A new Paleocene nyctitheriid insectivore from Inner Mongolia (China) and the origin of Asian nyctitheriids

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Nyctitheriids are primitive insectivores that were relatively abundant and diverse in North America and Europe during the middle Paleocene through to the middle Oligocene. The nyctitheriids from Asia are poorly known and show several distinctive characters. Here we describe the late Paleocene *Asionyctia guoi* gen. et sp. nov., the first fairly well known Asian nyctitheriid, from the Subeng locality near the city of Erlianhot (Erenhot) in Inner Mongolia, China. Among its most conspicuous features are the paraconid positioned high on p4, the rather primitive morphology and size of p3, the premolariform P4/p4 and the transverse upper molars with a small, straight postcingulum. Except for the paraconid positioned high on p4, these combined features are also present in other Asian nyctitheriids, but absent in North American or European forms. We performed a cladistic analysis, based on a set of 20 dental characters, to resolve higher-level phylogenetic relations within Nyctitheriidae. The strict consensus tree groups all Asian forms in a single clade, for which we propose the rank of a subfamily and the name Asionyctiinae subfam. nov. Within Nyctitheriidae, a semimolariform P4/p4, as in *Leptacodon tener*, is considered primitive, and we consider the morphologically simplified P4/p4 of Asionyctiinae derived within Nyctitheriidae. Asionyctiinae can be derived from an American, primitive *Leptacodon*-like ancestor migrating into Asia, with the reduction of P4/p4 occurring on the Asian continent. Considering the derived morphology and the relatively high diversity of Asionyctiinae during the Asian late Paleocene, and the inferred conservative nature of the family Nyctitheriidae, we suggest an early Tiffanian time for the migration of nyctitheriids into Asia.

Key words: Mammalia, Nyctitheriidae, Paleocene, Gashatan, Subeng, Inner Mongolia, China.

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Introduction

Nyctitheriids are relatively conspicuous components in many different local faunas in Europe and North America from the middle Paleocene to the middle Oligocene (Smith 1996). The members of this family are characterized by a strong retention of primitive tribosphenic characters, but a tendency towards dilambdodonty has occurred independently in different lineages; both these factors seriously complicate the reconstruction of phylogenetic relationships (Sigé 1976, 1997) and no attempt has been made to completely resolve the internal phylogenetic relations of the family. Equally, the phylogenetic position of Nyctitheriidae itself is uncertain: generally, nyctitheriids are considered a group of primitive soricomorph (Butler 1972; McKenna and Bell 1997) or erinaceomorph lipotyphlans (Robinson 1968; Sigé 1976), although *Nyctitherium* Marsh, 1872 and *Wyonycteris* Gingerich, 1987 were originally thought to be chiropterans, and *Leptacodon* Matthew and Granger, 1921 was first placed in the family Leptictidae. Recently Hooker (2001) classified the Nyctitheriidae within the Archonta, together with Primates, Plesiadapiformes, Dermoptera, and Scandentia, but not with Lipotyphla or Chiroptera. Therefore, although much nyctitheriid material has been found and studied, the affinities of nyctitheriids are still unclear.

Here we describe a new nyctitheriid from the late Paleocene Gashatan Asian Land Mammal Age (ALMA) of China. It is one of the most abundant forms at the Subeng mammal site, which is located in a small area called "Subeng" by the local shepherds, about 20 km south-west of the city of Erlianhot in Inner Mongolia, China. The Subeng area has been sampled a first time in 1976 by the Institute for Vertebrate Paleontology and Paleoanthropology and the Inner Mongolian Museum, but none of the specimens has been published. In 1995, 2000, 2001, and 2004, a multidisciplinary team from the Royal Belgian Institute of Natural Sciences and the Inner Mongolian Museum resampled the area. The first results included the study of the ostracod microfossils from Subeng (Van Itterbeeck and Bultynck 2004) and the description of the oldest Asian plesiadapiform (Smith et al. 2004).

The Asian nyctitheriids are poorly known, and in all cases the material is very fragmentary. The new form from Subeng is comparable in size to *Leptacodon dormaalensis* (Quinet, 1964) and *Oedolius perexiguus* Russell and Dashzeveg, 1986 and consists mainly of isolated teeth and jaw fragments. All of the cheek teeth were identified, making this new form from Subeng the most completely known Asian nyctitheriid.

Institutional abbreviations.—IMM, Inner Mongolian Museum, Hohhot, China; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Systematic paleontology

Order Lipotyphla Haeckel, 1866

Family Nyctitheriidae Simpson, 1928

Subfamily Asionyctiinae nov.

Type genus: *Asionyctia* gen. nov.

Genera included: *Bumbanius* Russell and Dashzeveg, 1986; *Oedolius* Russell and Dashzeveg, 1986; *Voltaia* Nessov, 1987; *Bayanulanius* Meng, Zhai, and Wyss, 1998.

Diagnosis.—Nyctitheriids characterized by a generally primitive nature but having a structurally reduced P4/p4. Differing from all other nyctitheriids by a completely unbasined talonid on p4, and by a transversely elongated trigon and a postcingulum with a straight posterior border on the upper molars. Differing from *Nyctitherium*, *Saturninia*, *Euronyctia*, and *Amphidozotherium* by the smaller postcingulum on the upper molars. Differing from *Wyonycteris*, *Amphidozotherium* and *Euronyctia* by their completely straight centrocrista on the upper molars. Further differing from all Amphidozotheriinae by the larger and more complex p3, and the less reduced size of m3.

Distribution.—Late Paleocene of China and Kazakhstan, early Eocene of Mongolia.

Genus *Asionyctia* nov.

Table 1; Figs. 1, 2.

Type and only known species: *Asionyctia guoi* sp. nov.

Etymology: Composed of "Asia" for its Asian origin, and "nyctia" (from Greek *nyx*, *nyctos*—night), a common suffix in the family Nyctitheriidae; together referring to the specific Asian character of this new nyctitheriid.

Diagnosis.—As for the type and only known species.

Asionyctia guoi sp. nov.

Holotype: IMM 2004-SB-1, left dentary fragment with p4–m1 and alveoli of p2–3.

Paratypes: IMM 2001-SB-9, left dentary fragment with p4 and alveoli of i1–p3; IMM 2004-SB-2, right dentary fragment with p3–4 and alveoli of c–p2 ; IMM 2001-SB-10, right dentary fragment with m1–2 and alveoli of m3; IMM 2001-SB-11, left m3; IMM 2004-SB-3, right P4; IMM 2001-SB-12, left M1; IMM 2001-SB-13, left M2; IMM 2001-SB-14, fragmentary right M3; IMM 2001-SB-15, fragmentary left M3.

Referred material: At present the collection of *Asionyctia guoi* from Subeng contains 8 more dentulous dentary fragments, 55 isolated teeth and 21 identifiable fragmentary cheek teeth.

Type locality and age: Subeng (N 43°31´50´´ E 111°44´04´´ 955 m above sea level), Erlian Basin, Inner Mongolia, China. Upper part of the Nomogen Formation, late Paleocene, Gashatan ALMA.

Etymology: In honor of the Chinese paleontologist Dian-Yong Guo (IMM) for his contribution to the knowledge of the fossil vertebrates of Inner Mongolia.

Diagnosis.—Asionyctiine nyctitheriid differing from all other Asionyctiinae by the paraconid positioned high on p4. Differ-

Table 1. Dental measurements of *Asionyctia guoi* (in mm). n: number of specimens measured; S.D.: standard deviation; C.V.: coefficient of variation. Values are based only on measurements of well-preserved specimens. When dimensions of additional specimens could be estimated, these values were taken into account and the results are noted between brackets.

		Mean	Minimum	Maximum	n	S.D.	C.V.
p3	length	0.88	0.85	0.95	6	0.03	2.92
	width	0.50	0.45	0.55	6	0.03	6.59
p4	length	1.23	1.10	1.35	11	0.07	6.01
	width	0.66	0.60	0.75	11	0.04	5.36
m1	length	1.36	1.20	1.50	16	0.08	5.96.
	width	0.87	0.75	0.95	16	0.04	4.79
m2	length	1.31	1.20	1.40	12	0.06	4.28
	width	0.90	0.85	0.95	12	0.04	3.95
m3	length	1.35	1.25	1.40	5	0.05	3.60
	width	0.83	0.75	0.90	5	0.04	4.45
P4	length	1.05 (1.04)	1.00	1.10	3 (4)	0.03 (0.03)	2.38 (2.43)
	width	1.50 (1.48)	1.50 (1.45)	1.50	1 (2)	0.03 (0.03)	– (2.12)
M1	length	1.26 (1.26)	1.18	1.35	6 (10)	0.06 (0.06)	4.81 (4.79)
	width	1.95	1.85	2.05	9	0.07	3.66
M2	length	1.25 (1.28)	1.20	1.30	2 (4)	0.05 (0.05)	4.29 (3.73)
	width	2.08	1.95	2.20	3	0.11	5.52
M3	length	(1.05)	(1.00)	(1.10)	(2)	(0.04)	(3.37)
	width	(1.70)	–	–	(1)	–	–

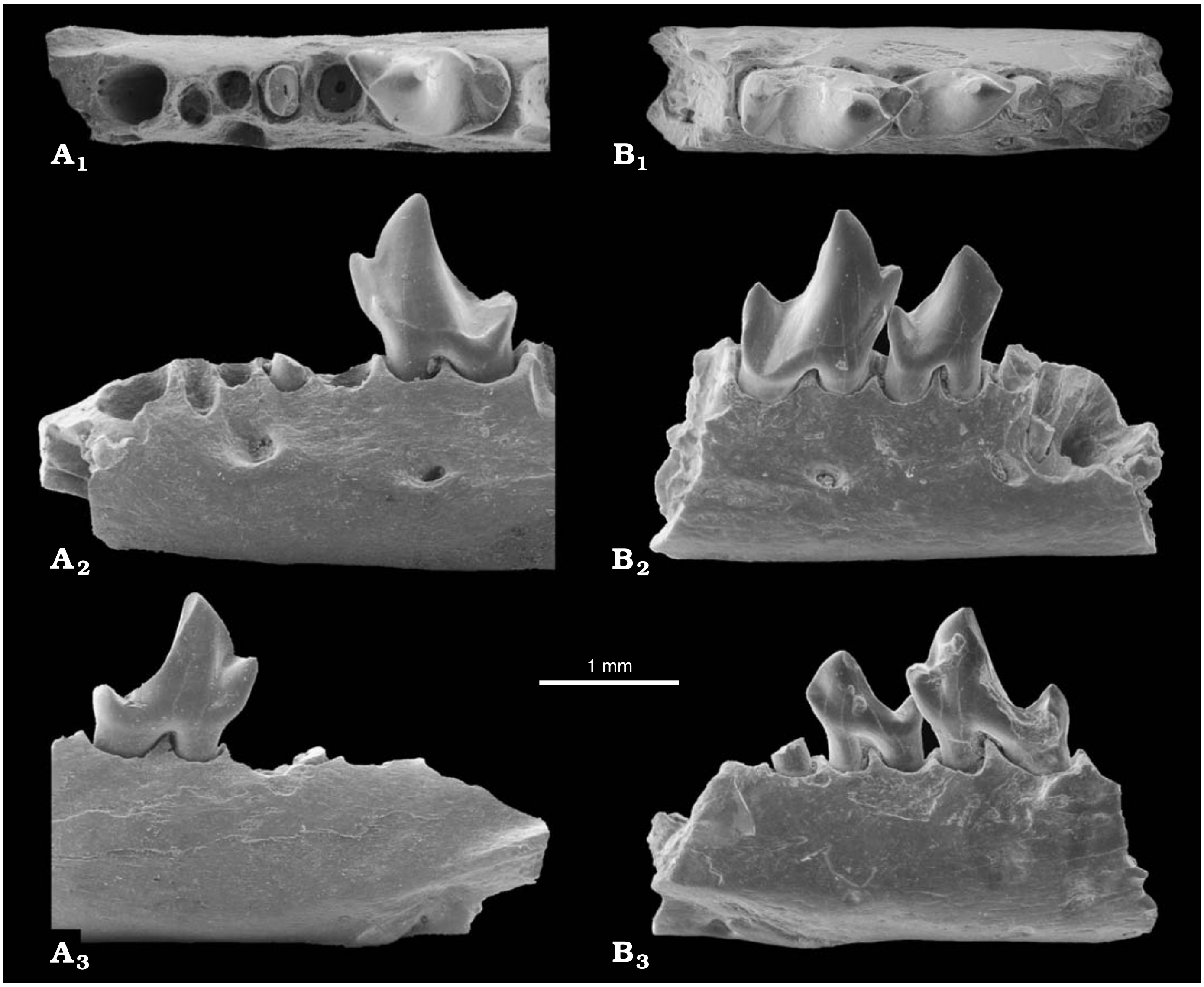


Fig 1. SEM micrographs of *Asionyctia guoi*, Gashatan ALMA (late Paleocene) from Subeng (Inner Mongolia, China). **A**. IMM 2001-SB-9, left dentary fragment with p4 and alveoli of i1–p3, in occlusal (A_1), labial (A_2) and lingual views (A_3). **B**. IMM 2004-SB-2, right dentary fragment with p3–4 and alveoli of c–p2, in occlusal (B_1), labial (B_2), and lingual (B_3) views.

ing from *Oedolius, Voltaia*, and *Bayanulanius* by the lower molars with an oblique crest that joins the trigonid low on the trigonid wall and the smaller hypoflexid. Further differing from *Oedolius* by its less reduced paraconid and the presence of an entocristid on the lower molars. Differing from *Bumbanius* by the absence of a metaconid on p4, from *Voltaia* by its single talonid cusp on p4 and the smaller and more reduced lower premolars, and from both by its smaller size.

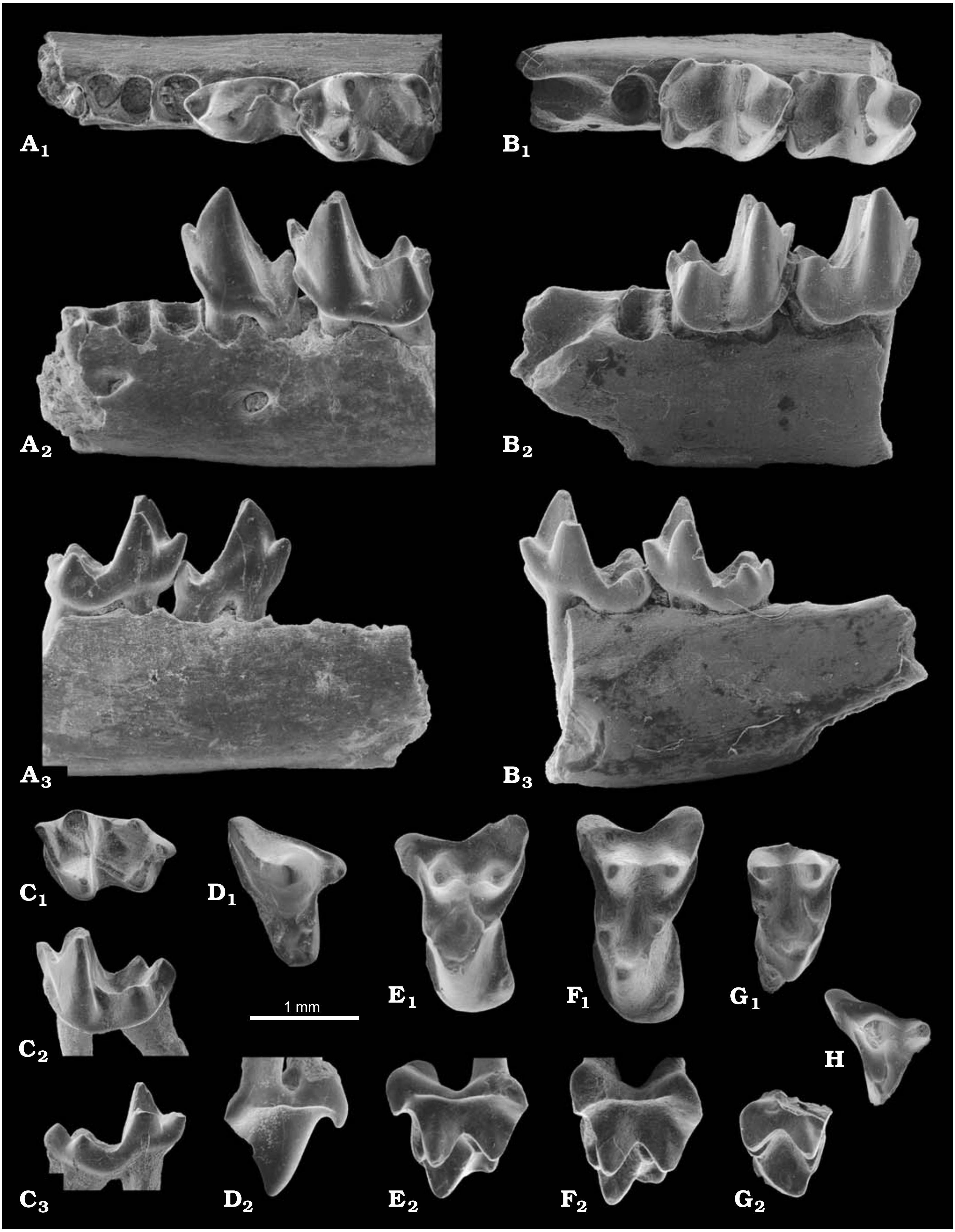
Measurements.—See Table 1.

Description

The mandible has two mental foramina, a large one positioned below the posterior root of p2 and the anterior root of p3 and a small one positioned below the roots of p4. It contains the alveoli for three anteriorly projecting incisors. The alveolus for i3 is followed by a large alveolus for the canine and by two small alveoli. No small uniradicular teeth fitting these alveoli were found and the position and size of these alveoli seems to indicate that p1 is absent and p2 is double-rooted and moderately smaller than p3. The absence of p1 would be unique among nyctitheriids; lacking further confirmation, we prefer to handle this feature with a certain care but at least it is clear that *Asionyctia guoi* has undergone a reduction of the anterior lower premolars but not of the other lower antemolar teeth.

The **p3** is double-rooted with a moderately high protoconid that is situated above the anterior root. The small paraconid is positioned high on the anterior side of the protoconid, and from the posterolingual side of the protoconid a ridge descends to a single median talonid cusp.

The **p4** is premolariform and larger than p3, subequal to m1 in length. p4 has a well-developed paraconid and para-


A1
B1
A2
B2
A3
B3
C1
D1
C2
1 mm
E1
F1
G1
H
C3
D2
E2
F2
G2

cristid, both positioned high on the protoconid, and a small anterolabial cingulum, but the metaconid is completely undeveloped. A strong crest descends posterolingually from the protoconid to a single, median talonid cusp. A talonid basin is not developed, but a small lingual notch is consistently present.

The **m1** has an anteriorly projecting paraconid that is crestiform and fused with the paracristid. The protoconid is slightly larger and higher than the metaconid. The anterolabial cingulum is well-developed and can continue along the base of the protoconid. The hypoconulid is slightly closer to the entoconid than to the hypoconid and is the smallest talonid cusp, while the hypoconid and entoconid are subequal in height. The ridge between hypoconid and hypoconulid often exhibits considerable wear and in worn specimens the hypoconid may be the lowest of the talonid cusps. The oblique crest joins the trigonid low on the trigonid wall.

The **m2** differs from m1 in having a slightly less anteriorly projecting paraconid, and a shorter and wider trigonid that is slightly larger than the talonid.

The **m3** resembles m2 but is somewhat smaller with a narrower talonid and a distinct hypoconulid.

P4 is premolariform and lacks a metacone, the crown consisting of a small parastyle, a large paracone and a large crest descending posterolabially from the paracone. Additional observations show the development of a small protocone and postcingulum, but neither conules nor hypocone are developed.

M1 is rectodont with a low, straight centrocrista. The paracone and protocone are subequal in height, and both are only slightly higher than the metacone. The ectocingulum bears a small parastyle; the metastylar crest and ectoflexus are moderately developed, but stylar cusps are absent. The trigon is transversely elongated, with two subequal conules, well-developed conule crests, and pre- and postprotocrista. The precingulum is small but always present; the postcingulum is relatively small with a hypocone and a remarkably straight posterior border.

M2 differs from M1 by its more labially orientated parastylar lobe, deeper ectoflexus and by its more transversely elongated trigon.

M3 is transversely shorter than M1 and M2. The labial side has a moderate parastyle; the lingual side presents a minute precingulum and a small postcingulum.

← Fig. 2. SEM micrographs of *Asionyctia guoi*, Gashatan ALMA (late Paleocene) from Subeng (Inner Mongolia, China). **A**. IMM 2004-SB-1, holotype, left dentary fragment with p4–m1 and alveoli for p2–3, in occlusal (A_1), labial (A_2), and lingual (A_3) views. **B**. IMM 2001-SB-10, right dentary fragment with m1–2 and alveoli of m3, in occlusal (B_1), labial (B_2), and lingual (B_3) views. **C**. IMM 2001-SB-11, left m3, in occlusal (C_1), labial (C_2), and lingual (C_3) views. **D**. IMM 2004-SB-3, right P4, in occlusal (D_1) and labial (D_2) views. **E**. IMM 2001-SB-12, left M1, in occlusal (E_1) and labial (E_2) views. **F**. IMM 2001-SB-13, left M2, in occlusal (F_1) and labial (F_2) views. **G**. IMM 2001-SB-14, fragmentary right M3, in occlusal (G_1) and labial (G_2) views. **H**. IMM 2001-SB-15, fragmentary left M3 in occlusal view.

Discussion

The molar teeth of *Asionyctia guoi* most closely resemble those of nyctitheriids. The lower molars possess a crestiform paraconid, subequal protoconid and metaconid, a relatively high trigonid, a marked but non-ascending oblique crest, and a hypoconulid that is slightly displaced towards the entoconid. The upper molars have a weak ectocingulum with a moderate ectoflexus, well-developed conules and conule crests, an anteroposteriorly compressed protocone, a small precingulum and a small postcingulum with a hypocone. These characters link *A. guoi* especially to the genus *Leptacodon*, generally considered the most primitive nyctitheriid genus (Robinson 1968; Sigé 1976; Butler 1988).

The family Nyctitheriidae is not well defined and therefore we limit our discussion to the European and North American forms that are most widely accepted to belong to this family. We examined all Asian taxa described as nyctitheriids but chose to analyse only the taxa where the attribution to the family Nyctitheriidae is unambiguous. The problematic Asian genera *Jarveia* Nessov, 1987 and *Praolestes* Matthew, Granger, and Simpson, 1929 have recently been considered nyctitheriids (Averianov 1995; Kondrashov et al. 2004). However, the morphological arguments for this are not unique to nyctitheriids. The upper molars of both genera show a very small to absent ectocingulum, poorly developed conules and conule crests, and the lack of a hypocone. These characteristics are unusual for nyctitheriids and the attribution of *Jarveia* and *Praolestes* to the family Nyctitheriidae is still uncertain and we did not consider them for further analyses.

Asionyctia guoi differs from all European and North American nyctitheriids by its upper molars with a transversely elongated trigon and a straight posterior border to the postcingulum. *A. guoi* differs from *Saturninia* Stehlin, 1940, *Amphidozotherium* Filhol, 1877, *Euronyctia* Sigé, 1997, and *Nyctitherium* by the much smaller postcingulum on the upper cheek teeth. *Asionyctia guoi* differs from *Amphidozotherium*, *Euronyctia*, *Nyctitherium*, and *Wyonycteris* by its low oblique crest and the complete lack of any characteristic linked to dilambdodont tendencies.

However, the most remarkable characteristics of *Asionyctia guoi* are in its premolars. Traditionally the family Nyctitheriidae is divided into two subfamilies: Nyctitheriinae and Amphidozotheriinae (Sigé 1976; McKenna and Bell 1997). Robinson (1968: 129) diagnosed Nyctitheriinae having a semimolariform P4/p4, double-rooted p2 and p3, a single-rooted p1, and a long and slender jaw with no apparent shortening; Sigé (1976) diagnosed Amphidozotheriinae having P4/p4 with a slightly attenuated (semi)molariform structure, and the median lower premolars, especially p3, reduced in size and tending to conserve only one root. In contrast, the P4 and p4 of *A. guoi* are completely premolariform and p3 is double-rooted and does not seem to have undergone any strong reduction. In *A. guoi*, the anterior lower premolars are reduced but the way this reduction occurred seems to be different from that seen in Amphidozotheriinae. Therefore, although the molar morphology places *Asionyctia* firmly within Nyctitheriidae, the morphology of the premolars of this new Asian species exclude it from both subfamilies known in Europe and North America.

Only few unambiguous nyctitheriids from Asia have been described, and the described species are very poorly known. Of these, *Bayanulanius tenuis* Meng, Zhai, and Wyss, 1998 and *Oedolius perexiguus* are comparable in size to *Asionyctia guoi*. However, the only known lower molar in *Bayanulanius tenuis* has an oblique crest ascending to the top of the metaconid, a deeper hypoflexid and a much smaller entoconid, and the upper molars of *B. tenuis* have better developed conule crests and an anteriorly orientated parastyle on M2. In *Oedolius perexiguus*, p4 has a strongly reduced paraconid and the lower molars have a relatively narrow talonid, with an oblique crest rising onto the trigonid wall and a lingually more open talonid basin. *Bumbanius rarus* Russell and Dashzeveg, 1986 differs from *Asionyctia guoi* by the presence of a large metaconid on p4, by its lower molars having an enlarged metaconid and by its more anteroposteriorly-compressed protocone on the upper molars. *Voltaia minuta* Nessov, 1987 has a premolariform p4 with a main median talonid cusp and a small, accessory lingual talonid cusp; the lower molars of *V. minuta* have a stronger oblique crest and a less crestiform paraconid. None of these species shows a reduction of the anterior lower premolars as observed in *Asionyctia guoi*.

Although our knowledge of unambiguous Asian nyctitheriids is limited, they show some important common features. In none of these species a semimolariform p4 is known, and all have a premolariform p4 with an unbasined talonid (only *Voltaia minuta* has a small accessory talonid cusp and only *Bumbanius rarus* has a metaconid on p4). Equally, where known, the upper molars of the Asian forms are transversely elongated with well-developed conules and conule crests, a small postcingulum with straight posterior border, and a complete lack of dilambdodonty. Russell and Dashzeveg (1986) and Meng et al. (1998) noted similarities among Asian nyctitheriids, and speculated on the possibility of uniting them in a new suprageneric taxon; here we explicitly confirm and expand these opinions. The material of *Asionyctia guoi* permits us to demonstrate clearly its nyctitheriid affinities, but also for the first time to define a unique set of characters grouping *Asionyctia*, *Bumbanius*, *Bayanulanius*, *Oedolius*, and *Voltaia* in a single clade apart from the European and North American nyctitheriids.

Cladistic analysis

In order to test the validity of this clade of Asian nyctitheriids, a cladistic analysis was performed, using PAUP 4.0b10 (Swofford 2003) and a set of 20 dental characters designed to resolve higher-level phylogenetic relations within Nyctitheriidae (Appendices 1 and 2). All unambiguous Asian nyctitheriids were included, as well as six European and North American nyctitheriid taxa. Five of these, *Leptacodon tener* Matthew and Granger, 1921, *Nyctitherium velox* Marsh, 1872, *Saturninia gracilis* Stehlin, 1940, *Amphidozotherium cayluxi* Filhol, 1877, and *Euronyctia montana* Sigé, 1997, are the type species of their respective genera and are fairly well known. The sixth one, *Leptacodon dormaalensis* was included because it is one of the oldest undoubted European nyctitheriids and has a well-known dentition of primitive nature (Smith 1996). Table 2 shows the age and the region of occurrence for the type material of all included species.

Because of the uncertain phylogenetic relations of the family Nyctitheriidae, a hypothetical taxon was constructed to be used as an outgroup. This was done by comparing the character states observed in *Leptacodon tener*, widely accepted as the most primitive nyctitheriid known, to those seen in *Paranyctoides* Fox, 1979, *Gypsonictops* Simpson, 1927, primitive leptictids, and primitive erinaceomorphs. All of these have been proposed to be at or near the origin of nyctitheriids and when serious conflicts arose between the observed character states, the character was scored "?" (unknown) in the outgroup. The resulting outgroup is not biased

Table 2. Correlative ages and localities for the type material of all species included in the cladistic analysis.

Taxa	Correlative ages	Localities
Leptacodon tener Matthew and Granger, 1921	Tiffanian (middle–late Paleocene)	Tiffany Beds, USA
Leptacodon dormaalensis (Quinet, 1964)	MP 7, Ypresian (early Eocene)	Dormaal, Belgium
Nyctitherium velox Marsh, 1872	Bridgerian (middle Eocene)	Bridger Basin, USA
Saturninia gracilis Stehlin, 1940	MP 18, Priabonian (late Eocene)	Gösgen, Switzerland
Euronyctia montana Sigé, 1997	MP 17, Priabonian (late Eocene)	Sossis, Spain
Amphidozotherium cayluxi Filhol, 1877	MP 19, Priabonian (late Eocene)	Caylus, France
Bumbanius rarus Russell and Dashzeveg, 1986	Bumbanian (early Eocene)	Naran Bulak, Mongolia
Asionyctia guoi gen. et sp. nov.	Gashatan (late Paleocene)	Subeng, China
Bayanulanius tenuis Meng, Zhai, and Wyss, 1998	Gashatan (late Paleocene)	Bayan Ulan, China
Oedolius perexiguus Russell and Dashzeveg, 1986	Bumbanian (early Eocene)	Naran Bulak, Mongolia
Voltaia minuta Nessov, 1987	Landenian (late Paleocene?)	Zhylga, Kazakhstan

by using *Leptacodon tener* as a starting point, but represents a generalized Eutherian type of dentition that is our nearest objective match for an outgroup to nyctitheriids. The outgroup has a maximal number of characters scored while remaining objective on more controversial points of nyctitheriid evolution such as the primitive shape of P4/p4.

Only parsimony-informative characters were included. Where the anteriormost teeth are unknown, sizes are based on the alveoli in this position (characters 2, 3). All characters were considered unordered except for characters 5, 8, 10, 11, and 20. For all these characters a gradual morphocline and an intermediate state can be observed, so their evolution is better considered ordered. Morphology was assessed through a review of the literature (McKenna 1968; Robinson 1968; Krishtalka 1976; Sigé 1976, 1997; Fox 1979; Russell and Dashzeveg 1986; Cifelli 1990; Smith and Smith 1995; Smith 1996; Meng et al. 1998; Archibald and Averianov 2001) and through study of casts.

The analysis yielded six equally most parsimonious cladograms of 37 steps with a consistency index of 0.7027 and a retention index of 0.8036. The major feature of the strict consensus tree (Fig. 3) is the grouping of all Asian Nyctitheriidae in a single clade that is supported by multiple clearly defined characters (characters 6, 13, and 18, and the not unambiguous character 7). These results confirm our earlier morphological observations and here we define a new, exclusively Asian clade of Nyctitheriidae, to which we accord the rank of subfamily and the name Asionyctiinae.

Within the Asionyctiinae, *Bumbanius rarus* is the most primitive member, being the only one where the metaconid on p4 was not lost. On the contrary, in *B. rarus* the metaconids of p4–m3 are enlarged compared to other nyctitheriids from Asia and elsewhere, probably representing a derived state and an early divergence from the other Asionyctiinae.

The consensus tree shows two polytomies for lower-level relationships. A first polytomy affects the phylogenetic relations of *Nyctitherium velox*, *Saturninia gracilis*, and (*Euronyctia montana* + *Amphidozotherium cayluxi*). In our view, this polytomy is the result of the convergence of characters in different independent lineages. We do not consider this unacceptable for the value of our analysis, because an exact resolution of lower-level relationships would require the inclusion of more taxa and more characters, and is beyond the scope of this article.

A second polytomy consists of three Asian Nyctitheriidae: *Bayanulanius tenuis*, *Oedolius perexiguus*, and *Voltaia minuta*. This result is not unexpected since these three genera are very poorly known. The available morphological information is sufficient to group them with the other Asian nyctitheriids and the development of the oblique crest unites these three taxa. At present, our knowledge of these taxa is insufficient to resolve their phylogenetic position completely. Nonetheless, it should be noted that all lower premolars of *V. minuta* are large and well-developed, more than currently known for any other Asian nyctitheriid, suggesting a rather basal position within the Asionyctiinae.

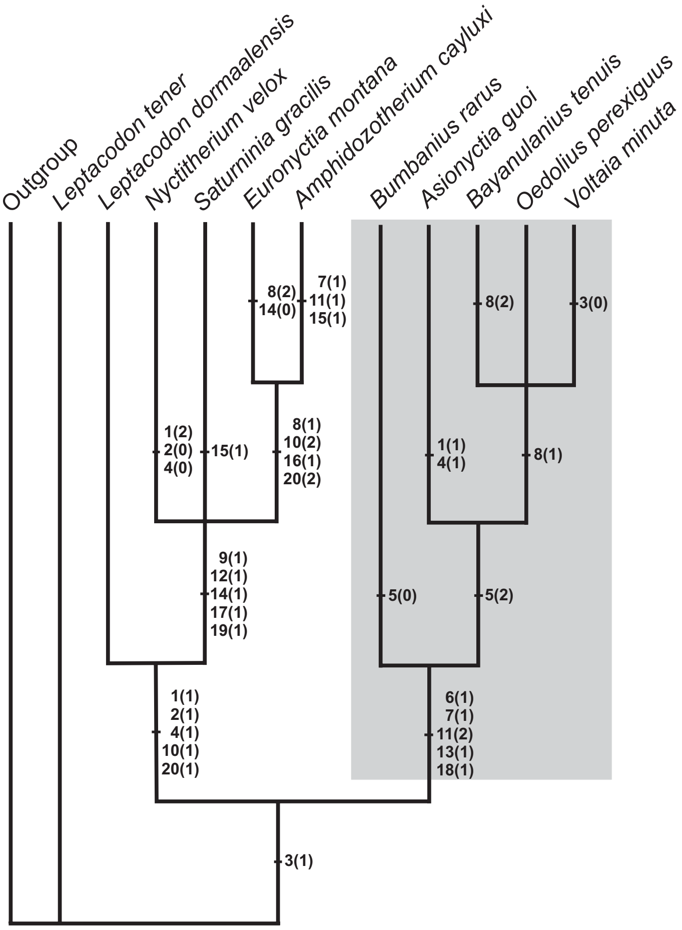


Fig 3. Strict consensus tree of six maximum-parsimony trees, based on the data matrix in Appendix 2. The shaded area indicates the position of the Asian nyctitheriids, grouped in the new subfamily Asionyctiinae. Characters have been mapped on the consensus tree, using the Acctran optimization for the maximum parsimony tree that corresponded completely to the consensus tree.

Phylogenetic and biogeographical implications

In their description of *Bayanulanius*, Meng et al. (1998) noted that *Bayanulanius* most closely resembles Asian *Bumbanius* and *Oedolius* and North American *Leptacodon.* Here we expand these ideas to all Asian Nyctitheriidae. All Asian nyctitheriids in our analysis are grouped in the exclusively Asian subfamily Asionyctiinae, best recognized by a structurally simplified P4/p4, and, among North American and European nyctitheriids, comparing most favorably to forms of the genus *Leptacodon*. It is generally agreed the genus *Leptacodon* served as a primitive stem group for the North American and European nyctitheriids (Sigé 1976; Krishtalka 1976; Smith 1996), but already in the Torrejonian there was a considerable morphological diversity. Asionyctiinae can be derived from an American *Leptacodon*-like form migrating into Asia, and this ancestor was closest to primitive forms such as *Leptacodon tener* or "*Leptacodon*" *packi* Jepsen, 1930 ranging from the late Torrejonian to latest Tiffanian (Krishtalka 1976; Scott 2003). "*Leptacodon*" *munusculum* Simpson, 1935 from the Torrejonian to Tiffanian is more derived by its more lingual hypoconulid on the molars and *Leptacodon catulus* Krishtalka, 1976 from the Wasatchian is more derived by the lingual expansion of the ectocingulum. *Leptacodon rosei* Gingerich, 1987 from the Clarkforkian closely resembles European *Leptacodon dormaalensis* and this lineage characterized by a more reduced p3 may be ancestral to the other European nyctitheriids (Smith 1996).

Our cladistic analysis suggests the structurally more simple P4/p4 of Asionyctiinae evolved by reduction of a more complex, semimolariform P4/p4 and this accords well to similar reductions observed in several lineages of late Eocene and Oligocene nyctitheriids in Europe (Sigé 1976; Sigé and Storch 2001). As North American nyctitheriids are fairly well known and none of them shows a P4/p4 with a reduced structure, the differentiation of the asionyctiine P4/p4 most likely took place on the Asian continent, only after migration of the North American ancestor. *Asionyctia* and *Bayanulanius* are found in faunas of Gashatan age, and at that moment in time a third lineage towards *Bumbanius* is supposed to have been present already. This means that already by Gashatan times the Asionyctiinae had fully developed a reduced P4/p4 and other synapomorphies, and that they had already diverged into at least three lineages with a morphology differing at the generic level. These morphological changes certainly required a considerable minimal period of isolated evolution on the Asian continent, especially for a group thought to be markedly conservative (Sigé 1976; Butler 1988). The Gashatan in Asia is generally accepted to be late Paleocene in age and is traditionally correlated to the Clarkforkian in North America (Meng and McKenna 1998; Ting 1998), although some authors suggest an even older age for the Gashatan faunas (Beard 1998; Wang et al. 1998; Beard and Dawson 1999).

Based on the late Torrejonian to late Tiffanian age of a convenient ancestor for Asionyctiinae, on the age correlations for the earliest representatives for Asionyctiinae, on the many derived characters of these earliest representatives and on the generally slow morphological evolution of Nyctitheriidae, we suggest the migration of the common ancestor of Asionyctiinae to have taken place during the early Tiffanian. Smith et al. (2004) noted the possibility of an early to middle Tiffanian migration of carpolestid plesiadapiforms into Asia and a simultaneous migration of both groups into Asia is a valid possibility.

According to this model for the origin of Asian nyctitheriids, other nyctitheriids are to be found in Asia in sites of an older age, including forms with an intermediate morphology showing a less reduced P4/p4. Once again, additional research on late Paleocene Asian mammal faunas can be a key for a better understanding of the early Paleogene mammals from Asia and their paleobiogeographical relations.

Conclusions

The molar morphology of *Asionyctia guoi* places it firmly within the family Nyctitheriidae, comparing most favorably with *Leptacodon*, among North American and European forms. Although knowledge of other Asian nyctitheriids is incomplete, they together with *Asionyctia guoi* can be united in the new higher-level clade Asionyctiinae, characterized by a structurally reduced P4/p4, and by transversely elongated upper molars having a small postcingulum with a straight posterior border. Within this subfamily, *Bumbanius* is set apart from the other Asionyctiinae, being the only one to have retained the metaconid on p4 and probably representing an early divergent lineage. Other internal phylogenetic relations within the Asionyctiinae are poorly resolved but we anticipate future discoveries of new asionyctiine fossils will confirm our conclusions and further clarify their phylogeny.

Asionyctiinae probably descended from a North American, primitive *Leptacodon*-like ancestor of late Torrejonian to late Tiffanian age that migrated into Asia. Because the evolution of Asionyctiinae appears to have taken place after this migration, because of their morphological diversity already in the Gashatan ALMA, and because of the generally slow morphological evolution of nyctitheriids, we suggest an early Tiffanian time for the migration of nyctitheriids into Asia.

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Appendix 1

List of characters and character definitions used in our cladistic analysis of higher-level relationships within Nyctitheriidae. Character states considered primitive are in bold.

1. **Jaw with premolar row slightly longer than molar row (0)**, premolar row shortened (1), premolar row lengthened (2).
2. **The c1 large (0)**, small (1).
3. **The p2 and/or p3 not reduced in morphology and size (0)**, reduced (1).
4. **The p4 paraconid situated low (0)**, moderately high to very high (1).
5. The p4 metaconid present and larger than the protoconid (0), present but not larger than the protoconid(1), absent (2).
6. The p4 talonid basin present (0), absent (1).
7. The p4 with 2 or 3 large talonid cusps (0), 1 main median talonid cusp (1).
8. **Oblique crest on lower molars low (0)**, weakly to moderately rising towards the metaconid (1), rising to the top of the metaconid (2).
9. Lower molars without postcingulid (0), postcingulid present (1).
10. **The m3 not reduced in size (0)**, slightly reduced (1), markedly reduced (2).
11. P4 metacone well-developed and differentiated from paracone (0), small and fused with paracone (1), absent (2).
12. **P4 without hypocone (0)**, with hypocone (1).
13. Upper molar trigon not transversely elongated (0), transversely elongated (1).
14. **Paraconule crests on the molars pronounced (0)**, reduced to absent (1).
15. **Metaconule crests on the molars pronounced (0)**, reduced to absent (1).
16. **Precingulum M1–2 present (0)**, vestigial to absent (1).
17. **Postcingulum M1–2 small to moderately sized (0)**, large (1).
18. Posterior border of postcingulum M1–2 rounded (0), straight (1).
19. **M2 transversely longer than M1 (0)**, equally long (1).
20. **M3 not reduced in size (0)**, slightly reduced (1), markedly reduced (2).

Appendix 2

Character matrix used to assess higher-level phylogenetic relations within Nyctitheriidae. Missing or unknown characters are marked “?”.

Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Outgroup	0	0	0	0	?	?	?	0	?	0	?	0	?	0	0	0	0	?	0	0
Leptacodon tener	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptacodon dormaalensis	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Nyctitherium velox	2	0	1	0	1	0	0	0	1	1	0	1	0	1	0	0	1	0	1	1
Saturninia gracilis	1	1	1	1	1	0	0	0	1	1	0	1	0	1	1	0	1	0	1	1
Euronyctia montana	?	1	1	1	1	0	0	2	1	2	0	1	0	0	0	1	1	0	1	2
Amphidozotherium cayluxi	1	1	1	1	1	0	1	1	1	2	1	1	0	1	1	1	1	0	1	2
Bumbanius rarus	0	?	1	0	0	1	1	0	0	0	?	?	1	0	0	0	0	1	0	?
Asionyctia guoi	1	0	1	1	2	1	1	0	0	0	2	0	1	0	0	0	0	1	0	0
Bayanulanius tenuis	?	?	?	?	?	?	?	2	0	?	?	?	1	0	0	0	0	1	?	0
Oedolius perexiguus	0	0	1	0	2	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Voltaia minuta	0	0	0	0	2	1	1	1	0	0	?	?	?	?	?	?	?	?	?	?