第49卷 第4期
2011年10月

古脊椎动物学报
VERTEBRATA PALASIATICA

pp.406－422
figs.1－8

现生毛猬 *Neotetracus* 属与 *Hylomys* 及 *Neohylomys* 属齿系和颅骨的比较

Burkart ENGESSER[1]　蒋学龙[2]

（1 瑞士巴赛尔自然历史博物馆　巴赛尔　CH－4001）

（2 中国科学院昆明动物研究所　昆明　650223）

摘要：鼩猬属 *Neotetracus* 是毛猬亚科 Hylomyinae 中一个个体小、对其知之甚少的成员。本文对其齿系（包括乳齿）和颅骨的特征进行了描述，并与毛猬属 *Hylomys* 及毛猬类其他近亲的齿系和颅骨形态进行了相应比较。由于现生的鼩猬属为一单型属，其惟一的种 *Neotetracus sinensis* 被一些研究者归入毛猬属，本文之所以进行这样的比较，目的是为了弄清楚这种归并是否合理。*Neohylomys hainanensis* 是毛猬类的另一属种，亦有学者将其归入 *Hylomys* 属。尽管这一属种的材料不多，在此同样作了比较研究。比较表明，毛猬亚科上述三属间在齿列上的几乎每一颗牙齿和某些头骨形态上都有明显的差别，研究的结果为保留 *Neotetracus*，*Neohylomys* 和 *Hylomys* 属的独立存在提供了证据，并根据这三个属在形态上的差异对其相互间的进化水平进行了评估。现代的毛猬亚科动物生活在亚洲东南部一个相对小的地区，总共有5属6种。地史上，特别是在中、晚中新世期间，这一亚科几乎散布整个北半球，从亚洲到欧洲和北非，从旧大陆到新大陆都有其踪迹。那时的种类也比现在的多，迄今描述的化石已有9属47种。因此，有理由认为毛猬亚科是一类孑遗动物。毛猬亚科分布地区缩小的原因还不清楚，为了探讨和认识这一有意思的课题，本文对其历史和分布做了简要的阐述。

关键词：云南；食虫目，毛猬亚科，鼩猬属，毛猬属，海南毛猬属；齿学，颅骨学；比较

中图法分类号：Q915.873　**文献标识码**：A　**文章编号**：1000－3118(2011)04－0406－17

ODONTOLOGICAL AND CRANIOLOGICAL COMPARISONS OF THE RECENT HEDGEHOG *NEOTETRACUS* WITH *HYLOMYS* AND *NEOHYLOMYS* (ERINACEIDAE, INSECTIVORA, MAMMALIA)

Burkart ENGESSER[1]　JIANG Xue-Long[2]

(1 *Naturhistorisches Museum Basel* Augustinergasse 2, CH－4001 Basel, Switzerland　burkart. engesser@ yahoo. com)

(2 *Kunming Institute of Zoology*, *the Chinese Academy of Sciences* Kunming 650223, China)

Abstract　The dentition and some cranial characters of *Neotetracus*, a small, little known member of the subfamily Hylomyinae are described and compared with corresponding parts of *Hylomys*, another closely related hylomyine erinaceid. The milk-dentition is included in these descriptions. Since the single species of the genus *Neotetracus*, *N. sinensis*, was placed by some authors in the genus *Hylomys*, the comparisons aim at finding out, whether the fusing of the two genera is justified or not. *Neohylomys hainanensis*, another hylomyine having been placed by some authors in the genus *Hylomys*, is, despite the scarce material at disposal, included in these comparisons as well. The comparisons yield distinct

收稿日期：2011－06－03

differences between these three hylomyines in almost each tooth and in some skull features, fully justifying the maintenance of the genera *Neotetracus*, *Neohylomys* and *Hylomys*. The differences found are also used to assess the evolutionary level of the three forms with respect to each other. The Hylomyinae are living today in a relatively small area in Southeast Asia and are represented by five genera with a total of six species. In the past, especially during the Middle and Late Miocene, this subfamily was spread over almost the whole northern hemisphere: from Asia to Europe and North Africa, and to North America. The Hylomyinae were also much more diverse than today, so far 9 fossil genera with 47 species having been described. Therefore it is justified to speak of the Hylomyinae as relict forms. To emphasize the shrinking of the distribution area of the Hylomyinae, the reasons for which are not yet understood, an abridged history of the subfamily is given.

Key words Yunnan; Insectivora, Hylomyinae, *Neotetracus*, *Hylomys*, *Neohylomys*; odontology, craniology; comparison

1 Introduction

Neotetracus (common name: shrew gymnure) is a small representative of the subfamily Hylomyinae Anderson, 1879, living today in China (provinces of Yunnan, Sichuan, and Guizhou), northern Myanmar, and northern Vietnam. The genus includes one species: *N. sinensis* Trouessart, 1909, with three subspecies: *N. s. sinensis* Trouessart, 1909, *N. s. fulvescens* Osgood, 1932, and *N. s. cuttingi* Anthony, 1941. Several authors (e.g. Frost et al., 1991) included the species *sinensis* together with (*Neohylomys*) *hainanensis* Shaw & Wong, 1959 into the genus *Hylomys* Müller, 1839.

The subfamily of the Hylomyinae (moonrats or hairy hedgehogs) is a very primitive group of insectivores, having had a huge area of distribution during the Middle and Late Miocene (about 15 ~ 10 million years ago). This area extended from Asia over Europe to Africa, and to North America. Especially in Europe the Hylomyinae were extremely abundant and produced a great variety of genera and species.

Today the distribution of the Hylomyinae is restricted to Southeast Asia (Southwest China, Burma, Laos, Vietnam, Kampuchea, Malaysia, Indonesia, and the Philippines), including only 5 genera (3 according to certain authors) with 6 species in total. Therefore it is justified to speak of the Hylomyinae as relict forms. For emphasizing the shrinking of the distribution area of the Hylomyinae, the reasons for which are not yet understood, we give here an abridged history of the subfamily.

Especially for palaeontologists the Hylomyinae living today are of great interest, because they can give an idea how the fossil relatives of the Recent moonrats could have lived. Since only the dentition is known for Tertiary Hylomyinae with few exceptions (*Galerix*, *Deinogalerix*), statements about the way of life and the ecology of the fossil forms are possible only to a very restricted extent.

The question, whether *Neotetracus* is a separate genus or whether the species *sinensis* should be classified within the genus *Hylomys* is still very much discussed (Corbet, 1988; Frost et al., 1991). We attempt to contribute to the solution of this problem by comparing the dentitions of *Neotetracus* and *Hylomys*. Since the dentitions of these hedgehogs so far have been neither described nor figured in detail, in connection with the comparisons we give detailed descriptions. At this occasion the milk dentition and the tooth replacement are described as well.

Our odontological and craniological comparisons are mainly based upon 43 *Neotetracus* and 10 *Hylomys* skulls of the collection of the Kunming Institute of Zoology (KIZ) and 2 *Neotetracus* and 1 *Hylomys* skulls of the Basel Natural History Museum (NMB).

The comparisons with *Neohylomys hainanensis* Shaw & Wong, 1959 are less extensive than those between *Neotetracus* and *Hylomys*, because only 4 skulls (one of them badly broken) from the Kunming Institute of Zoology were at our disposal, not permitting a statement about the vari-

ability of characters.

A second article on *Neotetracus* about its outward appearance, its biotope, its behaviour in captivity and DNA comparisons of *Neotetracus*, *Hylomys*, and *Neohylomys* will be published elsewhere.

2 Comparisons and descriptions

2.1 Comparison and description of the dentitions of *Neotetracus* and *Hylomys*

Neotetracus and *Hylomys* show many and various differences in the dentition. Almost each tooth shows features enabling the distinction of the two genera. In the following only those characters are mentioned that seem little subject to variability. There are other characters by which the two genera can be distinguished only with a great number of skulls at hand (e. g. the number of roots of the premolars). These characters are not treated here.

The most eyecatching difference in the dentition of *Neotetracus* and *Hylomys* having been mentioned already by different authors (Leche, 1902; Corbet, 1988; Frost et al., 1991) is the number of premolars: *Neotetracus* having three of them in the upper and the lower jaw, whereas *Hylomys* has four. These numbers are subject to little variability: among 43 skulls of *Neotetracus* of the collection of the KIZ there was only one, showing the left p2 reduced to a functionless vestige. Among 10 *Hylomys* skulls only one deviation was found with only three premolars in the lower jaw.

The teeth of the upper jaw I1: The I1 of *Neotetracus* is very large. It is by far the largest tooth in front of the P4. Its crown is slightly bent backwards and it shows a distal cutting edge but no basal cusp (Fig. 1A).

The I1 of *Hylomys* is distinctly smaller, its crown is hook-shaped, that means from the root it bends first forwards and then back again. Distally the I1 of *Hylomys* has a small basal cusp.

I2: The I2 of *Neotetracus* is quite large, its crown is straight and conical. It is separated from the I1 by a distinct diastema (Fig. 1A).

The I2 of *Hylomys* is smaller and its crown is bent backwards.

I3: The I3 of *Neotetracus* is distinctly smaller than the I2 and shows a straight, conical crown with a small anterior and sometimes a posterior cusp.

The I3 of *Hylomys* is very small with a slightly backwards bent crown and often with an anterior and a posterior basal cusp. In *Hylomys* there is a quite wide diastema between I3 and C, in *Neotetracus* being much narrower. All three incisors of *Neotetracus* and *Hylomys* are single-rooted.

C: The upper canine of *Neotetracus* is only a little larger than the I3 and has a triangular crown in labial view and weak anterior and posterior basal cusps. It has two strongly spread roots (Fig. 1A).

The C of *Hylomys* is much larger than that of *Neotetracus*, has a backwards bent crown, a quite strong posterior basal cusp, and two spread roots.

P1, P2, P3: The upper canine of *Neotetracus* is followed by two almost identical small teeth (P2 and P3) with conical crown and small anterior and posterior basal cusps. P2 and P3 are sometimes single- and sometimes double-rooted.

The P1 of *Hylomys* is a small, mostly single-rooted tooth with distinct anterior and posterior basal cusps, the posterior being stronger. The P2, mostly single-rooted too, is somewhat larger than the P1, but very similar (Fig. 1B).

The P3 of *Hylomys* is distinctly larger than the P2 and also larger than that of *Neotetracus*. It shows an anterior and a posterior basal cusp, a weak labial cingulum and always two roots.

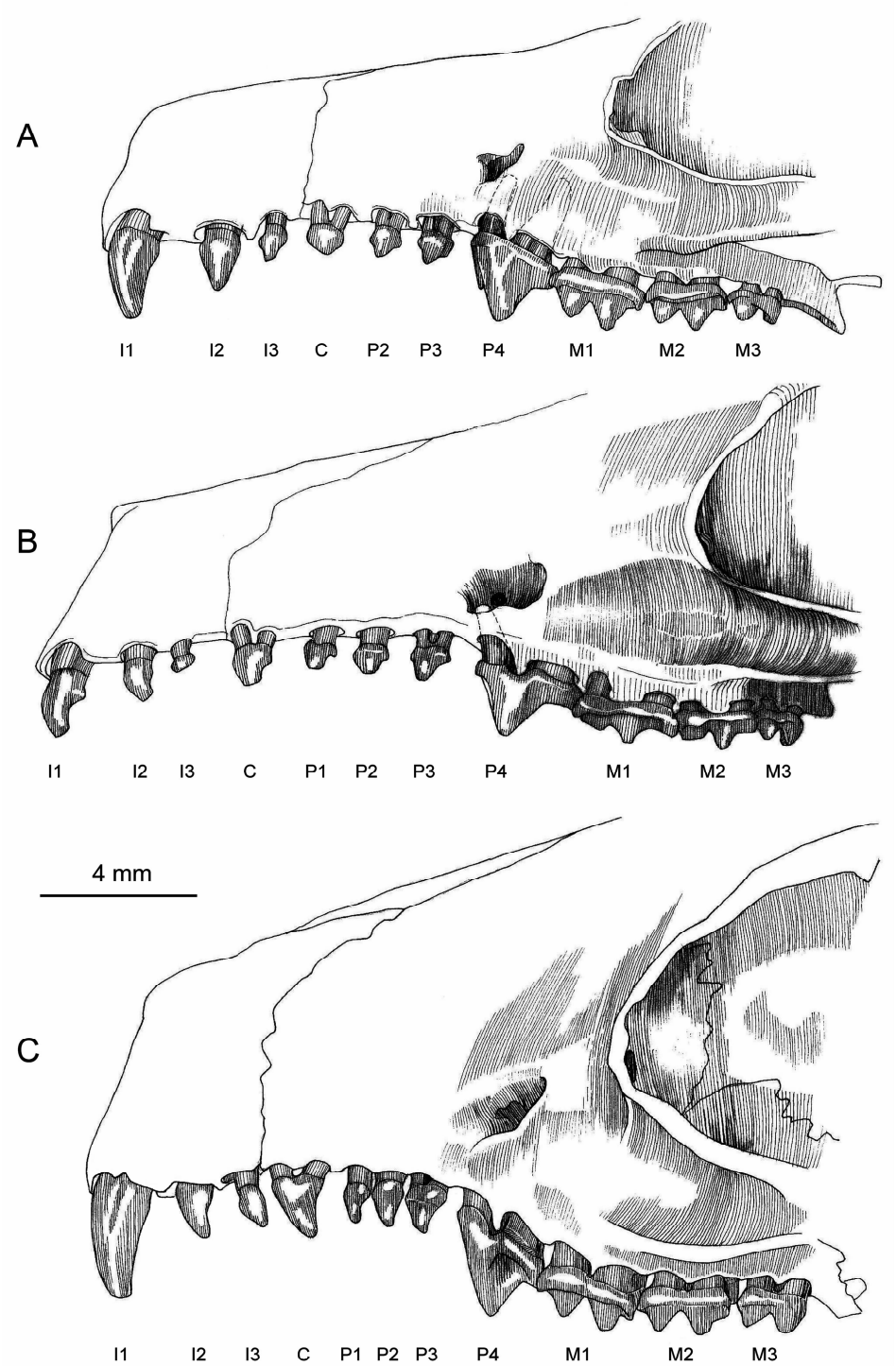

Fig. 1　Comparison of the upper dentition (I1-M3 sin.) of *Neotetracus*, *Hylomys* and *Neohylomys* in labial view
A. *Neotetracus sinensis* from Yunnan, KIZ 640154; B. *Hylomys suillus dorsalis* from northern Borneo, NMB 8892; C. *Neohylomys hainanensis* from Hainan, KIZ 201313

P4: The P4 of *Neotetracus* and *Hylomys* resemble each other in having a large main cusp and two smaller lingual cusps. However, the P4 of *Neotetracus* is much stouter and-the most important difference from *Hylomys*—is lacking a parastyle, which is very distinct in *Hylomys* and always present (Figs. 2A, B). The posterior lingual cusp of the P4 of *Neotetracus* is very low compared with that of *Hylomys*. In addition the P4 of *Neotetracus* is often as long as the M1, whereas in *Hylomys* the M1 is mostly longer. As in other Hylomyinae, the P4 shows the largest variability in size and morphology of all teeth.

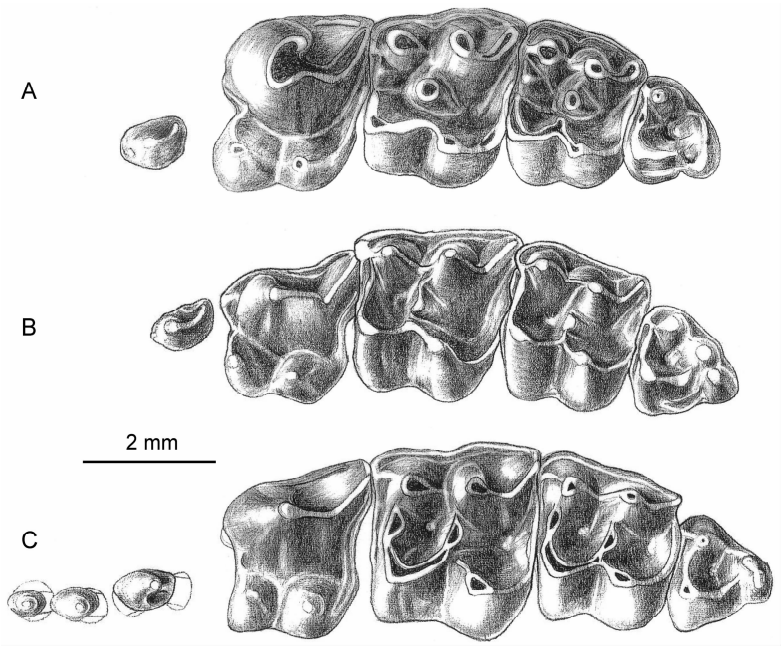

Fig. 2 Comparison of the upper cheek teeth of *Neotetracus*, *Hylomys* and *Neohylomys* in occlusal view
A. *Neotetracus sinensis* from Yunnan, KIZ 74116, P3-M3; B. *Hylomys suillus suillus* from Yunnan, KIZ 620034, P3-M3; C. *Neohylomys hainanensis* from Hainan, KIZ 201313, P1-M3 sin

M1/M2: In *Neotetracus* the M1 is only slightly larger than the M2, whereas in *Hylomys* this size difference is distinctly larger. The M1 and M2 of *Neotetracus* have a very large metaconule, round in occlusal view, and almost always separated from the posterior branch of the protocone in the M1, and mostly in the M2 (Fig. 2A), resembling very much the metaconule of M1 and M2 of *Lanthanotherium*.

In *Hylomys* the metaconule of M1 and M2 is much smaller, mostly crest-shaped and mostly (in M2 even more than in M1) connected with the posterior branch of the protocone (Fig. 2B. This is a very primitive character, being typical for Oligocene Hylomyinae like *Tetracus*).

From the metaconule of M1 and M2 of *Hylomys* often a ridge—the continuation of the posterior branch of the protocone—runs labially towards the metacone. To this extend, this feature is not observed in the M1 and M2 of *Neotetracus*.

An additional difference between the two genera is the diagonal extension (anterolingually/posterolabially) of the M1 and to some extent also of the P4 of *Neotetracus*, which is not so pronounced in *Hylomys*. In *Neotetracus* the M1 and M2 almost always show a protoconule, sometimes a very distinct one. In M1 and M2 of *Hylomys* this cusp is almost always lacking (Figs. 2A, B).

M3: The posterior talon of the M3 of *Hylomys* is almost always divided (in 8 of 9 specimens) into metacone and hypocone, in some specimens even very distinctly (Fig. 2B; KIZ

620034, KIZ 0611075). In the M3 of *Neotetracus* this subdivision is very rare (only in 2 of 12 specimens).

The teeth of the lower jaw　i1: The i1 is by far the largest tooth of the mandible of *Neotetracus* in front of the p4. It is obliquely inclined and its crown is shovel-shaped (Fig. 3A).

The i1 of *Hylomys* is very much smaller, not larger than i2 and c. It is almost horizontally implanted in the jaw and its crown is shovel-shaped (Fig. 3B).

i2: The i2 of *Neotetracus* is tiny with a rounded, button-like crown sitting on a long root. It is obliquely implanted, too.

The i2 of *Hylomys* is much larger than that of *Neotetracus*, about as large as the i1. This tooth with its flattened, shovel-like crown is anteriorly directed.

i3: The i3 of *Neotetracus* is distinctly larger than the i2. The root inserts ventral to the posterior part of the lingually flattened crown, triangular in lateral view (Fig. 3A).

The i3 of *Hylomys* is smaller than the i2. Its crown resembles that of the i3 of *Neotetracus*, but is less rounded.

c: In size and morphology the lower canine of *Neotetracus* is very similar to the i3, but it is less flattened on the lingual side. It is almost vertically implanted in the mandible.

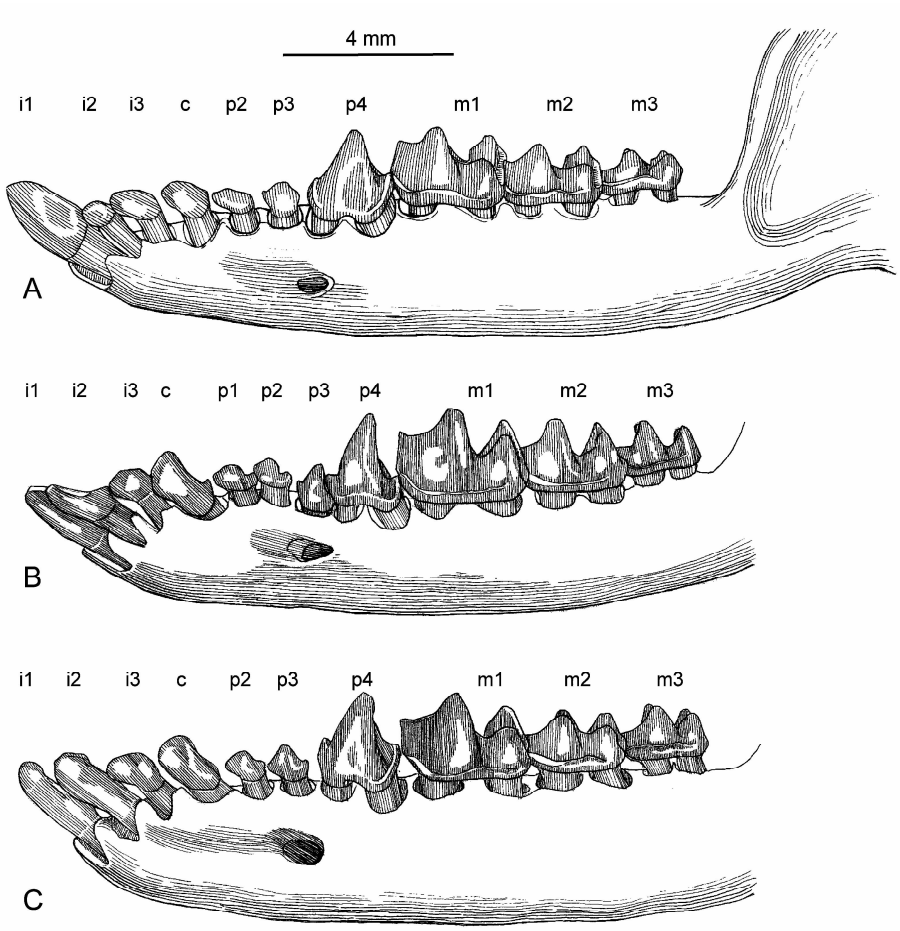

Fig. 3　Comparison of the lower dentition (i1-m3 sin.) of *Neotetracus*, *Hylomys* and *Neohylomys* in labial view
A. *Neotetracus sinensis* from Yunnan, KIZ 640154; B. *Hylomys suillus* from Yunnan, KIZ 0611075 (m3 reversed from the right side); C. *Neohylomys hainanensis* from Hainan, KIZ 201313

The lower canine of *Hylomys* is totally different: it is much larger, has a very long crown with a distinct posterior basal cusp, and it is anteriorly directed with posteriorly directed root (Fig. 3B).

p1-p3: Even *Neotetracus* having no p1, the p2 is situated closer to the c than the p1 in *Hylomys*. The p2 and p3 of *Neotetracus* are very similar to each other, the p3 usually being somewhat smaller. Both premolars are rounded, somewhat inflated, and show a weak posterior basal cusp.

The p1, p2, and p3 of *Hylomys* are very similar to each other. Their size increases from the front to the rear. They are less inflated than the p2 and p3 of *Neotetracus* and have stronger posterior basal cusps.

p4: The p4 of *Neotetracus* is a very strong "cracking" tooth, wider and more robust than in *Hylomys*. In front this p4 is about as wide as at the back, whereas that of *Hylomys* is distinctly narrower anteriorly (Figs. 3, 4). Whereas in *Hylomys* the labial side of the p4 is mostly surrounded by a continuous cingulum, in the p4 of *Neotetracus* this cingulum is only discernible anteriorly and posteriorly on the labial side.

The p4 of *Hylomys* is much more slender than that of *Neotetracus*. On the p4 of both genera distinct anterior and posterior cusps can be observed. It is very conspicuous that in *Neotetracus* the p4 is situated deeper in the jaw; i. e., the base of the crown is more ventral than that of the other teeth (Fig. 3A). This might be an indication, that this tooth is more subjected to strain than others.

In *Hylomys* the p4 is at the same level as the other teeth of the tooth row. All teeth of *Neotetracus* and *Hylomys* in front of p4 are single-rooted, but the p4 of both genera is double-rooted. The roots of the p4 of *Neotetracus* are much stronger developed than those of the p4 of *Hylomys* (Figs. 3A, B).

m1, m2, m3: The most obvious difference between the lower molars of *Neotetracus* and *Hylomys* are the entoconid crests, well developed in *Neotetracus*, but lacking in *Hylomys* (Figs. 4A, B). In *Neotetracus* these entoconid crests are most developed in the m2, somewhat less in the m1, and least in the m3. The m1 of *Hylomys* is distinctly larger than the m2. In *Neotetracus* this size difference is less pronounced. In addition the labial cingulum of lower molars is stronger in *Hylomys* than in *Neotetracus*. The m3 of *Hylomys* has a much stronger labial cingulum than that of *Neotetracus* (Figs. 4A, B).

The milk-dentition of *Neotetracus* and *Hylomys* (Figs. 5, 6) The following comparisons as far as *Hylomys* is concerned, are based only on one specimen with milk teeth. In the collection of the KIZ no second specimen was found, and in that of the Zoological Institute in Beijing there was no *Hylomys* skull with milk teeth at all.

The milk-teeth of the anterior part of the mandible in front of P4 and p4 are distinguished from their permanent successors mainly by their smaller size, and only little by their morphology. The differences between these teeth of *Neotetracus* and those of *Hylomys* are also slight, and these milk-teeth are subject to great morphological variability. Therefore it is not worth describing them in detail. The DP4 and dp4 of both genera on the other hand are completely different.

dp4: Like the p4 of *Neotetracus*, its dp4 is also stronger, stouter, and wider than that of *Hylomys*. Especially in the front part, *Hylomys* is very narrow, whereas *Neotetracus* is wider. The dp4 of *Hylomys* shows a very strong lingual cusp, whereas this cusp is weakly developed in the dp4 of *Neotetracus* or entirely lacking. Also the anterior cusp is more distinct in the dp4 of *Hylomys* than in that of *Neotetracus*.

DP4: The DP4 of *Hylomys* is more slim than that of *Neotetracus*. It has a very strong posterior lingual cusp, whereas this is poorly developed in the DP4 of *Neotetracus* or entirely lacking. The anterior lingual cusp of the DP4 of *Hylomys* is stronger, too. The DP4 of *Hylomys* shows an extremely anteriorly protruding parastyle, whereas that of *Neotetracus* is only poorly developed

(Figs. 6A, B). In the DP4 of *Neotetracus* the main cusp occupies almost the whole crown, but a wide talon lingual to the main cusp is found in the DP4 of *Hylomys*.

In *Neotetracus* and *Hylomys* the milk-dentition seems to be in function for quite a long time. This is proved by several skulls in the collection of the KIZ, having still all milk-teeth in the anterior part of the mandible while molars are distinctly worn. The DP4 and the dp4 seem to be replaced first, as shown by two skulls having already the P4 and p4 but in front of them all milk-teeth (Figs. 5C, D).

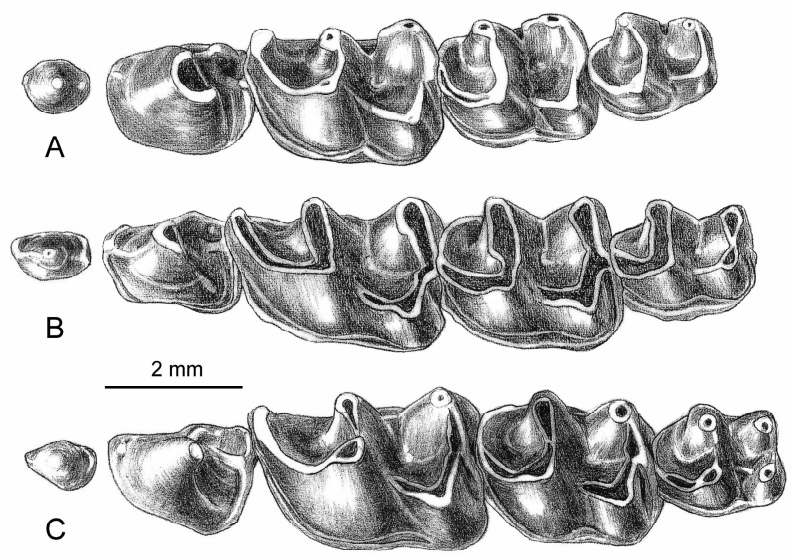

Fig. 4　Comparison of the lower dentition (p3-m3) of *Neotetracus*, *Hylomys* and *Neohylomys* in occlusal view
A. *Neotetracus sinensis* from Yunnan, KIZ 74116; B. *Hylomys suillus* from Yunnan, KIZ 810888; C. *Neohylomys hainanensis* from Hainan, KIZ 201313

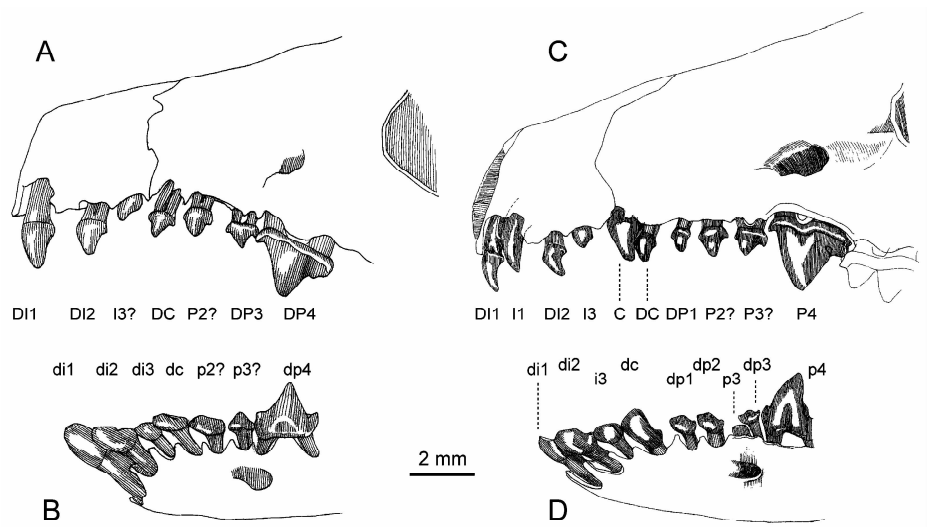

Fig. 5　The tooth replacement of *Neotetracus* and *Hylomys* in labial view
A-B. *Neotetracus sinensis* from Yunnan, KIZ 640137: A. upper dentition DI1-DP4 sin., B. lower dentition di1-dp4 sin.; C-D. *Hylomys suillus* from Yunnan, KIZ 620034: C. upper dentition DI1-P4 sin., D. lower dentition di1-p4 sin.

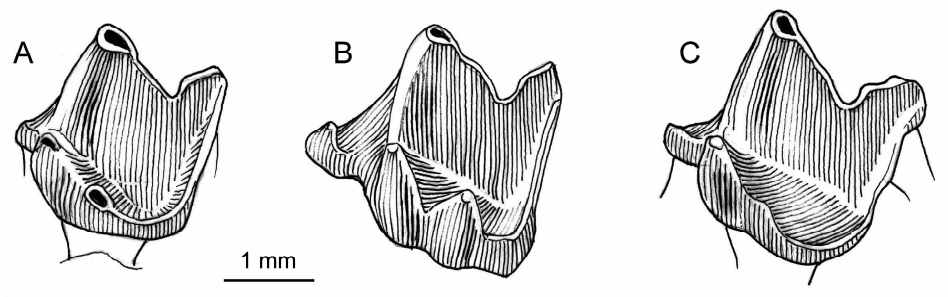

Fig. 6 Comparison of the last upper milk tooth (DP4) of *Neotetracus*, *Hylomys* and *Neohylomys* in lingual view
A. *Neotetracus sinensis* from Yunnan, DP4 sin., KIZ 820576; B. *Hylomys suillus* from Yunnan, DP4 dext. (reversed), KIZ 003397; C. *Neohylomys hainanensis* from Hainan, DP4 sin., KIZ 201312

2.2 The dentition of *Neohylomys hainanensis* in comparison with that of *Neotetracus sinensis* and *Hylomys suillus*

Upper teeth I1: The I1 of *Neohylomys* is very large and has a posterior cutting edge as in *Neotetracus*. In one specimen of the four *Neohylomys* stored in the KIZ, the I1 shows a small posterior basal cusp as in *Hylomys*. The I1 of *Neohylomys* is much larger than that of *Hylomys* and even of that of *Neotetracus* (Figs. 1A-C).

I2: *Neohylomys* has a relatively large I2 with a large, wide root and a slightly backwards bent crown. It is larger than that of *Hylomys* and without posterior basal cusp.

I3: The I3 of *Neohylomys* is a tiny single-rooted tooth. In contrast to that of *Hylomys* it has no posterior basal cusp (Fig. 1C).

C: The upper canine looks very much like that of *Hylomys*, being much larger than that of *Neotetracus*. It has a slightly posteriorly bent tip and two distinctly separated spread roots (Fig. 1C).

P1: *Neohylomys* has a very small, single-rooted P1, being very similar to the I3 in size and morphology and without the posterior basal cusp as that of *Hylomys*.

P2: The P2 of *Neohylomys* is almost equally large as the P1, but has a thicker root and no posterior basal cusp as found in *Hylomys*. In contrast to the P2 of *Neotetracus* the root is not divided.

P3: The P3 of *Neohylomys* is as high as the P2, but shows two clearly separated roots, a weak posterior basal cusp and a slightly backwards bent tip. It is elliptical in occlusal view, not triangular as in *Neotetracus* (Figs. 2A, C). The roots are more spread than in the P3 of *Hylomys*, which shows sometimes only one root.

P4: As in other Hylomyinae the P4 of *Neohylomys* shows a great variability: two of three specimens show a large parastyle, one none at all. The anterior lingual cusp is distinctly higher than the posterior one (Fig. 2C). The anterior labial root sometimes breaks through into the infraorbital foramen. The lingual root is slightly subdivided.

M1: In occlusal view the M1 of *Neohylomys* is almost square. It has a very weak, but discernible protoconule. The posterior branch of the protocone is well connected with the metaconule and with the hypocone (Fig. 2C). The posterior branch of the hypocone joins the posterior cingulum. The metaconule is elongated as in the M1 of *Hylomys* (not round as in *Neotetracus*). There is a strong labial cingulum.

M2: The M2 of *Neohylomys* is distinctly smaller than the M1 and square, too. The connections of the posterior branch of the protocone with the metaconule and the hypocone are very strong. The metaconule is elongated as in *Hylomys*. M1 and M2 have four roots.

M3: The M3 of *Neohylomys* is similar to that of *Hylomys* with slightly separated metacone and hypocone (in two of three specimens). These two cusps are situated more labially than in *Neotetracus*, between paracone and protocone (Fig. 2C). The M3 has three roots.

Lower teeth i1: The i1 of *Neohylomys* is not enlarged as in *Neotetracus*. It is shovel-

shaped and obliquely directed at an angle of about 45° (Fig. 3C).

i2: The i2 of *Neohylomys* is almost as big as the i1, thus much larger than that of *Neotetracus*. It is shovel-shaped and obliquely implanted.

i3: As in *Hylomys* the i3 of *Neohylomys* is distinctly smaller than i1 and i2. Its crown is triangular in labial view, extended anteriorly.

c: The lower canine of *Neohylomys* is much larger than that of *Neotetracus*. It is obliquely implanted, triangular in labial view, and has a small posterior basal cusp (Fig. 3C).

p1: All 4 specimens of *Neohylomys* of the KIZ collection lack p1.

p2 and p3: The p2 and p3 of *Neohylomys* are very similar to each other: single-rooted with triangular crown in labial view (Fig. 3C). Both teeth show a small posterior basal cusp, which is more pronounced in p2 than in p3.

p4: The p4 of *Neohylomys* is relatively strong, wider at the back than in front, and shows a small anterior cusp. One of two well preserved p4 of the KIZ collection shows a weak lingual cusp. The posterior cingulum, in which a cusp is integrated, is well developed.

m1: The m1 of *Neohylomys* is distinctly larger than the m2(Figs. 3C, 4C). Its trigonid is longer than the talonid. In contrast to the m1 of *Neotetracus* there is no entoconid crest. On the labial side there is a distinct cingulum ending at the base of the hypoconid as in *Neotetracus*.

m2: The m2 of *Neohylomys* is distinctly shorter than the m1 and less wide. Its trigonid is somewhat longer than the talonid. There is a narrow labial cingulum ending at the base of the hypoconid.

m3: The m3 of *Neohylomys* is very much reduced, its trigonid being much longer and above all much wider than the talonid. The entoconid and even more the hypoconid are developed as distinct cusps, much more than in *Neotetracus* and *Hylomys* (Figs. 4A-C). The crista obliqua ends more lingually (almost in the middle of the tooth) than in the two other genera. The labial cingulum is very weak.

The milk-teeth In the collection of the KIZ there is only one juvenile skull of *Neohylomys* showing the milk-dentition (YP 22624). In the collection of the Zoological Institute in Beijing there is no skull with milk teeth. Since the following descriptions are based only on a single specimen, it is not possible to say anything about the variability of the different characters. The milk-teeth in front of DP4 and dp4 show a very simple structure with few characters and are very similar to those of *Neotetracus* and *Hylomys*, a description of most of them being not worth while.

DC: The upper deciduous canine of *Neohylomys* is single-rooted as that of *Hylomys* (On the right side of the mandible the root is slightly laced). The DC of *Neotetracus* on the other hand shows two clearly separated roots.

DP3: The DP3 of *Neohylomys* shows a single root with a slight subdivision. Those of *Neotetracus* and *Hylomys* show two distinctly separated roots.

DP4: The DP4 of *Neohylomys* is triangular in occlusal view with a very strong parastyle as in *Hylomys* (Fig. 6C). The main cusp is slim. The anterior lingual cusp is very high and pointed, whereas the posterior one is very weak and situated close to the anterior one. There is a weak labial cingulum. The DP4 of *Neotetracus* has a stronger main cusp and a less prominent parastyle. Its anterior lingual cusp is not very high and the posterior one very weak or lacking (Fig. 6A). On the DP4 of *Hylomys* both lingual cusps are very high and pointed, the anterior one being higher (Fig. 6B).

dp4: The crown of the dp4 of *Neohylomys*, triangular in labial view, shows a slim and not very high main cusp, and no anterior cusp. The lingual cusp is very distinct as in *Hylomys*, being situated on a lingual bulge of the oval outline. This lingual cusp is very weak in *Neotetracus* or lacking entirely. The labial side is provided with a small wart instead of a true cingulum. In contrast to *Hylomys* the dp4 of *Neohylomys* shows no distinct posterior cusp. The two roots of the dp4 are slim and very much spread.

2.3 Differences between *Neotetracus*, *Hylomys* and *Neohylomys* in the skull and mandible

Infraorbital foramen On the skull of *Neotetracus* the infraorbital foramen is very narrow and opens to the front. It is always situated in front of the anterior labial root of the P4 (Figs. 1A, 7A). In *Hylomys* this foramen is larger and less compressed. It opens more laterally and extends more posteriorly than that of *Neotetracus*. Its posterior edge is superior to the middle of the P4. The P4 anterior labial root extends to the base of this foramen and in some specimens it breaks through into it (Figs. 1B, 7B). These differences in the infraorbital foramen seem to be very stable.

The infraorbital foramen of *Neohylomys* resembles that of *Hylomys*: it is very large, has a wide opening and is situated far back. Its posterior edge is above the posterior root of the P4 or even the front of the M1 (Figs. 1C, 7C).

Cranial bones On the surface of the skull of *Hylomys*, the posterior end of the premaxillary and the anterior tip of the frontal mostly come into contact (Fig. 7B). In *Neotetracus* the tips of these two bones fit closely the lateral suture of the nasal, but mostly do not come into contact (Fig. 7A). On all four skulls of *Neohylomys* of the KIZ, the frontal and the premaxillary have no contact (Fig. 7C).

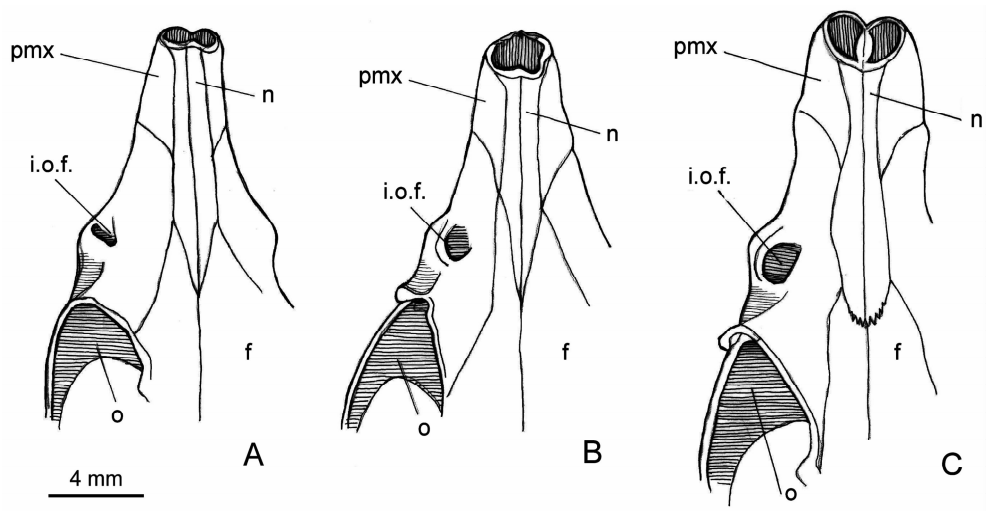

Fig. 7 The snout of the skull of *Neotetracus*, *Hylomys* and *Neohylomys* in dorsal view
A. *Neotetracus sinensis* from Yunnan, KIZ 206442; B. *Hylomys suillus* from Yunnan, KIZ 0611076; C. *Neohylomys hainanensis* from Hainan, KIZ 201310
Abbreviations: f. frontal; i. o. f. infra-orbital foramen; n. nasal; o. orbit; pmx. premaxillary

Anterior palatine foramina In *Neotetracus* the anterior palatine foramina are elongated and drop-shaped. They extend from about the middle of the I1 to the middle of I2. The suture between premaxillary and maxillary leads into the middle of the lateral side of this foramen (Fig. 8A).

In *Hylomys* these foramina are shorter and triangular. The premaxillary-maxillary suture leads into the lateral corner of the foramen (Fig. 8B). In *Neohylomys* these foramina are even shorter than in *Hylomys* and are D-shaped (Fig. 8C).

Although in body size *Hylomys* is somewhat larger than *Neotetracus*, and *Neohylomys* is larger than *Hylomys*, it is surprising that the length of the palate and of the tooth row of the three forms is about the same.

The mandible Generally the ramus horizontalis of the mandible is stronger in *Neotetracus* than in *Hylomys*. Especially in the anterior part in front of the p4, the mandible is distinctly deeper (Fig. 3A). With about an equal body size the mandible of *Hylomys* is generally some-

what longer than that of *Neotetracus*. In a specimen of the subspecies *Hylomys suillus dorsalis* from Sumatra, kept in the Basel Natural History Museum collection (NMB 8892) the mandible is longer than in any compared specimen of *Neotetracus*. In this specimen also the diastema between c and p4 is larger. Connected with the somewhat longer mandible might be the more anterior position of the mental foramen in *Hylomys*: in *Hylomys* below the p3, in *Neotetracus* below the anterior root of p4 (Figs. 3A, B).

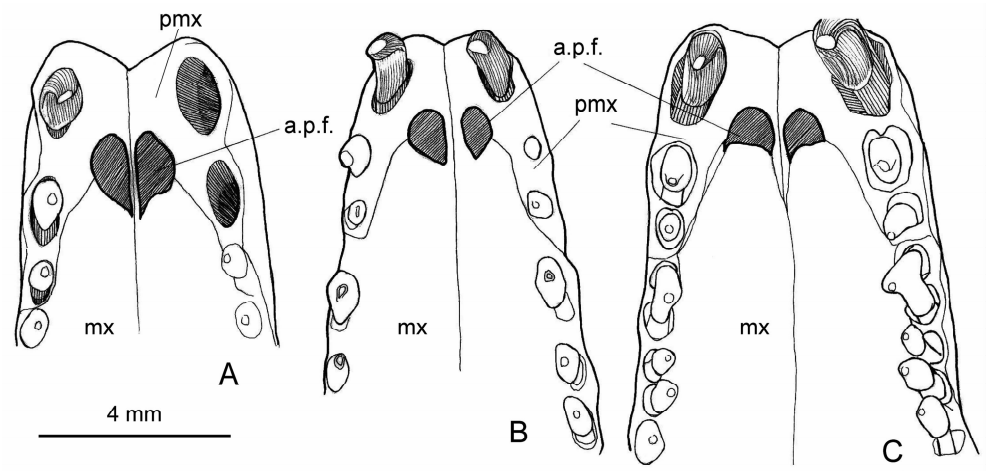

Fig. 8　The snout of the skull of *Neotetracus*, *Hylomys* and *Neohylomys* in ventral view
A. *Neotetracus sinensis* from Yunnan, KIZ 74116; B. *Hylomys suillus* from Yunnan, KIZ 8892; C. *Neohylomys hainanensis* from Hainan, KIZ 201313
Abbreviations: a. p. f. anterior palatine foramen; mx. maxillary; pmx. premaxillary

Although *Neohylomys* is somewhat larger in body size than *Neotetracus* and *Hylomys*, the length of its tooth row of the upper and the lower jaw as well is about the same. The mandible of *Neohylomys* is stouter and its ramus horizontalis is deeper than that of the two other genera (Figs. 3A-C). The mental foramen is very large and placed below the p3.

Table 1 shows the most important differences in dentition and skull of the three genera.

2.4　Comparison of the evolutionary level of the dentitions of *Neotetracus*, *Hylomys* and *Neohylomys*

In most characters permitting a statement about the evolutionary level, *Hylomys* is more primitive than *Neotetracus*. *Neohylomys* has an intermediate position between the two others.

Hylomys has a complete dentition with four premolars in the upper and in the lower jaw. In the dentition of *Neotetracus* P1 and p1 are lacking. *Neohylomys* also has a reduced dentition with 2 ~ 4 upper premolars and 3 lower premolars.

The posterior branch of the protocone in M1 and M2 of *Hylomys* and *Neohylomys* is mostly connected with the metaconule. This is a very primitive feature, well known from very old erinaceids like *Tetracus*. In M1 and M2 of *Neotetracus* this connection is rather rare, the metaconule mostly being isolated.

In *Hylomys* and *Neohylomys* M1 and m1 are distinctly larger than M2 and m2, whereas in *Neotetracus* M1 and m1 are only slightly larger than M2 and m2.

In *Hylomys*, in the posterior talon of M3 metacone and hypocone are mostly separated, in *Neohylomys* very distinctly, whereas in *Neotetracus* these two cusps are mostly fused.

The P4 of *Hylomys* has a well developed parastyle, a cusp lacking in the P4 of *Neotetracus*. In *Neohylomys* two of three specimens show a strong parastyle, one not at all.

Table 1 Synopsis of the most important differences in dentition and skull of *Neotetracus*, *Hylomys* and *Neohylomys*

	Neotetracus	*Hylomys*	*Neohylomys*
number of premolars	3/3	4/4	2 ~ 4/3
I1	large, with slightly curved conical crown	small, hook-shaped, with posterior basal cusp	like that of *Neotetracus*, but larger
I2	larger than that of *Hylomys* with straight conical crown	small, with backwards bent crown	as large as that of *Neotetracus*, with slightly backwards bent crown
I3	small	very small	small
C	small, stout, with 1 or 2 roots	larger than that of *Neotetracus* with backwards bent crown, 2 roots	as large or larger than that of *Hylomys*, without posterior basal cusp, 2 roots
P1	lacking	small, 1 root	small, sometimes lacking, 1 root
P2	1 ~ 2 roots	mostly 1 root	1 root
P3	1 ~ 2 roots, wider than that of *Hylomys*	slender, always 2 roots	slender, 2 roots
P4	very stout, without parastyle	slender, with strong parastyle	slender, with or without parastyle
M1 and M2	M1 only little larger than M2, metaconule large and rounded, not connected with protocone and hypocone	M1 distinctly larger than M2, metaconule small and crest-shaped, mostly connected with protocone and hypocone	M2 smaller than M1, protoconule small, crest-shaped, connected with protocone and hypocone
M3	metacone and hypocone mostly fused, lingually placed	metacone and hypocone mostly not fused, medially placed	metacone and hypocone slightly separated, medially placed
i1	very large, shovel-shaped	much smaller than in *Neotetracus*	much smaller than in *Neotetracus*
i2	very small, button-shaped	almost as large as i1, shovel-shaped	almost as large as i1, shovel-shaped
i3	larger than i2	smaller than i2	smaller than i2
c	small, with triangular crown, almost vertically implanted	larger than that of *Neotetracus*, with elongated crown, obliquely implanted	larger than that of *Neotetracus*, with elongated crown, obliquely implanted
p1	lacking	small, 1 root	lacking
p2 and p3	equal in size, 1 root	p2 smaller than p3, 1 root	p2 smaller than p3, 1 root
p4	very stout and wide, faint or no labial cingulum	more slender and narrower than in *Neotetracus*, distinct labial cingulum	back side wider than in *Hylomys*, no labial cingulum
m1 and m2	m2 almost as long as m1, with entoconid crests	m2 distinctly smaller than m1, without entoconid crests	m2 distinctly smaller than m1, without entoconid crests
m3	entoconid and hypoconid little separated	entoconid and hypoconid little separated	entoconid and hypoconid distinctly separated
mandible	mental foramen small, below p3	mental foramen mostly very long, position variable between anterior root of p4 and p2	mental foramen very long, position variable
skull	infraorbital foramen narrow, opening anteriorly, situated in front of anterior labial root of P4	infraorbital foramen wide, opening laterally, posterior edge above middle of P4	infraorbital foramen wide, opening laterally, posterior edge above posterior root of P4
	anterior palatine foramina very long, drop-shaped	anterior palatine foramina short, triangular	anterior palatine foramina very short, D-shaped
	premaxillary no contact with frontal	premaxillary in touch with frontal	premaxillary no contact with frontal

The dp4 of *Hylomys* and *Neohylomys* has a strong lingual cusp, whereas this cusp is very small in the dp4 of *Neotetracus* or completely lacking.

The DP4 of *Hylomys* has a well developed posterior lingual cusp. In the DP4 of *Neotetracus* this cusp is very small or lacking at all. In the single specimen of *Neohylomys* this cusp is very weak.

The only character in which *Neotetracus* is more primitive than *Hylomys*, is the mostly developed protoconule of M1 and M2. In these two molars of *Neohylomys* the protoconule is well developed, too.

3 Conclusions

The comparison of the dentitions of *Neotetracus*, *Hylomys* and *Neohylomys* yielded many and very distinct differences between these Hylomyinae. Quantitative character analyses proved most of the observed differences being quite stable and subject only little to variability. Even in the milk-teeth, according to Leche (1902) representing a more primitive stage of evolution than the permanent teeth, important differences between *Neotetracus*, *Hylomys* and *Neohylomys* can be observed.

The comparison of dental characters yielding information about the evolutionary level proves that *Neotetracus* is clearly more advanced than *Hylomys*. The evolutionary level of *Neohylomys* is intermediate in relation to the two other forms.

Neotetracus and *Hylomys* certainly have their own very long independent history, having been separated probably already since millions of years, as proved by the existence of species of both genera in the Early Miocene of Thailand (Mein and Ginsburg, 1997).

Therefore we came to the conclusion that alone on the basis of the dental differences, the three genera should be retained. This result is corroborated by Corbet's (1988) statement that the striking differences in the morphology of the penis speak in favor of a generic separation of *Neotetracus* and *Hylomys*.

The comparisons further prove the dentition of *Neotetracus* to be generally stouter and the mandible as more robust. According to this observation it can be expected that *Neotetracus* is adapted to a harder diet than *Hylomys*.

4 Abridged history of the Subfamily Hylomyinae Anderson, 1879

(= Galericinae < Galerices > Pomel, 1848, Gymnurinae Gill, 1872, Echinosoricidae Cabrera, 1921)

The Hylomyinae are a very old group of mammals having originated probably in the Eocene or even earlier in Asia. However, the oldest findings date from the Late Eocene (about 40 million years ago) from Kazakhstan (Gabunia and Gabunia, 1987) and China (Wang and Li, 1990). The Hylomyinae were once very diverse, so far 9 fossil genera with a total of 47 species having been described.

Today the Hylomyinae are represented by 5 (according to some authors 3) genera with totally 6 species:

Echinosorex Blainville, 1838
Hylomys Müller, 1839
Neotetracus Trouessart, 1909
Podogymnura Mearns, 1905
Neohylomys Shaw & Wong, 1959

Today all living Hylomyinae are restricted to Southeast Asia, to an area including China, Burma, Thailand, Malaysia, Sumatra, Java, Borneo, and the Philippines. Considering the fact that the geographical range of this subfamily once included a large part of the northern hemi-

sphere, the distribution area of today has to be described as relict.

Europe In Europe the Hylomyinae reached probably their fullest flowering, so far 6 genera with 32 species having been described. This diversity certainly is not only due to the fact, that Europe is palaeontologically better investigated than other continents. Especially in the European Miocene (23 ~ 5 million years ago) the Hylominae were extremely common. There is hardly a well documented fauna, in which these insectivores are lacking, and in many faunas they are among the most abundant animals.

In Europe the Hylomyinae are recorded for the first time after the "Grande Coupure" in the earliest Oligocene (MP 21, about 36 million years ago). As for other mammals showing up in Europe at about the same time (Talpidae, Cricetidae, Castoridae, Eomyidae, Rhinocerotidae, Anthracotheriidae), the Hylomyinae can be considered as immigrants from Asia (Crochet, 1995). In the Oligocene this subfamily is represented only by the genera *Tetracus* Aymard, 1850 and *Neurogymnurus* Filhol, 1877 each of them with two species. They were nowhere common during this epoch, and in the Late Oligocene they disappeared. From the latest Oligocene and the earliest Miocene a few findings, mainly isolated teeth, are recorded, but so far not a single species has been described.

By the Early Miocene (MN 3, about 18 million years ago) the genus *Galerix* appears, being recorded from then until the Late Miocene (MN 11). *Galerix* is probably an immigrant from Turkey, where the genus is recorded already in the latest Oligocene (MP 30, van der Hoek Ostende, 2001). During this long period 6 species developed and two evolutionary lines and three immigrations can be recognized (Ziegler, 1999).

The genus *Lanthanotherium*, very common during the Miocene as well, is documented by 7 species and has also to be considered as an immigrant. *Lanthanotherium* shows up for the first time in the Early Miocene (MN 4, about 16 million years ago) and is recorded until the Late Miocene (MN 11, 8 million years ago, Engesser and Ziegler, 1996).

Schizogalerix probably is an eastern genus having had its largest distribution in the Miocene of Turkey and Greece, where it probably also originated in the Middle Miocene (MN 5). So far 11 species of *Schizogalerix* have been described and three evolutionary lines can be distinguished (Engesser, 1980). *Schizogalerix* was common mainly in eastern countries of Europe (Greece, Austria), and reached the more western countries of Switzerland (Kälin and Engesser, 2001) and France (Farjanel and Mein, 1984) only relatively late (MN 9 ~ 11) and scantily.

Deinogalerix is an endemic genus with 5 species being restricted to the Gargano peninsula in southern Italy. During the Late Miocene this area was an island, on which under insular conditions the largest known Hylomyinae developed: *Deinogalerix koenigswaldi* with an estimated 56 cm length of head and body (Butler, 1980).

Africa The fact that the record of fossil Hylomyinae in Africa is scanty probably cannot be attributed only to poor exploration and unfavourable conditions for fossilisation (especially in central Africa). From the East African Miocene one species of *Galerix* is recorded (Butler, 1956). The specimen attributed to *Lanthanotherium* by Butler (1969) has proved to belong to *Galerix* with additional material (Butler, 1985).

The genus *Schizogalerix* is recorded from different Middle and Late Miocene localities (MN 8 ~ 12) of Algeria and Morocco (Engesser, 1980). Since this record is limited to a few isolated teeth, no species identification could be done. However it is possible to say, that these forms from North Africa show close relations to species from Turkey and Greece.

North America Also in North America, the Hylomyinae probably never were greatly distributed. In the case of the erinaceid from the Middle Eocene of Wyoming, attributed to the "Galericinae" by Novacek et al. (1985), it is very questionable, whether it belongs to this subfamily (Crochet, 1995). The Hylomyinae probably reached North America in the Late Oligocene, as proved by the genus *Ocajila* from the early Arikareean (about 26 million years ago)

from South Dakota (Macdonald, 1963). The genus *Lanthanotherium* is recorded with two species, showing up in the Middle Miocene (Barstovian) and documented until the Late Miocene (James, 1963).

Asia In Asia the so far oldest Hylomyinae are recorded. From this fact it can be concluded, that the subfamily originated there. In view of the size of the Asian continent and the poor palaeontological exploration, in the future many new finds can be expected, broadening and modifying our knowledge of the phylogeny of the Hylomyinae. Findings of Asian Hylomyinae being far apart from each other geographically and as well as stratigraphically, the phylogenetic relations are difficult to determine. Important finds are identified only in open nomenclature.

Already in the Middle Eocene of northeastern China, the genus *Eochenus* is recorded and attributed to the Hylomyinae by most authors (Wang and Li, 1990). Also in the Eocene and Oligocene of Kazakhstan isolated teeth were found, very probably belonging to the Hylomyinae, and partly having been identified as *Tetracus* (Gabunia and Gabunia, 1987). The genera *Ictopidium* Zdansky, 1930 and *Tupaiodon* Matthew & Granger, 1924 from the Eocene and Oligocene of Asia are included here in the subfamily Tupaiodontinae Butler, 1988.

As in Europe most Asian findings of Hylomyinae are from the Miocene. The genus *Galerix* is well documented in Turkey, being known from the latest Oligocene (MP 30) until the Early Miocene (MN 3, van den Hoek Ostende, 1992). Thus this genus appears in Turkey much earlier than in Europe. *Galerix* is also recorded in the Chinji Formation of Pakistan (Munthe and West, 1980) and probably in the Middle Miocene of China (Xiacaowan, about MN 4). From the latter locality *Lanthanotherium* is recorded, too (Qiu and Storch, 2005). This genus persists in China until the Late Miocene, being recorded in Lufeng, Yunnan (~MN 12).

In Turkey *Schizogalerix* undergoes a development, which can be followed from the Middle Miocene (MN 5) in different stages to Late Miocene (Engesser, 1980). *Schizogalerix* is also recorded in the Middle Miocene of Kazakhstan (Kordikova, 2000) and China (Halamagai Formation, about MN 6, Qiu and Storch, 2005).

Especially revealing for the present study are the finds from the Middle Miocene of Thailand: besides the fossil genus *Thaiagymnura* one species of the Recent genera *Neotetracus* and *Hylomys* were discovered (Mein and Ginsburg, 1997). These findings on the one hand demonstrate early separation of *Neotetracus* and *Hylomys* and on the other hand they prove, that these Recent genera are rightly called "living fossils".

Hylomys also is recorded in the Late Miocene of Yuanmou (Yunnan, Ni and Qiu, 2002) and Lufeng (Yunnan, Qiu and Storch, 2005) both about MN 12. In the Late Pliocene (MN 17) locality of Damiao (Hubei) *Neotetracus* and *Hylomys* were found together (Qiu and Storch, 2005).

Acknowledgements We are very grateful to the "Stiftungen für das Naturhistorische Museum Basel" (Foundations for the Basel Natural History Museum) for several grants, enabling us to travel and to do fieldwork in Yunnan. We are very much indebted to Larry Flynn (Peabody Museum, Harvard University, Cambridge, MA) for improving the English text and helpful criticism.

References

Butler P M, 1956. Erinaceidae from the Miocene of East Africa. Brit Mus Nat Hist, Fossil Mammal Afr, **11**: 1-75

Butler P M, 1969. Insectivores and bats from the Miocene of East Africa. In: Leakey L S B ed. Fossil Vertebrates of Africa 1. London and New York: Academic Press. 1-37

Butler P M, 1980. The giant erinaceid insectivore, *Deinogalerix* Freudenthal, from the Upper Miocene of Gargano (Italy). Scr Geol, **57**: 1-72

Butler P M, 1985. The history of African insectivores. Acta Zool Fenn, **173**: 215-217

Corbet G B, 1988. The family Erinaceidae: a synthesis of its taxonomy, phylogeny, ecology and zoogeography. Mammal Rev, **18**: 117-172

Crochet J Y, 1995. Le Garouillas et les sites contemporains (Oligocène, MP 25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertébrés, 4. Marsupiaux et insectivores. Palaeontogr, Abt A, **236**: 39-75

Engesser B, 1980. Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei. Schweiz Paläont Abh, **102**: 45-149

Engesser B, Ziegler R, 1996. Didelphids, insectivores, and chiropterans from the later Miocene of France, Central Europe, Greece, and Turkey. In: Bernor R L, Fahlbusch V, Mittmann H W eds. The Evolution of Western Eurasian Neogene Mammal Faunas. New York: Columbia University Press. 157-167

Farjanel G, Mein P, 1984. Une association de mammifères et de pollens dans la formation continentale des "Marnes de Bresse" d'âge Miocène supérieure, à Ambérieu (Ain). Géol France, (1-2): 131-148

Frost D R, Wozencraft W C, Hoffmann R S, 1991. Phylogenetic relationships of hedgehogs and gymnures (Mammalia: Insectivora: Erinaceidae). Smithson Contrib Zool, **518**: 1-69

Gabunia L K, Gabunia V D, 1987. Preliminary report on insectivore faunas from the Paleogene and Early Neogene of the Zaissan Depression (East Kazakhstan). New Acad Sci Georgia, Biol Ser 13, **6**: 406-411(in Russian)

Hoek Ostende L W van den, 1992. Insectivore faunas from the Lower Miocene of Anatolia, Part 1: Erinaceidae. Proc K Ned Akad Wet, **95**(4): 437-467

Hoek Ostende L W van den, 2001. A revised generic classification of the Galericini (Insectivora, Mammalia) with some remarks on their palaeobiogeography and phylogeny. Geobios, **34**(6): 681-695

James G T, 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley Badlands, California. Part 1. Geology, faunal interpretations, and systematic descriptions of Chiroptera, Insectivora, and Rodentia. Univ Calif Publ Geol Sci, **45**: 1-161

Kälin D, Engesser B, 2001. Die jungmiozäne Säugetierfauna vom Nebelbergweg bei Nunningen (Kanton Solothurn, Schweiz). Schweiz Paläont Abh, **121**: 1-61

Kordikova E G, 2000. Insectivora (Mammalia) from the Lower Miocene of the Aktau Mountains, South-Eastern Kazakhstan. Senckenbergiana lethaea, **80**(1): 67-79

Leche W, 1902. Zur Entwicklungsgeschichte des Zahnsystems der Säugethiere. 2. Theil: Phylogenie. Erstes Heft: Die Familie der Erinaceidae. 1-103

Macdonald J R, 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull Am Mus Nat Hist, **125**: 139-238

Mein P, Ginsburg L, 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systematique, biostratigraphie et paléoenvironnement. Geodiversitas, **19**(4): 783-844

Munthe J, West R M, 1980. Insectivora of the Miocene Daud Kehl local fauna, Mianwali District, Pakistan. Contrib Biol Geol Milwaukee Public Mus, **38**: 1-17

Ni X J, Qiu Z D, 2002. The micromammalian fauna from the Leilao, Yuanmou hominoid locality: implications for biochronology and paleoecology. J Hum Evol, **42**: 535-546

Novacek M J, Bown T M, Schankler D, 1985. On the classification of the Early Tertiary Erinaceomorpha (Insectivora, Mammalia). Am Mus Novit, (2813): 1-22

Qiu Z D, Storch G, 2005. China. In: Hoek Ostende W van den, Doukas C S, Reumer J W F eds. The Fossil Record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) Part 1. Scr Geol Spec Issue, **5**: 37-50

Trouessart E L, 1909. *Neotetracus sinensis*, a new insectivore of the family Erinaceidae. Ann Mag Nat Hist, **8**(4): 389-391

Trouessart E L, 1910. Description d'un insectivore nouveau de la famille des Erinaceidae. Bull Mus Hist Nat, (1): 1-6

Wang B Y, Li C T, 1990. First Paleogene mammalian fauna from Northeast China. Vert PalAsiat, **28**(3): 165-205(in Chinese and English)

Ziegler R, 1999. Order Insectivora. In: Rössner G E, Heissig K eds. The Miocene Land Mammals of Europe. München: Verlag Dr. Friedrich Pfeil. 53-74