Taxonomic revision of the holotype of Proboselaphus watasei Matsumoto, 1915 (Bovidae, Artiodactyla) from Chuanyu area, China Postprint

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Abstract

A taxonomic revision of Proboselaphus watasei Matsumoto, 1915 (Bovidae, Artiodactyla) from the Pleistocene of Chuanyu area, China demonstrates that this genus and species names are invalid. The holotype with a skull and mandibles was recently rediscovered in the fossil collection by Nobuo Naora, which is housed in the National Museum of Japanese History, Chiba Prefecture, Japan. Proboselaphus watasei was described as a closely-related species to living nilgai, or Boselaphus tragocamelus, in South Asia, based on general characteristics of pecorans, such as small bony horn-cores and hypsodont cheek teeth. However, the cranial and dental morphologies re-examined in the present study clearly show that the holotype has cervid-specific characteristics: e.g., the fronto-parietal surface curving dorsally, the basioccipital with a triangular outline, and molars with isolated anterior and posterior lobes. The molars of the holotype are comparable to those of Cervus unicolor, in having strong accessary structures (or spurs, cingulums/cingulids, and styles/stylids), and are as large as those of Cervus cf. C. unicolor from the Pleistocene deposits in southern China. This taxonomic change suggests that any crown-boselaphins had not dispersed into East Asia since the Pleistocene.

Full Text

Preamble

Taxonomic revision of the holotype of *Proboselaphus watasei* Matsumoto, 1915 (Bovidae, Artiodactyla) from Chuanyu area, China

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Abstract

A taxonomic revision of *Proboselaphus watasei* Matsumoto, 1915 (Bovidae, Artiodactyla) from the Pleistocene of the Chuanyu area, China, demonstrates that this genus and species name is invalid. The holotype, comprising a skull and mandibles, was recently rediscovered in the fossil collection of Nobuo Naora, housed in the National Museum of Japanese History, Chiba Prefecture, Japan. *Proboselaphus watasei* was originally described as a species closely related to the living nilgai (*Boselaphus tragocamelus*) of South Asia, based on general pecoran characteristics such as small bony horn-cores and hypsodont cheek teeth. However, re-examination of cranial and dental morphologies in the present study clearly reveals cervid-specific characteristics: e.g., the fronto-parietal surface curving dorsally, the basioccipital with a triangular outline, and molars with isolated anterior and posterior lobes. The molars of the holotype are comparable to those of *Cervus unicolor* in having strong accessory structures (spurs, cingulums/cingulids, and styles/stylids) and are as large as those of *Cervus* cf. *C. unicolor* from Pleistocene deposits in southern China. This taxonomic revision suggests that no crown-boselaphins dispersed into East Asia during the Pleistocene.

Keywords: China, Quaternary, mammal, Bovidae, Cervidae

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1. Introduction

Late Cenozoic mammalian fossil localities in the Chuanyu area (Sichuan and Chongqing), China have been surveyed by various overseas paleontologists since the 19th century (Owen, 1870; Koken, 1885; Schlosser, 1903; Matsumoto, 1915). A substantial mammalian fossil collection was obtained by the Central Asiatic Expeditions of the American Museum of Natural History in the 1920s, which became known as the Yanjinggou (= Yenchingkou) fauna from Wanxian and represents the Chinese Pleistocene mammals (Matthew and Granger, 1923; Osborn, 1929; Granger, 1932; Colbert and Hooijer, 1953). The Yanjinggou fauna comprises a mixture of extant and extinct taxa, including *Stegodon orientalis*, *Palaeoloxodon namadicus*, *Hesperotherium* (or *Nestoritherium*) *sinense*, and *Tapirus* (or *Megatapirus*) *augustus*. This combination of mammalian species indicates that the Yanjinggou fauna dates primarily to the middle Pleistocene or later stages, correlating with mammalian fossil assemblages from the Boulder Conglomerate in South Asia and the Zhoukoudian fissures in North China (Colbert and Hooijer, 1953; Chow, 1957; Pei, 1957; Kahlke, 1961; Li, 1981), though the lowest part may extend back to the lower Pleistocene (Teilhard de Chardin et al., 1935; Chen et al., 2013).

While the contributions of Colbert and Hooijer (1953) provided foundational systematic descriptions of the Yanjinggou mammals, previous papers contain important but enigmatic findings that warrant taxonomic reconsideration. Matsumoto (1915) described the genus *Proboselaphus* (Boselaphini, Bovidae, Artiodactyla), including *P. watasei* and *P. liodon*, which he considered closely related to extant *Boselaphus tragocamelus* in South Asia. His proposals have been frequently referenced in discussions of Asian boselaphin evolution (Pilgrim, 1939; Bibi et al., 2009; Nishioka and Vidthayanon, 2018; Nishioka et al., 2019). However, the taxonomy of *Proboselaphus* has not been re-examined since Matsumoto (1915) because he did not specify where the type specimens were housed.

In the present study, we systematically revise the taxonomic position of the holotype skull of *P. watasei*, noting the current depository and condition of the fossil materials. As this skull was tentatively identified as a cervid species in previous works (Harunari, 2008, 2017), it requires careful comparison with both bovids and cervids. Additionally, we provide preliminary comments on the other species, *P. liodon*.

Institutional abbreviations: BNHS, Bombay Natural History Society, Mumbai, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMB, Natural History Museum of Basel, Basel, Switzerland; NMJH, National Museum of Japanese History, Sakura, Japan; NMNS, National Museum of Nature and Science, Tokyo, Japan.

2. Material and Methods

Examined material. The holotype of *Proboselaphus watasei* Matsumoto (1915), comprising a skull with left and right mandibles (Fig. 1 [Figure 1: see original paper]), was taxonomically re-examined in this study. According to Matsumoto (1915), this holotype was collected from Wanxian in the Sichuan basin by T. Sakawa at least before 1915 and subsequently donated to Prof. Shozaburo Watase at the Zoological Institute, Faculty of Science, Imperial University of Tokyo (now the University of Tokyo), Japan. The holotype was recently rediscovered in Prof. Nobuo Naora's fossil collection, currently housed in the National Museum of Japanese History, Sakura City, Chiba Prefecture, Japan. The specimen had been intermixed with fossil assemblages from Quaternary deposits in Kuzuu Quarry, northeastern Japan, and was catalogued tentatively as 'a large deer skull (A-636-1-1-18-9-25)' and 'deer mandibles (A-636-1-1-18-9-6 and

A-636-1-1-18-9-8)’ (Naora, 1997; Harunari, 2008). Harunari (2017) suggested that the holotype was transferred to Prof. Shigeyasu Tokunaga, who supervised Naora at Waseda University. Although there are no reports or records of this specimen after Matsumoto’ s (1915) initial study, Naora (1954) seemingly compared the holotype of *P. watasei* with a ruminant mandible from the middle Pleistocene of Matsugae Cave, Fukuoka Prefecture, Japan.

According to Matsumoto (1915), the fossils from the Sichuan basin were divided into two faunas based on species composition and preservation. *Proboselaphus* species were categorized in the ‘Upper Pliocene’ group, along with *S. orientalis* and *Aceratherium blanfordi* var. *hipparionum*, which were recovered from brown clay in limestone. While the geological timescale has since been revised, the *S. orientalis* fauna is certainly younger than the Hipparion stage, dating primarily to the late Miocene to early Pleistocene in Asia.

The National Museum of Japanese History currently possesses only the skull with left and right mandibles of *P. watasei* and two fragmentary molars of *Stegodon orientalis* from the Sichuan basin, as most other fossil specimens described by Matsumoto (1915), including *P. liodon*, have been missing since then. Matsumoto’ s collection likely originated from a Chinese drugstore or fossil trader who purchased specimens from Chinese farmers working in limestone fissures or pits at Yanjinggou (Colbert and Hooijer, 1953), and is not associated with any geological or locality information.

Comparative material. We examined the following specimens for comparison with the holotype. **Living species:** *Alces alces* (NMB C.2198, C.3530); *Bos taurus* (authors’ private specimen); *Boselaphus tragocamelus* (BNHS 18183, 18184, 18186); *Cervus elaphus* (NMB 7551, 8267); *Cervus nippon* (NMNS M11391, M16022); *Cervus (Rusa) unicolor* (IVPP OV 567, OV 1210; NMNS M1146, M31214); *Cervus (Rusa) timorensis* (IVPP OV 1101); *Elaphurus davidianus* (NMNS M13066, M33873). **Fossil species from China:** *Cervus (Rusa)* cf. *C. unicolor* from Longgudong (Middle Pleistocene), Hubei (IVPP V 13469), Gongjishan (Middle or Late Pleistocene), Guangxi (IVPP V 19323), and Hejiang Cave (Middle Pleistocene), Guangxi (IVPP V 19323); *Cervus (Rusa) yunnanensis* from Sanhe Cave (Early Pleistocene), Guangxi (IVPP V 17102).

Methods. The classification of Cervidae follows Groves and Grubb (2011), with Eld’ s deer (*Panolia eldii*) included in the genus *Cervus* following Pitra et al. (2004). Groves and Grubb (2011) recognized six genera (*Dama*, *Axis*, *Rucervus*, *Cervus*, *Panolia*, and *Elaphurus*) in the tribe Cervini. While *Panolia eldii* was tentatively placed in the genus *Rucervus* (e.g., Grubb, 2005), it is currently included in *Cervus* (Pitra et al., 2004) or treated as an independent genus, *Panolia* (Groves, 2006). Recent molecular studies of cervids prefer lumping the genera *Cervus*-*Panolia* (possibly including *Elaphurus*) under a single genus, *Cervus* (e.g., Gilbert et al., 2006; Hu et al., 2019).

Dental terminology follows Bärmann and Rössner (2011) (Fig. 2 [Figure 2: see original paper]). Abbreviations are as follows: dP, upper deciduous premolar; M/m, upper/lower molar. Tooth measurements were obtained as maximum anteroposterior crown length and maximum buccolingual crown widths of anterior and posterior lobes.

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3. Systematic Paleontology

Artiodactyla Owen, 1848
Cervidae Goldfuss, 1820
Cervus Linnaeus, 1758
Cervus cf. *C. unicolor* Kerr, 1792 (Fig. 3 [Figure 3: see original paper])

Synonym. *Proboselaphus watasei* Matsumoto, 1915, p. 13, pl. 6–7.

Material. NMJH A-636-1-2-10-1-25 (previous numbers: A-636-1-1-18-9-25, A-636-1-1-18-9-6, and A-636-1-1-18-9-8), a skull with dP2-dP4 and M1-M2, a right mandible with m1-m2, and a left mandible with m1-m2, probably from the Pleistocene of Wanzhou (formerly Wanxian), Chongqing. Hereafter, these are referred to as the Matsumoto specimens.

Measurements. See Appendix 1.

Description. The fossil surface exhibits a whitish or orange coloration, with light-brown calcareous sediments from a limestone area. The skull was unnaturally damaged and eroded in the nasal and occipital regions. The maxillary portion is strongly compressed buccolingually and distorted from its original position. The skull belongs to a juvenile individual with deciduous premolars (dP2-dP4) and erupting molars (M1-M2).

The rostrum and neurocranium are anteroposteriorly elongate. The dorsal surface of the fronto-parietal region curves with a peak at the bregma. The frontal bone is weakly depressed between the orbits. A slender supraorbital foramen and small pit open above the right orbit.

A slender cylindrical bony appendage, or pedicle, follows immediately behind the posterodorsal part of the right orbit. The postcornual wall overhangs, forming a shallow temporal fossa. In the right orbit, a molar (possibly right M3) is buried in matrix. The parietal bone is smooth (without a rugose surface) and bears weak temporal crests extending from the postcornual part to the occipital bone. The supraoccipital bone shows a trapezoidal outline in dorsal view. The posterior surface of the occipital is narrow mediolaterally and has a weak median nuchal line. The occipital condyles are relatively large, with maximum intercondylar width nearly equal to brain case width. The basioccipital is flat and triangular, lacking deep constrictions or large tubercles.

The upper deciduous premolars are broken and strongly worn on both left and right sides. dP2 is constricted around the middle of the lingual wall, with a well-developed anterior lobe elongated anteroposteriorly. dP3 consists of a rectangular anterior lobe and triangular posterior lobe. The anterior cingulum is strong, extending to the occlusal surface. dP4 and upper molars are quadrate in occlusal view, with the anterior lobe separated from the posterior lobe by a deep valley (especially between the postprotocrista and premetaconulecrista).

In M1 or M2, the postprotocrista branches at the posterior end as a tiny fold into the anterior fossa. The preprotocrista of M2 also has one or two short folds extending into the anterior fossa. The postprotocrista approaches the anterior end of the premetaconulecrista but does not fuse with it. A clear metaconule fold extends from the postmetaconulecrista. The postmetaconulecrista connects approximately with the postmetacrista. The postparacrista connects with the lingual wall of the premetacrista. Buccal ribs and styles project prominently from the base (cervical line) to the occlusal surface. The mesostyle shows an S-shaped curve in buccal view. The entostyle is strong but shorter than crown height. The molars are moderately high-crowned: buccal crown height is nearly equal to anteroposterior occlusal length.

The mandibles preserve the posterior mandibular body with m1-m2 and the dorsal part of the ramus. According to Matsumoto (1915), the left mandible originally preserved the coronoid process with the articular condyle of the ascending ramus and the anterior horizontal ramus with dp4, while the right mandible originally preserved dp4 in situ on the anterior horizontal ramus (Fig. 1). These portions are missing in the current collection. The mandibular angle forms an obtuse corner and does not project ventrally or posteriorly. The mandibular foramen is situated on the extension of the occlusal surface. The buccal surface of the right mandibular body was artificially removed after Matsumoto’ s (1915) original description.

The lower molars, m1 and m2, are erupting. Each tooth comprises two triangular prismatic lobes. The anterior lobe has a strong anterior cingulid, forming a short cristid on m1 or a pillar on m2. The external postprotocristid is absent. The internal postprotocristid connects with the buccal wall of the internal postmetacristid and the anterior end of the preentocristid. The anterior end of the prehypocristid is isolated from any cristids by a deep valley. A shallow gap occurs between the postentocristid and posthypocristid. An accessory fold extends posterobuccally from the entoconid into the posterior fossa. The entostylid is pillar-shaped, reaching half of crown height. The lingual surface is well marked by distinct ribs and stylids. A tiny pillar occurs on the lingual base of m1.

Comparisons. Matsumoto (1915) established the genus *Proboselaphus* as closely related to *Boselaphus*, identified by “bovine” characteristics such as widely separated small horn-cores with triangular cross-section and hypsodont molars. Moreover, he believed *Proboselaphus* possessed some “Tetracerus-like” cranial characteristics: i.e., a more convex apical surface of the skull, weak temporal crests of the parietals, and less hypsodont molars. These characteristics are observed commonly in many cervid species, but Matsumoto only made comparisons with boselaphin bovids in his paper.

The Matsumoto specimens differ from bovid skulls, including *Boselaphus tragocamelus*, in having a dorsally curving fronto-parietal surface, supraorbital foramina above the anterior orbits, a long brain case, and a triangular basioccipital bone. The cheek teeth of the Matsumoto specimens undoubtedly exhibit a cervid dental pattern, characterized by isolation between anterior and posterior lobes, a strongly curved mesostyle in buccal view, well-developed spurs, and postentocristid-posthypocristid isolation. Moreover, the bifurcated postprotocrista is rarely found in bovids.

The skull and mandibles of the Matsumoto specimens were tentatively identified as a megacerin deer and *Alces alces*, respectively, and incorrectly documented as collected from Kuzuu Quarry, northeastern Japan (Naora, 1997:pl. 18; Harunari, 2008). As these previous observations indicated, the present reexamination confirms that the holotype of *P. watasei* should be reclassified as a young male deer belonging to the family Cervidae. Compared with Pleisto-Holocene cervids, the teeth of the Matsumoto specimens show more advanced morphology (e.g., high-crowned teeth with well-projected ribs and styles/stylids) than any species of tribes Muntiacini, Rangiferini, Capreolini, Alceini, and Megacerini. The molars of megacerin deer such as *Sinomegaceros* from the Pleistocene of China and Japan rarely have additional crests/spurs and cingulums on the occlusal surface (Naora, 1997; Vislobokova, 2013; Okumura et al., 2016). The molars of *Alces alces* also lack these characteristics and have a concave buccal surface without ribs on the posterior lobe. In contrast, such enamel surface complexities are prominently present in the Matsumoto specimens.

Among comparative Cervini material, the Matsumoto specimens resemble the teeth of *Cervus (Rusa) unicolor* in the following dental morphological features: molars of *C. unicolor* are characterized by strong spurs on the fossae, slender entostyles/ectostylids, and prominently projected cingulums/cingulids on anterior and posterior sides (Heckeberg, 2020). The cristid-like anterior cingulid is a diagnostic feature for the subgenus *Rusa*, as it is consistently present in *C. unicolor* (IVPP OV 567; NMNS M31214) and *C. timorensis* (IVPP OV 1101). This anterior cingulid also appears in *C. (Panolia) eldii* and *Rucervus duvaucelii* (Heckeberg, 2020), but is absent in *C. nippon* (NMNS M11391, M16022), *C. elaphus* (NMB 7551, 8267), and *Elaphurus davidianus* (NMNS M1168, M13066, M33873). Moreover, *E. davidianus* has more developed and flatter entostyles on upper molars than *C. unicolor*. *Axis* and *Dama* also lack strong anterior cingulids. *Rucervus duvaucelii* differs from the Matsumoto specimens in having upper molars with well-developed anterior cingulums, a concave posterolingual wall between the protocone and metaconule, and deeply projected buccal ribs and styles.

The Matsumoto specimens share many dental characteristics with *C. unicolor* and *C. eldii*. Based on fossil materials from the middle Pleistocene of Thailand, all tooth measurements of *C. unicolor* are clearly larger than those of *C. eldii* (Suraprasit et al., 2016). The Matsumoto specimens are 20%–30% larger than each upper and lower molar of *C. eldii* illustrated in Figure 19 [Figure 19: see original paper] of Suraprasit et al. (2016). In tooth measurements, the Matsumoto specimens are more comparable to cheek teeth of *C. unicolor* than to *C. eldii* (Fig. 4 [Figure 4: see original paper]; Appendices 1 and 2).

In China, *C. unicolor* is the only living species belonging to the subgenus *Rusa*, though several fossil species such as *C. elegans* (Teilhard de Chardin and Piveteau, 1930) and *C. yunnanensis* Lin et al., 1978 have been recovered from the lower Pleistocene (e.g., Dong, 1993; Leslie, 2011). These fossil species are distinguished by antler morphology, and their dental characteristics remain poorly defined due to the absence of complete skulls.

Chen (2004) described *Cervus* cf. *C. unicolor* from the lower Pleistocene of Longgudong Cave, southern China, which is slightly larger than living *C. unicolor* in both antler and tooth size. This author also allocated a smaller form to *C. yunnanensis* based on comparisons of numerous isolated teeth. Living *C. unicolor* is seemingly intermediate in molar length between *C. yunnanensis* and *Cervus* cf. *C. unicolor* from Longgudong Cave, though these species overlap broadly (Fig. 4). Other authors have identified isolated teeth of *Cervus* cf. *C. unicolor* and *C. yunnanensis* from Pleistocene cave deposits (e.g., Dong et al., 2011, 2014; Zhang et al., 2014), but we could not recognize any critical difference in dental morphology between these species. Compared solely with materials from Longgudong Cave, the Matsumoto specimens correspond to the maximum size group of *Cervus* cf. *C. unicolor* and are certainly larger than living *C. unicolor* (Fig. 4).

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4. Discussion

The taxonomic position of the holotype of *Proboselaphus watasei* is revised to *Cervus* cf. *C. unicolor*. Matsumoto (1915) described another species, *P. liodon*, based on three isolated teeth, though these specimens are currently missing. Judging from his plate illustrations, one of the upper molars exhibits typical bovid characteristics, showing a straight mesostyle and robust entostyle (Fig. 5 [Figure 5: see original paper]). It is generally impossible to classify bovid species based on isolated teeth, and the characteristics of *P. liodon* mentioned by Matsumoto (1915) are shared by all Quaternary bovids. Therefore, there is no evidential material to define the genus *Proboselaphus*, and this name should be regarded as invalid.

The crown group of Boselaphini, including *Boselaphus* and *Tetracerus*, is currently distributed in South Asia (the Indian subcontinent). Their origin and evolution primarily occurred in South and Southeast Asia, based on fossil records from Neogene and Quaternary localities (e.g., Pilgrim, 1939; Nishioka and Vidthayanon, 2018; Nishioka et al., 2019). The latter two authors suggested that faunal separation between South Asia and Southeast Asia increased since the late Miocene due to formation of a biogeographical boundary between the regions, and that crown-boselaphins were possibly isolated in South Asia before the Quaternary. The fossil record of *Proboselaphus* from China, which was believed to represent an ancestral form of *Boselaphus*, conflicted with this paleobiogeographical dispersal scenario for Boselaphini, but this contradiction is completely resolved by the present taxonomic revision.

The Matsumoto specimens (except for the aforementioned bovid molars) are classified as a species of *Cervus* similar to *C. unicolor* among various *Cervus* species in the Pleistocene of China. This result is acceptable because the Yanjinggou fauna commonly includes remains of *C. unicolor* (Colbert and Hooijer, 1953). More detailed taxonomic identification of the Matsumoto specimens will require rigorous examination of size variation among *Cervus* species in the Quaternary.

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Note: Figure translations are in progress. See original paper for figures.