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<td>Author(s)</td>
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Kyoto University
Early Pleistocene Javan rhinoceros
from the Irrawaddy Formation, Myanmar

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Abstract

We report dental fossils of Javan rhinoceros, \textit{Rhinoceros sondaicus} (Mammalia, Perissodactyla, Rhinocerotidae), discovered from the upper part of the Irrawaddy Formation, the lower Pleistocene of central Myanmar. This is the first discovery of \textit{R. sondaicus} from the Irrawaddy Formation, and these materials are possibly to be the oldest fossil record of this species in the world. The present materials consist of two fragmentary maxillae with \textit{M}\textsuperscript{3}. They are referable to those of \textit{Rhinoceros sondaicus} in having the following characteristics on the upper molars: moderately developed molar crochet, subhypsodonty, absence of the molar crista and antecrochet, absence of the protocone fold, absence of the metacone bulge on \textit{M}\textsuperscript{2}, sinuosity of the ectoloph, strong molar parastyle fold, and deeper median valley than the posterior valley. The discovery of early Pleistocene \textit{Rhinoceros sondaicus} in Myanmar fills geographical and chronological gaps between the late Miocene \textit{Gaindartherium} (a probable ancestor of the genus \textit{Rhinoceros}) from Indo-
Pakistan and middle Pleistocene \textit{R. sondaicus} from Java and Sumatra. It suggests that this species originated as early as early Pleistocene in continental Asia.

Introduction

The living rhinocerotid genus \textit{Rhinoceros} consists of two species, \textit{R. sondaicus} and \textit{R. unicornis}, and its geographical distribution is restricted. \textit{Rhinoceros sondaicus} (Javan rhinoceros = Asian lesser one-horned rhinoceros) inhabits in tropical rain forests of Indonesia and Vietnam; and \textit{R. unicornis} (Indian rhinoceros = Asian greater one-horned rhinoceros) lives in northern India. On the other hand, this genus was widely distributed in the Pleistocene of Asia: materials of fossil \textit{Rhinoceros} have been found in the Pleistocene of India, China, and Southeast Asia (Colbert, 1935, 1938; Hoojer, 1946; Colbert and Hooijer, 1953; Tougard, 2001).

In Myanmar, five species of the Family Rhinocerotidae (\textit{Aceratherium lydekkeri},...
Aceratherium perimense, Brachypotherium sp., Diceratherium naricum, and Rhinoceros sivalensis) have been recorded (Colbert, 1938; Cotter, 1938). In this article, we first report dental fossil specimens of Rhinoceros sondaicus discovered from the early Pleistocene deposits of the Irrawaddy Formation in near Pauk township, Magway Division (Figure 1). Although R. sondaicus was widespread in the upper middle Pleistocene to the upper Pleistocene of Laos, Vietnam, Cambodia, Thailand, Java, Sumatra, and Borneo, it is unknown in the early Pleistocene or older deposits.

Irrawaddy Formation (Fossil Wood Group: Theobald, 1837; Irrawaddian Series: Noetling, 1900) mainly consists of fluvatile sediments, transported from the Eastern Highlands (Shan Plateau), Eastern Himalayas, and Western Ranges (Rakhine Ranges) (Drury, 1987). It occurs extensively throughout central Myanmar and yields the remains of terrestrial and aquatic vertebrates. Although Bender (1983) used the term “Irrawaddy Group”, Myanmar geologists widely accept “Irrawaddy Formation” introduced by Aung Khin and Kyaw Win (1969). In this paper, we use the term “Irrawaddy Formation”.

At present, four mammalian order including 14 families are recorded from this formation and it can be correlated with the Siwalik Group of Indian Subcontinent (Takai et al., 2006). According to lithological and paleontological criteria, Irrawaddy Formation is traditionally divided into two parts, lower and upper parts. Although the stratigraphic position of this formation has not been fully understood due to the lack of geological age calibrated from radioisotope and paleomagnetism, some age estimates has been done using correlations of the vertebrate faunas. It has been suggested that the lower part of the formation is the late Miocene to Pliocene, and that the upper part is the early Pleistocene (Colbert, 1943; Bender,
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Based on this age estimate, *Rhinoceros sondaicus*, discovered from the upper part of the Irrawaddy Formation, is likely to be the oldest fossil record of this species in the world.

**Abbreviations**

NMMP-KU-IR, National Museum - Myanmar - Paleontology - Kyoto University - Irrawaddy (stored in the National Museum, Yangon, Myanmar, and in the Department of Geology, University of Yangon, Yangon, Myanmar).

**Systematic paleontology**

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Subfamily Rhinocerotinae Owen, 1845
Tribe Rhinocerotini Owen, 1845
Subtribe Rhinocerotina Owen, 1845
Genus *Rhinoceros* Linnaeus, 1758

*Rhinoceros sondaicus* Desmarest, 1822

*Newly discovered material.*—NMMP-KU-IR 0404, a right maxilla with M\(^1\)-M\(^3\); and NMMP-KU-IR 0408, a left maxilla with M\(^1\)-M\(^3\).

*Locality of the newly discovered material.*—Near Pauk Township, Magway Division, central Myanmar (Figure 1).
Formation and age of the newly discovered material.—The upper part of the Irrawaddy Formation; early Pleistocene (Colbert, 1943).

Description.—We follow the dental terminologies for rhinoceros by Guérin (1980) (Figure 3). Dental measurements are taken at the base of the crown according to Hooijer (1946). Dental measurements are given in Table 1. For M3, ectometaloph is measured for the external anteroposterior diameter.

In NMMP-KU-IR 0404, the teeth are subhypodont, and the crowns are moderately worn. The parastyle of M1 and crown portion of M3 are lost. M1 and M2 are roughly quadrate although M3 is triangular in occlusal view. The crochet is moderately developed, and molar crista and antecrochet are absent. The parastyle fold is strong. On M1, the protocone shows backward extension with no protocone constrictions. On M2, there is a wide median valley without protocone bulge and deeper median valley than posterior valley. There is no tubercle in this specimen. The protocone fold is absent in all molars. The anterior and posterior cingula are developed on the all molars although there is no lingual cingulum. The posterior cingulum is divided by a V-shaped incision, and shows crenulations. The ectoloph is concave in the posterior part showing sinuosity (Figure 2A).

In NMMP-KU-IR 0408, the teeth are roughly quadrate in occlusal view, and the crowns are moderately worn. M3 has a triangular shaped outline, and a small antecrochet is observed. There is a moderately developed crochet on each molar, and these teeth lack crista and antecrochet. A small tubercle is present in posterior valley of M1. The protocone bulge is absent, showing a wide median valley. The dental characteristic of this specimen is similar to the above described specimen although the former is smaller than the latter (Figure 2B).

Comparison and Discussion

Dental characteristics of these rhinocerotid materials from Myanmar are identical to those of *Rhinoceros sondaicus*, which have been reported from the middle Pleistocene to Recent of Java and Sumatra. They share the following dental characteristics: presence of the strong parastyle fold, concavity of the posterior part of the ectoloph showing sinuosity,
Table 1. Dental measurements of *Rhinoceros sondaicus*. Abbreviations: ap., anteroposterior; ext., external; int., internal; tr., tranverse. * = estimated measurements.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>NMMP-KU-IR 0404 (right)</th>
<th>NMMP-KU-IR 0408 (left)</th>
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<tbody>
<tr>
<td>M1</td>
<td>ext. ap. diameter *53.14</td>
<td>46.56</td>
</tr>
<tr>
<td></td>
<td>int. ap. diameter 38.76</td>
<td>34.58</td>
</tr>
<tr>
<td></td>
<td>protoloph length 61.26</td>
<td>62.01</td>
</tr>
<tr>
<td></td>
<td>metaloph length 59.25</td>
<td>57.82</td>
</tr>
<tr>
<td>M2</td>
<td>ext. ap. diameter 52.32</td>
<td>53.28</td>
</tr>
<tr>
<td></td>
<td>int. ap. diameter 39.30</td>
<td>35.78</td>
</tr>
<tr>
<td></td>
<td>protoloph length 68.79</td>
<td>62.64</td>
</tr>
<tr>
<td></td>
<td>metaloph length 59.44</td>
<td>46.64</td>
</tr>
<tr>
<td>M3</td>
<td>ext. ap. diameter *54.36</td>
<td>52.81</td>
</tr>
<tr>
<td></td>
<td>int. ap. diameter *43.04</td>
<td>43.80</td>
</tr>
<tr>
<td></td>
<td>protoloph length *45.69</td>
<td>55.54</td>
</tr>
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absence of the crista and antecrochet, and presence of the moderately developed crochet (Hooijer, 1946; Pocock, 1945). The present specimens are also similar to *Rhinoceros sinensis* from the Pleistocene of China in having the following characteristics: a backward extension on the protoloph, presence of the parastyle fold, and sinuosity of the ectoloph. However, *R. sinensis* differs from the Myanmar fossil rhino in showing generally larger size, and in having more hypsodont molars, a stronger molar crochet, and crista or small enamel projection into medifossette (Colbert, 1942). *Rhinoceros unicornis* from the middle Pleistocene to Recent of Java and India differs from the present specimens in presence of a flattened molar ectoloph and of a well-developed molar crista, which unites with crochet to form medifossette (Laurie *et al.*, 1983). *Rhinoceros sivalensis* from the Plio-Pleistocene of Indo-Pakistan is distinct from the fossil rhinoceros of Myanmar in having a distinct crochet which may unite with the protoloph to enclose a fossette and in being larger in size (Colbert, 1942). The fossil rhinoceros from Myanmar shares some primitive characteristics with the late Miocene genus *Gaindatherium* from the Siwaliks of Indo-Pakistan, such as sinuosity of the ectoloph and the prominent parastyle fold. However, it is larger in size than *Gaindatherium* (Colbert, 1934, 1938).

Molar size can not differentiate one species from another in the genus *Rhinoceros* due to a high intraspecific variation (Figure 4). However, fossil and sub-fossil specimens of *Rhinoceros* show larger in molar size than recent ones (e.g., the width of M1 of an extinct *R. sivalensis* is about 80 mm: Colbert, 1935), suggesting that body size dwarfing in this lineage occurred probably in the late Pleistocene or Holocene.

Colbert (1942) compared the cranial and dental characteristics of *Rhinoceros sondaicus* with *Gaindatherium* and suggested that *R. sondaicus* is morphologically primitive among extinct and extant *Rhinoceros* although its remains have been recovered from the middle and late Pleistocene of Asia. At present, the transition from the *Gaindartherium* lineage to the Pleistocene *Rhinoceros* species is poorly known (Hessig, 1989). Moreover, their earliest fossil remains of *R. sondaicus* had previously been recorded from the middle Pleistocene.
Djetis Bed and Trinil Bed of Java (Hooijer, 1957). Therefore, the discovery of the *Rhinoceros sondaicus* from the early Pleistocene of Myanmar fills the geological and chronological gap between primitive *Gaindarterium* and the middle Pleistocene *R. sondaicus* from Java. This discovery suggests *R. sondaicus* originated as early as the early Pleistocene in continental Asia, and its possible migration to island Southeast Asia during the late early Pleistocene and later ages.

**Conclusion**

The discovery of early Pleistocene *Rhinoceros sondaicus* in Myanmar suggests the early Pleistocene or late Pliocene origin of this lineage in continental Asia, and shows a primitive position of this species among the genus *Rhinoceros*. The molar size difference between extinct and extant *Rhinoceros* suggests body size dwarfing in this lineage occurred probably in the late Pleistocene or Holocene.

**Acknowledgments**

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