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亚洲始新世啮齿目一新科——争胜鼠科 (Zelomyidae)[1)]

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摘要 继 1990 年王伴月和李春田记述了发现在吉林桦甸中始新世的争胜鼠(*Zelomys*)之后,近年又在山西垣曲、河南卢氏、江苏溧阳等地的中始新世到晚始新世(Irdinmanhan-late Sharamurunian or Ergilian)的 5 个地点中陆续发现了一些与争胜鼠相近的新材料。经研究后,将所有材料归诸于创建的一新科:争胜鼠科(Zelomyidae fam. nov.)。它包括了争胜鼠及本文新记述的安氏鼠(*Andersomys* gen. nov.)、耗子(*Haozi* gen. nov.)和苏鼠(*Suomys* gen. nov.)共 4 属 6 种。新科的特征是:始啮型头骨 - 松鼠型下颌;门齿釉质层散系;颊齿具有发育的次尖和下次脊,后期种类上颊齿的外侧齿尖的唇侧发展成平凹到新月形。新科的系统关系不很清楚,尽管与始鼠科(Eomyidae)有某些相似之处,但它更可能是独立发展的一个支系。

争胜鼠属化石分布较广,在我国吉林、江苏和山西的中、晚始新世地层中都有发现,它的特征是下颊齿 p4-m2 宽度逐渐增大,p4-m3 具下前边尖,并与短的下原尖前臂相接。属中除属型种——东方争胜鼠(*Z. orientalis* Wang et Li)外,还建立了一个约翰争胜鼠新种(*Z. joannes* sp. nov.),一约翰争胜鼠相似种(*Z.* cf. *Z. joannes*)。同时认为 *Z. gracilis* Wang et Li, 1990 是 *Z. orientalis* 的同物异名。约翰种与属型种的区别在于个体稍大和下臼齿上缺少自下外脊伸出的附脊。安氏鼠属化石发现在山西中始新世晚期及有可能是晚始新世地层中,其特征是 P4 和 p4 分别大于 M1 和 m1;P4 前尖和后尖及 M1 后尖唇侧平;与争胜鼠属不同在于前臼齿和臼齿的大小比例和上颊齿具平的唇侧尖。安氏鼠包括两种:老文种(*A. laoweni* sp. nov.)和南堡头种(*A. austrarx* sp. nov.)。两种的不同在于后者个体稍大,P4 唇侧齿带较发育和 p4 前缘更显圆滑。耗子属仅有一种,简单耗子(*H. simplex* sp. nov.),与科中其他属的不同在于颊齿齿尖较呈丘形,P4 和 M1 大小接近,上颊齿的前附尖和后附尖很发育,P4 三角凹宽于跟凹。该属化石仅发现在河南中始新世晚期地层中。苏鼠属也只有新月苏鼠(*S. selenis* sp. nov.)一种,发现在江苏中始新世晚期到晚始新世地层中。该属的特点是 P4 比其他上颊齿大,具强的前齿带和唇侧齿带;P4-M2 的前尖和后尖及 M3 的前尖唇侧凹平,且向前、后延长,形成 W 形外壁,中附尖明显;下颊齿的唇侧尖也呈 W 形结构,使牙齿为新月形式样,这是与科中其他属明显不同的特征。

文中还对含化石地层时代问题做了评述。

关键词 亚洲东部,始新世,争胜鼠科

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ZELOMYIDAE, A NEW FAMILY OF RODENTIA (MAMMALIA) FROM THE EOCENE OF ASIA

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Abstract Six Eocene localities in eastern China, ranging geographically from Jilin to Jiangsu provinces and in age from Irdinmanhan to late Sharamurunian or Ergilian, have yielded four genera (*Haozi*, *Suomys*, and *Andersomys* named as new here and *Zelomys*) assigned to the new rodent family Zelomyidae. The family is characterized by a primitive protrogomorphous-sciurognathous zygomasseteric structure and pauciserial incisor enamel, but the cheek teeth are precocious in development of hypocone and hypolophid. Later members of the family exhibit a development of buccal flattening to selenodonty of the cusps of the cheek teeth. Relationships of the new family are unclear, although some dental similarities suggest affinities with the Eomyidae. On the other hand, differences from eomyids may suggest that the zelomyids are an independently derived Asian Eocene family.

Key words Eastern Asia, Eocene, Zelomyidae

1 Introduction

The Eocene rodent record in Asia differs distinctly from that of the comparable time in Europe and North America. In Asia the Paleogene endemic ctenodactyloids dominate during the Early Eocene, followed by increasing prominence in the Middle Eocene of cricetids, eomyids, and zapodids (Tong, 1997); ischyromyids are present but seem never to have been dominant (Dawson and Wang, 2001). In Europe, on the other hand, the Early Eocene dominance of ischyromyids is followed in the Middle Eocene by the origin of the presumably autochthonous theridomorphs and gliroids (Escarguel, 1999). The North American Paleogene faunas include dominant ischyromyids, but show the origin and increased diversity there by the late Early Eocene of the apparent ischyromyid derivatives, the Sciuravidae (Korth, 1984). The latter family is characterized by an early formation of quadrate upper molars, having a strongly developed hypocone, and lophate lower molars with a well developed hypolophid.

In several Asian Eocene faunas there are rodents that have been referred definitely or with question to the otherwise North American family Sciuravidae (Li, 1963; Dawson, 1964; Shevyreva, 1976; Hussain et al., 1978; Tong and Wang, 1980; Wang and Li, 1990). Later, some of these have been shown to be ctenodactyloids (Dawson, 1977; Wood, 1977; Dawson et al., 1984). One, the rodent *Zelomys* (Wang and Li, 1990), has been referred to the Eomyidae (Korth, 1994). Reexamination of *Zelomys* and several other of these problematic rodents, outside of the ctenodactyloids, has now shown that they represent a discrete rodent lineage, here recognized as the new family Zelomyidae.

As currently known, six Asian Eocene localities have produced representatives of the new family, ranging in age from probably Irdinmanhan (middle Middle Eocene) through Ergilian (latest Eocene). Their currently known geographic distribution encompasses southern Jiangsu, western Henan, southern Shanxi, and central Jilin provinces.

Abbreviations and terminology:

ALMA, Asian Land Mammal Age.

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

MP, Paleogene Mammalian Reference Level (European).

NALMA, North American Land Mammal Age.

a-p, anteroposterior length; trw, transverse width of trigon; taw, transverse width of talon; tri, transverse width of trigonid; tal, transverse width of talonid; mm, millimeter.

For the dental notation we use upper case letters for upper teeth and lower case letters for lower teeth; e.g. M1 indicates an upper first molar, m1 a lower first molar.

Hedi is the corrected Pinyin spelling for the formation in the Yuanqu Basin (Huang et al., 2001), which has also been spelled Hoti (Chow et al., 1973, using the Wade-Giles transliteration) and Heti (Li and Ting, 1983).

2 Age and geologic setting

All of the localities that have produced members of the new family occur in eastern China (Fig. 1); no zelomyids are currently represented in the relatively well known stratified deposits of Mongolia and Nei Mongol (Inner Mongolia) on which the Asian Eocene land mammal ages have been based (Russell and Zhai, 1987). These rodents have been found in discrete, isolated basins (Lushi, Yuanqu, Huadian) as well as in the Shanghuang fissures, Liyang, and in varying lithologies over a wide geographic area, ranging from the oil shales of central Jilin Province, at about 43° north latitude, to the fissure fillings of southern Jiangsu Province, at about 31°N. These geographic factors contribute substantially to the problem of correlating both between localities and into the Asian framework. Correlation by biostratigraphy is hampered by several factors, including probable differences in small mammals over this latitudinal span due to paleoclimatic/environmental differences and in ecological preference between, for example, animals that would be preserved in the oil shales of Jilin, the fresh water marls of Zhaili, and the karstic fissure fillings of Shanghuang.

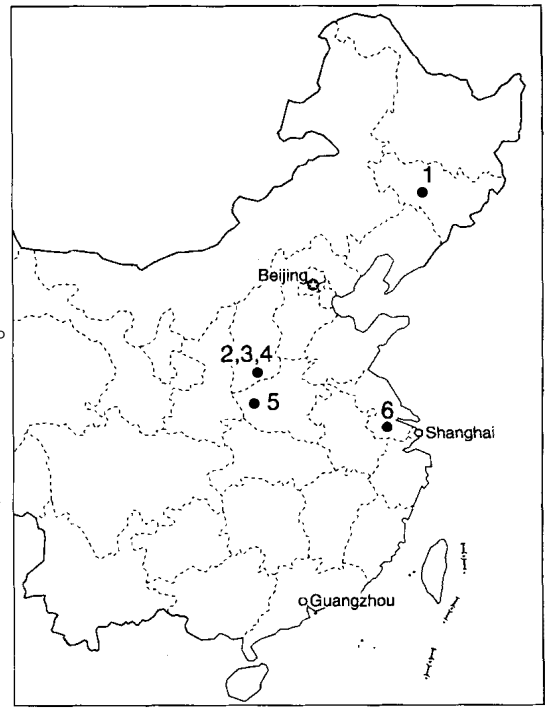

Fig. 1 Outline map of the eastern part of the People's Republic of China, showing localities in which fossil Zelomyidae have been found

1. Huadian Basin, Jilin Province; 2～4. Yuanqu Basin, Shanxi Province (Huoshipo, Zhaili, Nanbaotou faunas); 5. Lushi Basin, Henan Province (Chugouyu Fm.); 6. Shanghuang fissure fillings, Liyang County, Jiangsu Province

A recent evaluation of Eocene faunas from localities in the Yuanqu Basin (Huang et al., 2001), several of which contain members of the new family, provided the following sequence from oldest to youngest: Huoshipo (Huang et al., 1999; Zhang et al., 2001; Irdinmanhan ALMA); Rencun (Sharamurunian ALMA; no zelomyids have been recognized from this locality); Zhaili (Naduan ALMA); and Nanbaotou (Ulangochuan ALMA). While this sequence is almost certainly correct, the correlation to ALMAs outside of the Yuanqu Basin must be viewed with a great deal of caution. All of these ALMAs except Naduan are based on sequences in Nei Mongol. Naduan is an Asian land mammal age that was established (Tong, 1989) on the basis of faunas of mostly large mammals from the Nadu Formation in the Bose Basin of Guangxi Zhuang Autonomous Region in southern China. The Caijiachong fauna of Yunnan Province (Wang, 1985,

1997) , which contains numerous small mammals and has been correlated on a global scale with the North American Chadronian NALMA , was also referred to the Naduan age (Tong et al. , 1995) . The concept of a Naduan ALMA has been remarkably difficult to establish with precision. To avoid this difficulty , Russell and Zhai (1987) and Emry et al. (1998) have utilized the Ergilian ALMA for post-Sharamurunian , pre-Shandagolian Asian sites. This practice is followed here.

The rodents from the Zhaili fauna , which was referred to the Naduan ALMA by Huang et al. (2001) , appear to be older than those of the Caijiachong fauna. The entire Caijiachong fauna may be included in the Ergilian ("older than both the Ardyn Obo local fauna in Asia and MP 21 of Europe" in Wang , 1992 , 1997 ; Emry et al. , 1998) . Russell and Zhai (1987) have already extended the concept of a Sharamurunian ALMA to include the Zhaili fauna , a use that is followed here , with the Zhaili fauna considered to be late Sharamurunian in age.

The Nanbaotou local fauna , in the strict sense used here , comes from a limited area. The fossils , which are entirely small , have been obtained mostly through screen washing of sediments exposed in a ravine of restricted extent. While all of the rodents from the Nanbaotou local fauna have not been thoroughly studied , it is clear that they are more derived than those from Zhaili. However , there does not appear to be a large age difference between the two faunas. Ergilian rodents such as *Eucricetodon* and derived zapodids are not present in Nanbaotou. Accordingly , the Nanbaotou local fauna is here tentatively bracketed as latest Sharamurunian or Ergilian in age. The late or latest Eocene anthracothere *Brachyodus* was included in the Nanbaotou local fauna by Huang et al. (2001) , but the Baishui locality from which it comes (Wang and Hu , 1963) is separate geographically from the Nanbaotou micro-mammal locality and the two sites cannot yet be reliably correlated by stratigraphy , biostratigraphy , or magnetostratigraphy.

A zelomyid occurs in the Chugouyu Formation of the Lushi Basin , Henan , which overlies the faunally better known Lushi Formation (Li and Ting , 1983) . The Chugouyu Formation has been considered to be Sharamurunian in age (Tong , 1989) . The Shanghuang fissure fillings (Qi et al. , 1991 ; Beard et al. , 1994 ; Wang and Dawson , 1994) , also containing zelomyids , probably record several different times : fissures D and E may be Irdinmanhan or earliest Sharamurunian in age , whereas the known small mammals from fissures A , B and C appear to be considerably more derived , and are presumably later in age , possibly Sharamurunian (or and Ergilian) . Finally , the fauna of the Huadian Formation of Jilin Province , containing *Zelomys* , was correlated with the late Uintan NALMA (Wang and Li , 1990) , which has , in turn , been correlated with part of the Sharmurunian in the Asian land mammal chronology. Comparisons with other Asian faunas suggested to Wang and Li (1990) that the age of the Huadian "fauna must be earlier than or equivalent to that of the Zhaili member."

3 Systematic paleontology

Family Zelomyidae , new family

Type genus *Zelomys* Wang et Li , 1990.

Included genera *Zelomys* , *Andersomys* gen. nov. , *Suomys* gen. nov. , *Haozi* gen. nov.

Horizon and locality Irdinmanhan ALMA (early Uintan NALMA) through Ergilian ALMA (Chadronian NALMA) . Eastern Asia.

Diagnosis Rodents having a protrogomorphous-sciurognathous zygomasseteric structure ; masseteric fossa of mandible extending forward to below M2 ; dental formula 1 , 0 , 2 , 3/ 1 , 0 , 1 , 3 ; incisor enamel pauciserial , where known ; cheek teeth brachydont. Well developed , single rooted , conical P3 ; molariform P4 ; hypocone on P4-M2 subequal to protocone ; strong lingual valley between protocone and hypocone bounded by posterior arm of protocone and anterior arm of hypocone. Tendency toward flattening of buccal walls of upper molariform teeth. On p4-m3

ectolophid well developed, hypolophid transverse, intersecting the ectolophid anterior to the hypoconid. p4 relatively molariform.

Differs from Ischyromyidae in having prominent hypocone on P4-M2 and well developed hypolophid on p4-m3; differs from Sciuravidae in having well developed wall of V-shaped lingual valley on P4-M3 and P4/p4 larger relative to the molars; differs from Cylindrodontidae in having large molariform P4 and well developed hypocone on P4-M2; differs from Aplodontidae in having well developed hypocone and lacking conules on P4-M3; differs from Eomyidae in having protrogomorphous zygomasseteric structure, relatively posterior position of mandibular masseteric fossa, and from the eomyids except *Yoderimys* and *Litoyoderimys*, and from the possible eomyid *Metanoiamys*, in retaining P3.

Zelomys **Wang et Li, 1990**

Type species *Zelomys orientalis*.

Included species *Z. orientalis*, *Z. joannes* sp. nov., *Z.* cf. *Z. joannes*.

Horizon and localities Middle Eocene (Irdinmanhan to Sharamurunian ALMAs); Huadian Formation of Jilin Province, Hedi (see above, Abbreviations and Terminology) Formation of Shanxi Province, and Shanghuang Fissure Fillings, Jiangsu Province.

Diagnosis Zelomyid in which cheek teeth increase in width from p4 to m2; anteroconid present on p4-m3; short anterior arm of protoconid connects to anteroconid. Differs from *Haozi* in lacking distinct parastyle and metastyle.

Discussion Paleogene oil shales and coals in the Huadian Formation (Uintan equivalent, following Wang and Li, 1990) in northeastern China's Jilin Province provided the first evidence of the rodent *Zelomys*. The taxon was based on lower jaws and teeth and an associated but edentulous maxilla that appears to have a protrogomorphous zygomasseteric structure. The original assignment of *Zelomys* was to the otherwise North American family Sciuravidae, although its similarities to the North American eomyid rodent *Namatomys* were also noted (Wang and Li, 1990). The latter similarities were used by Korth (1994) as the grounds for referring *Zelomys* to the family Eomyidae.

Two species of *Zelomys* were originally described, *Z. orientalis* and *Z. gracilis* (Wang and Li, 1990). They were differentiated mainly on the basis of size, *Z. gracilis* having a shallower jaw. It must be noted that the holotype of *Z. gracilis*, IVPP V 8800, is an immature individual having dp4 (mistakenly identified as p4), and that the mandible of V 8800 is broken away below the incisor, making inaccurate any measurement of depth of jaw. Dental measurements of permanent teeth in the two named taxa overlap. Their morphological similarities indicate that *Z. orientalis* and *Z. gracilis* are synonyms, leaving *Zelomys orientalis* as the valid species from Jilin.

Zelomys orientalis **Wang et Li, 1990**

1990 *Z. gracilis* Wang and Li, p. 182～187; figs. 9～11; pl. Ⅳ

Type specimen IVPP V 8797, left jaw with incisor and p4-m3.

Horizon and locality Locality 85006 (V 8797, V 8800, V 8801), Gonglangtou Oil Shale Mine, and IVPP locality 85007 (V 8798 and V 8799), Daboji Oil Shale Mine, Gongjitun village, member Ⅲ of Huadian Formation, ? Sharamurunian ALMA (? late Uintan NALMA).

Revised diagnosis Species of *Zelomys* having short accessory lophids from the ectolophid into the lingual valley; enamel of talonid basin wrinkled. Differs from *Andersomys* in having p4 smaller than m1. Differs from *Suomys* in having p4 smaller than m1 and lacking crescentic development of cusps and crests of molariform teeth.

Zelomys joannes **sp. nov.**

(Fig. 2; Table 1)

Holotype IVPP V 13516, right lower jaw with dp4-m2 and talonid of m3.

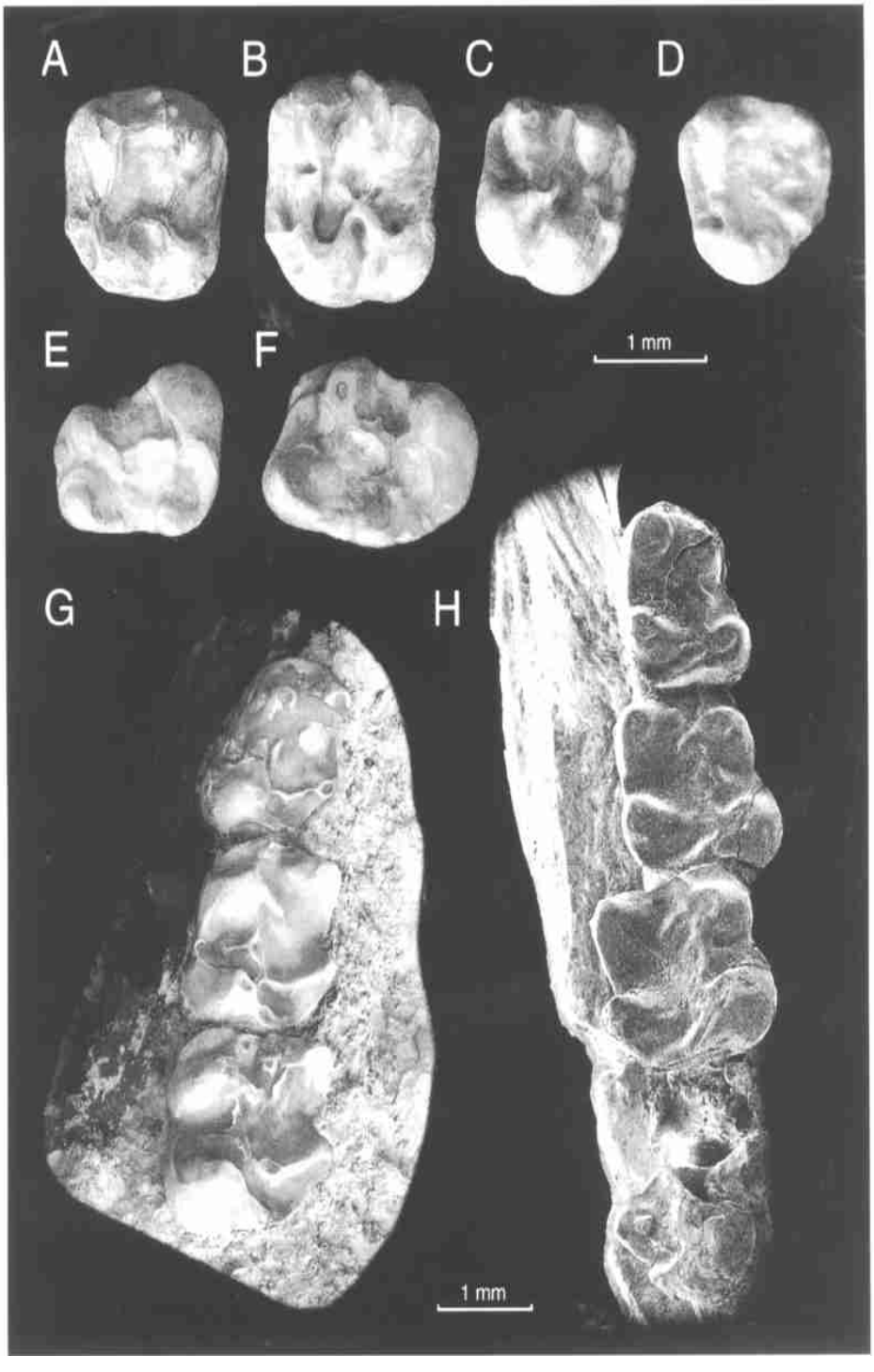

Fig. 2 *Zelomys joannes* sp. nov., occlusal views

A. IVPP V 13518.2, left M1 or 2; B. IVPP V 13518.1, left M 1 or 2; C. IVPP V 13518.3, right ? dP4; D. IVPP V 13518.4, left M3; E. IVPP V 13518.5, right p4; F. IVPP V 13518.6, right m3; G. IVPP V 13517, left mandible with dp4-m2; H. IVPP V 13516, holotype, right mandible with dp4-m3 (m3 broken)

Referred specimens　IVPP V 13517, incomplete left lower jaw with dp4-m2. Isolated teeth IVPP V 13518.1～28.

Horizon and locality　Middle Middle Eocene (Irdinmanhan ALMA); Yuli member of the Hedi Formation; Huoshipo, Guojia village, Yuanqu County, Shanxi Province.

Etymology　For John Kappelman, whose paleomagnetic work led to the discovery of the locality that produced the type and other specimens of this rodent.

Diagnosis　Species of *Zelomys* lacking accessory lophids from ectolophid into central valley of lower molars. Slightly larger than *Z. orientalis*. Differs from *Andersomys* and *Suomys* in lacking any buccal flattening or selenodonty of paracone and metacone of molariform teeth.

Description　Two lower jaws and twenty-eight isolated teeth represent this species. Both of the lower jaws appear to have dp4 in place, based on greater wear than on the associated m1 and on the divergence of the roots. The dp4 is basically a cuspate tooth, with very little development of lophids except for the hypolophid and ectolophid. The anteroconid is discrete. p4 is very similar to dp4 but has a relatively wider trigonid and stronger crests.

m1-3 are more lophate than p4, having a short posterior arm of the protoconid and elongation of the metaconid into the anterior valley. These lophs are, however, shorter than in *Zelomys orientalis*. Shared with *Z. orientalis* is the short anterior arm of the protoconid that extends to a cuspate anteroconid. m3 has a narrower talonid than trigonid and a more posteriorly protruding posterolophid than on m1-2.

One peg-like P3 with a long, straight root adheres to the lower jaw of IVPP V 13516. Association with this species seems probable. Outside of this tooth, sixteen isolated upper cheek teeth are here referred to Z. *joannes*. The upper molariform teeth differ from those known for other zelomyids in having the hypocone slightly smaller than the protocone and a shallower lingual valley. The simple, cuspate teeth have a well developed anterior cingulum and a variable mesostyle. The anterior arm of the protocone extends into the anterior valley in teeth that are presumed to be P4 but directly to the paracone in the presumed molars. The teeth that are probably dP4 are smaller than the referred permanent teeth, and have a short anterior arm of the protocone extending into the anterior valley.

The incisor of IVPP V 13517 was sectioned to reveal the enamel microstructure. The Schmelzmuster shows the pauciserial condition: two-layered with a Portio interna having transversely oriented Hunter-Schreger bands and Portio externa with radial enamel (personal communication, Daniela Kalthoff, April 5, 2002). This is the primitive state for rodent incisor enamel. *Zelomys* is the only member of the Zelomyidae that has been examined for the microstructure of the incisor enamel, but the condition has been tentatively extrapolated to characterize the family as a whole.

Table 1　Measurements of Zelomys joannes **sp. nov. (IVPP specimens)**　(mm)

	a-p	trw		a-p	trw
V 13518.3 ? dP4	1.42	1.52	V 13518.1 M1 or 2	1.59	1.7
V 13518.2 M1 or 2	1.42	1.56	V 13518.4 M3	1.49	1.49

	V 13516 (holotype)			V 13517			V 13518.5			V 13518.6		
	a-p	tri	tal	a-p	tri	tal	a-p	tri	tal	a-p	tri	tal
p4	1.56	0.95	1.22	1.49	1.02	1.29	1.56	1.08	1.29			
m1	1.59	1.29	1.56	1.56	1.36	1.56						
m2	1.7	1.49	1.63	1.63	1.56	1.7						
m3										1.76	1.42	1.29

Discussion　Although *Zelomys joannes* has simple cuspate teeth, it shows clearly the characteristic molarization of the upper molariform teeth and loph development of the lower molariform teeth of this family. Its closer similarities to *Zelomys orientalis* including proportions of

the lower teeth to one another and the connections of lophs on the trigonid, support assignment to this genus. *Z. joannes* is, however, more primitive than the genotype *Z. orientalis* in lacking extra lophids on the lower molars. Its upper molariform teeth also are in a more primitive stage of development than in other zelomyids known from upper teeth, as shown by the relatively smaller hypocone and shallow lingual valley.

Zelomys **cf.** Z. joannes
(Fig. 3)

Referred specimens IVPP V 11545.1～49, V 11560.1～2.

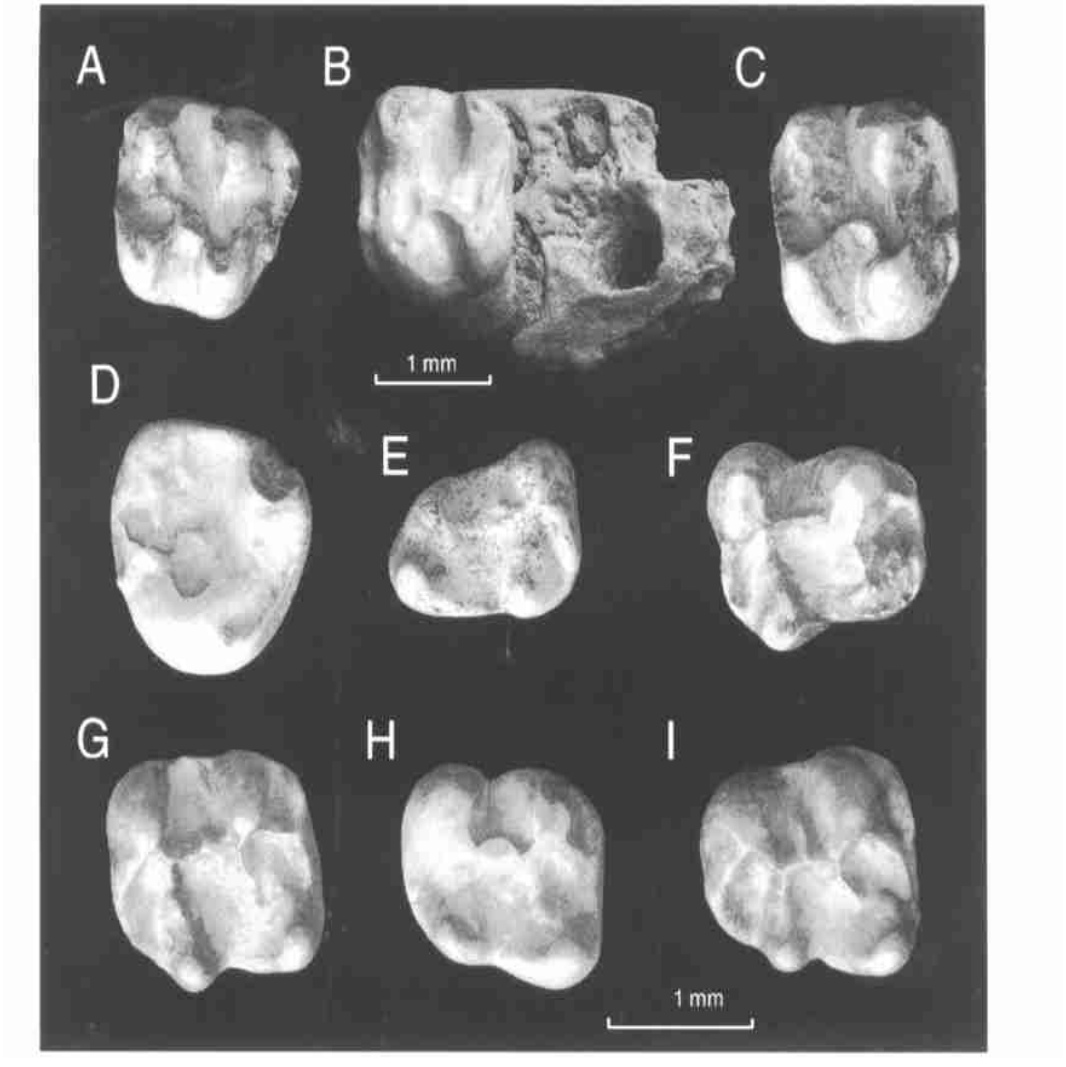

Fig. 3 *Zelomys* cf. *Z. joannes*, occlusal views of teeth
A. IVPP V 11545.4, right P4; B. IVPP V 11545.41, fragment of left maxilla with M1; C. IVPP V 11545.11, right M1 or 2; D. IVPP V 11545.19, right M3; E. IVPP V 11545.21, right p4; F. IVPP V 11545.1, left m1 or 2; G. IVPP V 11545.27, left m1 or 2; H. IVPP V 11545.38, left m3; I. IVPP V 11545.35, left m3

Horizon and locality Middle Eocene, fissure fillings D (IVPP loc. 93006D) and E (IVPP loc. 93006E) in Triassic Qinglong limestone, Shuimushan Quarry, near Shanghuang Village,

Liyang County, Jiangsu Province, China.

These isolated teeth are very close in most aspects of their morphology to the known sample of *Zelomys joannes*. The specimens do show, on average, a better developed posterior arm of the protoconid than in *Z. joannes*. In zelomyids the proportions of the teeth relative to others in the dentition are very important in determining affinities at generic and specific levels. Because there are no associated pieces in the currently sorted Shanghuang sample, relative sizes of teeth within the dentition cannot be established, so whether or not proportions are those of *Z. joannes* cannot be determined. Dental similarities provide the basis for the current reference as *Zelomys* cf. *Z. joannes*.

Andersomys **gen. nov.**

Type species *Andersomys laoweni* sp. nov.

Included species *A. laoweni* and *A. austrarx* sp. nov.

Horizon and locality Late Middle Eocene and probable Late Eocene, Shanxi Province, China.

Etymology For the late J. G. Andersson, Swedish discoverer, in 1916, of the first fossils from the River Section, Yuanqu Basin, Shanxi Province, type locality for *Andersomys laoweni*.

Diagnosis Zelomyid in which P4 and p4 are larger than M1 and m1; buccal side of paracone and metacone of P4 and metacone of M1 is flattened. Differs from *Zelomys* in proportions of premolars to molars and in having flattening of buccal cusps in the upper dentition. Differs from *Suomys* in having molariform teeth without selenodont cusps.

Andersomys laoweni **sp. nov.**

(Figs. 4, 5; Table 2)

Holotype IVPP V 13519, right mandible with p4-m3.

Referred specimens IVPP V 13520, left mandible with p4-m2; IVPP V 13521, right maxilla with P4-M2; IVPP V 13522, right maxilla with P4-M3; IVPP V 13523, right maxilla with P4-M2.

Horizon and locality Late Sharamurunian, Zhaili Member, Hedi Formation; River Section, locality 1, Tuqiaogou, east of Zhaili village, Yuanqu County, Shanxi Province.

Etymology For Wen Zhaohua of Zhaili village, the intrepid, skilled field assistant for the River Section Project.

Diagnosis Differs from *Zelomys orientalis* in having relatively strong ectolophid and lacking short transverse lophids from ectolophid into central valley. Larger than *Z. joannes* and having more buccally flattened paracone and metacone on P4 and metacone on M1. Smaller than *A. austrarx* and having less prominent buccal cingulum on P4.

Description Relatively complete specimens of *Andersomys laoweni* from the River Section, locality 1, make this the best known member of the Zelomyidae, and is thus the species on which some familial characters are most firmly based. Of the three maxillae, IVPP V 13521 and IVPP V 13523 preserve parts of the zygoma. The anterior root of the zygoma extends laterally anterior to a line with P3; a strong ridge forms the anteroventral edge of the zygoma, above which is the non-expanded (ca. 1.0mm transverse width), rounded infraorbital foramen. The incisive foramen extends back to approximately the anterior edge of the alveolus of P3, which suggests that this foramen was considerably larger than is usually found in rodents. There is a low but distinct ridge running forward from anteromedial to P3, paralleling the incisive foramen.

On the horizontal ramus of the mandible the anterior edge of the masseteric insertion is marked by a low, curved ridge that extends anteriorly to below the anterior edge of m2. There is a large mental foramen below the diastema.

All of the permanent cheek teeth are preserved except P3, the alveolus of which indicates that

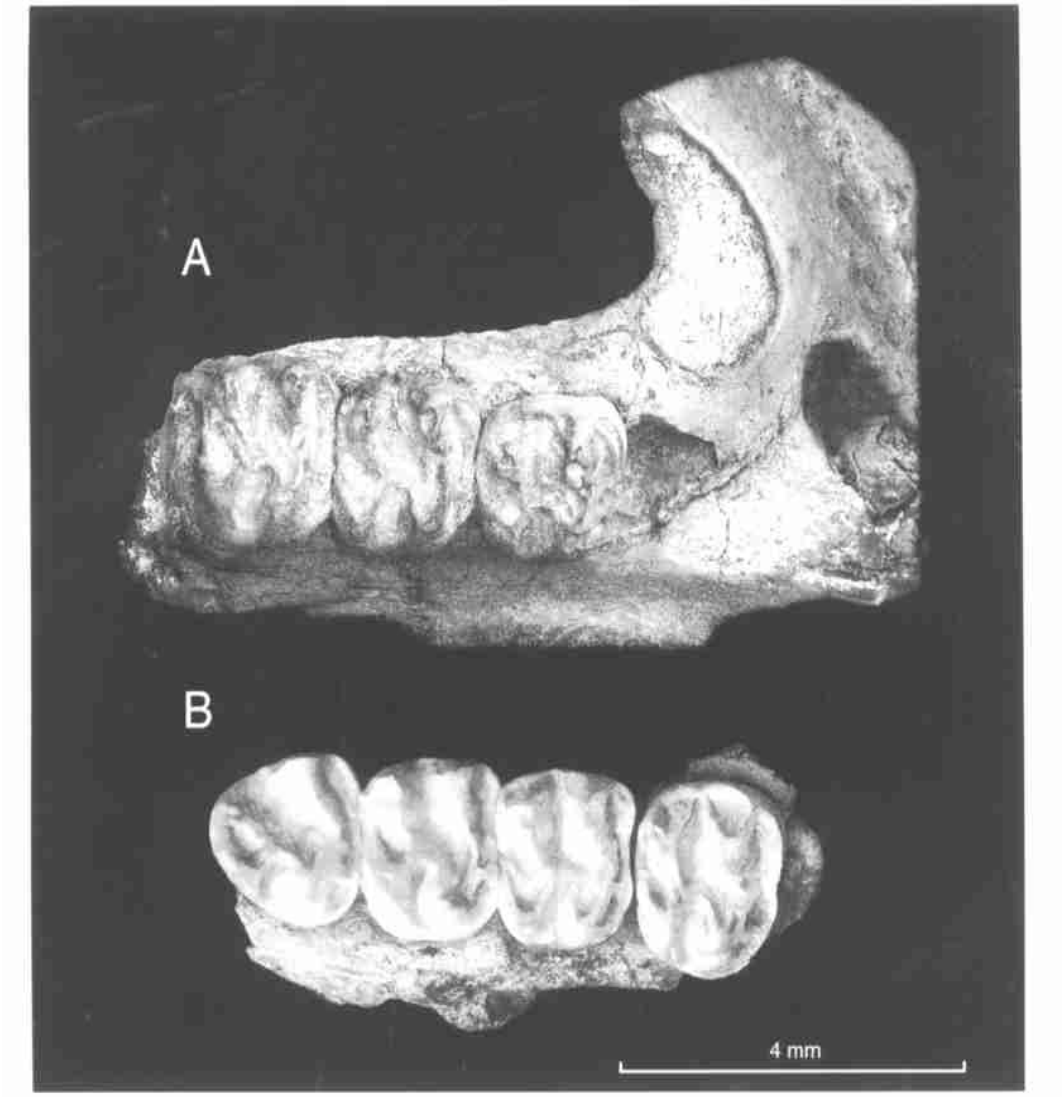

Fig. 4 *Andersomys laoweni* gen. et sp. nov., occlusal views of maxillae with teeth
A. IVPP V 13521, right maxilla with P4-M2; B. IVPP V 13522, right maxilla with P4-M3

it was a relatively large tooth. P4 is larger than M1 and completely molariform, having a hypocone subequal to that of the molars although the trigon is wider than the talon. The buccal cingulum is variably developed, but the anterior cingulum is consistently prominent. Buccally paracone and metacone are flattened. There is little development of the posterior arm of the paracone, whereas the well developed metaloph extends to the strong anterior arm of the hypocone. The protoloph crosses the valley between paracone and anterior cingulum and comes in contact with the cingulum. A second short bridge runs between the lingual end of the anterior cingulum and the protocone. The wide lingual fold is bordered by the posterior arm of the protocone and the anterior arm of the hypocone. M1-2 are similar in general character to P4, although the lingual fold is anteroposteriorly narrower and more anterobuccally oriented. On M2 the buccal cingulum is absent and paracone and metacone are more cuspate, less flattened buccally than on P4 and M1. The mesostyle is variable in development on M1-2, though never pronounced. M3 is a large three sided tooth on which the

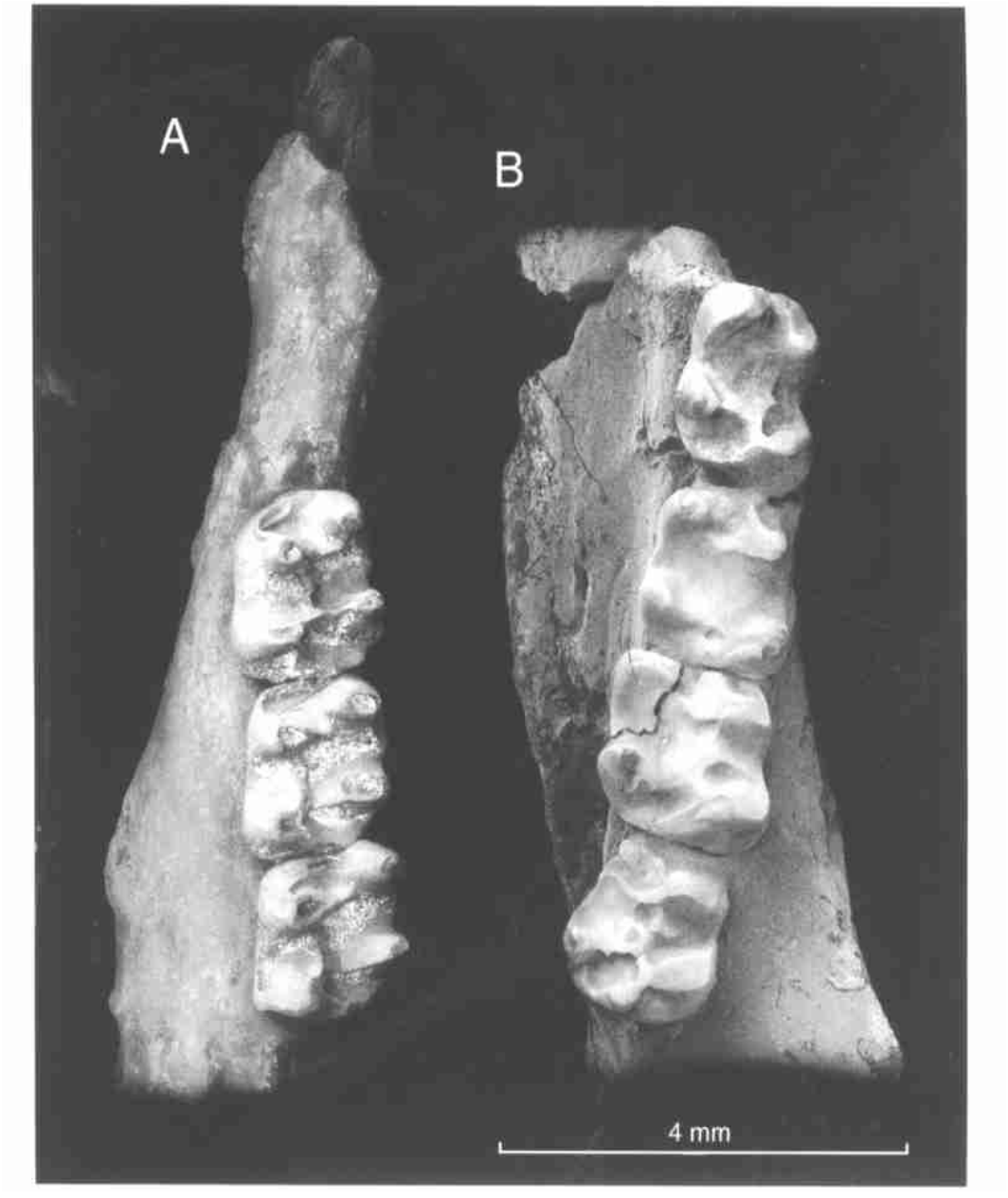

Fig. 5 *Andersomys laoweni* gen. et sp. nov. , occlusal views of mandibles with teeth
A. IVPP V 13520 , left mandible with p4-m2 ; B. IVPP V 13519 , right mandible with p4-m3 , holotype

anterior arm of the protocone extends to the paracone. The metacone and hypocone connect to form a ridge around the posterior and posterobuccal rim of the talon , and also there is a narrow but distinct loph connecting metacone to hypocone posterior to the central basin. As on the more anterior cheek teeth , the lingual fold is well developed.

The essentially molariform p4 of *A. laoweni* is larger than m1. p4-m2 have trigonids that are only slightly narrower than the talonids. p4 differs from m1-2 mainly in having a more cuspate metaconid that lacks a lophid extending toward the protoconid. Other characters shared by p4-m2

include two lophids from the protoconid, one extending anteriorly to the front edge of the tooth, and another reaching lingually to the posterior flank of the metaconid. In later stages of wear, the anteriorly extending lophid from the protoconid wears away and an occlusal facet develops (IVPP V 13520, Fig. 5A). A small mesoconid occurs on the well developed ectolophid. The hypolophid extends transversely to reach the ectolophid anterior to the hypoconid. There is a deep valley between the hypolophid and the thick posterolophid. m3 is preserved only in IVPP V 13519, and it is incomplete, having the metaconid broken away. As far as can be determined, it differs from the more anterior teeth in having trigonid and talonid extending approximately equally on the buccal side and the wider, more cuspate posterolophid reaching less far lingually.

Table 2 Measurements of Andersomys laoweni **gen. et sp. nov. (IVPP specimens)** (mm)

	V 13521		V 13523		V 13522	
	a-p	trw	a-p	trw	a-p	trw
P4	1.76	1.9	1.7	2.03	1.9	2.17
M1	1.7	1.9	1.63	1.76	1.7	1.97
M2	1.7	1.97	1.7	1.83	1.76	1.97
M3					1.97	1.97
P4-M3					7.0	
	V 13519 (holotype)			V 13520		
	a-p	tri	tal	a-p	tri	tal
p4	1.76	1.36	1.42	1.76	1.36	1.56
m1	1.7	1.27	1.42	1.7	1.42	1.56
m2	1.7	1.42	1.63	1.76	1.56	1.76
m3	1.63	1.42				
p4-m3	6.8					

Discussion Of all the currently known zelomyids, *Andersomys laoweni* is the best represented by complete dentitions and jaws, so it serves as a standard to which other members of the family can be compared. Its combination of large P4/p4 and flattening of the buccal cusps of the upper molariform teeth indicate that this is a more derived zelomyid than *Zelomys*.

Andersomys austrarx **sp. nov.**

(Fig. 6; Table 3)

Holotype IVPP V 13524, left p4.

Referred specimens IVPP V 13524.1, left dP4; V 13524.2, left P4; V 13524.3～5, left M 1 or 2; V 13524.6, 7, left M3; V 13524.8, left dp4; V 135234.9, 10, right m1 or 2.

Horizon and locality Latest Sharamurunian or Ergilian, Hedi Formation; near Nanbaotou village, Yuanqu County, Shanxi Province.

Etymology The locality name, Nanbaotou, is translated as "southern hill fort," which is here rendered as *austrarx*, from Latin *auster*, south, and *arx*, fortress, height.

Diagnosis Slightly larger than *A. laoweni* and with better developed buccal cingulum on P4 and more rounded anterior wall of p4.

Description A second species of *Andersomys*, known from isolated teeth, occurs at the Nanbaotou locality in the Yuanqu Basin. It is generally similar to *A. laoweni* but larger. P4 is a large, molariform tooth, that has a transversely wider trigon than talon due to an expanded buccal cingulum on the trigon. A distinct, though narrower cingulum, extends along the anterior side of the tooth. M1 and M2 cannot be differentiated with certainty. In ? M2 the anterior arm of the protocone connects directly to the paracone, whereas in ? M1 this arm extends into the valley anterior to the paracone and bifurcates, sending a short spur back to the anterolingual slope of that cusp. The

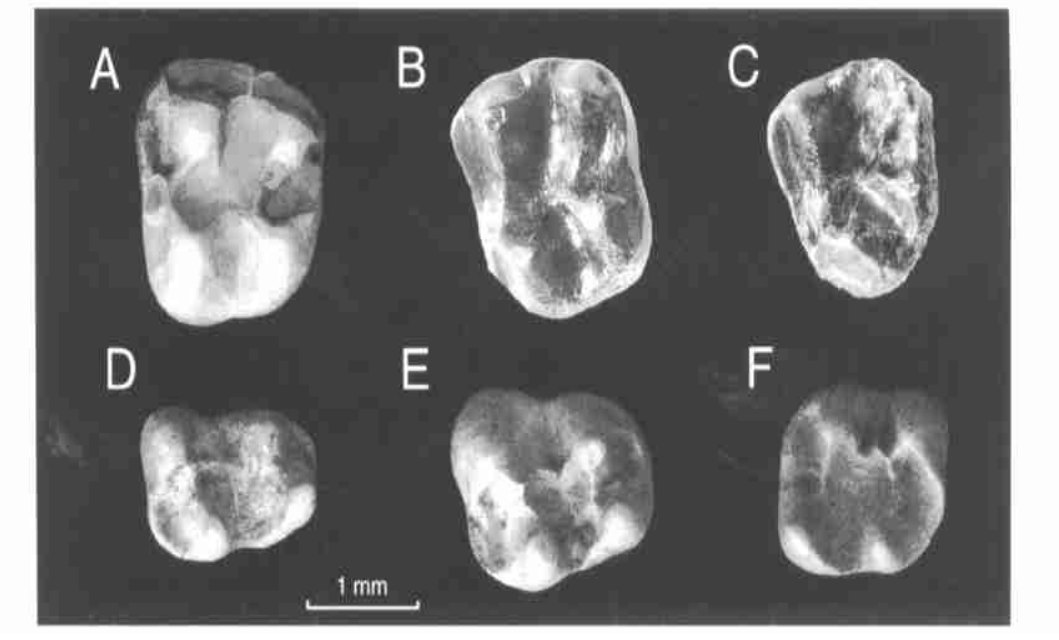

Fig. 6 *Andersomys austrarx* gen. et sp. nov. , occlusal views of isolated teeth
A. IVPP V 13524. 2 , left P4 ; B. IVPP V 13524. 3 , left M1 or 2 ; C. IVPP V 13524. 6 , left M3 ; D. IVPP V 13524. 8 , left dp4 ; E. IVPP V 13524 , left p4 , holotype ; F. IVPP V 13524. 9 , right m1 or 2

metaloph extends to the anterior arm of the hypocone. As in *A. laoweni* M3 has a narrower talon than trigon , due to reduction of metacone and hypocone. The lingual valley is oriented anterobuccally.

Only three lower teeth are here referred to *A. austrarx*. The almost unworn p4 has strong cusps and crests and a much wider talonid than trigonid. A discrete anteroconid occupies the center of the anterior wall. The metaconid is slightly elongated anterobuccally and the protoconid , posterolingually. The strong ectolophid is well set in and inclined anterolingually from hypoconid to protoconid. The hypolophid intersects the ectolophid anterior to the hypoconid. A distinct lingual valley occurs anterior to the posterolophid. A slightly smaller tooth may be dp4 ; it resembles p4 except in having a relatively narrower talonid and more elongate trigonid , a buccally expanded anteroconid , and a more buccally situated ectolophid. A single lower molariform tooth , m1 or m2 , is smaller than p4. Except for slightly larger size and a more anterolingually inclined posterior arm of the protoconid , it is very similar to lower molariform teeth of *A. laoweni*.

Table 3 Measurements of Andersomys austrarx **gen. et sp. nov. (IVPP specimens)** (mm)

	a-p	trw		a-p	tri	tal
V 13524. 2 P4	1. 9	2. 2	V 13524. 8 dp4	1. 9	1. 22	1. 42
V 13524. 3 M1 or 2	1. 86	2. 27	V 13524 p4	1. 97	1. 42	1. 7
V 13524. 6 M3	1. 86	2. 1	V 13524. 9 m1 or 2	1. 76	1. 63	2. 18

Discussion This relatively incompletely known species is the largest and presumably youngest *Andersomys* from the Yuanqu Basin. It appears to be closely related to , but slightly more derived than *A. laoweni*.

Haozi **gen. nov.**

1980 Sciuravidae Tong and Wang , p. 24

Type species *Haozi simplex* sp. nov.

Horizon and locality Sharamurunian, Chugouyu Formation; Lushi Basin, western Henan (Tong and Wang, 1980).

Etymology Chinese, *haozi* (treated as masculine), mouse.

Diagnosis More bunodont cusps than in other known zelomyids, and having only slight flattening of the buccal cusps of P4-M1. P4 subequal in size to M1. P4 trigon wider than talon. More distinct parastyle and metastyle than in other zelomyids.

Haozi simplex **sp. nov.**

(Fig. 7; Table 4)

Holotype IVPP V 13525, left maxilla with P3-M1, M2 broken off at level of the alveolus, both upper incisors.

Etymology Latin, *simplex*, referring to the uncomplicated molar pattern in this rodent.

Diagnosis Only known species of genus.

Description The type and only known specimen of *Haozi* is a well preserved maxilla that has a ventral ridge on the zygoma, a rounded, non-enlarged infraorbital foramen, and a slight ridge on the palate extending anteriomedially from near P3.

Haozi is the only zelomyid for which P3 is certainly known. It is a sturdy, single rooted tooth with a crown composed of a prominent rounded central cusp and a posterolingual cingulum. P4 is fully molariform, as in all zelomyids, having four subequal cusps and the trigon wider than the talon, as in *Andersomys* and *Suomys*. A narrow cingulum occurs on anterior, buccal and posterior sides of the tooth. On the buccal side distinct parastyle, mesostyle, and metastyle bracket the rounded paracone and metacone. The anterior arm of the protocone extends into the valley anterior to the paracone. The metaloph reaches from metacone to the anterior arm of the hypocone. The lingual valley is essentially transverse in orientation. M1 is a very similar tooth, except that the buccal cingulum is either absent or worn away, the anterior arm of the protocone has a slender ridge reaching to the paracone, parastyle and metastyle are more pronounced, and the lingual valley is oriented more obliquely anterobuccad.

Table 4 Measurements of Haozi simplex **gen. et sp. nov. (IVPP V 13525)** (mm)

P3		P4		M1	
a-p	trw	a-p	trw	a-p	trw
1.02	1.02	1.63	1.83	1.59	1.9

Haozi differs from *Zelomys*, *Andersomys* and *Suomys*, in having upper molariform teeth with the combination of more rounded, bunodont cusps and prominent styles, and from the latter two in having less flattening of the buccal cusps of the molariform cheek teeth. Although very incompletely known, its differences from the other known zelomyids indicate something of the range of diversity in tooth patterns that characterize this family.

Suomys **gen. nov.**

Type species *S. selenis* sp. nov.

Horizon and locality Sharmurunian (or and Ergilian), fissures A, B and C in Shuimushan Quarry, near the village of Shanghuang, Liyang County, Jiangsu Province.

Etymology *Su* is the Chinese abbreviation for Jiangsu Province, and Greek, *mys*, mouse.

Diagnosis Zelomyid in which P4 is larger than other upper cheek teeth, strong anterior and buccal cingula; paracone and metacone of P4-M2 and paracone of M3 are flattened buccally and have lengthened anterior and posterior crests, resulting in a W-shaped buccal wall; prominent mesostyle; buccal cusps of lower teeth also extended by crests to form a buccal W-shaped structure, giving a selenodont appearance to the cheek teeth. Differs from other zelomyids in having

pronounced selenodonty.

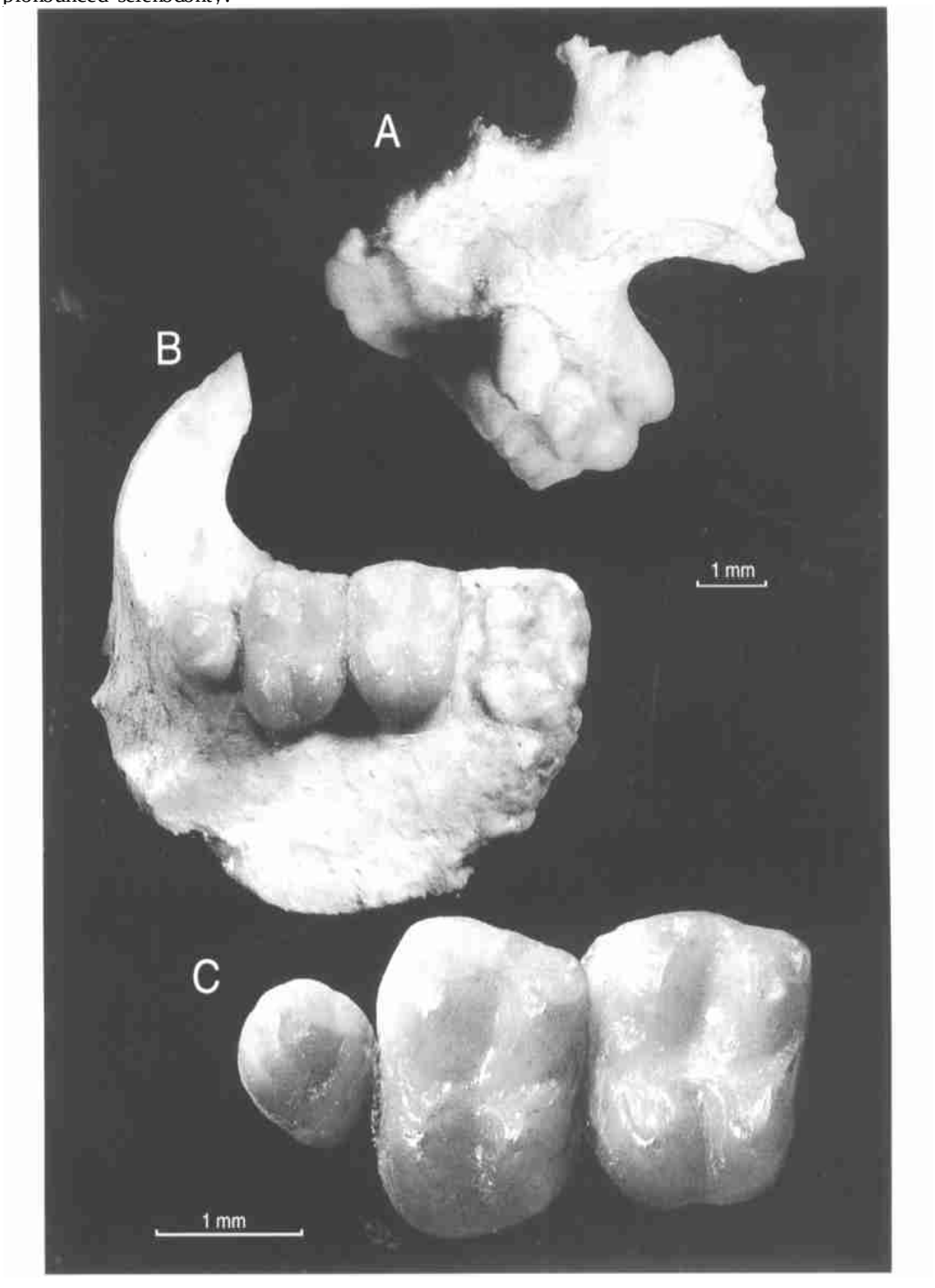

Fig. 7 *Haozi simplex* gen. et sp. nov. , IVPP V 13525 , holotype , left maxilla with P3-M1
A. anterior view showing infraorbital foramen and zygoma ; B. palatal view of specimen ; C occlusal view of P3-M1

Suomys selenis **sp. nov.**
(Figs. 8, 9; Table 5)

Holotype IVPP V 11643.1, right maxilla with alveolus for P3, P4-M2, IVPP locality 93006B.

Hypodigm IVPP V 11643.2, fragment of right maxilla with dP4 (93006B); IVPP V 11642.1, 2 (93006A), V 11643.3～107 (93006B), V 11644.1～85 (93006C), all isolated teeth.

Horizon and locality Sharamurunian (or and Ergilian), IVPP localities 93006A, 93006B and 93006C, fissures in the Triassic Qinglong limestone, Shuimushan Quarry.

Etymology Greek, *selenis*, crescentic.

Diagnosis Only known species of genus.

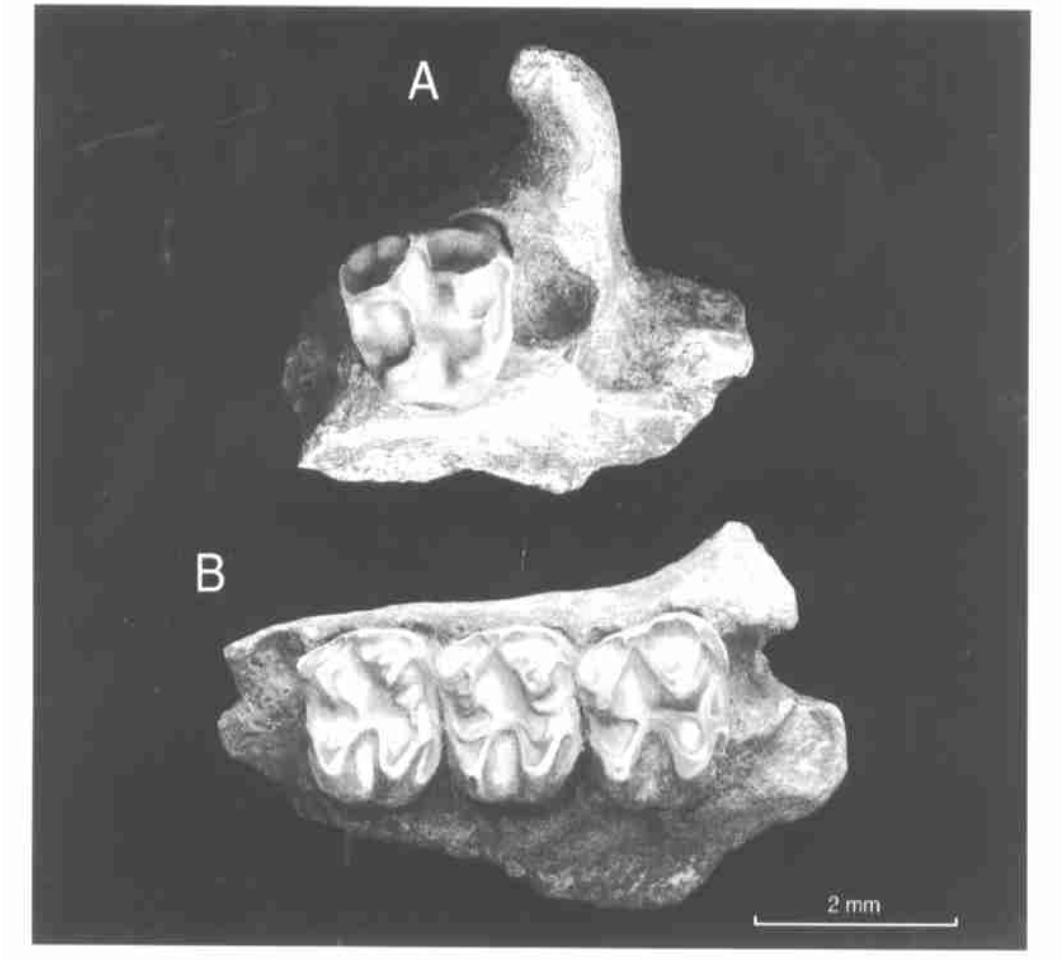

Fig. 8 *Suomys selenis* gen. et sp. nov., occlusal views of maxillae with teeth
A. IVPP V 11643.2, fragment of right maxilla with dP4; B. IVPP V 11643.1, right maxilla with P4-M2, holotype

Description Although most of the specimens of *Suomys* are isolated teeth, two partial right maxillae, V 11643.1 (Fig. 7B) and V 11643.2 (Fig. 7A), provide important information on the zygomasseteric and palatal morphology of this rodent. The zygoma and infraorbital foramen have the

protrogomorphous condition that is characteristic of the family, with a relatively small, low infraorbital foramen and no sign of scars for muscle attachment on what is preserved of the zygomatic plate. As in other zelomyids there is a ridge on the palate, extending anteriorly from in front of P3. The extent of the incisive foramen is not clear on either maxilla. The alveolus of P3 indicates that this tooth was at least as well developed as in *Haozi*.

The nearly unworn dP4 of IVPP V 11643.2 has a distinct anterior cingulum but only relatively narrow cingular shelves buccal to the paracone and metacone. The paracone and metacone are flattened buccally and extended by anterior and posterior crests. The anterior crest from the metacone meets the posterior crest from the paracone to form a protruding mesostyle. The protoloph extends into the valley anterior to the paracone. As in other zelomyids a posterior arm of the protocone meets the anterior arm of the hypocone to form a distinct V-shaped enamel ridge bordering the lingual valley. The metaloph joins the ridge just posterior to the lingual valley. DP4 is slightly wider transversely across the trigon than the talon, and is longer anteroposteriorly than transversely.

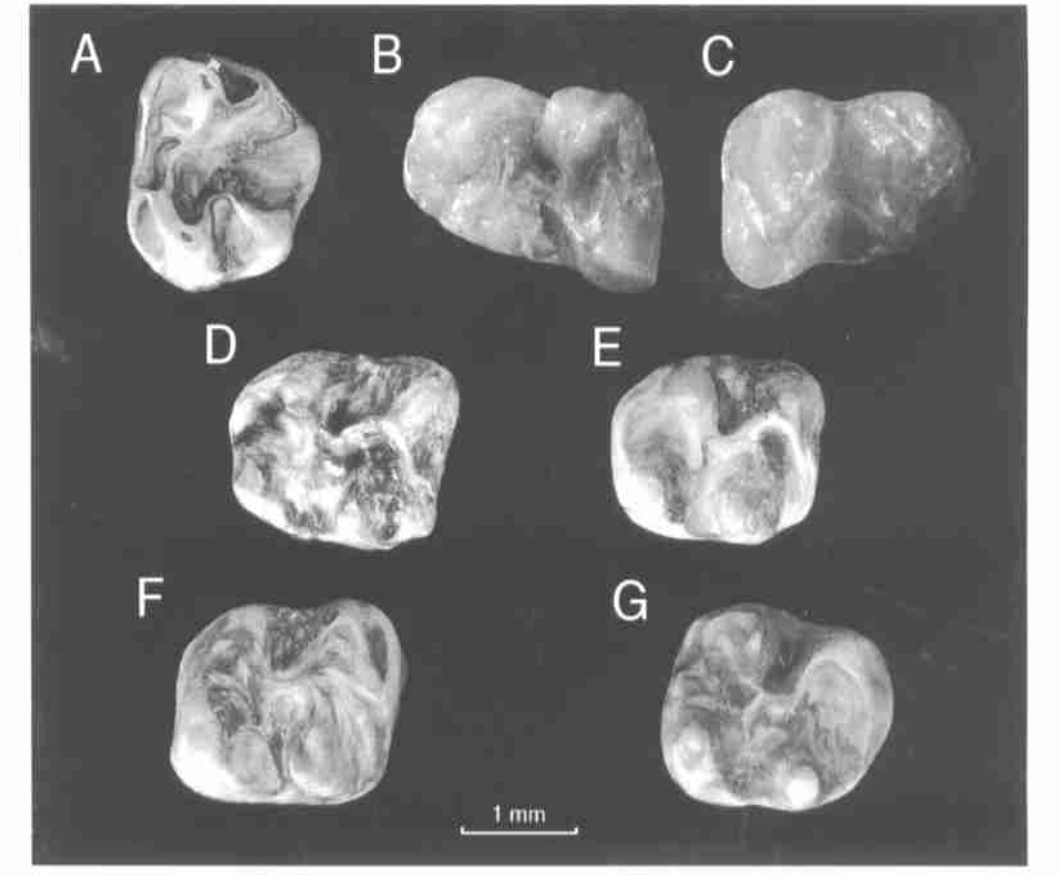

Fig. 9 *Suomys selenis* gen. et sp. nov., occlusal views of isolated teeth
A. IVPP V 11643.51, left M3; B. IVPP V 11643.58, left p4; C. IVPP V 11643.59, right p4; D. IVPP V 11643.65, right m1 or 2; E. IVPP V 11643.66, right m1 or 2; F. IVPP V 11643.93, right m1 or 2; G. IVPP V 11643.105, right m3

The permanent cheek teeth have strong cusps and crests. P4 is a sturdy wide molariform tooth with buccal and anterior cingula. Its trigon, which has an expanded buccal cingulum, forms the widest part of the upper tooth row. On P4-M2 paracone and metacone are flattened buccally, and each cusp has a crescentic appearance due to the development of strong anterobuccal and

posterobuccal crests. The subequal protocone and hypocone are separated by the well developed lingual fold formed by strong lophs from the lingual cusps. On P4 and M1 the lingual fold is transverse whereas on M2 it is more anterobuccally oriented. The protoloph extends from the protocone into the valley anterolingual to the paracone; it terminates freely on P4 and M1 but has a short loph contacting the paracone on M2. The short metaloph extends from the metacone to the enamel ridge of the lingual fold. The trigon of M3 is similar to those of the more anterior molars but the talon is reduced, narrower than the trigon, has a low, non-cuspate metacone and a more buccad position of the hypocone.

Of the lower dentition, dp4 cannot be identified with certainty, which is unexpected in view of the well represented dP4. Possibly some of the smaller teeth referred to p4 are actually deciduous, but no clear morphological differences were found among them. Well defined cusps, lophs, and valleys characterize the permanent lower cheek teeth, as they do the upper cheek teeth. p4 has a trigonid that is narrower transversely than the talonid. The anterior cingulum is short transversely and protrudes anteriorly. The ectolophid is concave buccally. The lingual cusps are higher than the buccal, with the metaconid a sturdy cusp that is elongated anterobuccally to posterolingually, and the entoconid continues into a hypolophid that reaches the ectolophid anterior to the hypoconid. The posteriorly convex posterolophid is thicker buccally and tapers lingually; the valley between it and the hypolophid is well developed. m1 and m2 are difficult to differentiate morphologically; by analogy with *Andersomys*, the larger teeth may be m2. On these teeth the trigonid is somewhat narrower than talonid, and the anterior arm of the protoconid curves from protoconid to metaconid. The posterior arm of the protoconid is short. The strong ectolophid is well set in as on p4. A well developed hypolophid extends from the large, cuspate entoconid to intersect the ectolophid anterior to the hypoconid. The posterolophid forms the strongly ridged posterior edge of the molars, behind a distinct valley. m3 has a wider trigonid than talonid, and the posterolophid is more strongly convex posteriorly than on the more anterior molars.

Table 5 Measurements of Suomys selenis **gen. et sp. nov. (IVPP V 11643)** (mm)

	V 11643.2			V 11643.1			V 11643.51		
	a-p	trw	taw	a-p	trw	taw	a-p	trw	taw
dP4	1.76	1.56	1.49						
P4				1.9	2.17	1.97			
M1				1.83	1.9	1.83			
M2				1.9	1.9	1.83			
M3							1.83	2.17	1.56

	a-p	tri	tal
V 11643.58 p4	1.9	1.15	1.36
V 11643.59 p4	1.8	1.02	1.15
V 11643.65 m1 or 2	1.9	1.36	1.53
V 11643.66 m1 or 2	1.97	1.36	1.42
V 11643.93 m1 or 2	2.03	1.56	1.63
V 11643.105 m3	2.1	1.63	1.56

Discussion *Suomys* is dentally the most derived of known zelomyids. Superimposed on the basic, and relatively primitive, zelomyid zygomasseteric structure and dental formula, this rodent has emphasized the tendency in the family toward a large, molarized P4/p4, well developed hypocone, and extreme flattening to selenodonty of the buccal cusps of the upper molariform teeth. Within the family, *Suomys* is closest to but more derived in selenodonty than *Andersomys*.

Within the Rodentia, which exhibit a much greater range of cheek tooth morphologies than any

other mammalian order, selenodonty has developed in several different lineages. Among Eocene rodents some development of selenodonty can be found in *Eohaplomys* (Wilson, 1949) and in the upper teeth of the theridomyid *Pseudosciurus suevicus* (Schmidt-Kittler, 1971). In later rodents, the aplodontids exhibit selenodonty (Rensberger, 1982), as does, in its most extreme form among rodents, the cricetid *Selenomys* (Wang, 1987). These are not closely related rodents. *Eohaplomys* and the aplodontids are protrogomorphous rodents but lack the large hypocone and loss of conules that characterize the zelomyids. The theridomyid *Psuedosciurus suevicus* is a characteristic theridomorph, with an enlarged infraorbital foramen and loss of P4, and large conules on the upper molariform teeth, all differences from the zelomyids. In *Suomys*, *Eohaplomys*, and *Pseudosciurus*, the selenodonty is basically developed on the buccal side of the upper molariform teeth, and this is combined with more cuspate lingual cusps. The buccal selenodonty results in a lengthening of the anteroposterior crest against which occlusion occurs. *Selenomys* has an extreme form of molar selenodonty superimposed on a basic cricetid morphology, with a large infraorbital foramen and reduced dental formula.

4 Zelomyids in the Asian Eocene

The Zelomyidae is a family of Middle to Late Eocene Asian rodents that have retained a number of primitive rodent characters. They resemble the other early rodent families Ischyromyidae, Sciuravidae, Cocomyidae, and Cylindrodontidae in combining the protrogomorphous/sciurognathous zygomasseteric structure, the complete dental formula for rodents (1,0,2,3/1,0,1,3), and a pauciserial Schmelzmuster in the incisor enamel, all primitive characters for Rodentia.

The cheek teeth, however, exhibit clearly some derived characters that set this family apart as a distinct lineage of early rodents. This is particularly pronounced in the essentially complete molarization of P4/p4 that occurs even in the less derived genera *Zelomys* and *Haozi*. Other derived features are the relatively large size of P4/p4, complete loss of conules, strong lingual valley between protocone and hypocone on the upper molariform teeth, and complete hypolophid on the lower molariform teeth. Additionally, the more derived zelomyids have a buccal flattening of the paracone and metacone of P4 and the metacone of M1. The extreme of this morphology is developed in *Suomys* in which the flattening has evolved into a kind of selenodonty that is present on its upper and lower molariform teeth.

The stratigraphic range of the zelomyids can not yet be precisely determined due to uncertainties in correlation. However, the range is likely to be Middle to Late Eocene (Irdinmanhan, for Shanghuang fissures D and E, through latest Sharamurunian or Ergilian, for Shanghuang fissures B and C). Geographically zelomyids occur only in eastern China, but in a long north-south axis, from Jilin Province to southern Jiangsu Province. Absence of a record of zelomyids in the productive and well sampled Irdinmanhan through Ergilian deposits of Nei Mongol, Mongolia, and eastern Kazakhstan suggests a restriction of these rodents to the probably more humid environments of eastern Asia.

Even in their relatively abbreviated time span, the zelomyids demonstrate both diversity and evolutionary changes. Diversity is exemplified by the transition from the relatively primitive state of *Zelomys* to the bunodont *Haozi* on the one hand and the highly modified, selenodont *Suomys* on the other. Uncertainty about the exact stratigraphic position of most of the localities that have produced zelomyids prohibit the demonstration of temporal sequences for the most part. Within the Yuanqu Basin, however, the stratigraphic succession reveals a general evolutionary sequence from the primitive *Zelomys joannes* to the increasingly more derived, but closely related, *Andersomys laoweni* and *A. austrarx*.

No zelomyids are currently known to be younger than the latest Sharamurunian or Ergilian. Their extinction may be related to the Middle Eocene origin and seemingly rapid dominance of the

cricetids and zapodids, both groups more derived in zygomasseteric structure than the zelomyids, in the eastern parts of Asia, and to the diversity of the ctenodactyloids in presumably drier Eocene habitats.

5 Relationships of the zelomyids

The combination of a primitive rodent morphology of the zygomasseteric structure with precociously molarized cheek teeth sets this family apart from other Eocene rodents. Nonetheless, previous allocations of various zelomyids to the Sciuravidae (Tong and Wang, 1980; Wang and Li, 1990) and Eomyidae (Korth, 1994) are based on very real similarities between these groups. Analysis of these similarities may help determine the interrelationships, if any, of these families.

The Sciuravidae, a family of North American Eocene rodents, resemble zelomyids in having a protrogomorphous/sciurognathous zygomasseteric structure, the complete rodent dental formula, and pauciserial incisor enamel, all primitive states for rodents. They also resemble the zelomyids in forming quadrate teeth through enlargement of the hypocone on the upper molariform teeth and of the entoconid-hypolophid on the lower molariform teeth. This "squaring up" of the grinding teeth has occurred numerous times among the rodents, as among many other herbivorous mammals, and may not be regarded as strongly indicative of close relationships. Differences from the sciuravids include, in all zelomyids, the precocious molarization and enlarging of P4/p4 and the strong ridges bordering the lingual valley of P4-M3; the flattening to selenodonty of the buccal cusps of the molariform teeth in the more derived zelomyids *Andersomys* and *Suomys* has no parallel among the sciuravids.

The Eomyidae, a family of Holarctic rodents, have been suggested to have their oldest record in the Middle Eocene of North America (Chiment and Korth, 1996; Emry et al., 1997, indicated that the genus *Zaisaneomys* Shevyreva, 1993, from the Middle Eocene of Kazakhstan, is not an eomyid as originally described but is either a zapodid or a cricetid). Although the zygomasseteric structure of *Metanoiamys*, presumed to be the oldest known eomyid, is unknown (Walsh, 1997), its lower jaw does show forward migration of the masseteric fossa, to below the anterior margin of m1, a marked difference from the more posterior position of this fossa in the zelomyids. *Metanoiamys* also has the strongly concave dorsal edge of the jaw below the diastema that is found in other eomyids, but not in zelomyids. Later eomyids have a sciuromorphous-sciurognathous zygomasseteric structure and a specialized eomyid type of uniserial incisor enamel (Wahlert and von Koenigswald, 1985), derived conditions not shared with zelomyids. In the morphology of the cheek teeth, on the other hand, the Chadronian yoderimyine eomyids *Yoderimys* and *Litoyoderimys* (Emry and Korth, 1993) share with zelomyids the presence of P3 (lost in the eomyines) and enlarged P4/p4 that have somewhat crescentic cusps. The former character is simply a primitive one, whereas the latter could make it possible to postulate a sister group relationship of zelomyids and eomyids. However, in the yoderimyines the strongly lophate pattern of the molariform teeth, with well developed mesoloph and mesolophid, appears to have little in common with the pattern characteristic of the zelomyids, and the dental similarities between the families may be homoplasies.

If the zelomyids are not the sister group to either the Sciuravidae or the Eomyidae, where can their affinities lie? A plausible interpretation can result from using available morphological, temporal, and geographic information, coupled with understanding of the high amount of homoplasy exhibited within the Rodentia. Accordingly, the zelomyids may be an endemic Asian family, traceable to origin from an Asian ischyromyid that developed molarized premolars and quadrate cheek teeth but retained a primitive zygomasseteric structure and incisor enamel in parallel to a similar derivation of the sciuravids from ischyromyids in North America.

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