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Taxonomic revision of lower Miocene pecorans (Mammalia, Artiodactyla) from Japan, with a new fossil record of stem Cervidae

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Taxonomic revision of lower Miocene pecorans (Mammalia, Artiodactyla) from Japan, with a new fossil record of stem Cervidae

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Abstract. The origin and early dispersion of crown groups (e.g. Cervidae and Bovidae) in pecorans are traced back to the late Oligocene or early Miocene in Eurasia. The fossil pecorans from the lower Miocene of Japan are highly fragmentary but form evidence of a zoogeographic connection between Japan and the Eurasian continent during this period. In this study, we described dental fossils (seven specimens) from five Burdigalian formations (Nakamura Fm. ~18.5 Ma; Hiramaki Fm. ~18 Ma; Misawa Fm. and Kitatage/Asakawa Fm. ~17 Ma; Kunimi Fm. ~16 Ma), and as a result of taxonomic revision we recognized four species, including a basal species of Cervidae, *Dicrocerus*? *tokunagai*, cf. *Palaeomeryx minoensis*, and *Amphimoschus* sp. These species have the basic occlusal patterns of cheek teeth inherited from primitive pecorans (e.g. *Amphitragulus*), but each species displays advanced characteristics, such as full selenodonty, a weak/no external postprotocristid, and a bicuspidate third lobe of m3 (*Amphimoschus*). The early group of crown pecorans composed of basal cervids (Lagomerycinae or

Procervulinae), *Palaeomeryx s.l.*, and *Amphimoschus*, had dispersed widely in Europe (early Orleanian or MN3) and East Asia (Shanwangian), including Japan. Our findings on the Japanese fossil records demonstrate that the dispersion of a basal cervid and palaeomerycid between Japan and the Eurasian continent had been completed before 18 Ma. Further studies with additional material would reveal detailed taxonomic relationships and evolutionary process of the Japanese pecorans in the Burdigalian.

Key words: *Amphimoschus*, *Amphitragulus*, Asia, Burdigalian, *Dicrocerus*, Neogene, *Palaeomeryx*, Ruminantia

Introduction

The Japanese archipelago began to be isolated from the Eurasian continent with the opening of the Sea of Japan, during the late Oligocene or early Miocene (e.g. Otofuji *et al*., 1985; Kano *et al*., 1991; Tamaki *et al*., 1992). Studies of this event have been focused primarily on structural geology and paleomagnetism so far (e.g. Hoshi, 2018; Nakajima, 2018), but it also attracted the attention of paleontologists of terrestrial mammals recently (e.g. Kimura *et al*., 2019; Handa, 2020). Such fossil records of terrestrial mammals are valuable as they allow us to discuss the faunal interchange of Far East Asia during the incomplete isolation of the Japanese archipelago.

One of the most important mammalian fossil assemblage concerning this event has been found in the lower Miocene part of the lower to middle Miocene Mizunami Group distributed across the Kani and Mizunami basins in central Japan (Kamei and Okazaki, 1974; Okazaki, 1977; Tomida *et al*., 2013). The fossil assemblages from these basins include a soricomorph (Oshima *et al*., 2017), rodents (Tomida *et al*., 1995; Tomida, 2011; Mörs and Tomida, 2018), a lagomorph (Tomida, 2012), perissodactyls (Qiu *et al*., 1991; Miyata and Tomida, 2010; Fukuchi and Kawai, 2011), artiodactyls (Matsumoto, 1918), and proboscideans (Matsumoto, 1924, 1926; Tassy, 1994, 1996), which consistently support a close faunal connection between Japan and the Eurasian continent. On the other hand, recent findings of small mammals indicated partial geographic isolation of the eastern margin of East Asia, including Japan, during the early Miocene (Mörs *et al*., 2016; Kimura *et al*., 2019).

In this study, we focus on Japanese lower Miocene pecorans (Ruminantia, Artiodactyla), which are still questionable taxonomically (Tomida *et al*., 2013; Nishioka and Ando, 2016; Nishioka *et al*., 2016). Body fossils of Miocene pecorans have been reported mainly on Honshu Island (Table 1 and Figure 1). Early Japanese paleontologists recognized two deer-like pecorans, *Amphitragulus minoensis* Matsumoto, 1918 and *Dicrocerus tokunagai* Matsumoto, 1927, and their identification spread widely, but there has been no reassessment to date. Before the 21st century, many Oligo-Miocene pecorans from Eurasia were tentatively regarded as species of the genus *Amphitragulus* or *Palaeomeryx* (e.g. McKenna and Bell, 1997), but later studies based on cranial morphology split up the genera more (Gentry *et al*., 1999; Rössner and Rummel, 2001; Prothero, 2007; Rössner, 2010; Mennecart, 2012; Mennecart *et al*., 2012). All fossils of the Japanese lower Miocene pecorans should be re-examined with reference to current paleontological knowledge and taxonomically updated materials. Here, we report new pecoran fossils from the lower Miocene of the Mizunami Group in central Japan, and provide a taxonomic and stratigraphic review on the Japanese lower Miocene pecorans.

Institutional abbreviations.—BSPG = Bavarian State Collection for Palaeontology and Geology, Munich, Germany; ICM = Iida City Museum, Iida, Japan; FPDM = Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; IGPS = Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai, Japan; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MFM = Mizunami Fossil Museum, Mizunami, Japan; MNHN = National Museum of Natural History, Paris, France; NMB = Natural History Museum, Basel, Switzerland; NMJH, National Museum of Japanese History, Sakura, Japan; NMNS = National Museum of Nature and Science, Tokyo, Japan; SNHM = Shanhai Natural History Museum, Shanhai, China.

Materials and methods

Fossil materials

We examined the dental materials of pecoran fossils from four lower Miocene localities in Japan (#1 Iwaki, #2 Daigo, #5 Kani, and #6 Fukui in Table 1 and Figure 1). Localities #1 Iwaki and #2 Daigo are situated in the northeastern region of Japan, and are known as the fossil localities of *Dicrocerus tokunagai*. NMJH A-636-1-1-9 is a right mandible collected from the Yanokura Formation of the Joban Coal Field in Ishiwaki, Iwaki City, Fukushima Prefecture (Matsumoto, 1927; Naora, 1997). Later studies focusing on diatom biochronology revised the fossil-bearing horizon to the Misawa Formation, Yunagaya Group that is dated around 17 Ma (Suto *et al*., 2005; Yanagisawa, 2011). ICM YH-3412 is an additional specimen of *D. tokunagai* from the bank of Kuzi River, Korofuji, Daigo-cho, Ibaraki Prefecture. Shikama and Ômori (1952) documented that the fossil comes from the conglomeratic sandstone of the lower part of the Asakawa Formation (middle Miocene), which includes a variety of plant fossils. In the current geological viewpoint, however, the outcrop yielding dense plant fossils in this area is the Kitatage Formation directly below the Asakawa Formation. The uppermost part of the Kitatage Formation contains the Osawaguchi Tuff Member (17.3–16.7 Ma by K-Ar dating: Tagiri *et al*., 2008) and preserves fossil footprints of cloven-hoofed animals (Koike *et al*., 2007). These updated data indicate that the fossil-bearing horizons of the localities #1 Iwaki and #2 Daigo correspond stratigraphically to the lower Miocene (*ca.* 17 Ma).

In central Japan, the lower Miocene fossil localities are distributed in the region extending across the southern part of Nagano and Gifu prefectures. The Mizunami

Group in locality #5 Kani, Gifu Prefecture, consists of the Hachiya, Nakamura, and Hiramaki formations, and the pecoran fossils have been recorded from all horizons (Tomida *et al*., 2013; Table 1). In this study, we newly describe two specimens (NMNS PV-20160 and NMNS PV-20161) from the Nakamura Formation in Dota, Kani City, Gifu Prefecture. The Nakamura Formation is distributed widely along the riverside in this area, and its uppermost part is unconfortably overlain by the Hiramaki Formation. The Nakamura Formation is well known for its fossiliferous beds including lower Miocene vertebrate animals and plants (Ina, 1981; Yasuno, 1982; Okumura *et al*., 1977; Tomida *et al*., 1995, 2013; Tomida, 2011; Mörs *et al*., 2016; Nishioka and Ando, 2016; Oshima *et al*., 2017; Mörs and Tomida, 2018; Kimura *et al*., 2019). The cervoid fossils examined by Nishioka and Ando (2016) and in this study were recovered from a tuffaceous muddy sandstone bed, including patchy, pebbly sandstone and pumice, which is situated at four meters below the boundary of the Nakamura and Hiramaki formations (Y. Ando and T. Goda, private communications in 2021). The base of the Hiramaki Formation is characterized by tuff breccia with boulders (*ca*. 18.4 Ma by fission-track dating: Shikano, 2003). A rough estimate of the deposition rate of the Nakamura and Hiramaki formations is 0.01 Ma/meter, judging from the chrono-stratigraphical data by Shikano (2003), and therefore previous studies have considered that there is a narrow difference (0.1 Ma, more or less) between the basal Hiramaki Formation and the fossil-bearing horizon of the upper Nakamura Formation. The same horizon has yielded small mammalian fossils, such as *Minocastor godai* Mörs *et al*., 2016 and *Plesiosorex fejfari* Oshima *et al*., 2017.

We redescribed a right mandible of *Amphitragulus minoensis* Matsumoto, 1918 from the Hiramaki Formation in Banjobora, Kani City, Gifu Prefecture. The sole specimen (holotype) of *A. minoensis* has been lost since then, and currently its plaster cast (IGPS 22059) is available at the Tohoku University Museum. The terrestrial mammalian fossils, such as *Gomphotherium annectens* (Matsumoto, 1924), from the Hiramaki Formation are dated to approximately 18 Ma, based on the stratigraphic and paleomagnetic relationships of the Mizunami Group (Tomida *et al.*, 2013).

FPDM-V-8462 is a right mandible of *Amphitragulus* sp. from the Kunimi Formation (#6) in Koniu, Fukui City, Fukui Prefecture (Takeyama, 1989). This author estimated that the fossil-bearing horizon corresponds to the *Miogypsina*-*Operculina* foraminiferan range, dated during the lower to lowest middle Miocene (Matsumaru *et al.*, 1979). According to Takeyama (1989), a series of fossils (there were 10 specimens at the time) was found above the Ito-o Formation, including the lower Miocene tuffaceous bed (*ca*. 16 Ma by fission-track dating: Hirooka *et al.*, 1972). On the other hand, palaeomagnetic data indicated that the lower limit of the Kunimi Formation extends to the lower Miocene (older than 16.5 Ma) (Nakajima *et al.*, 1992).

We did not include some of the dental materials of Miocene pecorans in our examination. Many pecoran fossils from the lower Miocene were recorded from the Akeyo Formation (*ca*. 18 Ma) of the Mizunami Group (# 4) and contemporaneous Tomikusa Group (#3) in the 1900s (e.g. Kamei and Okazaki, 1974; Okazaki, 1977; Anan Town Publications Editorial Committee, 1987), but the studies of those fossils still continue in detail. Nishioka *et al.* (2016) first reported cervoid dental fossils from the lower Miocene Koura Formation (#7) of southwestern Japan. This cervoid species is similar to the species from the Nakamura Formation, but a detailed examination should be attempted using additional materials. There are many fossil records of footprints of deer-like animals from the Miocene (Okamura and Takahashi, 2009), but such footprints could not be used in a taxonomic study.

Methods for systematic descriptions

A basal framework of systematic studies of Eurasian pecorans (families Giraffidae, Palaeomerycidae, Cervidae, Moschidae, and Bovidae) was established by Janis and Scott (1987), and since then it has been discussed in paleontological and molecular biological analyses (Hassanin and Douzery, 2003). The phylogenetic position of the Moschidae is a problem because this family is currently composed of only a single genus, *Moschus*. Recent studies have strongly supported the sister group relationship of Moschidae and Bovidae (Hassanin and Douzery, 2003; Marcot, 2007; Sánchez *et al*., 2010; Mennecart *et al*., 2021), although Fernández and Vrba (2005) argued that the Moschidae are rather close to the Cervidae. Some of the Oligo-Miocene pecorans without any cranial appendages, such as *Amphitragulus* and *Dremotherium*, were conveniently placed in the Moschidae or other family (Prothero, 2007), but we treated them together as primitive pecorans in the present study.

In the synonymy list, conventional qualifiers of Matthews (1973) are added after the publication year: *, the work validates the species; v, the authors have seen the original material of the reference; pars, the reference applies only in part to the species; no sign, the authors were unable to check the validity of the reference. In the comparisons, we referred to the pecoran fossils from the lower and middle Miocene of Europe and China (Appendix 1). The dental terminology followed Bärmann and Rössner (2011). Teeth were measured in the maximum antero-posterior length of the crown (L) and the maximum labio-lingual width of the crown (W: premolar; Wa: molar anterior lobe) (Figure 2).

Systematic paleontology

Order Artiodactyla Owen, 1848

Family Cervidae Goldfuss, 1820

Cervidae gen. et sp. indet.

Figure 3 A–C

Cervoidea fam., gen. et sp. indet. Nishioka and Ando, 2016 v, p. 40, fig. 3.

New material.—NMNS PV-20160, left M2; NMNS PV-20161, a left mandible with m1–m3.

Other material.—MFM18126, right m3.

Repository.—The new materials, National Museum of Nature and Science, Tokyo, Japan; MFM18126, Mizunami Fossil Museum, Mizunami, Japan.

Locality.—35°26′07″ N and 137°00′57″ E, the south bank of the Kiso River, Dota, Kani City, Gifu Prefecture, central Japan.

Horizon.—The uppermost part of the Nakamura Formation, Mizunami Group; lower Miocene (*ca*. 18.5 Ma; Shikano, 2003).

Characteristics for identification.—Low-crowned molars; upper molars with a short and not bifurcated postprotocrista, pyramidal labial styles, distinct labial ribs, a weak entostyle; lower molars with an external postprotocristid, no mesostylid, a strong metastylid, a postentocristid not connected with the posthypocristid, and a monocuspidate (no entoconulid) third lobe on m3.

Measurements.—Shown in Tables 2– 3.

Description of the new material.—NMNS PV-20160 is identified to M2 in that the tooth has faint facets both on the anterior and posterior walls of the crown and conforms the M2 position of NMNS PV-20161. The paracone-metacone distance of NMNS PV-20160 is the same in length as the distance between the m2 ectostylid and the m2-m3 boundary of NMNS PV-20161. M2 is low-crowned and in the early wear stage. The occlusal outline is quadrate and composed primarily of four cusps with a selenodont pattern. The anterior lobe is separated from the posterior lobe by a deep valley. The preparacrista does not connect with the preprotocrista. The postmetacrista connects with the postmetaconulecrista. The posterior end of the postparacrista approaches the anterolingual wall of the premetacrista, but they are separated by a deep gap. The postprotocrista is short and not branched without an internal postprotocrista (= neocrista in Gentry *et al*., 1999). Thus, the occlusal surface of the anterolingual lobe shows a V-shape. The postprotocrista approaches the premetaconulecrista, but they are not connected each other. There is a tiny bifurcation at the anterior end of the premetaconulecrista. The styles on the labial side are pyramidal, which are half as tall as the crown height. The parastyle and the mesostyle are isolated from any cristae in the occlusal surface. The metastyle is fused with the postmetacrista. The labial rib extending from the paracone is deeply folded as a pillar, while that from the metacone is relatively weak. Cingula on the lingual side surround from the anterior wall to the posterolingual wall. A small and tetraedric entostyle is developed between the paracone and the metaconule on the lingual side.

NMNS PV-20161 preserves a posterior part of the mandibular body with the m1 to m3 alveolus. The mandibular body has almost a uniform depth (*ca*. 22–24 mm in the lingual side), and its lower outline curves slightly below the anterior root of m3. The alveolar bone weakly swells out to the labial side. The inside of the oblique line (behind the m3) is concaved. The angular process curves at a right angle.

The lower molars are selenodont and low-crowned, or their cervical lines expose above the alveolar process. The axis consisting of the lingual cusps (conids and stylids) is oblique to the axis of the molar row, or the orientation of the antero-posterior length. The mesostylid does not develop as a pillar-shaped cusp. The external postprotocristids are present in all molars. Although the occlusal surface is strongly worn on NMNS PV-20161, there are deep gaps at three points: between the preprotocristid and the premetacristid (only in m1–m2), between the posthypocristid and the postentocristid (only in m1– m2), and at the anterior end of the prehypocristid. In m3, the posthypocristid connects to the postentocristid via the triangle-shaped entostylid. The third lobe of m3 is separated from the second lobe in front of the prehypoconulidcristid and the preentoconulidcristid. The third lobe of m3, composed of the hypoconulid, forms a crescent-shaped occlusal surface. The entoconulid is strongly reduced or absent. The ectostylid of each molar is well-developed. There is a tiny posterior ectostylid on m3. The folding structures of the lingual wall are prominent below the metastylid and between the first (anterior) lobe and the second (posterior) lobe. The anterior cingulid of each molar is inscribed on the anterolabial wall, but never forms a crest-shaped fold on the occlusal surface. There is a weak cingulid on the posterolingual side of m3.

Remarks.—The upper molar, NMNS PV-20160, belongs to a relatively young individual at the different wearing stage from that of the lower molars (NMNS PV-20161), but the main cusps of NMNS PV-20160 are located on the m2 talonid and m3 trigonid basins of NMNS PV-20161. While the dental characteristics (see the Characteristics listed above) of these specimens are substantially inherited from primitive pecorans, such as *Amphitragulus* and *Dremotherium*, the molars of NMNS PV-20160 and NMNS PV-20161 are somewhat more advanced in selenodonty compared to the molars of the primitive pecorans. According to Sánchez *et al.* (2009), selenodonty of ruminants (especially tragulids) is determined by the longitudinal extension and the vertical development of the cristids, and by the flattening of the main cusps. The primitive pecorans from the Oligocene and the lower Miocene were still at a developmental stage from bunoselenodont to full selenodont (e.g. Mennecart, 2012; Mennecart *et al.*, 2012). Even *Amphitragulus*, which is one of the close genus to crown Pecora, has almost complete selenodont molars but partially retains bunodonty (cuspidate metaconid and entoconid) in the lower molars (Mennecart, 2012; Métais *et al.*, 2017). In terms of upper molars, NMNS PV-20160 is characterized by more developed labial rib and metastyle than the molars of *Amphitragulus* and *Dremotherium*. Comparing major genera of lower and middle Miocene pecorans in simplified upper molar patterns, NMNS PV-20160 is similar to the pattern of *Dremotherium* or cervids, and it is different from the upper molar of the earliest bovids, *Eotragus*, in that it has a clear separation between the anterior and posterior lobes (Figure 4). *Amphimoschus* is seemingly categorized into an intermediate between cervids and bovids in the upper molar patterns, but the genus is characterized by a relatively long postprotocrista approaching the anterior end of the premetaconulecrista, like bovids.

The isolated m3 (MFM18126) previously described as Cervoidea fam., gen. et sp. indet. by Nishioka and Ando (2016) corresponds to the additional specimen (NMNS PV-20161) in tooth size and shape (Table 3). MFM18126 is at an early wear stage, but it shares all of the characteristics of m3 of NMNS PV-20161. As mentioned by Nishioka and Ando (2016), the lower molars have many primitive features, and lack the synapomorphic features seen in Bovidae and Moschidae, such as the connection between the postentocristid and the posthypocristid. Moreover, the entoconulid of m3 is not cuspidated like that of *Amphimoschus* (Figure 5). A combination of upper and lower molar characteristics strongly indicates that the present pecoran species from the Nakamura Formation belongs to the Cervidae.

The stem Cervidae includes two major groups (Figure 4). One is the "ancestral" deer (Procervulinae and Dicrocerinae), which are relatively close to the crown clade of the Cervidae (Gentry *et al*., 1999; Mennecart *et al*., 2017). The species included in the Procervulinae or Dicrocerinae (e.g. *Procervulus*, *Heteroprox*, and *Dicrocerus*) are commonly characterized by dichotomous antlers without a burr, and they have upper molars with a distinct bifurcation of the postprotocrista (Figure 4). The bifurcated postprotocrista (or appearance of the internal postprotocrista) is clearly developed in younger genera, such as *Heteroprox* and *Dicrocerus*, whereas it appears with several morphotypes in the earliest genus *Procervulus* (Rössner, 1995). Based on observations of nearly 200 specimens of *P. praelucidus* from Wintershof-West (MN3, Germany), the bifurcation is present more often in M2–M3 than in M1 (Rössner, 1995). Moreover, the angle made by the preprotocrista and the postprotocrista tends to become a right or obtuse angle regardless of the presence or absence of bifurcation in all molars (Rössner, 1995). Based on our direct observation of the BSPG specimens referred in Rössner (1995), the same crest pattern as NMNS PV-20160 was rarely found in M2 (4%, n = 198). In addition, NMNS PV-20160 has clearer labial ribs (especially on the metacone) than M2 of *P. dichotomus* (BSPG 1979XV555) from Rauscheröd (MN4), Germany, although these specimens are almost identical in tooth measurements (Table 2). The lower molars (NMNS PV-20161) are also similar to those of *P. dichotomus* in both the occlusal patterns and measurements (Figure 5; Table 3).

The other group of early cervids is the Lagomerycinae, which are characterized by cranial appendages distally multi-furcated. Lagomerycin deer, such as *Lagomeryx* and *Ligeromeryx*, have been classified based mainly on antler morphology, and thus isolated dental materials may not be useful in genus or species identification. *Lagomeryx* from Europe and Thailand retains a simple postprotocrista without bifurcation (Rössner, 2010; Suraprasit *et al*., 2014), which shares a molar pattern with NMNS PV-20160. Qualitative and quantitative comparisons of dental morphology indicate a close relationship between the present Japanese species and *Ligeromeryx* from the lower Miocene of Europe and China (Figures 4 and 5; Tables 2 and 3). The species of *Ligeromeryx*, such as *Ligeromeryx triacuminatus* (Colbert, 1936) and *Ligeromeryx colberti* (Young, 1937), are the representative pecorans in the Shanwang mammalian fauna (Qiu *et al*., 2013). These species are possibly related to the European species, *Ligeromeryx praestans* (Stehlin, 1937) Azanza and Ginsburg, 1997, which was established based on fragmentary antlers. The dental morphology of any species of *Lagomeryx* has not been examined using sufficient materials, but the Chinese *Ligeromeryx* does not have the bifurcated postprotocrista on all upper molars, based on observations of unpublished specimens listed in Appendix 1. Dental measurements of NMNS PV-20161 are similar to those of European *Ligeromeryx praestans* (MNHN specimens in Appendix 1), rather than Chinese *Ligeromeryx* (SNHM 4376).

The comparisons mentioned above comprehensively suggest that the cervid species from the Nakamura Formation is placed in the basal lineage of the Cervidae closely related to the species of *Procervulus* or *Ligeromeryx*.

Genus *Dicrocerus* Lartet, 1837

Dicrocerus? *tokunagai* Matsumoto, 1927

Figure 3D–E

Dicrocerus tokunagai Matsumoto, 1927 v*, p. 290.

Dicrocerus hirabayashii (Tokunaga). Takai, 1938 v pars, p. 751.

Dicrocerus tokunagai Matsumoto. Shikama and Ômori, 1952 v, p. 569, figs. 1–6.

Dicrocerus tokunagai Matsumoto. Naora, 1997 v, p. 8, fig. 3.

Material.—NMJH A-636-1-1-9, a right mandible with p4–m2 (holotype of *Dicrocerus tokunagai*); ICM YH-3412, a left mandible with m1–m3.

Repository.—NMJH A-636-1-1-9, National Museum of Japanese History, Sakura, Japan; ICM YH-3412, Iida City Museum, Iida, Japan (previously stored in the Geological Institute of Yokohama National University, Yokohama, Japan).

Locality.—NMJH A-636-1-1-9, Kusano-mura, Iwaki City, Fukushima Prefecture, northeastern Japan; ICM YH-3412, the bank of Kuzi River, Kamiogawa-mura, Daigo-cho, Ibaraki Prefecture, northeastern Japan.

Horizon.—NMJH A-636-1-1-9, Misawa Formation, lower Miocene (*ca*. 17 Ma; Suto *et al*., 2005; Yanagisawa, 2011); ICM YH-3412, possibly Kitatage Formation, lower Miocene (*ca*. 17 Ma; Tagiri *et al*., 2008).

Characteristics for identification.—Low-crowned cheek teeth; relatively short p4; p4 anterior valley open; relative to Cervidae gen. et sp. indet. from the Nakamura Formation, slightly smaller lower molars with weaker external postprotocristid; the other characteristics are same as those of Cervidae gen. et sp. indet.

Measurements.—Shown in Table 3.

Description.—NMJH A-636-1-1-9 is a fragmentary right mandible with p4–m2 at a late wear stage. The alveolar bone weakly swells out to the labial side. The cheek teeth are low-crowned, or their cervical lines expose above the alveolar process. The crown of p4 is antero-posteriorly shortebed. A branch between the anterior stylid and the anterior conid is poorly recognizable because of the lack of the anterolingual margin of the tooth. The anterior and posterior valleys are open, or the mesolingual conid does not extend antero-posteriorly, without the anteriolingual and posterolingual cristids. The labial wall between the mesolabial conid and the posterolabial conid is weakly folded. The posterior valley is shallow but clearly separates the posterolingual conid from the mesolingual conid. The posterior stylid (probably synonym for "posterior arm" in Matsumoto, 1927) and the back valley are reduced. The anterolabial cingulid is vestigial, and the anterolingual cingulid extends from the base of the mesolingual conid. The characteristics of lower molars (NMJH A-636-1-1-9 and ICM YH-3412) are basically same with those of Cervidae gen. et sp. indet. (NMNS PV-20161 and MFM18126) (see also original description by Matsumoto, 1927 and Shikama and Ômori, 1952). Matsumoto (1927) described a clear "*Palaeomeryx*-fold" (= external postprotocristid) of NMJH A-636-1-1-9, whereas Naora (1944) pointed out a weakness of this characteristic. In our viewpoint, both NMJH A-636-1-1-9 and ICM YH-3412 have the external postprotocristid on each lower molar, but they are strongly worn or indistinct by cracking.

Remarks.—H. Matsumoto (in Tokunaga, 1927) originally proposed a new species name, *Dicrocerus tokunagai*. According to his description, *D. tokunagai* is similar to "*D*". *furcatus* (combined with the genus *Euprox* by Stehlin, 1928) from Europe, but *D. tokunagai* is more primitive than *Euprox furcatus*, having a clear external postprotocristid, a short posterior stylid on p4, a shallow back valley, and the presence of a basal cingulum in the anterior valley. These characteristics of *D. tokunagai* were recognized in later studies (Naora, 1944, 1997; Shikama and Ômori, 1952), although a taxonomic position of this species have not been reassessed so far. Takai (1938) argued synonymy of *D. tokunagai* with *Cervavus oweni hirabayashii* Tokunaga, 1926 from the upper Miocene of central Japan, but morphological difference, including size, between these species is undoubtedly clear (Matsumoto, 1927; Naora, 1997). As mentioned in the comparative discussion on Cervidae gen. et sp. indet. from the Nakamura Formation, lower molars of stem cervids are characterized by the lingual cusps obliquely lined, always opening between the postentocristid and the posthypocristid, a presence of the external postprotocristid, and relatively low ectostylids. NMJH A-636-1-1-9 and ICM YH-3412 are more advanced in terms of selenodonty than *Amphitragulus*, and share the above characteristics with stem cervids. As Matsumoto (1927) perceived, a weakly-developed posterior part at p4 (NMJH A-636-1-1-9) usually appears in basal cervids, like *Procervulus*, and it is a crucial difference from the premolars of any species of *Dicrocerus*. We do not completely agree with him in this point because the reduction of the posterior stylid on p4 is not remarkable in *Dicrocerus* but commonly appears in *Euprox furcatus* from Austria (Aiglstorfer *et al*., 2014) and from Germany (NMB specimens in Appendix 1). The anterolingual cingulum of p4 maybe also one of identification keys for *Euprox* and *Heteroprox*.

NMJH A-636-1-1-9 and ICM YH-3412 share most dental characteristics with Cervidae gen. et sp. indet. from the Nakamura Formation, but they are slightly smaller in mandibular and tooth size (Figure 3; Table 3). Moreover, the external postprotocristid of NMJH A-636-1-1-9 is faintly weaker than NMNS PV-20161 in spite of the similar wear stage each other. These characteristics exhibited in a species from the Misawa and Kitatage formations (*ca*. 17 Ma) are morphologically more advanced relative to Cervidae gen. et sp. indet. from the Nakamura Formation (*ca*. 18.5 Ma). We have not found diagnostic features defining *D. tokunagai* as an independent species both in NMJH A-636-1-1-9 and ICM YH-3412, but tentatively leave this name as *D*.? *tokunagai* until more evidential materials will be examined.

Family Palaeomerycidae Lydekker, 1883

Genus *Palaeomeryx* von Meyer, 1834

cf. *Palaeomeryx minoensis* (Matsumoto, 1918)

Figure 6A

Amphitragulus minoensis Matsumoto, 1918 *, p. 77, fig. 1, pl. 13 (figs. 1–3).

"*Palaeomeryx minoensis*" Nagasawa, 1932, p. 220 (schematic drawing), p. 223.

Amphitragulus minoensis Matsumoto. Takai, 1938, p. 748.

Amphitragulus minoensis Matsumoto. Kamei and Okazaki, 1974, p. 275, pl. 93 (fig. 3).

?*Amphitragulus minoensis* Matsumoto. Kamei and Okazaki, 1974 pars, p. 276.

Amphitragulus minoensis Matsumoto. Okumura *et al*., 1977, p. 40, pl. 15 (fig. 2).

Amphitragulus minoensis Matsumoto. Okumura *et al*., 1977 pars, p. 41.

"*Palaeomeryx minoensis*" Nagasawa. Naora, 1997, p. 7.

Material.—IGPS 22059, a plaster cast of a right mandible with p3–m2.

Repository.—The Tohoku University Museum, Sendai, Japan.

Locality.—Banjo-bora, Mitake-cho, Kani-gun, Gifu Prefecture.

Horizon.—The lower part of the Hiramaki Formation (Matsumoto, 1918), Mizunami Group; lower Miocene (*ca*. 18 Ma; Tomida *et al*., 2013).

Characteristics for identification.—Large size ruminant; low-crowned cheek teeth; p1 present; p3 with an antero-posteriorly longer crown than p4, compressed labio-lingually; lower molars with a faint external postprotocristid, no mesostylid, a strong metastylid, a postentocristid not connected with the posthypocristid, and a preprotocristid not connected with the premetacristid.

Measurements.—Shown in Table 4.

Description.—IGPS 22059 preserves a middle part of the mandibular body with p3–m2 and the alveolus of p1 and p2. The lower outline of the mandibular body gently curves from the diastema to the position of m1. The alveolar bone less swells out to the labial side. The root socket for p1 shows a rounded triangular outline elongated antero-posteriorly, and behind that there are two elliptical sockets for p2. The cheek teeth are strongly worn and low-crowned, or their cervical lines expose above the alveolar process. The outlines of p3 and p4 are rounded triangular in occlusal view. The crown of p3 is more compressed labio-lingually than that of p4. In the occlusal morphology of the premolars, the anterior stylid is clearly branched from the anterior conid (but IGPS 22059 is vaguely replicated in this part). The mesolabial conid is more developed than the mesolingual conid. The transverse cristid extends posteriorly from the mesolabial conid to the mesolingual conid. The anterior and posterior valleys are open because of the lack of antero-posterior extension from the mesolingual conid. The posterolingual conid is separated from the posterior stylid by a shallow back valley on p3, while the surface between the mesolingual conid and the posterior stylid is integrated by wearing. The basal cingulum is present only on the anterolingual side.

The lower molars are selenodont. The axis consisting of the lingual cusps (conids and stylids) is slightly oblique to the orientation of the antero-posterior length. Owing to a strong wear stage the molars do not clearly show development of accessory structures, such as stylids, ribs, cingulids, and the external postprotocristid. In m2, the connections between the preprotocristid and the premetacristid and between the posthypocristid and the postentocristid are not fully fused. The external postprotocristid faintly remains, judging from the existence of a tiny notch on the posterolabial wall of the anterior lobe. The anterior ectostylid is slender. The anterior cingulid is weakly present on m2. The other characters are described in detail in Matsumoto (1918).

Remarks.—Matsumoto (1918) classified a single fragmentary mandible from the Hiramaki Formation as a new species, *Amphitragulus minoensis*, and later Nagasawa (1932) reported a different new species, "*Palaeomeryx minoensis*" (we nomenclaturally distinguish this name from our combined name), based on an isolated M2 from the same horizon. Because these holotype specimens were owned by the Tono Highschool and an individual respectively, they are missing at present. Matsumoto (1918) supposed that the Eurasian *Amphitragulus* evolved into the North American *Palaeomeryx* (currently replaced by the other genera, such as *Bouromeryx* and *Dromomeryx*) possibly via the Japanese *Amphitragulus*. However, his hypothesis is premised on knowledge when taxonomy of fossil pecorans had been confused. Nagasawa (1932) recognized that the Japanese palaeomerycids are more similar to *Palaeomeryx* than *Amphitragulus*, whereas he did not mention a relationship between "*P. minoensis*" and *A. minoensis*. Takai (1938) synonymized these species without any systematic revision, while Naora (1997) (this book was edited from his unpublished notes written probably in the 1940s) believed the opinion of Nagasawa (1932) because the materials of *A. minoensis* (lower teeth) and "*P. minoensis*" (upper molar) were not comparable to each other. However, the name *A. minoensis* spread more generally in later studies (Kamei and Okazaki, 1974; Okumura *et al.*, 1977).

Matsumoto (1918) placed the present specimen from the Hiramaki Formation to the genus *Amphitragulus*, based mainly on the presence of p1 and the external postprotocristid, with noting some uncertain taxonomic problems. The presence of p1 with a single root characterizes stem pecorans or basal cervoids (traditionally including Palaeomerycidae and Cervidae). In terms of the external postprotocristid Matsumoto (1918) misidentified a fold on the anterior end of the posterior fossa on m2 as the "*Palaeomeryx*-fold", but we confirmed it on the actual position in IGPS 22059. In contrast with these primitive characters, the lower molars of IGPS 22059 are completely selenodont and considerably larger than those of stem pecorans, including *Amphitragulus*.

Tooth measurements undoubtedly indicate size similarities between IGPS 22059 and Eurasian palaeomerycid species (Table 4). We are not able to identify characters of the upper molar of "*Palaeomeryx minoesis*" owing to a strongly worn occlusal surface (Nagasawa, 1932), but as Nagasawa suggested, it is similar in tooth measurements to the upper molars of species of *Palaeomeryx* from the lower Miocene of Europe. As a result, our observations supported the viewpoint of Takai (1938), but we tentatively used the name cf. *Palaeomeryx minoensis* (Matsumoto, 1918), combining *A. minoensis* with the genus *Palaeomeryx*.

Recent studies based on cranial morphology (Rössner, 2010; Sánchez *et al.*, 2015) have recognized seven genera of Eurasian palaeomerycids (= Palaeomerycinae): i.e. *Palaeomeryx*, *Triceromeryx*, *Ampelomeryx*, *Sinomeryx* (synonymous with *Palaeomeryx* in McKenna and Bell, 1997), *Tauromeryx*, *Germanomeryx*, and *Xenokeryx*. Eurasian palaeomerycids defined by dental materials in the 19th century have been included into a single genus, "*Palaeomeryx*" (or *Palaeomeryx s.l.*), and the differences among the classic species, such as "*P.*" *kaupi* (von Meyer, 1834) and "*P.*" *magnus* (Lartet, 1851), are still questionable in the genus identification (Rössner, 2010). As previously suggested (e.g. Ginsburg, 1999), comparisons of tooth measurements supported a size increase from the early Miocene palaeomerycids ("*P.*" *kaupi* from Europe, *S. tricornis* from China, and cf. *P. minoensis* from Japan) to the middle Miocene species ("*P.*" *bojani* and "*P.*" *magnus* from Europe) (Table 4). We consider that species identification of palaeomerycids without cranial material is difficult, but the proportion of premolars (especially the labio-lingual compression of p3) of cf. *P. minoensis* could be an evidential characteristic for defining this species.

Family indeterminate

Genus *Amphimoschus* Bourgeois, 1873

Amphimoschus sp.

Figure 6B

Amphitragulus sp. Takeyama, 1989 v, p. 12, fig. 1.

Material.—FPDM-V-8462 (previously catalogued as FPM-81181), a right mandible with m1–m3.

Repository.—Fukui Prefectural Dinosaur Museum, Katsuyama, Japan.

Locality.—Koniu, Fukui City, Fukui Prefecture, Japan.

Horizon.—Middle part of the Kunimi Formation (Takeyama, 1989); uppermost lower

Miocene (*ca*. 16 Ma; Hirooka *et al*., 1972).

Characteristics for identification.—Hypsodonty and selenodonty of lower molars are more advanced than those of stem pecorans; lower molars labio-lingually compressed; lower molars with an anterior lobe isolated from the posterior lobe, no external postprotocristid, an (internal) postprotocristid close to the prehypocristid (but not connected each other), a well-developed postentocristid but not connected with the posthypocristid, a preprotocristid not connected with the premetacristid, a bicuspidate (with a strong entoconulid) third lobe on m3, and a tall ectostylid.

Measurements.—Shown in Table 5.

Description.—FPDM-V-8462 preserves a posterior part of the mandible with m1 to m3. The mandibular body is thin and weakly swells out to the labial side at the alveolus. The incisura vasorum is weak. The mandibular angle is partially broken but its outline likely shows a semicircle. The ramus is tall and bulges at the bottom. The coronoid process is slightly constricted by the mandibular notch.

The lower molars are completely selenodont and high-crowned compared to other Oligocene and lower Miocene pecorans. The cervical lines are situated at the alveolus (m1) or buried under the alveolar process (m2 and m3) because these are in the middle of eruption. The lingual cusps (conids and stylids) are almost aligned in parallel with the orientation of the antero-posterior length. The mesostylid and the entostylid are weak. The metastylid develops as a pillar extending from the crown base to the occlusal surface. The lingual surface is relatively flat, with weakly projected ribs. The external postprotocristids are absent in all molars. The cristids approach each other, but are not fused at the anterolingual corner, the posterolingual corner, and the end of the prehypocristid. The connection between the posthypocristid and the postentocristid on m1 is not integrated in spite of a moderately wearing tooth. The third lobe of m3 is bicuspidate, composed of well-developed hypoconulid and entoconulid. The end of the preentoconulidcristid intrudes into the posterior fossa between the posthypocristid and the postentocristid. The ectostylid of each molar is tall and slender. No cingulids are visible on the molars.

Remarks.—Takeyama (1989) collected a total of 10 fossil specimens, including postcranial remains, of *Amphitragulus* sp., but only the mandible, FPDM-V-8462, is currently stored. Takeyama documented that FPDM-V-8462 was similar to *Amphitragulus* and *Palaeomeryx* in terms of the presence of a "*Palaeomeryx*-fold" (= external postprotocristid), but we did not find this characteristic on any molars of FPDM-V-8462. Moreover, Takeyama did not mention the cuspidate entoconulid that is a decisive characteristic of the genus *Amphimoschus* and moschids (Bourgeois, 1873; Sánchez *et al*., 2010; Mennecart *et al*., 2021). FPDM-V-8462 is distinguished from *Amphitragulus* and the other stem pecorans in having high-crowned molars and no external postprotocristid. The molar crown of FPDM-V-8462 is relatively higher and flatter on the lingual surface than that of stem cervids, including the Lagomerycinae, Procervulinae, and Dicrocerinae. FPDM-V-8468 is more advanced than the molars of stem pecorans and Cervidae in dental morphology (e.g. high crown and the bicuspidate third lobe of m3), whereas does not develop a fusion between the postentocristid and the posthypocristid, which is one of synapomorphic features of bovids and moschids.

The morphological character of FPDM-V-8468 corresponds to that of *Amphimoschus* redefined by Mennecart *et al*. (2021) after compiling the cranial and dental morphology of European species, *Amphimoschus ponteleviensis* from MN3–6 localities (e.g. Artenay and Pontlevoy) (see also Figure 5). The molar crown height of FPDM-V-8462 also similar to that of *Amphimoschus*. FPDM-V-8462 is slightly larger in molar measurements than *Amphimoschus ponteleviensis* from Artenay (MN3) (Table 5), but it is included in a range of this species obtained by Mennecart *et al*. (2021). There are some fossil records of *Amphimoschus* from the lower Miocene of China (Li *et al*., 1983; Wang, B. *et al*., 2003; Wang, X. *et al*., 2003; Li *et al*., 2021). *Amphimoschus xishuiensis* from Tiejianggou Formation (*ca*. 19.7–17 Ma) of the Tabenbuluk area, Gansu Province was established by skull and dental materials (Li *et al*., 2021). FPDM-V-8462 is approximately as large as the holotype (IVPP V 25521.1) of *Amphimoschus xishuiensis* in the measurements of m2 and m3 (Table 5). The antero-posterior length of m1 of FPDM-V-8462 is longer than that of IVPP V 25521.1. Regarding lower molar characteristics, *Amphimoschus xishuiensis* differs from *Amphimoschus ponteleviensis* by the presence of well-developed metastylid on m1–m3 and an additional lingual stylid on m1–m2 (Li *et al*., 2021). These characteristics are not found in FPDM-V-8462, but the Japanese material is insufficient to determine the species at present.

Discussion

The taxonomic positions of the Japanese Miocene pecorans examined in this study were narrowed down. Our revision confirmed four species of pecorans, including an indeterminate species of the basal cervids, *Dicrocerus*? *tokunagai*, cf. *Palaeomeryx minoensis*, and *Amphimoschus* sp. These pecorans are still indeterminate taxonomically in the species or genus level, but no specimens were allocated to primitive pecorans, such as *Amphitragulus* and *Dremotherium*. In the Neogene, these genera are limited to the Agenian (MN1–2: 23–19.5 Ma: Hilgen *et al*., 2012) in Europe, and there are no certain fossil records in Asia (Figure 7). *Amphitragulus* and *Dremotherium* are basically components of upper Oligocene fossil assemblages from Mongolia and Pakistan (Vislobokova and Daxner-Höck, 2002; Métais *et al*., 2017), although Vislobokova (1997) listed a species of *Amphitragulus* from the lower Miocene fossils in Kazakhstan. The absence of *Amphitragulus* in the lower Miocene (strictly Burdigalian) fauna of Japan is consistent with the result showing no fossil records of *Amphitragulus* from contemporaneous Xiejian and Shanwangian faunas of China (Qiu *et al*., 2013). Moreover, the appearances of *Ligeromeryx* (basal cervids) and *Sinomeryx* (*Palaeomeryx s.l.*) are an index of the Shanwang fossil biota (*ca*. 18–16 Ma: Deng *et al*., 2019). Many previous papers suggested that the taxonomic composition of the Japanese Burdigalian mammals is correlated with that of the Shanwangian mammalian fauna (e.g. Tomida and Setoguchi, 1994; Miyata and Tomida, 2010; Fukuchi and Kawai, 2011), and our reappraisal based on the pecoran fossils also arrived at the same result.

The early group of crown pecorans in Eurasia are represented by basal cervids (lagomerycines and procervulines), large-sized palaeomerycids (*Palaeomeryx s.l.*), and *Amphimoschus* (e.g. Gentry *et al*., 1999; Qiu *et al*., 2013; Mennecart *et al*., 2021). These taxa occurred in Europe during the early Orleanian (MN3: 19.4–17.2 Ma) and in China during the Shanwangian (19.5–16 Ma). Some Chinese local faunas indicate that the earliest occurrences of *Amphimoschus* and lagomerycine cervids in Asia possibly date back to the basal stage of the Shanwangian, or around 19.5–19 Ma (Qiu *et al*., 2013; Wang *et al*., 2019; Li *et al*., 2021). The findings of a basal cervid species and cf. *Palaeomeryx minoensis* from the Nakamura and Hiramaki formations, respectively, suggested that the early dispersal event of the crown pecorans had occurred even in the marginal region of Far East Asia.

The fossils of relatively derived genera of cervids, such as *Dicrocerus* and *Euprox*, have been discovered primarily from the middle Miocene of Europe (MN5 or younger) and Asia (Tunggurian) (e.g. Mein, 1989; Ye, 1989; Gentry *et al*., 1999; Wang and Zhang, 2011; Hou, 2015; see also Figure 7). The fossil records of *Dicrocerus*? *tokunagai* from the lower Miocene (*ca*. 17 Ma) in northeastern Japan would indicate the earliest dispersion of this genus if this generic identification is true, but we demonstrated that the attributed specimens display a different dental morphology from *Dicrocerus*. The occurrence of *Amphimoschus* from the Kunimi Formation (*ca*. 16 Ma) provided a new insight on stratigraphic distribution of this genus in Asia. *Amphimoschus ponteleviensis* is recorded from many localities in Europe, ranging from MN3 to the beginning of MN6 (Mennecart *et al*., 2021), while *Amphimoschus xishuiensis* from China is a member of the Xishuigou fauna that is the early stage (*ca*. 19.5–19 Ma) of the Shanwangian (Wang, X. *et al*., 2003; Qiu *et al*., 2013; Li *et al*., 2021). The fossil-bearing age in the Kunimi Formation is younger than that of the Chinese *Amphimoschus*, but the genus survived throughout the Burdigalian in East Asia as in Europe.

Compiled geological and paleontological evidence has made possible the reconstruction of an incomplete separation of the Japanese archipelago on the eastern margin of the Eurasian continent in the Burdigalian (Figure 1; Kano *et al*., 1991; Noda and Goto, 2004). As mentioned above, most fossil mammals, including pecorans, suggest a strong faunal connection throughout the Eurasian continent during this period; further, they more or less show speciation between the Japanese and other species. Kimura *et al*. (2019) considered that one of the eomyid rodents, *Japaneomys yasunoi*, from the lower Miocene part of the Mizunami Group had possibly diverged in the late Oligocene through allopatric speciation from *Asianeomys* in the inner-continental regions of Asia. The other taxa, including both large and small mammals, from the Mizunami Group are also morphologically specialized enough to define endemic genus or species (Fukuchi and Kawai, 2011; Tomida, 2011, 2012; Mörs *et al.*, 2016; Oshima *et al.*, 2017; Mörs and Tomida, 2018). *Anchitherium* (Equidae) from the Mizunami Group was tentatively assigned to an affinity species of *A. gobiense* from the Tunggur Formation (younger than 15 Ma), Inner Mongolia, but the Japanese form has a relatively primitive dental morphology (Miyata and Tomida, 2010). In pecorans, there is no major difference in dental morphology between the Japanese and other species, but we preliminarily noted some unique characteristics observed in the premolars of cf. *Palaeomeryx minoensis*. Because the fossil materials of the Japanese lower Miocene mammals are fragmentary in all taxa, further research and discussion will be needed to confirm whether or not the Japanese species evolved endemically due to geographical isolation.

Conclusion

In the lower Miocene of Japan, we have recognized four pecoran species: one indeterminate cervid, *Dicrocerus*? *tokunagai* (Cervidae), cf. *Palaeomeryx minoensis* (Palaeomerycidae), and *Amphimoschus* sp. (family indeterminate). The components of pecoran fauna of the lower Miocene of Japan are comparable with contemporaneous faunas from China (Shanwangian fauna) and Europe (mainly MN3–4 fauna), which are characterized by the occurrences of basal species of cervids, *Palaeomeryx s.l.* and *Amphimoschus*. The dispersion of basal cervids and *Palaeomeryx s.l.* in Japan dates back to 18.5 Ma and 18 Ma, respectively, when the Japanese archipelago was a part of the eastern margin of the Eurasian continent. *Amphimoschus* sp. from the Kunimi Formation possibly records the youngest occurrence of the genus in Asia at present. This study supports the notion that the genus *Amphitragulus* is not recorded in the lower Miocene of Japan.

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Figure and Table captions

Figure 1. Fossil localities and chrono-stratigraphy of the lower Miocene pecorans (only body fossils) from Japan. A paleogeographic map of Japan and East Asia in 20 Ma was referred from Noda and Goto (2004). The locality numbers correspond to the numbers in Table 1. Geomagnetic polarity timescale (GPTS) follows Raffi *et al*. (2021). The biostratigraphic correlation of European MN zones and Chinese land mammal stage/age (LMS/A) follows Hilgen *et al*. (2012) and Qiu *et al*. (2013).

Figure 2. Dental terminology (after Bärmann and Rössner, 2011) and measuring points of left cheek teeth of pecorans. **A,** upper molar. **B,** lower premolar. **C,** lower molar.

Figure 3. Cervidae gen. et sp. indet. (A–C) and *Dicrocerus*? *tokunagai* (D–E) from the lower Miocene of Japan. **A,** left M2 (NMNS PV-20160): **A1,** occlusal view; **A2,** labial view; **A3,** lingual view. **B,** a left mandible with m1–m3 (NMNS PV-20161): **B1,** occlusal view; **B2,** labial view; **B3,** lingual view. **C,** right m3 (MFM18126 in Nishioka and Ando, 2016): **C1,** occlusal view; **C2,** labial view; **C3,** lingual view. **D,** a right mandible with p4–m2 (NMJH A-636-1-1-9): **D1,** occlusal view; **D2,** labial view; **D3,** lingual view. **E,** a left mandible with m1–m3 (ICM YH-3412): **E1,** occlusal view; **E2,** labial view; **E3,** lingual view.

Figure 4. Comparisons of the left upper molar patterns commonly found in the examined pecoran specimens in Appendix 1. The phylogenetic tree was drawn by compiling the data of Suraprasit *et al*. (2014), Sánches *et al*. (2015), and Mennecart *et al*.

(2017).

Figure 5. Comparisons of m3 of Miocene pecorans. **A,** Cervidae gen. et sp. indet. (NMNS PV-20161, mirror image). **B,** *Ligeromeryx praestans* (NMB S.O.2060, mirror image). **C,** *Procervulus dichotomus* (BSPG 1979XV555). **D,** *Eotragus clavatus* (NMB Ss.5789). **E,** *Amphimoschus ponteleviensis* (NMB S.O.72). **F,** *Amphimoschus* sp. (FPDM-V-8462). Abbreviations: ipopc, internal postprotocristid; enld, entoconulid; ens, entostylid.

Figure 6. Cf. *Palaeomeryx minoensis* (A) and *Amphimoschus* sp. (B) from the lower Miocene of Japan. **A,** a right mandible with p3–m2 (IGPS 22059): **A1,** occlusal view (resin cast molded from IGPS 22059); **A2,** labial view (original cast); **A3,** lingual view (original cast). **B,** a right mandible with m1–m3 (FPDM-V-8462): **B1,** occlusal view; **B2,** labial view; **B3**, lingual view with the ramus.

Figure 7. The first appearance of the major genera of pecorans in the early and middle Miocene in Eurasia. The sources of Asia are based on the fossil records from China, Mongolia, and Thailand (Ginsburg and Ukkakimapan, 1983; Qiu *et al*., 2013; Suraprasit *et al*., 2014; Mennecart *et al*., 2019). The sources of Europe follows Mein (1989), Gentry *et al*. (1999), Rössner (2010), and Böhme *et al*. (2012).

Table 1. Records of the body fossils of the lower Miocene pecorans from Japan. The sources of numerical ages are documented in the text.

Table 2. Measurements (in mm) of M2 of Miocene cervids examined in this study (Appendix 1), with means, range, and number of specimens.

Table 3. Measurements (in mm) of p4–m3 of Miocene cervids examined in this study (Appendix 1), with means, range, and number of specimens.

Table 4. Measurements (in mm) of p3– m2 of Miocene palaeomerycids examined in this study (Appendix 1), with means, range, and number of specimens.

Table 5. Measurements (in mm) of m1– m3 of the species of *Amphimoschus* examined in this study (Appendix 1), with means, range, and number of specimens.

Appendix 1. List of the specimens examined in this study.

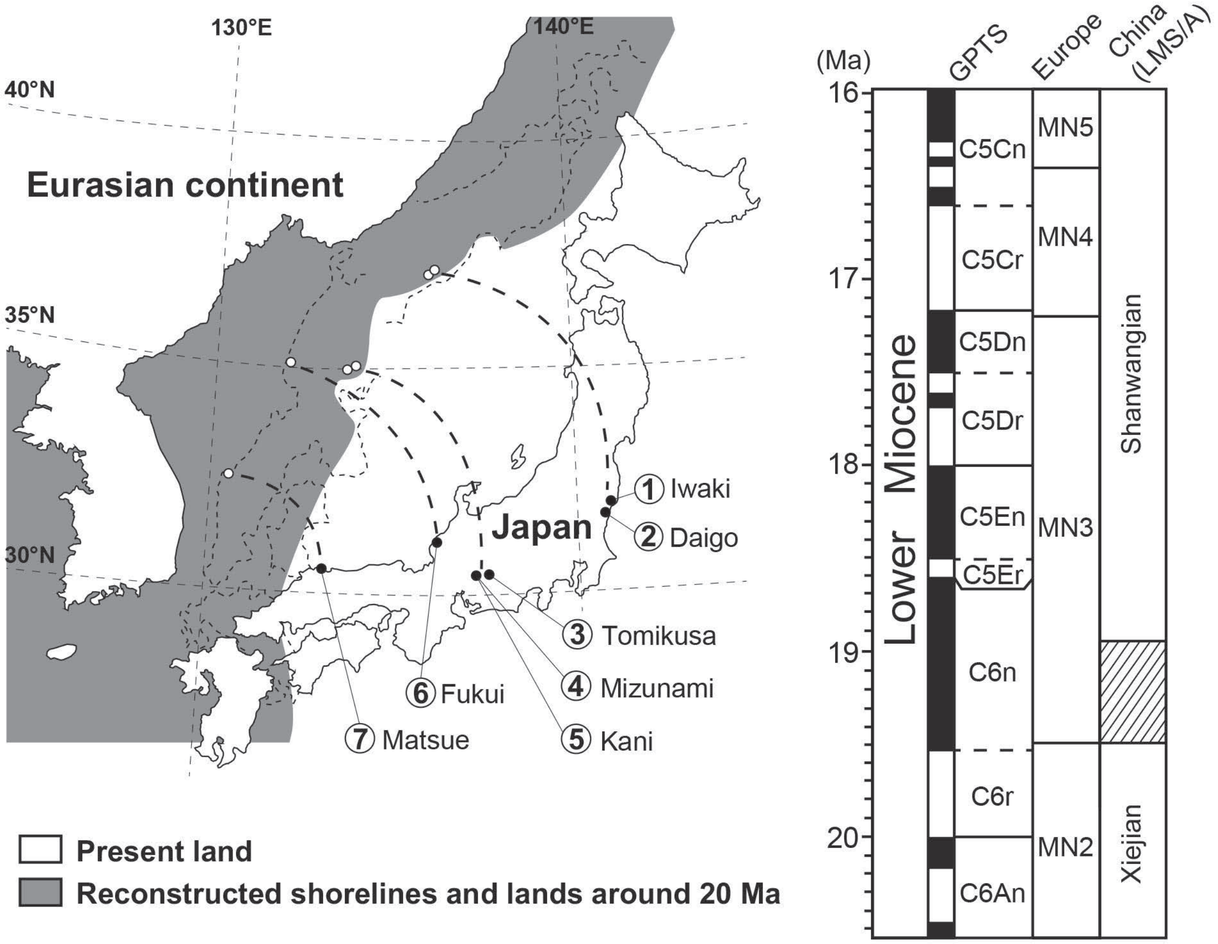

Fig.1 Nishioka et Tomida (1x)

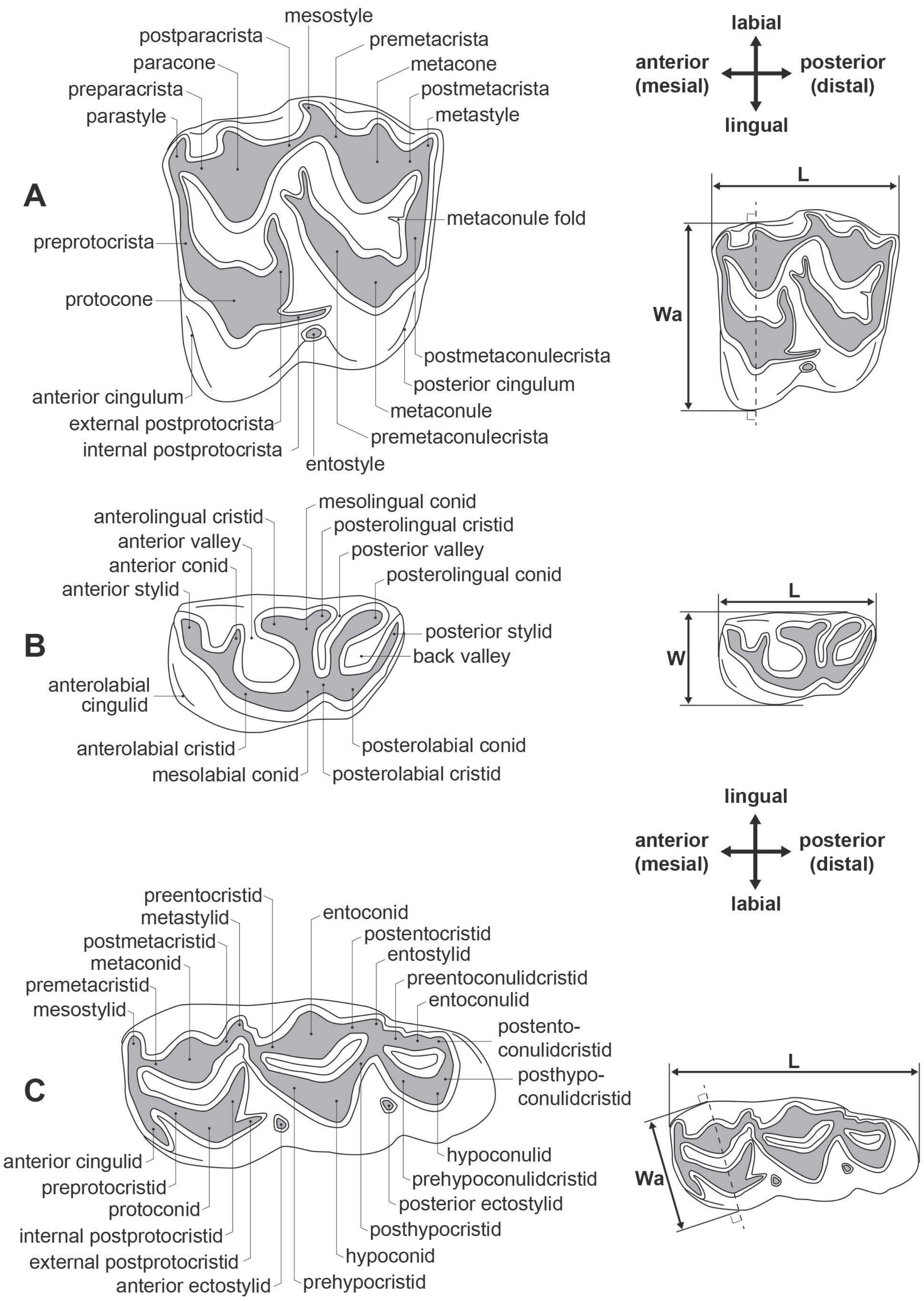

Fig.2 Nishioka et Tomida (1x)

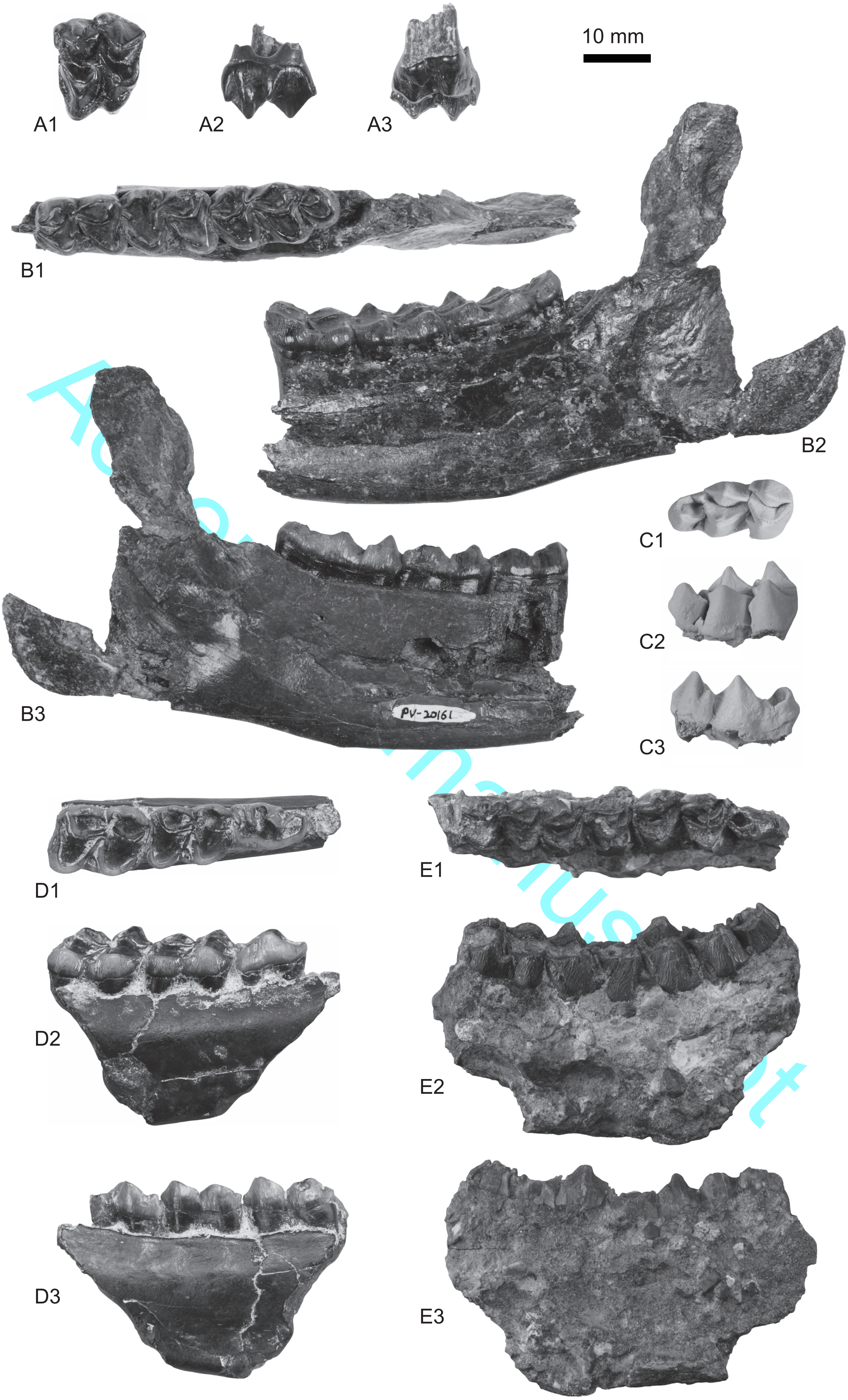

Fig.3 Nishioka et Tomida (1x)

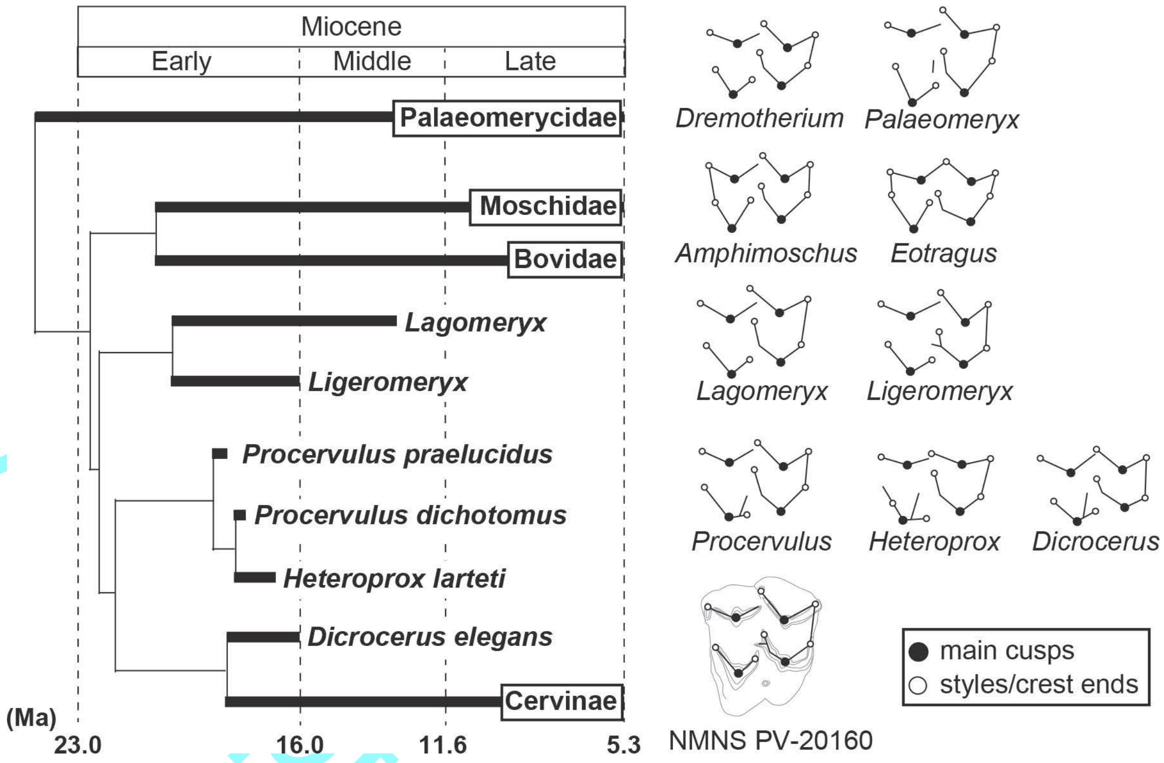

Fig.4 Nishioka et Tomida (1x)

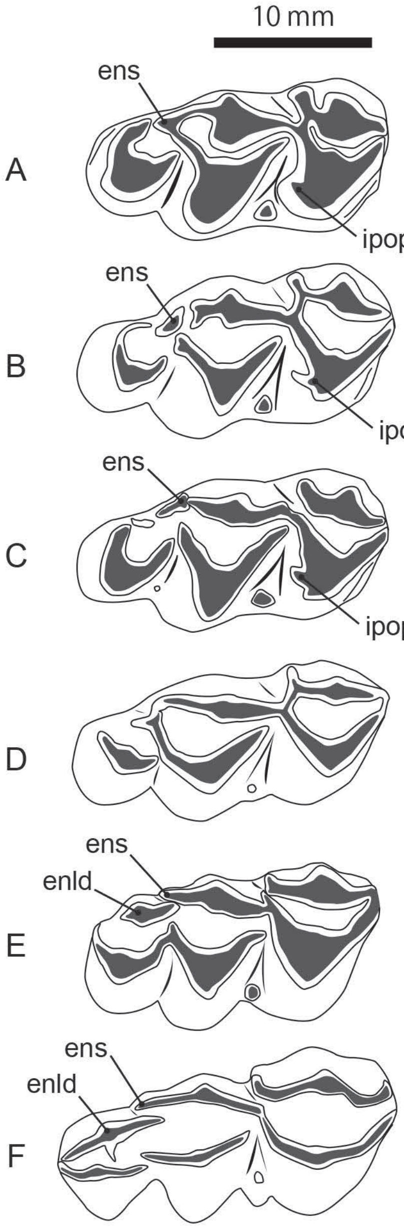

Fig.5 Nishioka et Tomida (1x)

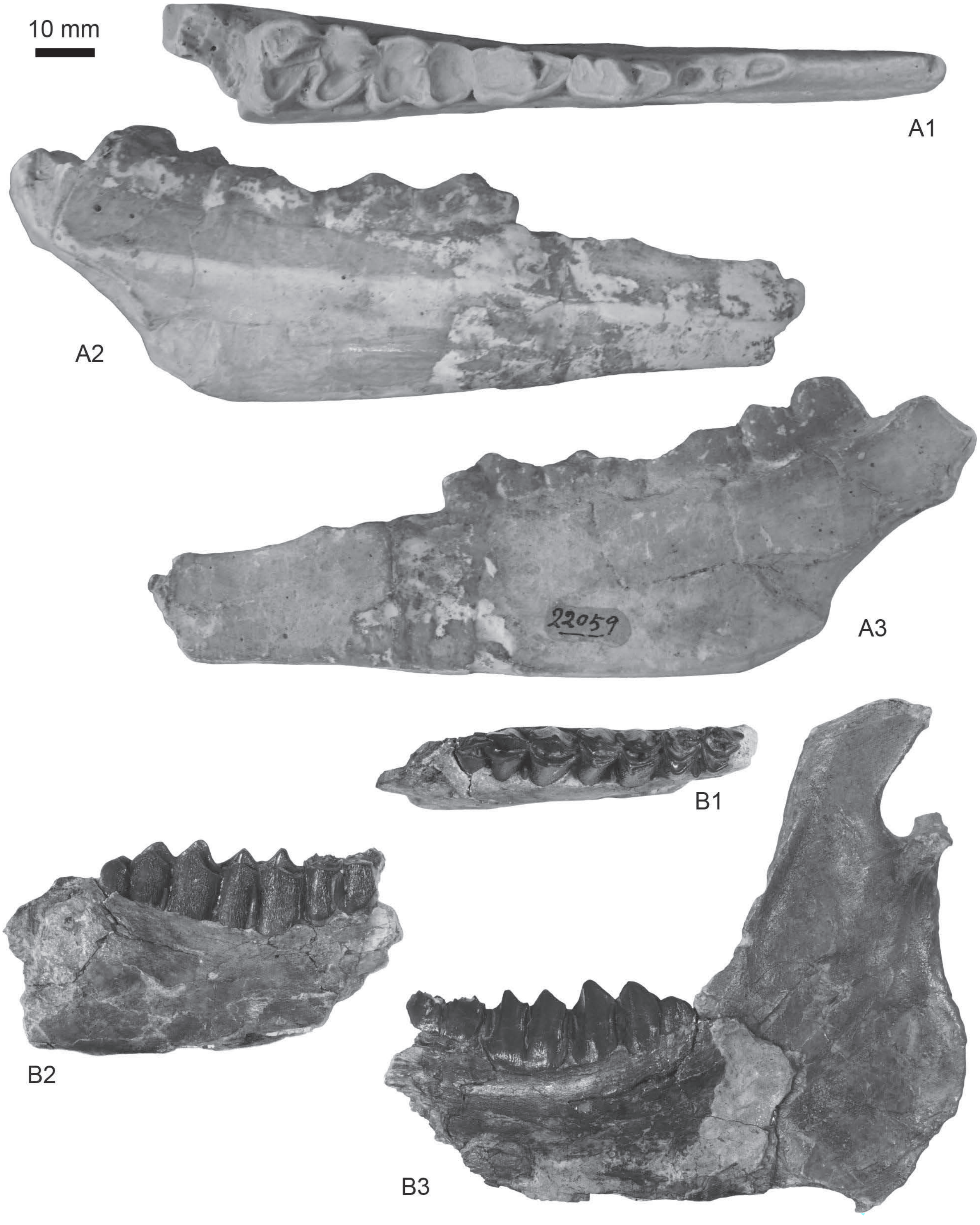

Fig.6 Nishioka et Tomida (1x)

Stratigraphic Stage	Japan	Asia		Europe	
Serravalian		Tunggurian LMS/A	*Palaeotragus* *Lagomeryx* *Dicrocerus* *Euprox* *Micromeryx* *Eotragus*	MN7/8	
Langhian				MN6	*Euprox*
				MN5	*Paradicrocerus* *Heteroprox* *Dicrocerus*
Burdigalian	*Amphimoschus* 17Ma *Dicrocerus?* 18Ma cf. *Palaeomeryx* stem Cervidae 20Ma	Shanwangian LMS/A	*Sinomeryx* *Ligeromeryx* *Stephanocemas* *Amphimoschus*	MN4	
				MN3	*Palaeomeryx s.l.* *Lagomeryx* *Ligeromeryx* *Procervulus* *Amphimoschus*
Aquitanian		Xiejian LMS/A		MN2	*Dremotherium* *Amphitragulus*
				MN1	

Fig.7 Nishioka et Tomida (1x)

Table 1.

	Locality	Horizon (formation)	Age (Ma)	Original identification	Identification by this study	Material	Papers
①	Iwaki	Misawa F.	17	*Dicrocerus tokunagai*	*Dicrocerus*? *tokunagai*	teeth	Matsumoto (1927)
②	Daigo	Kitatage/Asakawa F.	17	*Dicrocerus tokunagai*	*Dicrocerus*? *tokunagai*	teeth	Shikama and Ômori (1953)
③	Tomikusa	Oshimojo F.	18?	No description	—	teeth, postcranial	Anan Town Publications Editorial Committee (1987)
④	Mizunami	Akeyo F.	18	?*Amphitragulus minoensis*[*]	—	teeth, postcranial	Kamei and Okazaki (1974); Okazaki (1977)
⑤	Kani	Hiramaki F.	18	*Amphitragulus minoensis*	cf. *Palaeomeryx minoensis*	teeth	Matsumoto (1918)
	Kani	Hiramaki F.	18?	"*Palaeomeryx minoensis*"	cf. *Palaeomeryx minoensis*	teeth	Nagasawa (1932)
	Kani	Nakamura F.	18.5	Cervoidea fam., gen. et sp. indet.	Cervidae gen. et sp. indet.	teeth	Nishioka and Ando (2016); this study
	Kani	Nakamura F.	19–18.4	*Amphitragulus minoensis*	—	teeth, postcranial	Okumura *et al*. (1977)
	Kani	Hachiya F.	22–21?	*Amphitragulus minoensis*	—	postcranial	Shikano and Ando (2000)
⑥	Fukui	Kunimi F.	16	*Amphitragulus* sp.	*Amphimoschus* sp.	teeth, postcranial	Takeyama (1989)
⑦	Matsue	Koura F.	19	Cervoidea fam., gen. et sp. indet.	—	teeth	Nishioka *et al*. (2016)

[*] Possibly including several species.

Table 2.

	M2*L*	M2*Wa*
Cervidae gen. et sp. indet. (NMNS PV-20160)	13.72	15.62
Ligeromeryx praestans (MNHN specimens)	14.69 [14.27–15.11] (n = 3)	15.48 [14.69–16.18] (n = 3)
Procervulus dichotomus (BSPG 1979XV555)	13.92	15.43
Procervulus praelucidus (BSPG specimens)	10.76 [10.48–11.04] (n = 2)	11.71 [10.98–12.43] (n = 2)
Procervulus praelucidus (NMB specimens)	11.64 [11.63–11.64] (n = 2)	13.06 [12.92–13.19] (n = 2)
Euprox furcatus (NMB specimens)	12.08 [11.46–12.61] (n = 4)	14.08 [13.46–14.39] (n = 4)
Dicrocerus elegans (NMB specimens)	15.23 [15.03–15.54] (n = 3)	17.63 [17.33–17.78] (n = 3)

Table 3.

	p4*L*	p4*W*	m1*L*	m1*Wa*	m2*L*	m2*Wa*	m3*L*	m3*Wa*
Cervidae gen. et sp. indet. (NMNS PV-20161)	—	—	13.72	15.62	13.21	10.18	19.31	9.86
Cervidae gen. et sp. indet. (MFM18126)*	—	—	—	—	—	—	18.6	9.3
Dicrocerus? *tokunagai* (NMJH A-636-1-1-9)	10.04	6.34	11.42	8.57	12.81	10.62	—	—
Dicrocerus? *tokunagai* (ICM YH-3412)	—	—	11.48	7.34	13.29	8.65	19.75	8.64
Ligeromeryx praestans (MNHN specimens)	11.94 [10.32–13.20] (n = 19)	7.05 [6.57–7.88] (n = 19)	11.95 [11.24–12.74] (n = 16)	9.31 [8.53–9.88] (n = 16)	13.39 [11.98–14.92] (n = 25)	10.12 [9.11–11.08] (n = 25)	18.90 [17.43–20.76] (n = 20)	9.93 [8.85–10.76] (n = 20)
Ligeromeryx colberti (SNHM 4376)	8.17	—	9.68	7.00	11.44	7.82	16.5	8.43
Procervulus dichotomus (BSPG 1979XV555)	10.78	6.97	11.1	7.81	12.24	9.08	19.18	9.39
Procervulus praelucidus (BSPG 1979II12018)	9.34	5.12	9.99	6.72	10.25	7.77	14.82	7.17
Procervulus praelucidus (NMB specimens)	9.73 [9.17–10.50] (n = 5)	5.16 [4.80–5.44] (n = 6)	10.76 [8.85–11.72] (n = 9)	6.82 [6.35–7.52] (n = 10)	11.51 [10.85–11.94] (n = 14)	7.79 [7.09–8.59] (n = 14)	15.79 [14.27–17.14] (n = 13)	7.65 [7.01–8.35] (n = 14)
Euprox furcatus (NMB specimens)	10.59 [10.44–10.81] (n = 3)	6.61 [6.14–6.94] (n = 3)	11.02 [10.61–11.51] (n = 3)	7.42 [6.61–8.37] (n = 3)	11.96 [10.69–12.86] (n = 5)	8.75 [7.94–9.57] (n = 5)	17.36 [16.36–18.24] (n = 5)	8.99 [8.26–9.81] (n = 5)
Dicrocerus elegans (NMB specimens)	11.83 [10.74–13.25] (n = 4)	7.61 [6.85–8.22] (n = 4)	13.02 [12.55–13.79] (n = 6)	9.23 [8.92–9.70] (n = 6)	14.31 [13.22–15.39] (n = 65)	10.93 [10.16–11.42] (n = 6)	20.22 [19.40–21.17] (n = 6)	10.75 [10.20–11.52] (n = 6)
Dicrocerus grangeri (IVPP specimens)	11.44	6.08	12.04 [11.37–12.81] (n = 6)	8.50 [7.78–9.28] (n = 6)	13.81 [12.03–15.76] (n = 15)	9.76 [8.40–11.80] (n = 15)	18.85 [15.92–21.21] (n = 13)	9.45 [8.21–10.43] (n = 11)

*Data from Nishioka and Ando (2016).

Table 4.

	p3*L*	p3*W*	p4*L*	p4*W*	m1*L*	m1*Wa*	m2*L*	m2*Wa*
cf. *Palaeomeryx minoensis* (IGPS 22059)	16.35	7.84	16.53	9.80	15.78	11.68	19.82	14.47
Sinomeryx tricornis (IVPP specimens)	—	—	16.88	10.72	19.86 [17.36–22.35] (n = 2)	14.24 [12.34–16.13] (n = 2)	21.83 [19.85–23.81] (n = 2)	17.02 [15.50–18.53] (n = 2)
"*Palaeomeryx*" *kaupi* (BSPG specimens)	—	—	17.29	10.02	—	—	18.97 [18.64–19.30] (n = 2)	13.94 [13.70–14.17] (n = 2)
"*Palaeomeryx*" cf. *kaupi* (NMB specimens)	17.17 [16.68–17.66] (n = 2)	9.31 [8.92–9.70] (n = 2)	17.82 [16.99–18.75] (n = 4)	11.18 [11.06–11.50] (n = 4)	17.98 [16.97–18.53] (n = 5)	12.65 [12.18–13.11] (n = 5)	20.52 [20.21–20.76] (n = 3)	15.03 [14.49–15.48] (n = 3)
"*Palaeomeryx*" *bojani* (BSPG and NMB specimens)	—	—	—	—	22.49	15.49	21.96 [19.90–23.66] (n = 3)	16.79 [15.46–18.72] (n = 3)
"*Palaeomeryx*" *magnus* (MNHN specimens)	—	—	19.85 [19.64–20.05] (n = 2)	12.87 [12.42–13.31] (n = 2)	21.08 [21.05–21.10] (n = 2)	14.92 [14.58–15.26] (n = 2)	21.72 [21.10–22.11] (n = 3)	16.69 [15.26–18.44] (n = 3)

Table 5.

	m1*L*	m1*Wa*	m2*L*	m2*Wa*	m3*L*	m3*Wa*
Amphimoschus sp. (FPDM-V-8462)	>14.28	9.01	14.72	10.73	21.29	10.86
Amphimoschus xishuiensis (IVPP V25521.1)*	11.3	10.4	14.9	11.3	21.8	10.6
Amphimoschus ponteleviensis (NMB specimens)	12.03 [11.19–12.93] (n = 4)	8.00 [7.79–8.10] (n = 4)	13.63 [13.17–13.97] (n = 6)	9.60 [9.16–10.30] (n = 6)	19.37 [17.79–20.29] (n = 6)	9.52 [9.09–10.17] (n = 6)

*Data from Li *et al*. (2021).

Appendix 1.

Institute	No.	*Species*	LR	Material	Country	Locality	Horizon	Age	Remarks
Cervidae									
NMNS	PV-20160	Cervidae gen. et sp. indet.	L	M2	Japan	Dota, Kani City, Gifu Prefecture	upper Nakamura Fm	E. Miocene	
NMNS	PV-20161	Cervidae gen. et sp. indet.	L	mandible (m1–m3)	Japan	Dota, Kani City, Gifu Prefecture	upper Nakamura Fm	E. Miocene	
MFM	18126	Cervidae gen. et sp. indet.	R	m3	Japan	Dota, Kani City, Gifu Prefecture	upper Nakamura Fm	E. Miocene	
MNHN	BEI315	*Ligeromeryx praestans*	R	M2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	BEI534	*Ligeromeryx praestans*	R	M2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3023	*Ligeromeryx praestans*	R	M2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS2397	*Ligeromeryx praestans*	L	mandible (p4–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS2399	*Ligeromeryx praestans*	L	mandible (m2)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS363	*Ligeromeryx praestans*	L	mandible (m2–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3639	*Ligeromeryx praestans*	L	mandible (m2–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3666	*Ligeromeryx praestans*	L	mandible (p4–m1)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS858	*Ligeromeryx praestans*	L	mandible (m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	Lavé40	*Ligeromeryx praestans*	L	mandible (m2–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS223	*Ligeromeryx praestans*	R	mandible (m1–m2)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS2398	*Ligeromeryx praestans*	R	mandible (p4–m2)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3163	*Ligeromeryx praestans*	R	mandible (p3–m1)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3609	*Ligeromeryx praestans*	R	mandible (m1–m2)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS364	*Ligeromeryx praestans*	R	mandible (m2–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	Lavé39	*Ligeromeryx praestans*	R	mandible (m2–m3)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	Lavé43	*Ligeromeryx praestans*	R	mandible (p3–m1)	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS2492	*Ligeromeryx praestans*	L	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS269	*Ligeromeryx praestans*	L	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3173	*Ligeromeryx praestans*	L	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3592	*Ligeromeryx praestans*	L	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3596	*Ligeromeryx praestans*	L	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS270	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3000	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS349	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3591	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3593	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS6118	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS789	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS790	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS799	*Ligeromeryx praestans*	R	p4	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS1005	*Ligeromeryx praestans*	L	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3011	*Ligeromeryx praestans*	L	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3649	*Ligeromeryx praestans*	L	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3650	*Ligeromeryx praestans*	L	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS758	*Ligeromeryx praestans*	L	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3661	*Ligeromeryx praestans*	R	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3891	*Ligeromeryx praestans*	R	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS5318	*Ligeromeryx praestans*	R	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS5319	*Ligeromeryx praestans*	R	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS907	*Ligeromeryx praestans*	R	m1	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS244	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3006	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3596	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3600	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3887	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3893	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS5320	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS766	*Ligeromeryx praestans*	L	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS1965	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS253	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3049	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3598	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3653	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3665	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS763	*Ligeromeryx praestans*	R	m2	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS1911	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS2345	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3014	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3017	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS352	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS356	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS357	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS359	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS885	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS894	*Ligeromeryx praestans*	L	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS3170	*Ligeromeryx praestans*	R	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS737	*Ligeromeryx praestans*	R	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
MNHN	FS902	*Ligeromeryx praestans*	R	m3	France	Falun Touraine et Blaisois	MN3 or MN5	E. Miocene	
SNHM	4376	*Ligeromeryx colberti*		skeleton	China	Xiejiahe, Shandong Province	Shanwang Fm	E. Miocene	
BSPG	1979XV555	*Procervulus dichotomus*		skeleton	Germany	Rauscheröd	MN4	E. Miocene	
BSPG	1937II12203	*Procervulus praelucidus*	R	maxilla (M1–M3)	Germany	Wintershof-West	MN3	E. Miocene	
BSPG	1937II12236	*Procervulus praelucidus*	R	maxilla (P4–M3)	Germany	Wintershof-West	MN3	E. Miocene	
BSPG	1937II12018	*Procervulus praelucidus*	L	mandible (p3–m3)	Germany	Wintershof-West	MN3	E. Miocene	holotype
NMB	SO.654	*Procervulus praelucidus*	L	maxilla (P2–M3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.1284	*Procervulus praelucidus*	R	maxilla (M1–M3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.56	*Procervulus praelucidus*	L	mandible (m1–m2)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.55	*Procervulus praelucidus*	L	mandible (m1–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.1277	*Procervulus praelucidus*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.1299	*Procervulus praelucidus*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene	

NMB	SO.2299	*Procervulus praelucidus*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.3530	*Procervulus praelucidus*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.4070	*Procervulus praelucidus*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.1562	*Procervulus praelucidus*	L	mandible (p2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.267	*Procervulus praelucidus*	L	mandible (p3–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.4069	*Procervulus praelucidus*	L	mandible (p4–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.6185	*Procervulus praelucidus*	R	mandible (dp4–m1)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.2641	*Procervulus praelucidus*	R	mandible (m1–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.2300	*Procervulus praelucidus*	R	mandible (m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.2104	*Procervulus praelucidus*	R	mandible (p3–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.459	*Procervulus praelucidus*	R	mandible (p3–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.269	*Procervulus praelucidus*	R	mandible (p4–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	Sth.245a	*Euprox furcatus*	L	maxilla (M1–M3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.172a	*Euprox furcatus*	L	maxilla (P2–M3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.170a	*Euprox furcatus*	R	maxilla (P3–M3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.227	*Euprox furcatus*	R	maxilla (P3–M3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.246a	*Euprox furcatus*	L	mandible (m2–m3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.223	*Euprox furcatus*	L	mandible (p2–m3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.250a	*Euprox furcatus*	R	mandible (m2–m3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.224	*Euprox furcatus*	R	mandible (p4–m3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	Sth.747	*Euprox furcatus*	R	mandible (p4–m3)	Germany	Steinheim am Albuch	MN7/8	M. Miocene	
NMB	SS.749	*Dicrocerus elegans*	L	maxilla (M1–M3)	France	Sansan	MN6	M. Miocene	
NMB	SS.748	*Dicrocerus elegans*	L	maxilla (P3–M3)	France	Sansan	MN6	M. Miocene	
NMB	SS.3993	*Dicrocerus elegans*	R	maxilla (M2–M3)	France	Sansan	MN6	M. Miocene	
NMB	SS.39	*Dicrocerus elegans*	R	mandible (m1–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.5402	*Dicrocerus elegans*	R	mandible (m1–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.10	*Dicrocerus elegans*	R	mandible (p2–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.5451	*Dicrocerus elegans*	R	mandible (p3–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.11	*Dicrocerus elegans*	R	mandible (p4–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.5401	*Dicrocerus elegans*	R	mandible (p4–m3)	France	Sansan	MN6	M. Miocene	
IVPP	V8589.4	*Dicrocerus grangeri*	L	mandible (m2–m3)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.1	*Dicrocerus grangeri*	R	mandible (m1–m2)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.2	*Dicrocerus grangeri*	R	mandible (m1–m2)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.3	*Dicrocerus grangeri*	R	mandible (m2–m3)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8591.1	*Dicrocerus grangeri*	R	mandible (m2–m3)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8590	*Dicrocerus grangeri*	R	mandible (p3–p4)	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.?	*Dicrocerus grangeri*	L	m1	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.24?	*Dicrocerus grangeri*	L	m1	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.28	*Dicrocerus grangeri*	L	m1	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.?	*Dicrocerus grangeri*	R	m1	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.16	*Dicrocerus grangeri*	L	m1/2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.4?	*Dicrocerus grangeri*	R	m1/2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.?	*Dicrocerus grangeri*	L	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.?	*Dicrocerus grangeri*	L	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.14	*Dicrocerus grangeri*	L	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.23	*Dicrocerus grangeri*	L	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.26	*Dicrocerus grangeri*	L	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.21	*Dicrocerus grangeri*	R	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.6	*Dicrocerus grangeri*	R	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.8	*Dicrocerus grangeri*	R	m2	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.12	*Dicrocerus grangeri*	L	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.17	*Dicrocerus grangeri*	L	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.18	*Dicrocerus grangeri*	L	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.10	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.11	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.12	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.13	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.26	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.31	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8589.5	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8592	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
IVPP	V8593	*Dicrocerus grangeri*	R	m3	China	Xinjiang Autonomous Region	Halamagai Fm	M. Miocene	
NMJH	A-636-1-1-9	*Dicrocerus? tokunagai*	R	mandible (p4-m2)	Japan	Kusano-mura, Iwaki City, Ibaraki Prefecture	Misawa Fm	E. Miocene	holotype of *Dicrocerus tokunagai*
ICM	YH-3412	*Dicrocerus? tokunagai*	L	mandible (m1–m3)	Japan	Kamiogawa-mura, Daigo-cho, Ibaraki Prefecture	Kitatage/Asakawa Fm	E. Miocene	
Palaeomerycidae									
IGPS	22059	cf. *Palaeomeryx minoensis*	R	mandible (p3-m2)	Japan	Banjo-bora, Mitake-cho, Kani-gun, Gifu Prefecture	Hiramaki Fm	E. Miocene	cast of the holotype
IVPP	V7730.1	*Sinomeryx tricornis*	R	mandible (p4–m3)	China		Shanwang/Halamagai Fm	E./M. Miocene	
IVPP	V8594.2	*Sinomeryx tricornis*	L	m1	China		Shanwang/Halamagai Fm	E./M. Miocene	
IVPP	V8594.1	*Sinomeryx tricornis*	L	m2	China		Shanwang/Halamagai Fm	E./M. Miocene	
BSPG	1893I501	'*Palaeomeryx*' *kaupi*	R	mandible (p4–m3)	Germany	Georgensgmünd	MN5	M. Miocene	syntype
BSPG	1893I502	'*Palaeomeryx*' *kaupi*	L	m1/m2	Germany	Georgensgmünd	MN5	M. Miocene	syntype
NMB	SO.641	'*Palaeomeryx*' cf. *kaupi*	L	mandible (p2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.408	'*Palaeomeryx*' cf. *kaupi*	L	mandible (p4–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.37	'*Palaeomeryx*' cf. *kaupi*	R	mandible (p2–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.563	'*Palaeomeryx*' cf. *kaupi*	R	mandible (p4–m3)	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SO.3919	'*Palaeomeryx*' cf. *kaupi*	L	m1	France	Artenay-Autroche	MN3	E. Miocene	
NMB	SS.4963	'*Palaeomeryx*' *bojani*	L	mandible (m1–m2)	France	Sansan	MN6	M. Miocene	
NMB	SS.51	'*Palaeomeryx*' *bojani*	L	mandible (m2–m3)	France	Sansan	MN6	M. Miocene	
NMB	SS.158	'*Palaeomeryx*' *bojani*	R	mandible (m2–m3)	France	Sansan	MN6	M. Miocene	
BSPG	1893I28	'*Palaeomeryx*' *bojani*	L	m2–m3	Germany	Georgensgmünd	MN5	M. Miocene	syntype
MNHN	SI166	'*Palaeomeryx*' *magnus*	L	mandible (m1–m3)	France	Malartic, Simorre	MN6	M. Miocene	
MNHN	SML60	'*Palaeomeryx*' *magnus*	L	mandible (p4–m3)	France	Malartic, Simorre	MN6	M. Miocene	
MNHN	SML44	'*Palaeomeryx*' *magnus*	R	p4	France	Malartic, Simorre	MN6	M. Miocene	
MNHN	SI168	'*Palaeomeryx*' *magnus*	L	m2	France	Malartic, Simorre	MN6	M. Miocene	
Amphimoschus									
FPDM	V-8462	*Amphimoschus* sp.	R	mandible (m1m3)	Japan	Koniu, Fukui City, Fukui Prefecture	Kunimi Fm	M. Miocene	

NMB	SO.4071	*Amphimoschus ponteleviensis*	L	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene
NMB	SO.3511	*Amphimoschus ponteleviensis*	R	mandible (m1–m3)	France	Artenay-Autroche	MN3	E. Miocene
NMB	SO.72	*Amphimoschus ponteleviensis*	R	mandible (m1–m3)	France	Artenay-Autroche	MN3	E. Miocene
NMB	SO.74	*Amphimoschus ponteleviensis*	R	mandible (m2–m3)	France	Artenay-Autroche	MN3	E. Miocene
NMB	SO.3510	*Amphimoschus ponteleviensis*	R	mandible (p2–m3)	France	Artenay-Autroche	MN3	E. Miocene
NMB	SO.4079	*Amphimoschus ponteleviensis*	R	mandible (p3–m3)	France	Artenay-Autroche	MN3	E. Miocene