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Sivachoerus (Artiodactyla, Suidae, Tetraconodontinae) from the Pliocene of Myanmar

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Abstract

The phylogenetic status of *Sivachoerus* is re-evaluated according to the new materials recovered from the central Myanmar. *Sivachoerus* had also been known from the Pliocene Siwalik sediments of Indian Subcontinent. Compared to Siwalik specimens, Myanmar specimens are poorly known and have not been confirmed their geological age yet. New evidence for the discovery of *Sivachoerus* from the Irrawaddy Formation presumed that *Sivachoerus* has appeared during the Pliocene in Myanmar, Southeast Asia. Dental morphology and chronology of *Sivachoerus* strongly support the 'African origin' hypothesis than the 'Asian origin' of this genus. *Sivachoerus* probably evolved from the African *Nyanzachoerus* rather than the Asian *Conohyus*, during the Late Miocene, and migrated to Asia during the latest Miocene.

Key words: Africa, Asia, *Conohyus*, Myanmar, *Nyanzachoerus*, origin, *Sivachoerus*

Introduction

Sivachoerus Pilgrim, 1926 is a large tetraconodont suid, frequently discovered from the Pliocene of Indian Subcontinent. It had also been recorded from the deposits of Irrawaddy Formation (Aung Khin and Kyaw Win, 1969) Myanmar (Pilgrim, 1926). In Indian Subcontinent, the discovery of *Sivachoerus* from the Pliocene is confirmed by radioisotopic and paleomagnetic dating (e.g., Barry *et al.*, 1982). On the contrary, in Myanmar, the discovered horizon and associated fauna of *Sivachoerus* was not well documented so that it was difficult to determine the geological age of this taxa in Myanmar.

During our recent paleontological works, well preserved dentognathic specimens of *Sivachoerus* are newly discovered from the central Myanmar. That discovery prompted us to re-evaluate the age and phylogenetic status of *Sivachoerus*.

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Materials and Methods

All materials were collected in central Myanmar (Figure 1). They are now stored at the National Museum (Yangon, Myanmar) and the Department of Geology, University of Yangon (Yangon, Myanmar). Dental terminology and measurement method used are according to Thaung-Htike *et al.* (2005). Dental measurements of some Myanmar specimens and other correlated foreign suid specimens were adopted from Pilgrim (1926), Pickford (1988) and Made (1999). The length of first molar have been considered to express the less size variation and chosen for the diagnoses of tetraconodont suids to compare the body size differences.

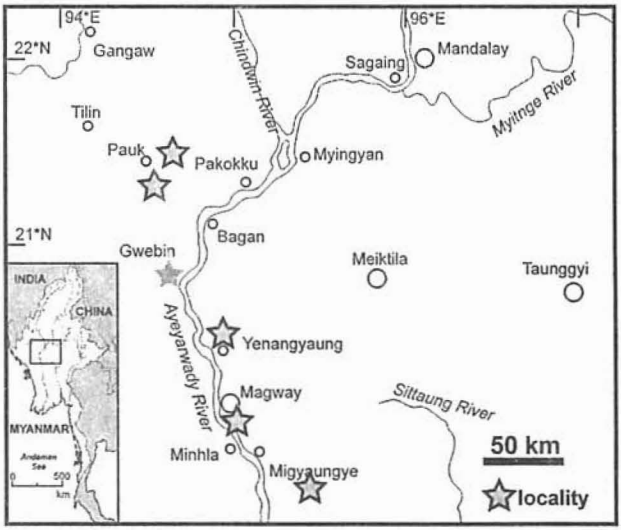

Figure 1. *Sivachoerus* fossil localities in central Myanmar

Systematic Paleontology

Genus *Sivachoerus* Pilgrim, 1926

Dental diagnosis.—Medium sized tetraconodont with relatively wide, hypsodont posterior premolars. The lower third molar is relatively elongated, having complex talonid with additional cusps. Lower third premolar has three separates roots.

Type species.—*Sivachoerus prior* Pilgrim, 1926 is type and only species.

Distribution.—*Sivachoerus* has been discovered from the Pliocene deposits of Siwalik and Irrawaddy Formation of Myanmar. There were some records from Africa most of these have been revised to *Nyanzachoerus*.

Sivachoerus prior Pilgrim, 1926

Figure 2, 3

Sivachoerus prior gen. et sp. nov. Pilgrim, 1926, pp.20-21, pl. 3, fig. 3, pl. 20, fig. 5.

Sivachoerus cf. *giganteus* (Falconer & Cautley) Pilgrim, 1926, pp. 21-22, pl. 4, fig. 1.

Tetraconodon minor, Pilgrim, 1926, pp. 18-19, pl. 3, fig. 1, pl. 4, fig. 2.

Lectotype.—GSI B 1, complete mandible with left P_1-M_3 and right P_1-M_2, figured by Lydekker (1884, pl. 11, fig. 1). (P = premolar; M = Molar)

Type locality.—Hasnot, Pakistan.

Type horizon and age.—Tatrot Formation, the Early Pliocene.

Dental diagnosis.—As for genus. M_1 length is about 25 mm and M_3 length about 53 mm. Talon of M^3 is small and simple compare to talonid of M_3.

New materials.—NMMP-KU-IR 0140 & 0141, right lower canine, right mandibular fragment with P_2-M_2 and left M_3, NMMP-KU-IR 0361, a right mandibular fragment with P_3-M_3 and root of P_2, NMMP-KU-IR 0328, left M^3, NMMP-KU-IR 0553, a left M^3, NMMP-KU-IR 0329, a right M^3, NMM NKE-2, a left mandibular fragment with M_1, trigonid of M_2 and alveolus of P_4, YUDG-KPN 2, a right mandibular fragment with P_2, P_4-M_1, root of canine and alveolus of P_3, NMMP-KU-IR 0594, a fragment of the anterior part of skull (teeth are broken).

Associated fauna.—*Hexaprotodon iravaticus*, *Propotamochoerus hysudricus*, *Merycopotamus dissimilis*, cf. *Hemibos* sp., *Stegolophodon* sp.,

Stegodon sp., *Agriotherium* sp., *Sinomastodon* sp., *Rhinoceros sivalensis*, *Selenoportax* sp.

Locality of the new material.—NMMP-KU-IR 0140 & 0141 was discovered from CHZ 15 (21° 32' 3"N; 094 ° 31' 4.8" E) near Chaingzauk Village, NMMP-KU-IR 0328 and 0329 were discovered near Chaingzauk Old Village (21° 31' 31.8" N; 094° 31' 25.8" E), NMMP-KU-IR 0553 and 0594 were discovered near Chaingzauk Village (21° 35' 34.2" N; 094 ° 32' 7.2" E) Pauk Township, Magway Division; NMM NKE-2 was discovered near Nwegwe Village, Chaung-U Township, Sagaing Division; YUDG-KPN 2 was discovered near Kyitpyin Village, Seik Pyu Township, Magway Division; NMMP-KU-IR 0361 was discovered near Sulegone Village (21° 20' 57" N; 094° 39' 39" E) Pauk Township, Sagaing Division.

Horizon and age of the new material.—Middle part of the Irrawaddy Formation, the Pliocene.

Description.—Morphology of the dental and skull of *Sivachoerus prior* are already reported by previous authors (Pilgrim, 1926; Pickford, 1988). Here, only

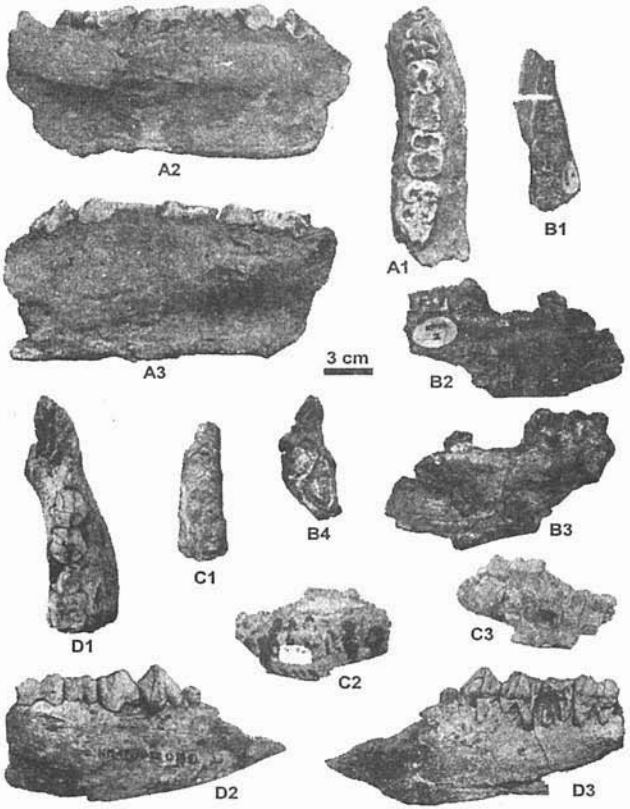

Figure 2. A-D, *Sivachoerus prior*. A, NMMP-KU-IR 0361, right mandibular fragment with P_3-M_3 and root of P_2: A1, occlusal view; A2, buccal view; A3, lingual view. B, YUDG-KPN 2, right mandibular fragment with P_2, P_4-M_1, root of canine and alveolus of P_3: B1, occlusal view; B2, buccal view; B3, lingual view; B4, anterior view. C, NMM NKE-2, left mandibular fragment with M_1, trigonid of M_2 and alveolus of P_4: C1, occlusal view; C2, buccal view; C3, lingual view. D, NMMP-KU-IR 0140, right mandibular fragment with P_2-M_2: D1, occlusal view; D2, buccal view; D3, lingual view.

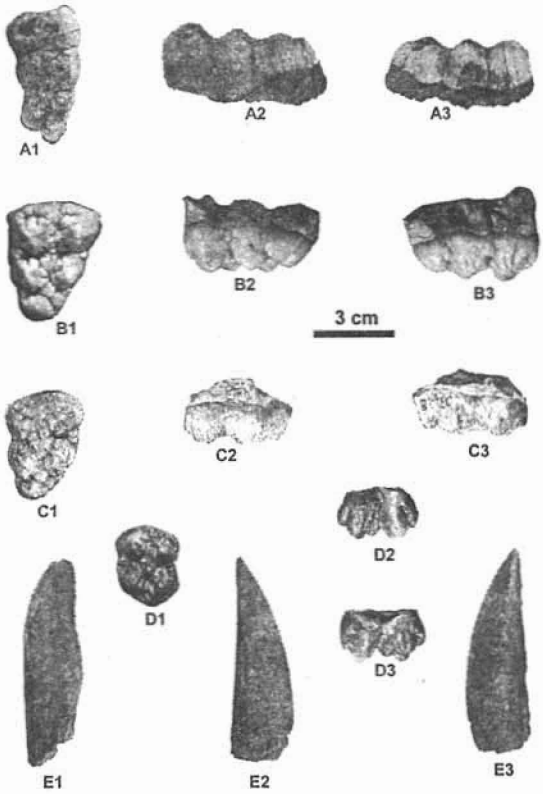

Figure 3. A-E, *Sivachoerus prior*. A, NMMP-KU-IR 0141, left M_3: A1, occlusal view; A2, buccal view; A3, lingual view. B, NMMP-KU-IR 0553, left M^3: B1, occlusal view; B2, buccal view; B3, lingual view. C, NMMP-KU-IR 0328, left M^3: C1, occlusal view; C2, buccal view; C3, lingual view. D, NMMP-KU-IR 0329, right M^2: D1, occlusal view; D2, buccal view; D3, lingual view. E, NMMP-KU-IR 0140, right lower canine: E1, mesial view; E2, buccal view; E3, lingual view distinct dental characters of present specimens are described and discussed.

Cheek teeth show typical bunodont suid morphology. The mandible is robust and its depth below M_1 is up to 95 mm. The cross-section of C_m (C = canine; $_m$ = male) shows intermediate type of scrofic and verrucosic, which has nearly same posterior and labial widths and wider lingual width.

Molars are bunodont with poorly wrinkled and thick enamel but thinner than enamel of *Tetraconodon* (Suidae, Tetraconodontidae)

Only M^2 and M^3 are known for upper molar in present specimens. They are moderately complex in morphology, both in furchen plan and development of minor cusplets at the ends of the median valley. Crenulated ridges are distinct between the furchen of unworn M^2. Anterior and posterior cingula are very distinct. Buccal and lingual cusplets of median valley are long and can be seen as cingula. Four major cusps (paracone, protocone, metacone and hypocone) and minor cusps of protopreconule and hypopreconule are distinct. Pentacone is small but distinct.

M^3 is wider and longer than M^2 and has small talon of pentacone. The anterior two lobes are similar in morphology with M^2.

Two types of P_2 can be seen in present specimens. P_2 of NMMP-KU-IR 0140 is distinctly smaller than that of YUDG-KPN 2. Both of them are tiny compare to P_3. Protoconid is distinct and situated at the center of crown. Other cusps are indistinct. Precristid is distinct in both of them.

P_3 is narrower but slightly longer than P_4. Both of them show same morphology. Protoconid is very high and situated at the center of crown. Metaconid is indistinct. Hypoconid is very low and distinct. Prestylid are very distinct in YUDG-KPN 2 and NMMP-KU-IR 0361, and very poor in NMMP-KU-IR 0140.

M_1 and M_2 are highly worn in all specimens and their occlusal morphology can not be traced. The occlusal outline show narrower and longer than that of *Tetraconodon*. Anterior cingulum is small but distinct in both of M_1 and M_2. $M_2 > M_1$.

M_3 is distinctly longer and wider than M_2 and elongated and narrower distally. Like in P_2, two type of M_3 can be seen in preset specimens. NMMP-KU-IR 0140 with smaller P_2 shows longer M_3 than NMMP-KU-IR 0361 with larger P_2. Anterior two lobes have four main cusps (protoconid, metaconid, hypoconid and entoconid) and moderately deep furchen. Both NMMP-KU-IR 0140 and 0361 show complex talonid. Only pentaconid with distinct pentaectoconulid and lingual minor cusplets can be seen in talonid of M_3 in NMMP-KU-IR 0361, however, the talonid of M_3 in NMMP-KU-IR 0141 (same individual with IR 0140) show 3 additional main cusps with separate roots, which can be correlated with pentacone, hexacone and heptacone of Made (1996).

Comparison.—Distinctly larger third and fourth premolars with minute second premolar indicate the diagnosis of Tetraconodontinae. Three separate roots in P_3 and longer M_3 with complex talonid in present specimens are the characters of *Sivachoerus*.

Among the tetraconodont suids, *Sivachoerus* and *Nyanzachoerus* are very similar in dental morphology where the posterior premolars of later is slightly smaller than former (Figure 4). These two genera have been separated by three separate roots in P_3 for *Sivachoerus* and two roots in P_3 for *Nyanzachoerus*. Made (1999) introduced some additional species of *Sivachoerus*; all of them are former Asian *Conohyus* and primitive *Nyanzachoerus*. However, *Sivachoerus prior* has been accepted as one and only Asian species on the world.

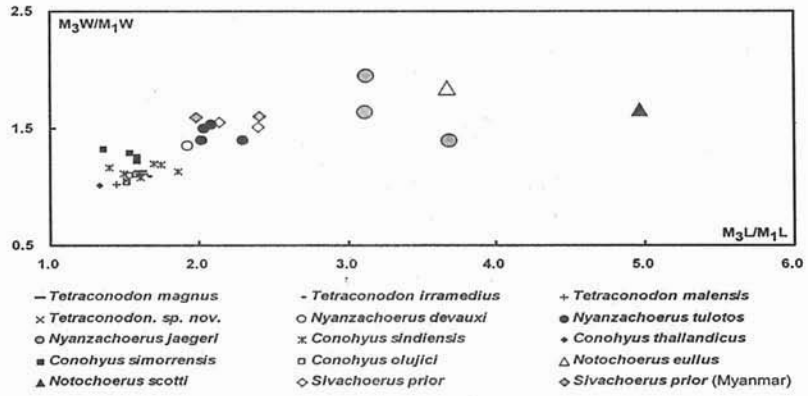

Figure 4. Size proportion of lower third molar relative to first molar in

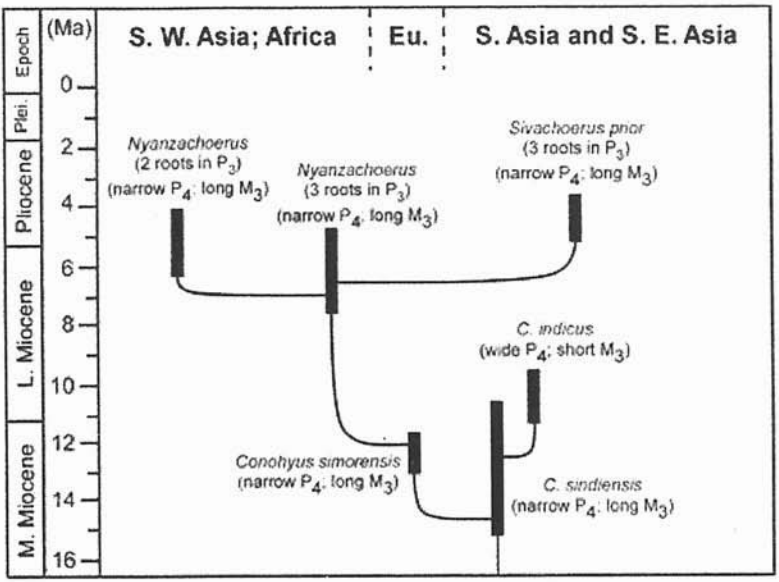

Figure 5. Phylogenetic relationship between *Sivachoerus* and its probable ancestors.

Discussion

The two hypotheses have been proposed for geographic origin of *Sivachoerus*, 'African origin' and 'Asian origin' hypotheses. In the 'Asian origin' hypothesis, *Conohyus*, a small tetraconodont from the Middle Miocene of South and Southeast Asia, has been suggested for the ancestor of *Sivachoerus*. Pilgrim (1926) discussed that *Sivachoerus* did not evolved from Asian *Conohyus* and *Tetraconodon* because relatively smaller and hypsodont posterior premolars and much longer third molar with complex talonid seen in *Sivachoerus* are distinct feature from *Tetraconodon*. On the contrary to Pilgrim's idea, Colbert (1935) insisted that both *Tetraconodon* and *Sivachoerus* evolved from Asian *Conohyus* during the Late Miocene, and relatively smaller and hypsodont posterior premolars and larger third molar of *Sivachoerus* are derived characters.

The 'African origin' hypothesis for *Sivachoerus* appeared after the description of *Nyanzachoerus* from the Late Miocene and Pliocene deposits of Africa. These two genera are very similar in dental morphology. Leaky

(1958) mentioned that *Sivachoerus* is distinguished from *Nyanzachoerus* by the number of the roots of P_3 (three in *Sivachoerus* and two in *Nyanzachoerus*). However, it was found that recently described materials of the latest Miocene *Nyanzachoerus* also have three-rooted P_3 (Made, 1999). It is now questioned whether *Nyanzachoerus* and *Sivachoerus* are really different from each other because dental measurements of some materials for *Nyanzachoerus tulotos* and *Nyanzachoerus pattersoni*, are very similar to those of *Sivachoerus* (Figure 4). However, the relative sizes of the last two premolars of the Pliocene *Sivachoerus* are distinctly larger than those of the Pliocene *Nyanzachoerus*. Therefore, Pickford (1989) suggested that *Sivachoerus* evolved from the Late Miocene *Nyanzachoerus*, and migrated into South and Southeast Asia during the latest Miocene.

On the other hand, Made (1999) replaced the *Conohyus* origin for *Sivachoerus* again. He followed the Leaky's idea (1958), and revised all three-rooted *Nyanzachoerus* to *Sivachoerus*. Moreover, he used the term *Sivachoerus* for all Asian *Conohyus*, and concluded that both of three-rooted *Nyanzachoerus* and *Sivachoerus* have derived from the same ancestor, Asian *Conohyus* respectively. Many researchers criticized his classification and disagreed especially to his changing Asian *Conohyus* to *Sivachoerus* (e.g., Pickford and Gupta, 2001; Harris and Leaky, 2003).

According to the recent stratigraphical data of Irrawaddy Formation (Chit-Sein, 2006; Thaung-Htike, 2008), the discovered horizon of *Sivachoerus* is much higher than other Late Miocene mammals, and the contemporaneous mammalian fauna are mostly the Pliocene equivalent fauna of Siwalik (e.g., *Agriotherium* sp.). Therefore, it suggests that the first appearance of *Sivachoerus* in Myanmar is not earlier than Pliocene.

The Pliocene appearance for *Sivachoerus* in Myanmar and Siwalik is chronologically much younger than the early Late Miocene last appearance of Asian *Conohyus*. Made (1999) described that *Sivachoerus prior* evolved from *Conohyus indicus*, which is a derived form of *C. sindiensis*. In *C. indicus*, relative size of posterior premolars with respect to first molar are larger and relative size of third molar is smaller than its ancestor, *C. sindiensis*, and these characters have been accepted for derived characters of *Conohyus* lineage (Colbert, 1935; Made, 1999). However, *Sivachoerus* shows relatively small posterior premolars and relatively large third molar compared to *C. indicus* and more similar in relative dental size to *C. sindiensis*. Therefore, evolution of *Sivachoerus* from *C. sindiensis* via

C. indicus does not show linear dental morphological changes, which is deviated from the evolutionary pattern of Suidae. There are morphological gap and chronological gap within the Pliocene *Sivachoerus* and Middle Miocene *C. sindiensis*.

Compared to *Conohyus*, morphological and chronological gaps between *Sivachoerus* and *Nyanzachoerus* are much smaller. Moreover, character of the gradually reduction of P_2 associated with expansion M_3 can be seen in both genera, and it suggests that the 'African origin' hypothesis is more appropriate than 'Asian origin' for *Sivachoerus*. It suggests that *Sivachoerus* is derived from the African *Nyanzachoerus* during the Late Miocene, and migrated into Asia during the latest Miocene or Early Pliocene (Figure 5).

Conclusion

In Myanmar, fossil materials of *Sivachoerus* are recovered from the Irrawaddy Formation. The newly discovered dental materials of this taxa indicate only *Sivachoerus prior* is discovered in Myanmar. The additional dental morphology of *Sivachoerus* which are considered from the new specimens suggests that *Sivachoerus* has appeared during the Pliocene in Myanmar, Southeast Asia. The dental morphology and geological age of *Sivachoerus* strongly support the hypothesis that the origin of this genus is 'African'. *Sivachoerus* probably derived from an African tetraconodont, *Nyanzachoerus* during the Late Miocene, and migrated to Asia in the latest Miocene.

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