamyinae (Ischyromyidae) Gen. et sp. indet.
Early Eocene (early Ypresian) ~54–53 Ma	Cambay Shale Formation, Vastan (Surat District, Gujarat), peninsular India (Bajpai <i>et al.</i> 2007; Rana <i>et al.</i> 2008)	Ailuravinae (Ischyromyidae) <i>Meldimys musak</i>

early middle Eocene localities of Indo-Pakistan (Kalakot, Metka, Ganda Kas, Chorlakki) nor in the older Subathu assemblage described here (table 2).

The age of the Subathu rodents treated here is almost certainly late-early Eocene (late Ypresian), as indicated by the foraminiferal biostratigraphy (Mathur and Juyal 2000). It is clearly younger than that of the Vastan assemblage and is closer to the youngest known Eocene (Lutetian or early-middle Eocene) rodent assemblages from India and Pakistan, as also corroborated by their similar familial and in some cases generic affinities and the presence of a combination of chapattimyid and yuomyid characters in the presently described teeth from the older Subathu red beds (Sahni and Khare 1973; Hussain *et al.* 1978; Kumar *et al.* 1997a, b).

5.3 Familial status of early Eocene Subathu rodents

The new Subathu rodents described here exhibit a combination of chapattimyid (Ch) and yuomyid (Yu) characters rather than characters of a single family as in case of Vastan rodents (Ischyromyidae) or those from the middle Eocene levels of the Subathu and Kuldana Formations (Chapattimyidae and Yuomyidae). For example: (i) in all but two upper cheek teeth in the present collection, the metacone is quite inflated (Ch) but it does not join the protocone, leaving the metaloph incomplete/interrupted (Yu), whereas in two other teeth (WIMF/A 1623 and 1629) the metaloph is clearly connected to the protocone (Ch) and in another (WIMF/A 1621) it is weakly connected to the protocone (Ch), (ii) in all except two teeth, the

protocone and hypocone are subequal in size (Ch), while in two other teeth (WIMF/A 1620 and 1636), the hypocone is considerably smaller than the protocone (Yu), (iii) in a few teeth (e.g., WIMF/A 1622, 1628 and 1629), the position of hypocone is more lingual in relation to protocone (Ch), whereas in others it is nearly at the same level as the protocone (Yu), (iv) in all except one tooth, the protoconule is indistinct and merged with the protoloph (a character common to chapattimyids and yuomyids), however, in another tooth (WIMF/A 1625) the protocone is quite inflated and not merged with protoloph. Both the P4s in the collection are molariform as in chapattimyids as well as yuomyids. Like the upper teeth, lower molars also show a mixture of chapattimyid and yuomyid characters: (i) in two molars (WIMF/A 1626 and 1631), the hypoconulid and entoconid are connected by posterolophid as in chapattimyids, whereas in the other three (WIMF/A 1627, 1632 and 1634), these conids are separated by a valley as in yuomyids, (ii) in four teeth (WIMF/A 1627, 1631, 1632 and 1634), the metalophulid II is short and weak as in chapattimyids and yuomyids, but in one tooth (WIMF/A 1626), it is longer and prominent terminating near the metaconid, (iii) in most teeth, the anterior arm of entoconid is either absent or small as in chapattimyids and yuomyids, but in one m3 (WIMF/A 1631) it appears conspicuously high. The lower premolars, whose size and shape are important characters to distinguish chapattimyids (=p4 smaller or subequal to m1 and oval) from yuomyids (=p4 larger than m1 and wasted) are unfortunately not represented in our collection.

The ctenodactylid families Chapattimyidae and Yuomyidae were found on fossils from the early middle Eocene horizons (Hussain *et al.* 1978; Hartenberger 1982; Dawson *et al.* 1984; Kumar *et al.* 1997a, b). In fact, during the middle Eocene, the central and eastern Asiatic rodents were dominated by the Yuomyidae and the south Asiatic by the Chapattimyidae, which have been labelled as vicars of Yuomyidae and Ctenodactylidae by Flynn *et al.* (1986). Their diagnostic characters are more or less identical and the main differences are in size and shape of p4s, inflated or otherwise shape of metaconule, complete/uninterrupted or incomplete/interrupted metaloph, size and the position of hypocone in respect to protocone, etc. (Wang 1994; Marivaux *et al.* 2004). According to Hartenberger (1982) and Dawson *et al.* (1984), the similarities between the chapattimyids and yuomyids are mostly in primitive characters and the two are distinct otherwise. Wang (1994) opined that these two families may belong to a single family, Chapattimyidae, though she refrained from merging the two due to inadequate data on Chapattimyidae. Following Wang (1994),

Averianov (1996) broadened the definition of Chapattimyidae to include Yuomyidae into it. This arrangement, however, was not followed by some of the later workers (e.g., Dashzeveg and Meng 1998; Marivaux *et al.* 2002, 2004) who maintained the validity of Yuomyidae. Meanwhile, McKenna and Bell (1997) downgraded Yuomyidae and Cocomyidae to the subfamily level and included them under the Chapattimyidae along with Chapattimyinae and Baluchimyinae. It is indeed difficult to maintain the validity of two families based on insufficient diagnostic features and it appears more reasonable to separate them at the subfamily level as done by McKenna and Bell (1997). However, the same cannot necessarily be said about the downgrading of Cocomyidae by McKenna and Bell (1997), which are distinguished from chapattimyids and yuomyids by their non-molariform premolars. The presence of a combination of chapattimyid and yuomyid characters in the presently described teeth from Subathu supports the downgrading of yuomyids and therefore yuomyids are treated here as a subfamily under the Chapattimyidae. It further suggests that the chapattimyids and the yuomyids have evolved from a common ancestor and diverged later in the middle Eocene. More complete specimens are needed to assess the relationship between the Subathu rodents and other ctenodactylids.

5.4 ?Chapattimyids from Europe

Peláez-Campomanes *et al.* (1989) described a few isolated rodent cheek teeth from the middle Eocene of Spain attributing them to cf. Chapattimyidae indet. and aff. Chapattimyidae indet. These were later attributed to a new genus and species, *Zamoramys extraneus* under an indeterminate family by Peláez-Campomanes and López-Martínez (1996). Subsequent workers considered these teeth to be allied to theridomyids rather than to Asian ctenodactylids (Vianey-Liaud *et al.* 1994; Escarguel 1999; Dawson 2003). More recently, however, Quer and Agustí (2010) included *Zamoramys* in a new family Remyidae along with *Remys*, *Pairomys* and a new genus *Frontanyamys*. Remyids differ from theridomyids mainly in having upper molars with very well-developed metaconule, from ischyromyids in having lophodont and hypsodont teeth and from chapattimyids in well-developed posterior arm of protoconid on lower molars, a metaconule nearly as large as metacone on upper molars and a paracone lingually positioned with respect to metacone on P4 (in *Frontanyamys*), and P4 much smaller than molars (in *Zamoramys*). It may be noted here that resemblance of remyids, particularly of *Zamoramys* and *Frontanyamys* and

especially of their upper teeth with those of chapattimyids and yuomyids in features such as subequal protocone and hypocone (in *Zamoramys*), lingually shifted hypocone, protoloph and metaloph convergent towards the protocone and inflated metaconule, etc., is rather striking and should be probed further with more material to know their relationships with the Asian ctenodactyloids, particularly chapattimyids.

5.5 Limited spread of ailuravines and dominance of chapattimyids on India

The earliest rodents that lived on the Indian subcontinent were apparently the ailuravines (Ischyromyidae), which are presently known by a single taxon *Meldimys musak* from the early Eocene (~54–53 Ma) of western peninsular India (Rana *et al.* 2008). Ailuravine assemblages are well known from the Eocene of Europe (Ypresian–Bartonian) and North America (Ypresian–Priabonian) (e.g., Michaux 1968; Korth 1988, 1994; Escarguel 1999). The lone ailuravine from India, *Meldimys musak* is somewhat more derived than the earliest Eocene European taxa, such as *Euromys cardosoi* and *Euromys* sp., which occur near the Paleocene–Eocene (P/E) boundary and more primitive than the late-early Eocene taxa, *E. inexpectatus* and *Ailuravus michauxi*. Morphologically, it is more similar to European than to American lineages and evolutionary level of the Indian species appears to be close to those occurring in Europe around 52 Ma. The common occurrence of *Meldimys* in the early Eocene of India and Europe points to a faunal exchange between these two widely separated regions near the P/E transition. Though it is unclear at this stage as to whether ailuravines originated in southern Asia and migrated to Europe or *vice versa*. The derived nature of *M. musak* compared to the more diverse earliest Eocene ailuravines from Europe (known by three genera and eight species) for now seems to favour a European origin for the subfamily.

Ailuravines survived in Europe until the latest middle Eocene (late Bartonian) and in North America throughout the Eocene (Wasatchian–Chadronian), but they are yet to be found in the younger Eocene (Lutetian) faunas of the Indian subcontinent. Unfortunately, rodents in Vastan have so far been recovered only from a single level, therefore there is no way to know whether or not ailuravines survived beyond early Eocene even in the Vastan local fauna. Also it is not known whether ailuravines could ever spread to the sub-Himalayan region and lived alongside the chapattimyids and yuomyids at any point of time. In otherwise very rich and quite diverse

Vastan vertebrate fauna with plenty of predators, especially snakes, the presence of just one rodent species is rather surprising and may be an artefact.

The apparent lack of diversification of ailuravines in the Vastan fauna, where other small mammals such as bats and primates show rather high diversity, and their apparent absence in the successively younger rodent faunas of the subcontinent (e.g., Barbara Banda and Ganda Kas in Pakistan, and Subathu and Kalakot in India) seems to suggest that they may not have survived on the subcontinent beyond early Eocene and may have been replaced by the chapattimyids, which originated on the subcontinent and spread rather quickly in the central Asia, including Kazakhstan, China and Mongolia. Chapattimyids survived until the Miocene (Baluchimyinae, Flynn *et al.* 1986), though there is no record of chapattimyines beyond middle Eocene.

Morphologically, the ailuravines and chapattimyids are distinct and there appears to be no ancestor-descendant relationship between them. This would suggest that these two rodent groups originated independently at different points of time from different ancestors, but the question arises whether they originated on different continents or on the same continent. Additional material from the sub-Himalayan as well as western peninsular Indian localities is expected to throw light on this.

5.6 Terrestrial faunal exchange between India and Europe near the P/E transition

The occurrence of a European ailuravine rodent genus, *Meldimys* in the early Eocene vertebrate fauna from Vastan (western peninsular India) was the first strong indication of a possible terrestrial faunal exchange between India and Eurasia close to the P/E transition (Rana *et al.* 2008). Although initially considered rather tenuous, owing principally to the existence of Turgai Strait (=West Siberian Sea) between Europe and Asia, and the Tethys Sea between India and Asia, which would have been formidable physical barriers for any cross-infiltration of land vertebrates around the P/E, the evidence has since become stronger. Apart from the ailuravine rodents, there are now several other elements in the Vastan fauna, which also have European or North American affinities. These include diacodexeid artiodactyls, notharctid and omomyid primates, chiropterans (bats), esthonychine tillodonts, and also birds (Smith *et al.* 2007; Rana *et al.* 2008; Rose *et al.* 2009a, b, 2013; Kumar *et al.* 2010; Mayr *et al.* 2010). India–Europe faunal link also gets support from studies

on dinoflagellate cysts by Iakovleva *et al.* (2001), which indicate lowering of sea level around the P/E, and on Eocene primate *Teilhardina* by Smith *et al.* (2006). Movement of fauna to and from India across the Tethys could have been facilitated by the presence of some hypothetical microcontinents and islands north of India as envisaged by Gaetani and Garzanti (1991) and Gingerich *et al.* (1997) or through potential land connections with Afro-Arabia during the northward drift (Gingerich *et al.* 1990; Chatterjee and Scotese 1999; Murphy *et al.* 2001). It may be mentioned here that Rose *et al.* (2014), while demonstrating that the mammalian group Perissodactyla originated in India opined that the stem taxa of perissodactyls could have entered India from Afro-Arabia possibly during the Paleocene.

Significantly, there is now substantial evidence of terrestrial faunal exchange between Asia and Europe also at the Cretaceous/Tertiary (K/T) transition – good ~10 Ma before ailuravines and others crossed-over. Adapisoriculid mammals (e.g., *Deccanolestes*) after their origin during the Maastrichtian on India quickly dispersed into Europe possibly via eastern Africa or directly across the Tethys into Europe and then to Africa (Boyer *et al.* 2010; Prasad *et al.* 2010; Smith *et al.* 2010; Goswami *et al.* 2011; De Bast *et al.* 2012). So if adapisoriculids could migrate to Europe from India around the K/T boundary, similar dispersal may also have happened around the P/E boundary. However, it remains to be seen whether P/E and K/T dispersals followed similar routes, and what were those routes?

The early Eocene Subathu horizons have so far yielded only rodents though there are definite indications of presence of other small mammal remains. It would be interesting to study their affinities and see if they are closer to European and American faunas or to the Asian faunas and also their relationship with the Vastan local fauna. The bulk screen-washing of the older Subathu red beds is likely to yield a more representative assemblage, including the small mammal groups such as primates, artiodactyls and chiropterans, etc., of the fauna that thrived in the sub-Himalayan region during the early Eocene.

6. Summary and conclusions

Chapattimyid rodents from the early Eocene horizons of the sub-Himalaya are represented by two new taxa, namely, *Subathumys solanorius* gen. et sp. nov. and *Subathumys globulus* gen. et sp. nov., and three others, including, *Birbalomys* cf. *sondaari*, *Birbalomys* sp. and cf. *Chapattimys* sp. All are found on/identified by upper molars, and

the lower cheek teeth have been described provisionally as indeterminate chapattimyids pending definitive taxonomic assignments when additional material is forthcoming. The moderate diversity of the early Eocene Subathu rodents indicates their early radiation in this fauna.

The co-occurrence of typical chapattimyid and yuomyid characters in the presently described cheek teeth suggests that the two rodent groups may have evolved from a common ancestor and diverged later in the middle Eocene. It also supports the downgrading of Yuomyidae to a subfamily level and bringing it under the Chapattimyidae by McKenna and Bell (1997). More complete specimens are needed to assess the relationship between the Subathu rodents and other ctenodactyls.

The early Eocene chapattimyid-yielding section at Subathu is chronologically intermediate between the Vastan mine section (Gujarat) of peninsular India and the Kalakot–Metka and Ganda Kas–Chorlakki sections of northern India and Pakistan, respectively. It is probably also younger than the Barbara Banda section of Pakistan. Chronologically, it is closest to the early middle Eocene rodent-yielding sections of northern India and Pakistan as also supported by the close similarity of certain early Eocene taxa with those from the middle Eocene.

Contrary to the earlier belief based on data from Kalakot–Metka and Subathu in India and Ganda Kas–Chorlakki in Pakistan (Hussain *et al.* 1978; Kumar *et al.* 1997a, b), the chapattimyids originated in the early Eocene on the subcontinent rather than in middle Eocene and were probably the dominant rodent group during early and middle Eocene, which did not allow the migrant ailuravines to flourish beyond early Eocene. However, the oldest known fossil rodents from India belonged to the cosmopolitan family Ischyromyidae rather than to endemic Chapattimyidae, and it is not clear if the two distinct groups ever lived together.

Ailuravines appear to have failed to disperse into the sub-Himalayan region, even though other groups such as diacodexids, whose oldest Indian record is also from the peninsular India could do so and are also known from the Lutetian horizons in the sub-Himalaya.

An extensive and systematic collecting in the older red beds of the Subathu Formation can be expected to yield a more representative assemblage, including other small mammal groups such as primates, artiodactyls and chiropterans, etc., of the fauna that thrived in the sub-Himalayan region during the early Eocene and help understand their relationship and palaeobiogeography *vis-à-vis* Eocene terrestrial faunas from peninsular India, Pakistan, Europe and North America.

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