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日本九州西部赤崎组和中甑组始新世哺乳动物:初步结果及其与亚洲陆相哺乳动物分期的对比

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摘要:日本已知时代最早的古近纪哺乳动物化石产自九州西部熊本县天草(Amakusa)地区始新世地层赤崎(Akasaki)组以及鹿儿岛县甑岛(Koshiki Islands)相当层位的中甑(Nakakoshiki)组。初步研究显示这两个组产出的哺乳动物分异度较高,包括9个目的至少18种动物。赤崎动物群有3种trogosine裂齿类、2种冠齿兽科全齿类、1种等脊貘科奇蹄类、2种dichobunoid偶蹄类、1种下齿兽科踝节类、1种西瓦兔猴科灵长类、1种未定食虫类以及2种可能的梳趾鼠类。中甑动物群包括1种冠齿兽科全齿类、2种小型雷兽科奇蹄类、1种高冠的下齿兽科踝节类、2种啮齿类和1种细齿兽科食肉类。这两个日本哺乳动物组合很接近早-中始新世界线。由于出现了trogosine裂齿类和雷兽,它们的时代要晚于伯姆巴动物群,极有可能与亚洲大陆阿山头期哺乳动物群相当。这两个动物群还包含了在亚洲大陆没有发现过的几个新种,并具有独特的哺乳动物组合。

关键词:日本九州,始新世,阿山头期,赤崎组,中甑组,哺乳动物

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EOCENE MAMMALS FROM THE AKASAKI AND NAKAKOSHIKI FORMATIONS, WESTERN KYUSHU, JAPAN: PRELIMINARY WORK AND CORRELATION WITH ASIAN LAND MAMMAL AGES

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Abstract The earliest known Paleogene mammals from Japan are reported from the Eocene Akasaki Formation, Amakusa area, Kumamoto Prefecture and from the stratigraphically equivalent Nakakoshiki Formation, Koshiki Islands, Kagoshima Prefecture, western Kyushu. Preliminary work has revealed a high diversity of mammals from these formations, including at least 18 different species from nine orders. The Akasaki fauna is represented by three trogosine tillodonts, two coryphodontid pantodonts, an isectolophid perissodactyl, two dichobunoid artiodactyls, a hyopsodontid condylarth, a sivaladapid primate, an unidentified insectivoran, and two possible ctenodactyloid rodents. The mammal fauna from the Nakakoshiki Formation includes a coryphodontid pantodont, two small brontotheriid perissodactyls, a hypsodont hyopsodontid condylarth, two rodents, and a miacid carnivoran. These Japanese mammal assemblages are from near the Early/Middle Eocene boundary, which is previously poorly known in Asia. Given the occurrences of trogosine tillodonts and brontotheriid perissodactyls, the Akasaki and Nakakoshiki faunas are younger than Bumbanian faunas and are most likely correlated with Arshantan faunas on the Asian mainland. The Japanese faunas contain several new taxa unknown from the Asian mainland, and there are unique faunal combinations in the mammal assemblages.

Key words Kyushu, Japan; Eocene; Arshantan; Akasaki Formation; Nakakoshiki Formation; mammals

1 Introduction

Paleogene land mammals in Japan have been described sporadically since the first report of an Oligocene anthracotheriid artiodactyl, "*Brachyodus*" *japonicus* Matsumoto (Tokunaga, 1925). However, Paleogene mammal fossils from Japan are never abundant (Appendix 1), and field work aimed at improving the Paleogene record of Japanese mammals has been intermittent. In most cases, a rock unit has yielded a single or a few remains of one or two species, making it difficult to evaluate the biostratigraphic and biogeographic significance of such small samples. Among the known Paleogene mammal-bearing formations, the Eocene Akasaki Formation in Amakusa area, Kumamoto Prefecture and the coeval Nakakoshiki Formation in the Koshiki Islands, Kagoshima Prefecture, have produced the most diversified and oldest known Cenozoic faunas in Japan. The two formations represent the basal part of the Paleogene sequence in western Kyushu.

One of us (K. Miyata) has investigated the stratigraphy and paleontology of the Akasaki and Nakakoshiki formations since 1992. The first mammal fossil from the Akasaki Formation was discovered at Akase-machi (Akase Town), Uto City, Kumamoto Prefecture in 1993, and it was described as a unique trogosine tillodont, *Higotherium hypsodon* Miyata & Tomida, 1998a. Later, seven specimens belonging to four orders (Tillodontia, Pantodonta, Perissodactyla, and Rodentia) were reported from the Akasaki Formation (Miyata and Tomida, 1998b). From the Nakakoshiki Formation, remains of mammals, including a coryphodontid pantodont and two brontotheriid perissodactyls, were found in 1999 (Miyata, 2003; Miyata and Tomida, 2003). Pending formal description of most of the fossil mammals from the Akasaki and Nakakoshiki formations, this paper discusses the biochronological significance of these faunas with respect to the established sequence of Asian Land Mammal Ages.

2 Geological setting

The Akasaki Formation (approximately 70~400 m in thickness) is distributed in the Amakusa area in the western part of Kumamoto Prefecture, while the Nakakoshiki Formation (approximately 890 m in thickness) outcrops on Kamikoshiki Island, which is part of the Koshiki Islands in the northwestern part of Kagoshima Prefecture, western Kyushu, Japan (Fig. 1). The fossiliferous horizons are concentrated in the upper and middle parts of the Akasaki Formation and in the middle part of the Nakakoshiki Formation. Both formations are basal units of the Eocene sequence unconformably overlying the Cretaceous Himenoura Group.

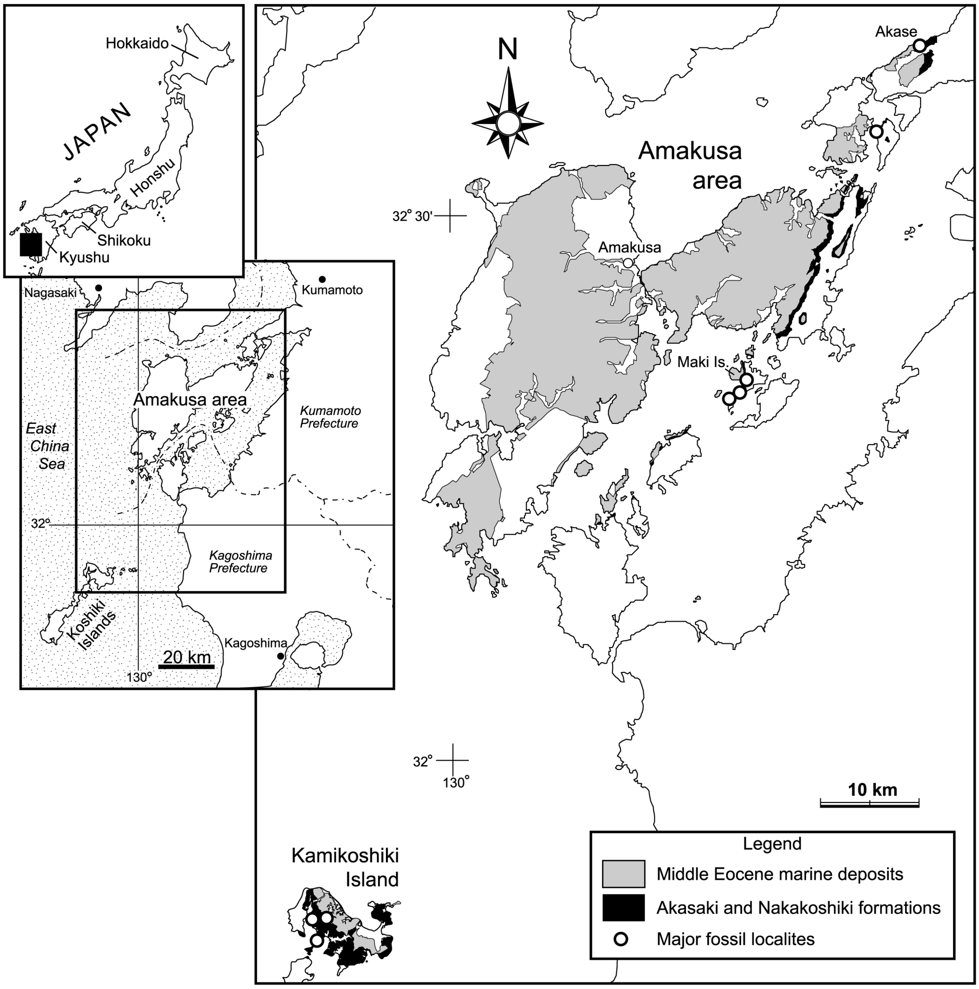

Fig. 1　Map showing the major fossil localities in the Amakusa area, Kumamoto Prefecture, and Kamikoshiki Island, Kagoshima Prefecture, western Kyushu, Japan

The Akasaki Formation comprises fluvial deposits consisting mainly of conglomerate, red siltstone, and gray-blue siltstone. The Akasaki Formation is constrained to be no younger than early Middle Eocene on the basis of overlying marine strata, the Fukuregi and Shiratake formations (Fig. 2), both of which bear various molluscan fossils and large foraminifera, *Nummulites* and *Discocyclina* (Hanzawa and Urata, 1964; Miki, 1975; Miyata and Tomida, 1998a). The Fukuregi Formation and the stratigraphically higher Kyoragi (Kyouragi) Formation (= Shikiyama Formation in Okada, 1992) have yielded early Middle Eocene nannofossils pertaining to the Cp 13a subzone (approximately 47.3 ~46.1 Ma in Berggren et al., 1995; approximately 46.6 ~ 45.0 Ma in Luterbacher et al., 2004) (Okada, 1992). Aside from these stratigraphic constraints, there is no direct chronological evidence bearing on the age of the Akasaki Formation and the length of the hiatus between the Akasaki Formation and the overlying marine strata (the Fukuregi and Shiratake formations).

Miyata (2007) suggested that the age of the Akasaki Formation potentially could extend from the late Early to early Middle Eocene based on the paleomagnetic data provided by Miki and Matsueda (1985). The paleomagnetic results of Miki and Matsueda (1985) indicate that

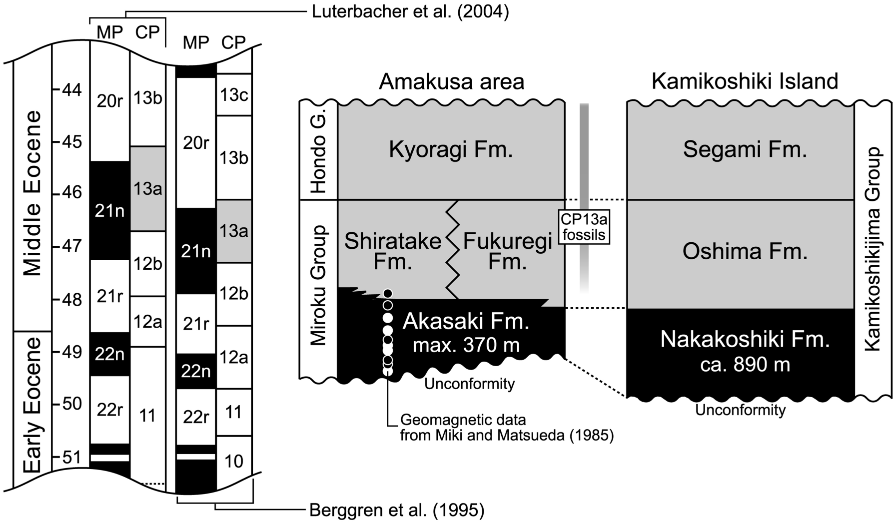

Fig. 2 Simplified stratigraphic correlation of the Eocene strata discussed in the text and standard global chronostratigraphic scales (Berggren et al., 1995; Luterbacher et al., 2004) showing the magnetic polarities (MP) and the interval of Cp 13a subzone

the Akasaki Formation preserves three magnetozones (Fig. 2). Because the Cp 13a subzone correlates with the normal interval of Chron 21 (Fig. 2; Berggren et al., 1995; Luterbacher et al., 2004), the Akasaki Formation is potentially correlated with the older geomagnetic intervals of Chrons 21 and 22, assuming that the results of Miki and Matsueda (1985) are reliable. Ishikawa (1997) recognized strata exhibiting stable reversed polarity from red beds of the Akasaki Formation, but he interpreted this as secondary chemical remanences based on a hypothetical derivational model of hematite in the red beds proposed by Miki and Matsueda (1985). Nevertheless, we hypothesize that the Akasaki Formation probably has preserved primarily reversed polarities in several red beds based on preliminary geomagnetic tests, and we further confirmed the presence of stable reversed polarities from red beds of the Nakakoshiki Formation, supporting a coeval relationship between the two formations.

The Nakakoshiki Formation, the basal part of the Paleogene Kamikoshikijima Group, primarily consists of conglomerate, sandstone, red, gray-blue, and brown mudstone. The Nakakoshiki Formation consists of fluvial deposits, whereas the overlying Oshima and Segami formations are shallow and offshore marine deposits, respectively (Inoue et al., 1979, 1982). Although the geological age of the Kamikoshikijima Group is unclear, Inoue et al. (1982) concluded that these rock strata represent a southwestern extension of the Eocene sedimentary basin in the Amakusa area. Inoue and his colleagues proposed that the Nakakoshiki, Oshima, and Segami formations are stratigraphically correlated with the Akasaki, Shiratake (plus Fukuregi), and Kyoragi formations in the Amakusa area, respectively (Fig. 2; Inoue et al., 1982). Toshimitsu et al. (2004), however, reported fission-track dates indicating 39.2 ± 2.5 and 36.4 ± 3.2 Ma from two different tuff beds in the Nakakoshiki Formation. These radioisotopic dates are somewhat younger than the ages expected based on the stratigraphic relationships mentioned above (Toshimitsu et al., 2004) and from the mammal fossils from the Nakakoshiki Formation. We assume that the Akasaki and Nakakoshiki formations are roughly contemporaneous strata dating near the Early/Middle Eocene boundary, although further geochronological evidence pertaining to these two mammal-bearing formations is needed.

3 Faunal elements

Based on our preliminary work, we have recognized a high diversity of mammals from the Akasaki and Nakakoshiki formations, consisting of at least 18 different species from nine orders (Table 1; Figs. 3, 4). Brief comments are summarized below, pending more detailed study, but precise locality data are omitted.

Table 1 Tentative list of mammal taxa from the Akasaki and Nakakoshiki formations

Akasaki Formation	Nakakoshiki Formation
Tillodontia, Esthonychidae, Trogosinae	
Higotherium hypsodon	
Trogosus cf. *T. latidens*	
Cf. *Trogosus* sp.	
Pantodonta, Coryphodontidae	
Gen. et sp. nov.	Gen. et sp. indet.
Asiocoryphodon sp.	
Condylarthra, Hyopsodontidae	
Hyopsodus sp. nov. A	*Hyopsodus* sp. nov. B
Perissodactyla, Isectolophidae	Brontotheriidae
Isectolophus sp. nov.	Gen. et sp. nov. A
	Gen. et sp. nov. B
Artiodactyla, Dichobunoidea	
Gen. et sp. nov. A (large)	
Gen. et sp. nov. B (small)	
Primate, Sivaladapidae	
Gen. et sp. nov.	
Rodentia, Ctenodactyloidea	
Gen. et sp. indet. A	Gen. et sp. indet. C
Gen. et sp. indet. B	Gen. et sp. indet. D
Insectivora	
Gen. et sp. indet.	
Carnivora, Miacidae	
	Gen. et sp. indet.

Tillodontia Three tillodonts belonging to the subfamily Trogosinae Gazin, 1953 have been formally described from the Akasaki Formation (Miyata and Tomida, 1998a,c; Miyata, 2007). The derived trogosine *Higotherium hypsodon*, represented by a right mandibular fragment with hypsodont m2-3 (Fig. 3A), and cf. *Trogosus* sp., documented by seven fragmentary teeth, were recovered from the uppermost part of the formation. A large species of *Trogosus* (Fig. 3B, *Trogosus* cf. *T. latidens*), described from the middle part of the formation, is represented by 12 teeth including brachydont molars, mandibular fragments, and cervical vertebrae (Miyata, 2007). These three trogosines from the Akasaki Formation can be readily distinguished from the smaller trogosine *Kuanchuanius* and the enigmatic *Chungchienia* from the Middle Eocene of China.

Pantodonta Coryphodontid specimens have been reported from the middle parts of both the Akasaki and Nakakoshiki formations (Miyata and Tomida, 1998b; Miyata, 2003; Miyata and Tomida, 2004, 2005; Miyata et al., 2006). One of the two Akasaki species (gen. et sp. nov.) is represented by the skull and mandible of a single juvenile individual and an adult mandible (Fig. 3C, D). It is a derived species with bilophodont, hypsodont molars differing from all known Asian coryphodontids; its dental structure suggests a closer affinity with Arshantan *Heterocoryphodon* or *Eudinoceras* than with Bumbanian *Wutucoryphodon* (Miyata and Tomida, 2005; Miyata et al., 2006). Another Akasaki species represented by a mandibular frag-

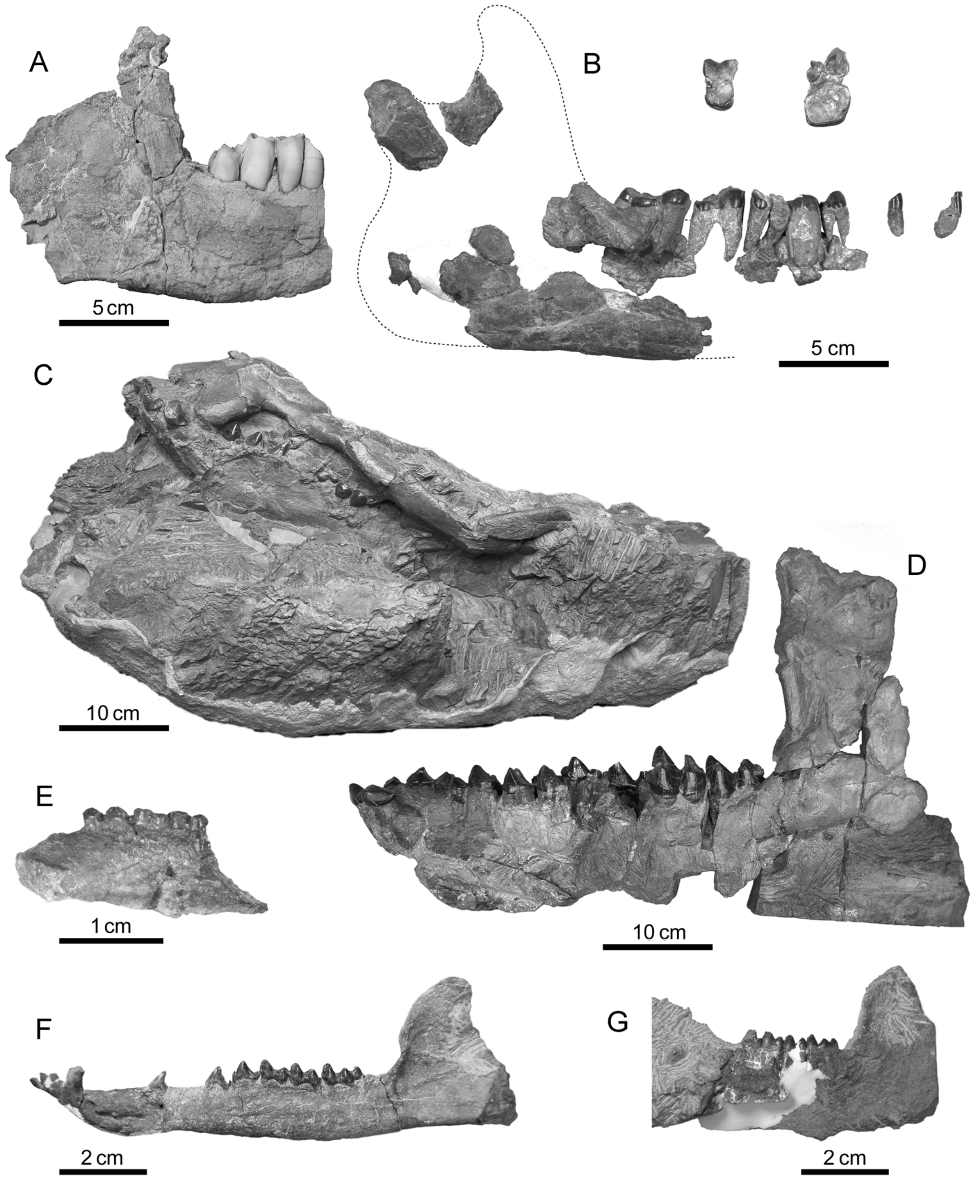

Fig. 3 Selected mammal specimens from the Akasaki Formation

A. right mandibular fragment with m2-3 of *Higotherium hypsodon* Miyata & Tomida, 1998a, lateral view; B. fragments of the right mandible and upper (right P4, M2, occlusal view) and lower teeth (left i1, lingual view; right i3, p3-m3, lateral view) of *Trogosus* cf. *T. latidens* described by Miyata (2007); C-D. juvenile skull with mandible in matrix (C) and adult mandible (D) of an unnamed hypsodont coryphodontid gen. et sp. nov., lateral view; E. right mandibular fragment with p3-m2 of *Hyopsodus* sp. nov. A, lingual view; F. left mandible of an unnamed dichobunoid gen. et sp. nov. A (large species), lateral view; G. right mandibular fragment with matrix of an unnamed dichobunoid gen. et sp. nov. B (small species), lingual view

ment with p3-m1 is a smaller species of *Asiocoryphodon*. These two coryphodontid species were recovered from nearly the same horizon of the Akasaki Formation on Makishima (Maki Island), Goshoura Town, Amakusa City (Fig. 1). A coryphodontid specimen from the Nakakoshiki Formation includes a posterior lower premolar and an anterior lower molar, which resemble those of large and hypsodont taxa such as *Heterocoryphodon* or *Eudinoceras*.

Condylarthra Two species of hyopsodontid condylarths, which likely belong to *Hyopsodus*, have been recognized (Miyata and Tomida, 2004). The Akasaki *Hyopsodus* is represented by a right mandibular fragment with p3-m2 from the upper part of the formation (Fig. 3E); the mandible is robust, and the cheek teeth are brachydont with a clear enamel fold on the p4 trigonid. Another species is known from two right mandibles with p4-m3 and m2-3, which were found in the middle part of the Nakakoshiki Formation (Fig. 4A). The Nakakoshiki *Hyopsodus* has hypsodont molars with stronger entoconid and hypoconulid than in the Akasaki species.

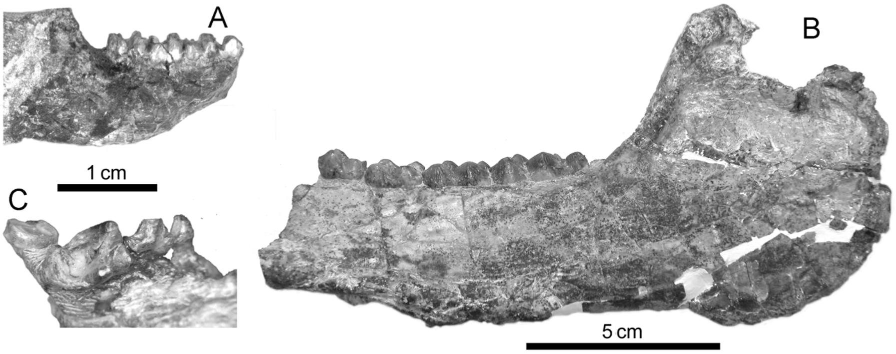

Fig. 4 Selected mammal specimens from the Nakakoshiki Formation
A. incomplete right mandible with p4-m3 of *Hyopsodus* sp. nov. B, lateral view; B. incomplete left mandible with p4-m3 of an unnamed *Eotitanops*-like brontotheriid gen. et sp. nov. A, lateral view; C. left p3-m2 of an unnamed miacid carnivoran gen. et sp. indet., lingual view

Three or four *Hyopsodus* species were previously described from Early Eocene strata in Mongolia and Early and Middle Eocene strata in China (Dashzeveg, 1977; Tong, 1989a; Huang, 1995; Kondrashov and Agadjanian, 1999). The Akasaki and Nakakoshiki *Hyopsodus* are relatively large species differing from the Bumbanian *H. orientalis* and are more similar in size to *H. fangxianensis* from the Early Eocene or *H. huashigouensis* from the Middle Eocene of China.

Perissodactyla Two upper molars of a small isectolophid, comparable in size to *Orientolophus*, were previously reported from the middle part of the Akasaki Formation (Miyata and Tomida, 1998b). Some additional dental material of the same individual was recently recovered, demonstrating that the Akasaki isectolophid is clearly distinguishable from all known species of Early Eocene *Orientolophus*, *Homogalax*, and *Chowliia*. It possibly represents a new species of Middle Eocene *Isectolophus*, although Bowen et al. (2002) and Tsubamoto et al. (2004) listed it as "cf. *Orientolophus hengdongensis*" without taxonomic justification.

Two small brontotheriid specimens were recovered from different levels of the middle part of the Nakakoshiki Formation (Miyata and Tomida, 2003). One specimen (gen. et sp. nov. A) is represented by a left mandible with p4-m3 (Fig. 4B) and several postcranial elements including atlas, ulna, femur, and scapulae. The length of the lower molar series indicates that it is a smaller brontothere than *Microtitan* and *Pygmaetitan* from Asia, being comparable in size to *Eotitanops* of early Bridgerian age in North America. The other specimen (gen. et sp. nov. B) is represented by an isolated left P4 that was recovered from a stratigraphic level about 300 m higher than that of the mandible mentioned above. The P4 is larger than that of *Eotitanops* and differs morphologically from those of *Microtitan*, *Pygmaetitan*, and *Nanotitanops*; it resembles that of small species of *Palaeosyops* from the Bridgerian of North America.

Artiodactyla Two possible dichobunoid species were recognized from the upper part of the Akasaki Formation (Miyata and Tomida, 2004). One is represented by the upper cheek tooth series, left mandible with nearly complete dentition, and some postcranial material. The mandible has long diastemata between the canine and p3 as in the Irdinmanhan *Gobiohyus* (Fig. 3F), but the upper dental characters differ from those of all known Asian artiodactyls. The second taxon is a smaller species (25 percent smaller in tooth dimension) known from a right mandibular fragment with p4 to m3 (Fig. 3G).

Primates An isolated, lower molariform tooth from the upper part of the Akasaki Formation is a right m1 or m2 of a sivaladapid primate, which belongs to a new genus and new species. It is the earliest record of the family.

Rodentia, Insectivora, and Carnivora Rodent, insectivoran, and carnivoran specimens remain unprepared, but these specimens will eventually become important for clarifying the biochronological framework. The rodent specimens were recovered from the upper and middle parts of the Akasaki Formation and the middle part of the Nakakoshiki Formation. Most of the rodent specimens are isolated molariform teeth, that clearly belong to four different species including two ctenodactyloids. An insectivoran specimen consisting of a mandibular fragment with p3-m1 was recovered from the uppermost part of the Akasaki Formation. A miacid carnivoran specimen from the middle part of the Nakakoshiki Formation includes a lower canine and left p3-m2 (Fig. 4C).

4 Discussion

In East Asia, various modern mammalian orders appeared in the Early Eocene Bumbanian, and this was followed by a period of perissodactyl dominance in the subsequent Arshantan (Meng and McKenna, 1998). The perissodactyl families that are abundant in Arshantan faunas include Brontotheriidae, Hyracodontidae, Rhinocerotidae, and Deperetellidae (Fig. 5; Meng and McKenna, 1998). The Arshantan has traditionally been correlated to the North American Bridgerian land mammal age (e. g., Li and Ting, 1983; Tong, 1989b; Tong et al., 1995), and both of these ages have been considered to extend from the late Early to the early Middle Eocene (Luterbacher et al., 2004; Woodburne, 2004). However, independent chronological evidence constraining the age of early Paleogene faunas in Asia is sparse (Wang et al., 2007). In fact, there seems to be almost no chronological data constraining the Bumbanian/Arshantan and Arshantan/Irdinmanhan boundaries aside from the recent magnetostratigraphic data from early Paleogene strata in the Erlian Basin, Nei Mongol, China (Wang et al., 2009, 2010). According to Sun et al. (2009), the Arshanto Formation in the Erlian Basin probably correlates with the reversed interval of Chron 21 and older geomagnetic intervals, supporting the idea that the Arshanto Formation traverses the Early/Middle Eocene boundary (Wang et al., 2009, 2010).

Further fossils and associated chronological data from the Akasaki and Nakakoshiki formations are required to clarify the position of the mammalian faunal samples from these formations with respect to Asian Land Mammal Ages. However, considering the available paleomagnetic data from the Akasaki Formation and the stratigraphic superposition of marine strata bearing Cp13a nannofossils mentioned before, the age of the Akasaki and Nakakoshiki faunas can be placed near the Early/Middle Eocene boundary. This correlation suggests that the Japanese faunas are contemporary with early Bridgerian faunas in North America and Arshantan faunas in the Asian mainland. Given the occurrences of trogosine tillodonts and brontotheriid perissodactyls, the Akasaki and Nakakoshiki mammal faunas are apparently younger than Bumbanian faunas and most likely correlate with the Arshantan age, although the Japanese faunas lack the perissodactyl dominance that seems to characterize Arshantan faunas in China and Mongolia (Miyata and Tomida, 2004). Several new taxa documented in the Japanese faunas enhance our under-

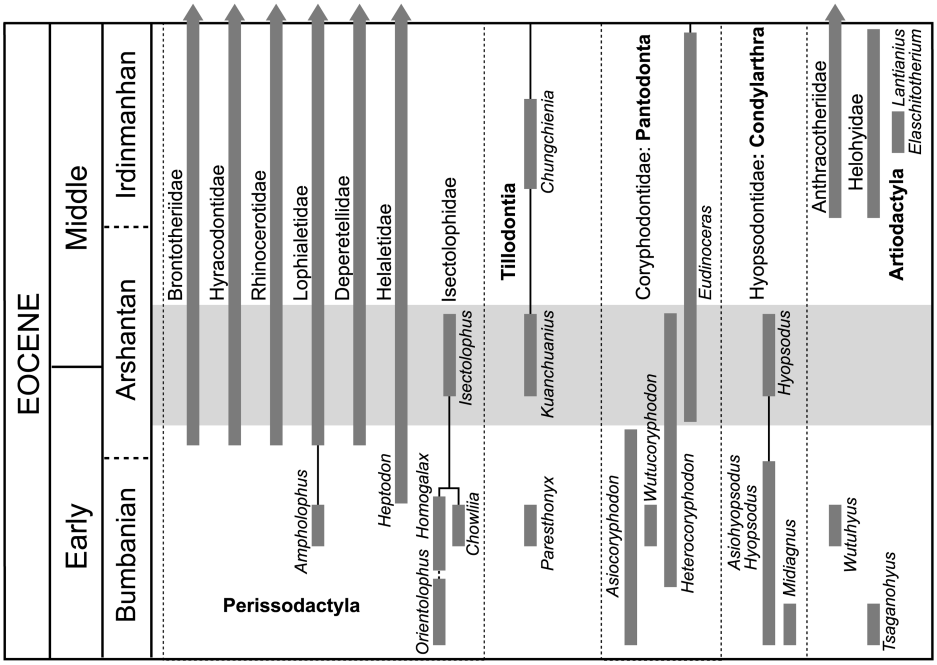

Fig. 5 Temporal distributions of Early and Middle Eocene herbivorous mammals (tillodonts, coryphodontid pantodonts, hyopsodontid condylarths, perissodactyls, and artiodactyls) from China and Mongolia, that are related to Japanese taxa discussed here

The distributions are derived from Tong (1989b), Lucas (1998, 2004), Meng and McKenna (1998), Ting (1998), Tong and Wang (1998, 2006), Bowen et al. (2002), Kondrashov (2004), Kondrashov et al. (2004), and Métais et al. (2004). Light gray area shows the preferred chronological and biostratigraphic zone related to the mammal taxa from the Akasaki and Nakakoshiki formations

standing of East Asian mammalian assemblages of this age. Artiodactyls and hyopsodontid condylarths are very rare elements in Arshantan assemblages on the Asian mainland. The Japanese faunas apparently sample a more coastal habitat or biome that differed appreciably from those which yield typical Arshantan assemblages from the Asian mainland.

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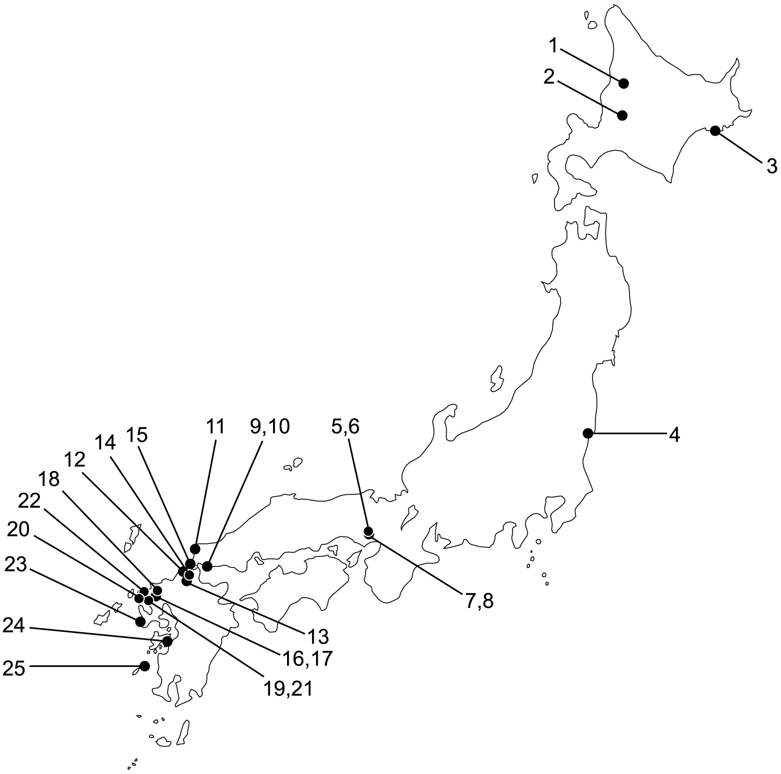
Appendix List and locality map of Paleogene land mammals in Japan with references

List: Asterisk (*) indicates undescribed specimen; Obelisk (†) means specimens from more than two individuals. The age is based on a current geochronology (Luterbacher et al., 2004) and recent references regarding the age of fossils.

No.	Taxa (or specimen)		Formation and Group	Age	Locality	Reference
1	Perissodactyla	*Amynodon watanabei* (Tokunaga, 1926)	Showa Fm. [38] or Itarakaomappu Fm. [56] , Uryu G.	late Middle or Late Eocene	Numata-cho (Uryu Coalfield) , Uryu-gun, Hokkaido	[40, 41] ; age: [56]
2	Perissodactyla	*Plesiocolopirus grangeri* (Tokunaga, 1933a) *	unknown, probably Ishikari G.	probably middle or late Middle Eocene	Miruto, Iwamizawa City, Hokkaido	[7] ; age: [43, 44]
3	Perissodactyla	*Plesiocolopirus kushiroensis* (Tomida, 1983)	Tenneru Fm., Urahoro G.	late Middle Eocene	Kushiro-cho, Kushiro-gun, Hokkaido	[50, 52] ; age: [16, 21]
4	Artiodactyla	*Entelodon* sp. cf. *E. orientalis* Dashzeveg, 1965	Iwaki Fm., Shiramizu G.	most likely Late Eocene	Iwasaki Colliery (Joban Coalfield) , Iwaki City, Fukushima	[42, 51] ; age: [9, 10]
5	Artiodactyla	*Bothriodon sandaensis* Tsubamoto, 2007 (in [55])	Yokawa Fm., Kobe G.	latest Middle or Late Eocene	Fujigaoka, Sanda City, Hyogo	[33, 55]
6	Perissodactyla	Cf. *Hyrachyus* sp.				
7	Perissodactyla	*Zaisanamynodon* cf. Z. protheroi Lucas, 2006* †			Akamastsudai, Kita-ku, Kobe City, Hyogo	[32, 33, 55]
8	Perissodactyla	*Zaisanamynodon* cf. Z. protheroi Lucas, 2006*			Kouzudai, Kita-ku, Kobe City, Hyogo	
9	Perissodactyla	*Amynodon watanabei* (Tokunaga, 1926) †	Ube coal-bearing Formation, Ube G.	probably late Middle and Late Eocene	Okinoyama Colliery, Ube City, Yamaguchi	[40, 41, 46, 47] ; age: [8]
10	Perissodactyla	“*Desmatotherium*” *grangeri* Tokunaga, 1933a		Late Eocene		[30, 31, 39] ; age: [8]
11	Artiodactyla	“*Brachyodus*” sp.	Taoyama Fm., Hioki G.	Late Oligocene	Nabeshima, Houhoku-cho Shimonoseki City, Yamaguchi	[24] ; age: [5, 28]
12	Pantodonta	Coryphodontid*	Oyake (Ooyake) Fm, Nogata G.	Middle Eocene	Yoshidome, Munakata City, Fukuoka	[34] ; age: [29]
13	Perissodactyla	Rhinocerotoidea gen. et sp. indet.	Uwaishi Fm., Nogata G.	Middle Eocene	Kamoo, Kama City, Fukuoka	[27] ; age: [29]
14	Perissodactyla	Amynodontidae gen. et sp. indet.	Ideyama Fm., Otsuji G.	Late Eocene or Early Oligocene	Tonno, Nogata City, Fukuoka	[26, 27] ; age: [29]

No.	Taxa (or specimen)		Formation and Group	Age	Locality	Reference
15	Perissodactyla	*Amynodon*? sp. *	Jinnobaru Fm., Ashiya G.	late Early or early Late Oligocene	Umashima (Uma Island) , Kokurakita-ku, Kitakyushu City, Fukuoka	[22] ; age: [20]
16	Perissodactyla	Cf. *Zaisanamynodon borisovi* Belyaeva, 1971	Yoshinotani Fm. Ochi G.	Late Eocene	Tatsukawa Colliery (Imari Coalfield) , Imari City, Saga	[54] ; age: [15, 16, 19, 20]
17	Perissodactyla	“Titanothere gen. et sp. indet. ”*				
18	Perissodactyla	Amynodontid? *	Kishima Fm, Kishima G.	latest Eocene or earliest Oligocene	Kitahatatakeari or Kitahatakamihirano, Karatsu City, Saga	[25] ; age: [20, 29]
19	Artiodactyla	“*Brachyodus*” *japonicus* Matsumoto, 1925 (in [45])	Nakazato Fm., Sasebo G.	likely Early Oligocene	Ikeno Colliery (Hokushou Coalfield) , Sasebo City, Nagasaki	[45] ; age: [19, 35]
20	Artiodactyla	Anthracotheriid (referable to “*B.* ” *japonicus*) *	Fukui Fm., Sasebo G.	Late Oligocene	Kosaza-cho, Sasebo City, Nagasaki	[14] , Kato T (per. comm.) ; age: [19]
21	Rodentia	*Steneofiber* sp.			Yoshii-cho, Sasebo City, Nagasaki	[12, 13] ; age: [19]
22	Artiodactyla	Bovidae gen. et sp. indet. *	Kase Fm., Sasebo G. (Kato T, per. comm.)	latest Oligocene or earliest Miocene	Shisa-cho, Matsuura City, Nagasaki (Kato T, per. comm.)	[11, 36] , Kato T (per. comm.) ; age: [35]
23	Unknown	Mammalian humeral remain, previously referred to hadrosaurid *Nipponosaurus**	likely Kouyagi Fm., Akasaki G. (Miyata K, pers. observ.)	perhaps early Middle Eocene	Takashima (Takashima Colliery) , Nagasaki City, Nagasaki	[6, 23] ; age: [20]
24		See Table 1	Akasaki Fm., Miroku G.	late Early and/or early Middle Eocene	Amakusa area, Kumamoto	See Geological setting section
25		See Table 1	Nakakoshiki Fm., Kamikoshiki G.	late Early and/or early Middle Eocene	Kamikoshikijima (Kamikoshiki Island) , Satsumasendai City, Kagoshima	See Geological setting section

The taxonomic status of “*Brachyodus*” specimens (“*Brachyodus*” sp., no. 11; “*B.*” *japonicus*, no. 19 in the list) and “*Desmatotherium*” *grangeri* (no. 10 in the list, see also Tokunaga, 1933a, b; Takai, 1944) are debatable. Dineur (1982) and Ducrocq and Lihoreau (2006) proposed that the “*Brachyodus*” specimens from Japan are “very probably” referable to the genus *Elomeryx*, whereas Kato (1997) and Kato and Otsuka (1999) noted that “*B.*” *japonicus* is probably assignable to the genus *Bothriodon*. Takai (1944) described the “*D.*” *grangeri* specimen consisting right p2, p4, and a fragment of m1 from the Ube Group, Yamaguchi Prefecture. Later, Russell and Zhai (1987) listed it as “*Colodon?*” *grangeri* based on the taxonomic comments of Radinsky (1965) for the holotype and referred specimens of “*D.*” *grangeri* from the Hosan Coalfield, North Korea (Democratic People's Republic of Korea). “*Desmatotherium*” *grangeri* or “*Colodon?*” *grangeri* from North Korea is reassigned to the genus *Plesiocolopirus* Schoch, 1989 by Tomida and Li (2004). However, Radinsky (1965) and later other workers have not examined the “*D.*” *grangeri* specimen from Ube Group directly (probably missing) and not clarified its taxonomic status; thus, we retain it here as problematic “*Desmatotherium*” *grangeri*. On the other hand, Iihoshi and Nakaya (2010) recently reported a tapiroid specimen probably referable to *Plesiocolopirus grangeri* (Tokunaga, 1933) from Hokkaido (no. 2 in the list); their assignment is based on the comparison and the similarity with the North Korean *P. grangeri*.



Locality map: the numbers (1–25) correspond to those of the list

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