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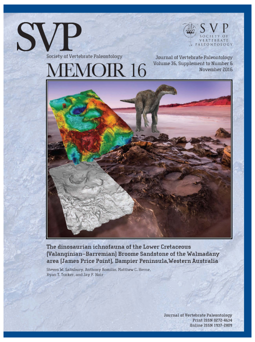

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ARTICLE

NEW SPECIES OF *YUOMYS* (RODENTIA, CTENODACTYLOIDEA) FROM THE UPPER EOCENE OF EASTERN NINGXIA, CHINA

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ABSTRACT—A new species, *Yuomys robustus* of the ctenodactyloid rodent *Yuomys*, is described in the paper. It is from the Western margin of the Ordos Basin District in eastern Ningxia Hui Autonomous Region, China. *Yuomys robustus* is characterized by a combination of features: large size, high tooth crown, having a postparacrista on M2 and lacking hypocone on P4. We also emended the diagnosis of type species of *Yuomys*, *Y. cavioides*. It is characterized by the absence of hypocone on P4, having a distinct ridge connecting the metaconule to the protocone on M1–M3, a postparacrista on M1, a mesostyle on M2, and a small ridge or spur on the mesial side of the protoloph on P4 and M1; the hypoconid smaller than the protoconid and is elongated, the paraconid absent and the mesostylid faintly visible on p4, but well developed on m1–m3; the talonid basin, sinusid, and posteroflexid are large and open on lower cheek teeth. The occurrence of *Lophiomeryx angarae* in the same stratigraphic layer as *Y. robustus* indicates that the horizon is possibly late Eocene in age, not early Oligocene as suggested by previous workers. Body mass estimations of *Y. cavioides*, *Y. eleganes*, and *Y. robustus* show that their weights are roughly in the range of 485–880 g, which is in between those of extant *Myospalax* and *Ratufa*. From the middle Eocene to the late Eocene, *Yuomys* exhibited a trend of gradually enlarging the cheek teeth, and increasing the tooth crown height and body mass.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Yuomys is a genus of rodents with hystricomorphous skull and sciurognathous mandibles, and its phylogenetic position is still incongruent (Li, 1975; Wood, 1977; Dawson et al., 1984; Averianov, 1996; Marivaux et al., 2004; Li and Meng, 2015; Marivaux and Boivin, 2019). Recent studies place *Yuomys* within the superfamily Ctenodactyloidea but of an indeterminate family (Li and Meng, 2015; Li and Tong, 2019). *Yuomys* is distinct from other related genera in Ctenodactyloidea (e.g., *Petrokozlovia*, *Advenimus*, *Saykanomys*) by the following combination of characters: it is a large-sized ctenodactyloid rodent; P4 is larger than M1 with an absent or weakly developed hypocone; the protoloph and metaloph are almost parallel on P4; the hypocone on M1 and M2 is always present and equal to or slightly smaller than the protocone, and the metaloph and protoloph are convergent towards the protocone on M1–M3; on P4–M3, anterocone is undifferentiated on the anteroloph, the anteroloph is connected to the protocone, and the metaconule is sub-equal to the metacone; on the lower cheek teeth, the mesoconid is absent; the ectolophid connecting the hypoconid to the protoconid; the entoconid is mesial to the hypoconid, and the hypolophid is transversely connected to the middle of the ectolophid; the hypoconulid is connected to the hypoconid; the posterolophid is distinct; the talonid basin and the posteroflexid are opened lingually; the preprotocristid connecting the protoconid to the metaconid on m1–m3, and the postprotocristid are short, so the trigonid basin is restricted to a very narrow valley and opened posterolingually (Dawson, 1964; Shevyreva, 1972; Li, 1975; Averianov, 1996; Dashzeveg and Meng, 1998; Li and Meng, 2015; Li and Tong, 2019). *Yuomys* originally was named by Li (1975), and currently comprises nine species, including the type species *Y. cavioides* Li, 1975, and the referred species *Y. eleganes* Wang, 1978, *Y. minggangensis* Wang and Zhou, 1982, *Y. weijingensis* Ye, 1983, *Y. huangzhuangensis* Shi, 1989, *Y. yunnanensis* Huang and Zhang, 1990, *Y. huheboerhensis* Li and Meng, 2015, *Y. altunensis* Wang, 2017, and *Y. magnus* Li, 2017. In addition, other specimens have been referred to undetermined species of *Yuomys* (Wang, 2001; Li and Meng, 2015; Li et al., 2016). Known specimens of *Yuomys* are mainly from the middle Eocene of the northern, northwestern, southwestern, and eastern parts of China (Fig. S1A). *Yuomys* was then a genus endemic to China and its widespread geographic distribution in that region may serve as a biostratigraphic marker.

GEOGRAPHIC AND GEOLOGICAL SETTINGS

The new *Yuomys* fossil material comes from the Bujiamiaozi Ravine, about 11 km northwest of the town of Majiatan, city of Lingwu, in the eastern part of Ningxia Hui Autonomous Region, China. In Ningxia, Cenozoic mammalian fossils are commonly found in its central and southern parts, such as the early

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Oligocene Qingshuiying Fauna in Lingwu, and Neogene mammalian faunal sequence in Tongxin-Haiyuan area, but are reported rarely in the eastern part (Hu, 1962; Wang et al., 1994, 2016). Tectonically and stratigraphically, the Ningxia region can be divided into four districts: the North Qilian District, the Hexi Corridor District, the Western Margin of the Ordos Basin District, and the Ordos Basin District (Wang et al., 2002). The area that produced the new *Yuomys* material belongs to the Western Margin of the Ordos Basin District. The northwest side of the fossiliferous area is a hillock named Yangjiadiwan Shan that is formed by the Cretaceous Yijun Formation. A series of ravines are distributed along the eastern slope of the hillock, and the longest of them is called the Bujiamiaozi Ravine (Fig. S1B, C). The Bujiamiaozi Ravine is northwest-southeasterly oriented and extends for nearly 12 km. The Paleogene sediments are well exposed on both sides of the ravine, and they are composed mainly of conglomerates, sandstones, and sandy mudstones. Those sediments can be divided roughly into three horizons from bottom to top: lower red sandy mudstone beds, middle white sandstone beds, and upper red sandy mudstone beds with gravel belts. The new *Yuomys* fossils were recovered from the middle white sandstone beds. The age of this set of Paleogene strata in the Bujiamiaozi Ravine is considered traditionally to be early Oligocene (BGMRNHAR, 1990; Wang et al., 2002). Previous geological surveys indicate that there are no Paleocene strata in the Ningxia region, and only the Eocene Sikouzi Formation, the Lower Oligocene Qingshuiying Formation, and the Upper Oligocene Hejiakouzi Formation had been formally named (BGMRNHAR, 1990; Liu et al., 2019). Lithologically, the Paleogene Bujiamiaozi Ravine strata cannot be directly correlated with any of these named formations due to the long distance and lack of exposure. Future in-depth stratigraphic work should be conducted to help establish the potential correlation among them.

The Bujiamiaozi fossil represents a new member of the late evolutionary stage of *Yuomys* due to its large size and high tooth crowns. This present study increases our knowledge of the temporal and spatial distribution of *Yuomys* and the evolutionary trend observed in its dental morphology. In addition, it provides new insight into the biochronology of Paleogene strata in eastern Ningxia.

Abbreviations—**BJMZ**, the Bujiamiaozi Ravine, in Lingwu of Ningxia, China, prefix to the IVPP field numbers; **V**, prefix to vertebrate fossils of the IVPP.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **BGMRNHAR**, Bureau of Geology and Mineral Resources of Ningxia Hui Autonomous Region, Ningxia, China; **CAS**, Chinese Academy of Sciences, Beijing, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology of CAS, Beijing, China; **SDM**, Shandong Museum, Shandong, China.

MATERIALS AND METHODS

The *Yuomys* material includes a right fragmentary maxilla with P4–M2 (IVPP V26875) collected from the locality BJMZ20200531LQ02. The material referred to as *Lophiomeryx* is a right m3 collected from the locality BJMZ20200531FU01. Both specimens are in the middle white sandstone beds, the same layer of the Paleogene Bujiamiaozi Ravine strata, and they were collected during the 2020 field season. The specimens are housed in the IVPP of CAS, Beijing, and are available for examination. Dental terminology for *Yuomys* follows Li and Meng (2015) and Li and Tong (2019), and for *Lophiomeryx* we use the terminology from Bärmann and Rössner (2011) and Mennecart (2015) (Fig. S2). The length and width measurements are the maximum mesiodistal and buccolingual distances, respectively. The crown height is the vertical distance between the top of the crown surface and the lowest point of the dental tract. The teeth were measured with a calibrated optical reticule on an Olympus SZX7 microscope to the nearest 0.01 mm. Body mass estimation equations are taken from Freudenthal and Martín-Suárez (2013): log(body mass) = (3.023log(tooth row length) − 0.993) * exp(0.382 ^ 2/2) based on the upper tooth row for the hystricognaths; log(body mass) = (2.788log(tooth row length) − 0.610) * exp(0.517 ^ 2/2) based on the lower tooth row for the sciurognaths. We also scanned the specimens using the 100 kV computerized tomography (CT) scanner with a resolution of 20 μm at the Key Laboratory of Vertebrate Evolution and Human Origins of the IVPP, CAS. The renderings of the 3D digital models of the fossil specimens were performed using VGstudio Max 2.2 software (Volume Graphics) installed in the laboratory.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Superfamily CTENODACTYLOIDEA Simpson, 1945
Family incertae sedis
Genus *YUOMYS* Li, 1975

Type Species—*Yuomys cavioides* Li, 1975.

Referred Species—*Y. eleganes* Wang, 1978, *Y. minggangensis* Wang and Zhou, 1982, *Y. weijingensis* Ye, 1983, *Y. huangzhuangensis* Shi, 1989, *Y. yunnanensis* Huang and Zhang, 1990, *Y. huheboerhensis* Li and Meng, 2015, *Y. altunensis* Wang, 2017, *Y. magnus* Li, 2017, and *Y. robustus* sp. nov.

Emended Diagnosis—A large-sized ctenodactyloid rodent; P4 is larger than M1 with an absent or weakly developed hypocone; the protoloph and metaloph is almost parallel on P4; the hypocone on M1 and M2 is always present and equal to or slightly smaller than the protocone, and the metaloph and protoloph are convergent towards the protocone on M1–M3; on P4–M3, the anterocone is undifferentiated on the anteroloph, the anteroloph is connected to the protocone, and the metaconule is subequal to the metacone; on the lower cheek teeth, the mesoconid is absent; the ectolophid connecting the hypoconid to the protoconid; the entoconid is mesial to the hypoconid, and the hypolophid is transversely connected to the middle of the ectolophid; the hypoconulid is connected to the hypoconid; the posterolophid is distinct; the talonid basin and posteroflexid are opened lingually; the preprotocristid connecting the protoconid to the metaconid on m1–m3, and the postprotocristid are short, so the trigonid basin is restricted to a very narrow valley and opened posterolingually.

Remarks—When Li (1975) established *Yuomys*, he dubiously assigned this genus to the subfamily Paramyinae within the superfamily Ischyromyoidea. All later workers including Wang (1978), Wang and Zhou (1982), and Ye (1983) followed Li's (1975) taxonomic treatment. However, Wood (1977) considered that Ischyromyoidea has a hystricomorphous skull and hystricognathous mandibles, and thus *Yuomys* should be placed in the Ctenodactylidae instead of the Ischyromyidae. Dawson et al. (1984) divided Ctenodactyloidea into three families, the Ctenodactylidae, Cocomyidae, and Yuomyidae (comprising *Yuomys*, *Petrokozlovia*, *Advenimus*, and *Saykanomys*). When Shi (1989) described *Y. huangzhuangensis*, and Huang and Zhang (1990) named *Y. yunnanensis*, they followed Dawson et al.'s (1984) taxonomy. Averianov (1996) suggested that Eocene Ctenodactyloidea includes three families, the Alagomyidae, Chapattimyidae (= Yuomyidae = Advenimurinae), and Tamquammyidae (= Cocomyidae = Orogomyidae), and that *Yuomys* should be placed in the Chapattimyidae as first proposed by Hussain et al. (1978).

McKenna and Bell (1997) followed Averianov's (1996) view, and they suggested that *Yuomys*, *Bandaomys*, *Advenimus*, *Petrokozlovia*, *Euboromys* and *Dianomys* constitute the Yuomyinae within the Chapattimyidae. Based on phylogenetic analyses of cheek teeth morphology, Marivaux et al. (2004) suggested that *Yuomys* instead should not be referred to the Chapattimyidae, but the Yuomyidae (consisting of *Yuomys*, *Advenimus*, *Petrokozlovia*, *Anadianomys*, and *Bandaomys*). Furthermore, it is one of the earliest representatives of Ctenodactyloidea. Li and Meng (2015) conducted a phylogenetic analysis of Ctenodactyloidea, and their results supported that *Chapattimys*, *Birbalomys*, *Dianomys*, *Petrokozlovia*, and *Yuomys* form a clade. Thus, Li and Meng (2015) supported that *Yuomys* should be referred to Ctenodactyloidea, but that it cannot be confidently placed in any recognized family. After that, when Li (2017) established *Y. magnus* and Wang (2017) erected *Y. altunensis*, they followed Li and Meng's (2015) taxonomy. Recently, Marivaux and Boivin (2019) suggested that *Yuomys* is the closest relative of *Petrokozlovia*, and is distantly related to the *Advenimus* + *Saykanomys* clade within Yuomyidae. Here, we follow Li and Meng's (2015) taxonomic treatment (i.e., *Yuomys* as part of Ctenodactyloidea without a familial attribution).

YUOMYS CAVIOIDES Li, 1975
(Figs. 1A–D, S3–S4)

Yuomys cavioides Li, 1975:58, fig. 1, plates I, II.4.
Yuomys cavioides Li, 1975: Tong, 1997:86.

Holotype—Specimen IVPP V4796.1–4, a skull, a fragmentary maxilla, and two associated mandibles, possibly belonging to the same individual (Fig. 1A–D).

Type Locality—Mianchi, Henan Province, China.

Referred Specimens—A left mandible with m1–m3, IVPP V4797 (Fig. S4A1–3); a left maxilla with P4–M2, IVPP V4798 (Fig. S4B1–3); a right mandible with m1–m3, IVPP V4799 (Fig. S4C1–3); a left mandible with p4–m1, IVPP V4800 (Fig. S4D1–3); six isolated cheek teeth including two right m1s, two left m3s, a left M2, and a left M3, IVPP V4801 (Fig. S4Ea–Ef); IVPP V4797–4801 are from Mianchi, Henan (see Li, 1975). A left maxilla with M2–M3, IVPP V10263.1 (Fig. S4G1–3) and a left mandible with m2, IVPP V10263.2 (Fig. S4H1–3), Mianchi, Henan (see Tong, 1997).

Age—Middle Eocene.

Emended Diagnosis—P4 is larger than M1 with an absent hypocone. The protocone and hypocone subequal in size on M1 and M2, but the hypocone obviously smaller than the protocone on M3. The metaconule and protocone usually connected by a distinct extra ridge on M1–M3. The postparacrista on M1 and the mesostyle on M2 always present. A small ridge or spur on mesial side of the protoloph sometimes present and mesially extending to the precingulum on P4 and M1. As for lower cheek teeth, p4 larger than m1, the hypoconid smaller than the protoconid and is elongated, the paraconid absent, and the mesostylid faintly visible on p4 but well developed on m1–m3. The preprotolophid and postprotolophid are short on p4, so the trigonid basin opened both anteriorly and posterolingually. The talonid basin, sinusid, and posteroflexid are large and open on lower cheek teeth.

Remarks—*Yuomys cavioides* was established by Li (1975) based on the specimens from three different localities: Mianchi and Jiyuan Counties in Henan Province, and Ula Usu in Nei Mongol (Inner Mongolia) Mongolian Autonomous Region, China. The holotype (IVPP V4796.1–4) comes from Mianchi, Henan Province, and Tong (1997) referred two additional specimens (IVPP V10263.1–2) to *Y. cavioides*. We examined the holotype and noticed that its dental morphology differs from Li's (1975) original description. On the holotype, there is a distinct extra ridge that connects the metaconule to the protocone. In addition, a loph or a spur is developed from the mesial side of the protoloph and extends mesially to the precingulum. That character state is present only on P4 and M1 of the holotype, and cannot be seen on the originally referred specimens of *Y. cavioides* (Fig. 1C–D).

A fragmentary skull of a juvenile individual (IVPP V4802) from Jiyuan County, Henan Province was referred to *Y. cavioides* by Li (1975), and it preserves a partial left tooth row (P3, DP4 and M1) and a right one with DP4–M2 (Fig. 2D–H). Its cheek teeth are significantly larger, and their crowns also are higher than that of the holotype (see Table S1). There also is no extra ridge connecting the metaconule to the protocone (Fig. 2G–H). Considering its larger size, higher tooth crown, and because the dental morphology is extremely similar to that of the new material from the Bujiamiaozi Ravine (described below), we recommend that IVPP V4802 from Jiyuan should be excluded from *Y. cavioides* and transferred to *Y. robustus* sp. nov.

Li (1975) also referred a right mandible with m1–m3 (IVPP V4803) from Ula Usu, Erlian Basin, Nei Mongol to *Y. cavioides* (Figs. 1E, S4F1–3). Compared with the mandibles of the holotype (IVPP V4796.1–2), IVPP V4803 possesses some obvious differences including that the dimension of m1–m3 tooth row is slightly shorter and wider than that of the holotype, the mesostylids on m1–m3 are well developed, and there is a distinct paraconid mesial to the metaconid on m1 (see Table S1 and Figs. 1E, S4F1–3). Given the rarity of the fossil material, we treat this specimen as *Yuomys* cf. *Y. cavioides*.

YUOMYS ROBUSTUS, sp. nov.
(Fig. 2)

Yuomys cavioides Li, 1975:58, plate II.1–3.

Etymology—The specific epithet is from Latin *robustus*, which refers to its large size, high tooth crown, and strong cusps and lophs.

Holotype—Specimen IVPP V26875, right fragmentary maxilla with P4–M2 (Fig. 2A–C).

Type Locality—Locality BJMZ20200531LQ02 (37°51′15.475″ N, 106°41′34.799″E), the Bujiamiaozi Ravine, Lingwu City, Ningxia Hui Autonomous Region, China (Fig. S1C).

Referred Specimens—Specimen IVPP V4802, broken skull with left P3, DP4 and M1, and right DP4–M2; Jiyuan, Henan Province (Fig. 2D–H, Li, 1975).

Age—Late Eocene.

Differential Diagnosis—Largest species of the genus with the highest cheek tooth crown. *Yuomys robustus* differs from *Y. cavioides* in having a hypocone smaller than the protocone, a lack of connection between the metaconule and the protocone, the absence of a loph or a spur on mesial side of protoloph that would extend to the precingulum on M1 and M2, the absence of a postparacrista on M1 and the mesostyle on M2, and in having a postparacrista on M2. *Yuomys robustus* differs from *Y. eleganes* in having a hypocone smaller than the protocone, having a well-developed parastyle, and exhibiting a separation between the metaconule and the protocone on M2. *Yuomys robustus* is distinguished from *Y. weijingensis* in lacking a mesostyle, a lack of connection between the metaconule and the protocone on M1, and having a postparacrista on M2. *Yuomys robustus* differs from *Y. huangzhuangensis* in lacking both the hypocone and protoconule on P4, in having a hypocone smaller than the protocone, and in lacking the protoconule on M1 and M2. *Yuomys robustus* differs from *Y. huheboerhensis* in having a larger size, lacking a hypocone on P4, having a hypocone distinctly smaller than the protocone on M1 and M2, a separation of the metaconule and protocone on P4–M2, the absence of a mesostyle on M1 and M2, and in having the postparacrista on M2. *Yuomys robustus* is unlike *Y. altunensis* in having a greater

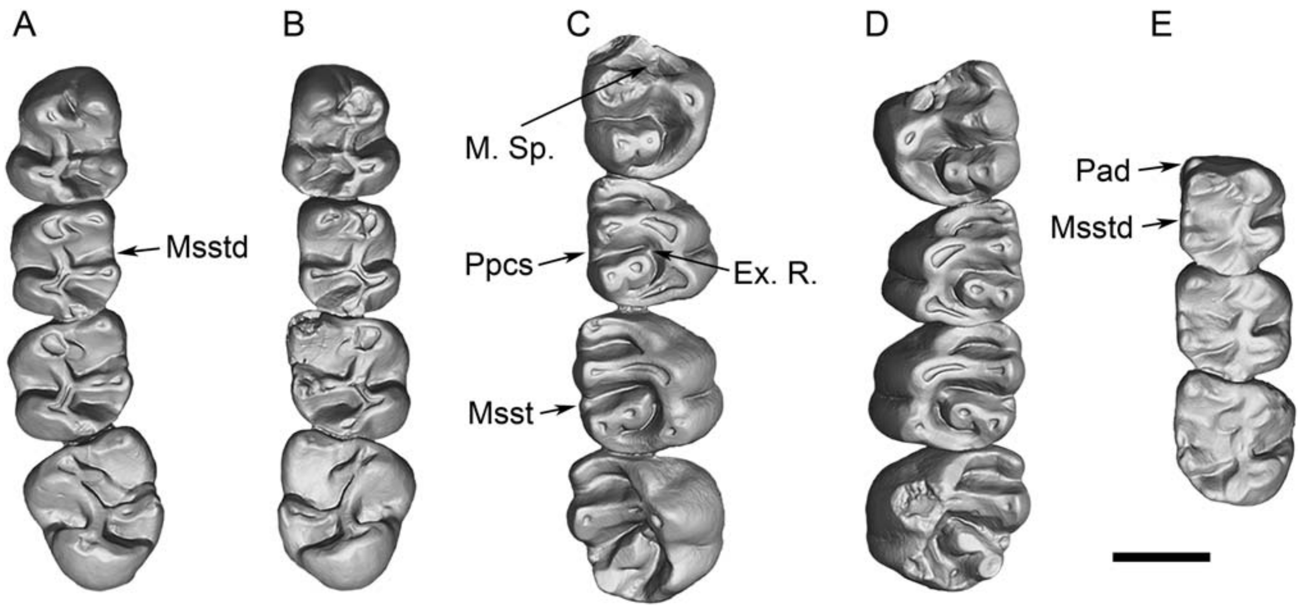

FIGURE 1. Occlusal view of the specimens originally attributed to *Yuomys cavioides* by Li (1975). **A–D**, holotype of *Y. cavioides*, Mianchi, Henan Province: **A**, left p4–m3, IVPP V4796.1; **B**, right p4–m3, IVPP V4796.2; **C**, right P3–M3, IVPP V4796.3; **D**, left P4–M3, IVPP V4796.4; **E**, right m1–m3, IVPP V4803, Ula Usu, Nei Mongol. **Abbreviations**: **Ex. R.**, extra ridge connecting the metaconule and the protocone; **Msst**, mesostyle; **Msstd**, mesostylid; **M. Sp.**, mesial spur of the protoloph; **Pad**, paraconid; **Ppcs**, postparacrista. Scale bar equals 3 mm.

ratio between the length and width on M1 and M2, and in having a postparacrista, but in lacking a mesostyle on M2. *Yuomys robustus* is distinguished from *Y. magnus* in lacking the protoconule, in displaying a metaconule separated from the protocone on P4–M2, in lacking a hypocone on P4, in having a greater ratio between length and width, a hypocone smaller than the protocone on M1 and M2, and in lacking a mesostyle on M1.

Description—Specimen IVPP V26875 is a fragmentary maxilla preserving P4–M2. Its teeth are heavily worn, so this specimen likely comes from an elderly individual. The teeth are robust, buno-lophodont, and lingually hypsodont. P4 is longer than M1, but both teeth are sub-equal in width, with M2 slightly larger than M1 (see Table S1).

P4 has a rounded triangular outline in occlusal view. It is molariform with a distinct paracone, a metacone, and a well-developed protocone, but the hypocone is absent. On the buccal side, the parastyle, paracone and metacone increase in height from the mesial to distal end, and the parastyle is significantly lower than the other two. The parastyle and precingulum are fused, and the anterocone is absent. The paracone is connected to the protocone via a robust protoloph lacking a protoconule. The metaconule is well developed and slightly larger than the metacone. The metaconule is connected to the metacone with a short metaloph but not connected to the protocone. The metaloph and protoloph are almost parallel. The postcingulum is low and reaches the distal base of the metacone. The mesial valley is relatively large and open, whereas the middle valley is also large, but nearly closed. There is no postparacrista, mesostyle, or premetacrista on the edge of the middle valley. The distal valley is relatively small and lingually connected to the middle valley in an arc. The tooth has three roots.

M1 and M2 have square outlines in occlusal view, and they also have three roots. On M1, the hypocone is well developed and slightly smaller than the protocone. The hypocone is separate from the protocone by a vertical sinus extending from the occlusal surface down to the base of the crown. On the buccal side, the metacone is smaller than the paracone, the parastyle is low and small, and it is fused with the precingulum. The anterocone is absent. The paracone is connected to the protocone through a robust protoloph lacking a protoconule. The metaconule is well developed and sub-equal to the metacone. They are connected via a short metaloph. The metaconule is not connected to the protocone. The metaloph and protoloph converge towards the protocone. The postcingulum is low and reaches the distal base of the metacone. The mesial valley is relatively large, while the middle valley is narrow and nearly closed. There is no postparacrista, mesostyle, or premetacrista on the edge of the middle valley. The distal valley is almost entirely erased. The morphology of M2 is very similar to that of M1, but differs in that the protoloph and metaloph converge towards the protocone, and they have a distinct postparacrista. For a detailed description of the referred IVPP V4802 specimen from Jiyuan, see Li (1975).

Comparison—The morphology and characters of IVPP V26875 from Bujiamiaozi are consistent with the dental characteristics of *Yuomys*, with the cheek teeth buno-lophodont, the upper cheek teeth lingually hypsodont, the P4 larger than M1, the hypocone absent or undeveloped on P4 (whereas it is developed and slightly smaller than the protocone on M1 and M2); and subequally sized metaconules and metacones (Li, 1975; Li and Tong, 2019).

Among the known nine species of *Yuomys*, *Y. minggangensis* and *Y. yunnanensis* are only known from lower cheek teeth, and *Y. cavioides*, *Y. eleganes*, *Y. weijingensis*, *Y. huheboerhensis* and *Y. magnus* have specimens of both upper and lower cheek teeth, which makes it possible to compare IVPP V26875 with them. The cheek tooth measurements demonstrate that IVPP V26875 is distinctly larger and has a higher crown than the dentition of all known species of *Yuomys* (see Table S1 and Fig. S5). Furthermore, the morphology of seven species of *Yuomys* that preserve upper cheek teeth differs from IVPP V26875 by the following characteristics.

The emended *Y. cavioides* differs from *Y. robustus* in that the protocone and hypocone are subequal in size on M1 and M2,

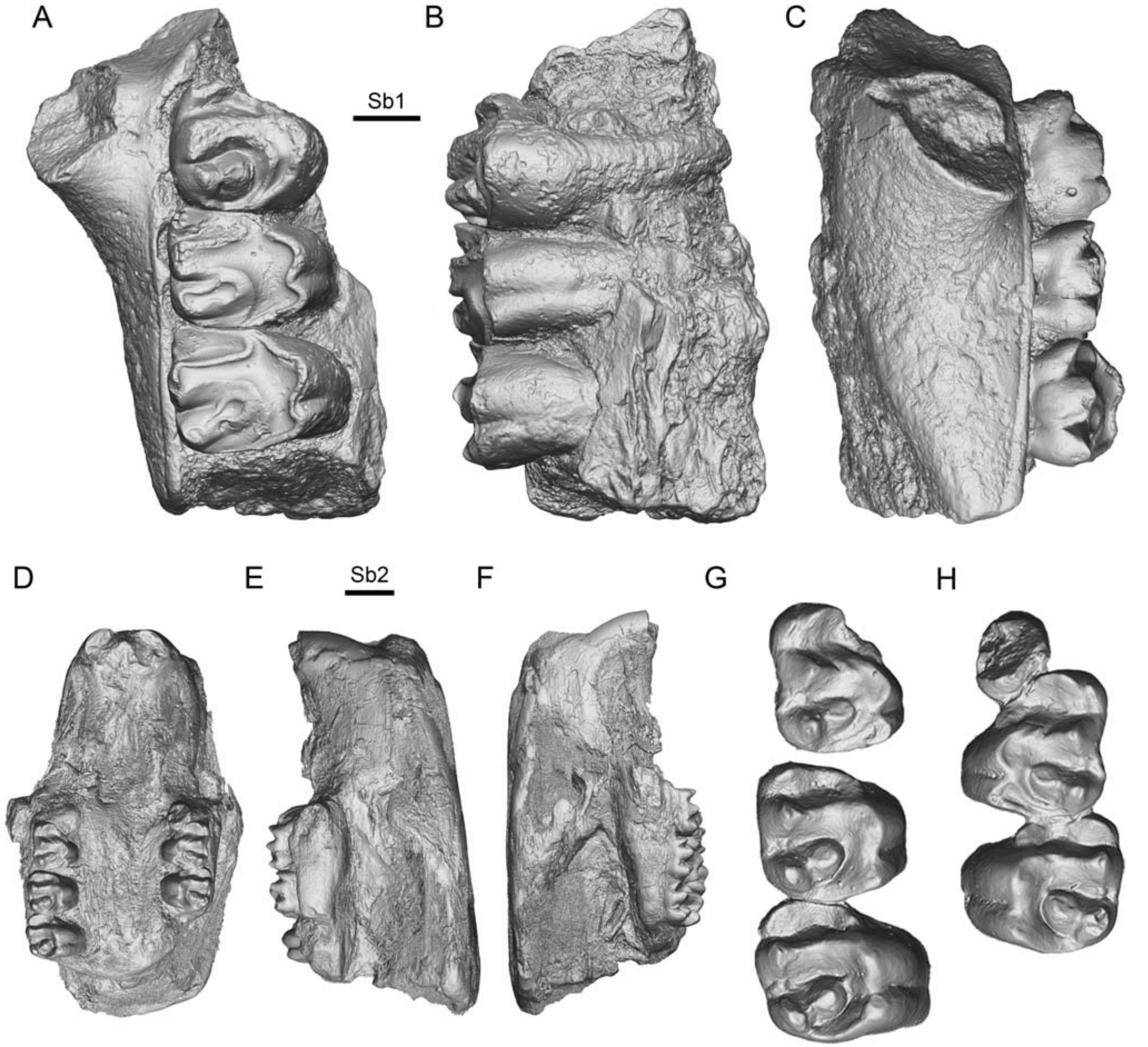

FIGURE 2. The holotype (IVPP V26875) and the referred specimen IVPP V4802 of *Yuomys robustus* sp. nov. (in this text). **A**–**C**, IVPP V26875, right maxillary fragment with P4, M1–2: **A**, occlusal view; **B**, lingual view; **C**, buccal view; **D**–**H**, IVPP V4802: **D**, inferior view; **E**, left view; **F**, right view; **G**, right DP4, M1–2; **H**, left DP3–4, M1. **Abbreviations**: **Sb1** = Scale bar 1, equals 2 mm (**A**–**C** and **G**–**H**); **Sb2** = Scale bar 2, equals 5 mm (**D**–**F**).

the metaconule and protocone are connected by a distinct extra ridge on M1 and M2, the postparacrista on M1 and the mesostyle on M2 are present, a postparacrista on M2 is absent, and a small loph or a spur on the mesial side of the protoloph is present and extends mesially to the precingulum on P4 and M1.

Wang (1978) described *Y. eleganus* based on two mandibles and an isolated M2 from the Lishigou Formation of the middle Eocene of Tongbai County, Henan Province. The latter species is different from *Y. robustus* in that the protocone and hypocone are sub-equal in size, the parastyle is faintly visible, and the metaconule and protocone are linked together by an extra ridge on M2.

Ye (1983) erected *Y. weijingensis* based on a left fragmentary maxilla bearing M1–M2 and a left m2 from the Ulan Shireh Formation (= Irdin Manha Formation + Tukhum Formation in Wang et al., 2012) of the middle Eocene of Ulan Shireh (= Wulan-taolegai in Wang et al., 2012), Erlian Basin, Nei Mongol. This species can be distinguished from *Y. robustus* in displaying the metaconule and the protocone linked by a distinct extra ridge, the mesostyle is present on M1, and the postparacrista is absent on M2.

Shi (1989) named *Y. huangzhuangensis* based on a left fragmentary maxilla preserving P4–M2 from the Huangzhuang Formation of the middle Eocene of Huangzhuang Village, city of Qufu, Shandong Province. It differs from *Y. robustus* in having a small hypocone on P4, the protocone sub-equal to the hypocone on M1–M2, and in the presence of a protoconule on P4–M2.

Li and Meng (2015) established *Y. huheboerhensis* based on 17 isolated upper and lower cheek teeth from the Irdin Manha Formation of the lower middle Eocene of Huheboerhe, Erlian Basin, Nei Mongol. Li et al. (2017) referred three additional cheek teeth from the middle part of the ‘Basal White’ beds (= lower part of the Irdin Manha Formation) of the lower middle Eocene from Erden Obo in Erlian Basin to *Y. huheboerhensis*. This species is different from *Y. robustus* in being clearly smaller in size, the presence of a small hypocone on P4, a faintly visible parastyle on P4 and M1, a hypocone sub-equal to the protocone on M1 and M2, a connection between the metaconule and the protocone via an extra ridge on P4–M2, a mesostyle present on M1 and M2, and in the absence of a postparacrista on M2.

Wang (2017) described *Y. altunensis* based on four fragmentary maxillae from the Xishuigou Formation of the middle Eocene of Caihong Gou, Altun Shan, Xinjiang Uygur Autonomous Region. It differs from *Y. robustus* in having a width greater than its length on M1 and M2, and in having a mesostyle on most M2s.

Li (2017) established *Y. magnus* based on 15 specimens, including fragmentary maxillae, mandibles, and isolated cheek teeth from the 'Lower Red' beds (= the Shara Murun Formation) of the upper middle Eocene of Erden Obo, Erlian Basin, Nei Mongol. This species is distinct from *Y. robustus* in having M1 and M2 that are wider than long, a protoconule, the metaconule connected to the protocone by an extra ridge on P4–M2, a small hypocone on P4, the protocone and hypocone sub-equal in size on M1–M2, and in displaying a mesostyle on most M1s.

DISCUSSION

Biostratigraphy

Wang (2001) referred two upper molars (IVPP V12528.1–2) from the Houldjin Formation of Erenhot, Nei Mongol to *Yuomys* sp. The age of the Houldjin Formation is generally accepted to be late Eocene (Wang, 1997a, 1997b; Li and Qiu, 2015; Wang et al., 2019). However, the species of *Yuomys* from Houldjin is quite small and distinctly smaller than almost all other species of *Yuomys* except for *Y. huheboerhensis*. Furthermore, the upper teeth of the Houldjin *Yuomys* specimens have a metaloph and protoloph almost parallel and a metaloph perpendicular to the entoloph, directed towards the hypocone. These characters contrast with those of all known species of *Yuomys*, where the protoloph and metaloph always converge towards the protocone to varying degrees. Given the limited amount of comparative material, we cannot make further taxonomic identification of those teeth. If the Houldjin specimens referred to as *Yuomys* were excluded from the genus, all other prior records of *Yuomys* would be restricted to the middle Eocene.

Yuomys robustus from the Bujiamiaozi Ravine has a remarkable large size and high tooth crowns. Therefore, we estimated that its relative age is possibly younger than the middle Eocene. This relative age estimate is supported by our discovery of a right m3 of a lophiomerycid (IVPP V26888, Fig. S6A) from the locality BJMZ20200531FU01 (37°51′12.811′′N, 106°41′48.356′′E) in the Bujiamiaozi Ravine (Loc. 2 in Fig. S1C). This specimen was collected in the middle white sandstone beds, which is the same layer having yielded *Y. robustus*. In the family Lophiomerycidae, the m3 is a key dental locus for alpha taxonomic identifications. There are some Eocene genera referred to as the Lophiomerycidae, such as the European *Iberomeryx*, Southeast Asian *Krabimeryx*, South Asian *Nalameryx* and northern Chinese *Zhailimeryx* (Gabunia, 1964; Guo et al., 2000; Métais et al., 2001, 2009). The Bujiamiaozi lophiomerycid m3 differs from the aforementioned genera in having imperfect selenodont metaconid and entoconid, only one hypoconulid, and in lacking a premetacristid, postentocristid, posthypoconulidcristid and distal basin. These features are consistent with an identification as *Lophiomeryx* Pomel, 1853. At present, while there are 11 species referred to *Lophiomeryx*, only two species are known in China. They are *L. shinaoensis* and *L. gracilis* from the Shinao Basin, Guizhou Province (Miao, 1982; Métais et al., 2009; Fig. S6C, D). Chiu (1965) described specimens assigned to *Lophiomeryx* sp. from the Junggar Basin in Xinjiang, but those specimens lack the m3, thereby limiting the scope of the comparisons with IVPP V26888 from the Bujiamiaozi Ravine. The latter specimen differs from m3 of *L. shinaoensis* and *L. gracilis* in having a larger size, a higher hypoconulid, a weak posthypoconulidcristid, no metastylid, and in having both mesial and distal basins open lingually. IVPP V26888 is identical both in size and morphology, to the m3 of *L. angarae* discovered by Matthew and Granger (1925) from Ardyn Obo, Mongolia, and most likely should be referred to that species (see Table S2 and Fig. S6B). Current opinion regarding the age of the Ardyn Obo Fauna is consistent with the late Eocene hypothesis (Dashzeveg and Devyatkin, 1986; Vislobokova, 1997; Meng and McKenna, 1998; Vislobokova and Daxner-Höck, 2001; Vandenberghe et al., 2012). The occurrence of *L. angarae* in the middle white sandstone beds producing *Y. robustus* in the Bujiamiaozi Ravine, strengthens support for the hypothesis that these deposits are late Eocene rather than early Oligocene in age as previously suggested (BGMRNHAR, 1990; Wang et al., 2002).

Evolutionary Trends in *Yuomys*

The oldest known species of *Yuomys* is *Y. huheboerhensis* from the Irdin Manha Formation in Huheboerhe and middle part of the 'Basal White' beds (= lower part of the Irdin Manha Formation) in Erden Obo, Erlian Basin, Nei Mongol. Their age is generally considered to be early middle Eocene (Li, 2016, 2017; Li et al., 2017). *Yuomys minggangensis*, *Y. weijingensis*, and *Y. yunnanensis* also are known from the lower middle Eocene, but are slightly younger than *Y. huheboerhensis* (Li and Tong, 2019). *Yuomys cavioides*, *Y. eleganes*, *Y. huangzhuangensis*, *Y. magnus*, and *Y. altunensis* are all from upper middle Eocene sites, and only the proposed new species here *Y. robustus* would be from the upper Eocene (Li, 1975; Wang, 1978; Wang and Zhou, 1982; Ye, 1983; Shi, 1989; Huang and Zhang, 1990; Li and Meng, 2015; Li et al., 2016, 2017; Li, 2017; Wang, 2017).

We selected the best preserved specimens of the different species of *Yuomys*, and arranged their cheek teeth by size and crown height with respect to their hypothesized chronological placement (Fig. 3). The earliest *Yuomys*, *Y. huheboerhensis* from the lower middle Eocene is the smallest species, and has the lowest tooth crown. In contrast, the other species from the middle Eocene are larger than *Y. huheboerhensis* and are higher crowned. *Yuomys magnus* is the largest species in the late middle Eocene, but it is slightly smaller than *Y. robustus*, and its crown is also distinctly lower than the latter. Furthermore, the proposed late Eocene *Y. robustus* is the youngest species and has the highest tooth crown.

Most physiological and life-historical traits are associated with body mass in mammal species, including lifespan, metabolic rate, diet, developmental rate, fecundity, interspecific relations, locomotion, etc. (Schmidt-Nielsen, 1984; Peters, 1986; Calder, 1996, 2001). So, it is essential to reconstruct the body mass of a fossil animal to understand its paleoecology (Hopkins, 2008; Millien and Bovy, 2010; Freudenthal and Martín-Suárez, 2013).

The body mass estimation equations of Freudenthal and Martín-Suárez (2013) are based on the maximum length of upper or lower tooth rows. Only five specimens from two species of *Yuomys* preserve complete tooth rows: including IVPP V4796.1–4 of *Y. cavioides* and IVPP V5308 of *Y. eleganes*. The estimated body mass of *Y. cavioides* ranges from 571–693 g, whereas that of *Y. eleganes* is about 485 g (Table S3). Because the tooth rows of the whole specimens recognized as documenting *Y. robustus* are incompletely preserved, we cannot directly calculate their body masses, and need to estimate their tooth rows length first. Based on the measurements of all complete tooth rows length, we assume

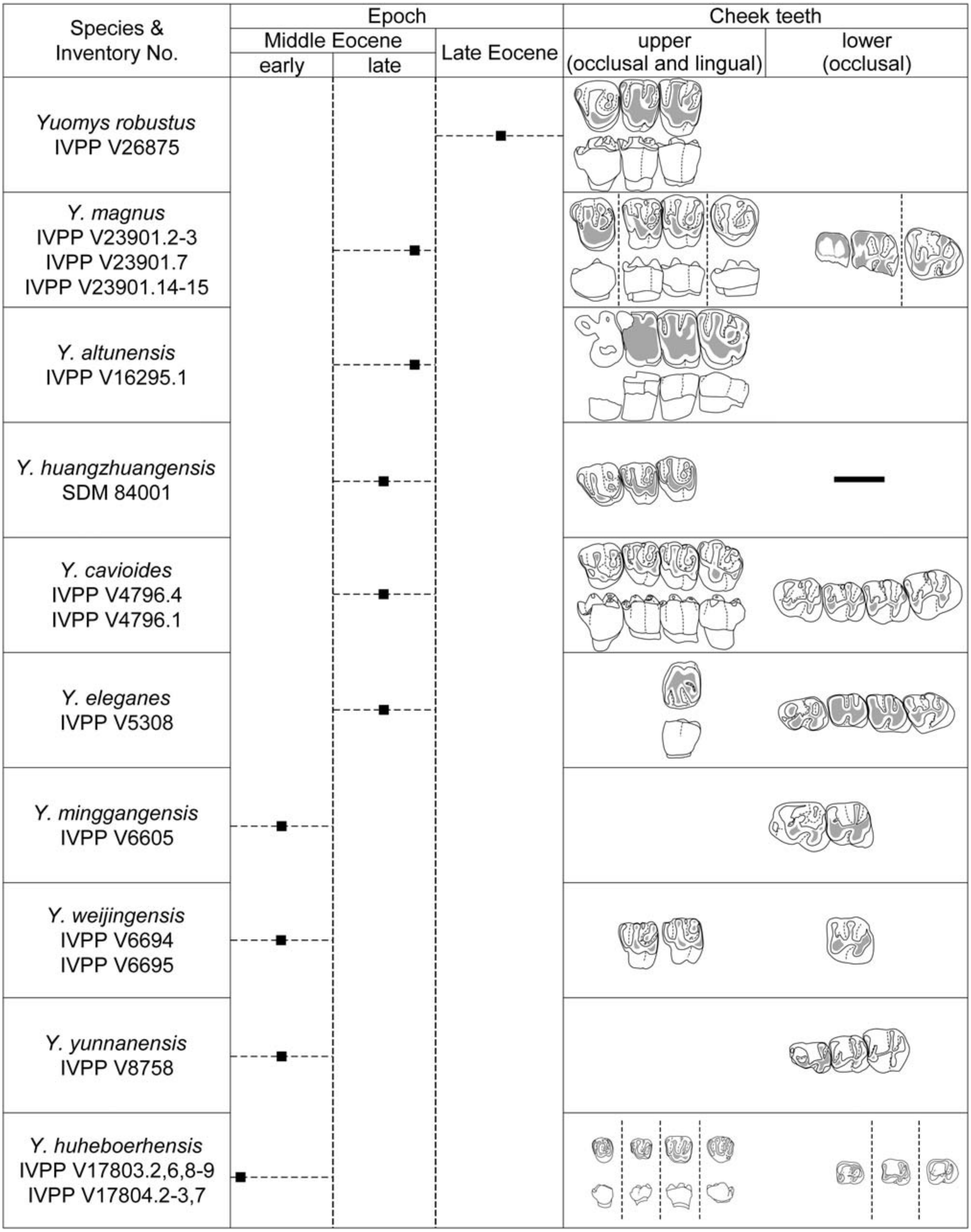

FIGURE 3. Hypothesized biostratigraphic distribution of the 10 species of *Yuomys* and the morphological evolutionary trend of their cheek teeth. Scale bar equals 5 mm.

that the ratio of P4–M2 length/P4–M3 length has no dramatic change during the evolution of *Yuomys*. The average ratio of P4–M2 length/P4–M3 length of the IVPP V4796.3–4 (*Y. cavioides*) is 0.72. Using this value, we estimated the 'complete' tooth row lengths of the two specimens of *Y. robustus*, which are 17.93 mm for the holotype IVPP V26875 and 17.95 mm for the IVPP V4802 (right upper). As a result, the body mass of *Y. robustus* is estimated around 880 g, and as such is significantly heavier than those of *Y. cavioides* and *Y. eleganes* (Table S3). Due to the paucity of complete tooth rows, we did not conduct further body mass estimations for the other species of *Yuomys*. Compared with those of some extant rodents, the estimated body masses of *Y. cavioides*, *Y. eleganes*, and *Y. robustus* range between zokor *Myospalax* (225–314 g) and giant squirrel *Ratufa* (875–3,000 g) (Fig. S7).

From these observations, it appears that from the middle Eocene to the late Eocene, *Yuomys* has a trend of increasing tooth size, tooth crown height, and correlated body mass, which is congruent with hypotheses previously advocated by Wang (2017) and Li (2017).

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