Review on the taxonomic status of *Hexaprotodon iravaticus* (Mammalia, Artiodactyla, Hippopotamidae) from the Neogene of Myanmar

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Abstract

The taxonomic status of the primitive hippopotamuses, *Hexaprotodon iravaticus*, is re-evaluated. This species is interested for its smaller size and narrow symphysis which are the characters of the primitive *Hexaprotodon* species. Because of the lectotype is not an adult specimen and poorly known on its recovered horizon and age, *Hex. iravaticus* has been rejected from the phylogenetic analyses and discussion of Asian Hippopotamidae. Recently, well preserved dental and partial skull materials of fossil hippopotamuses are newly discovered from the Neogene sediments of Myanmar. That discovery prompted to reclassify the fossil hippopotamuses of Asia, resulting the adult specimens has also shown distinguishable taxonomic characters and the Pliocene discovery for *Hex. iravaticus.*

Key words: *Hexaprotodon iravaticus*, taxonomy, Myanmar

Introduction

Although living hippopotamuses can be seen only in Africa at present, they were widely inhabited in southern part of Europe, South Asia and Southeast Asia during the Neogene. The first record of Asian fossil hippopotamuses was described by Clift (1828), which was collected by Crawford in1826 at Myanmar, 250 miles below Ava (Inwa) on the left bank of the Irrawaddy (=Ayeyarwady) River. Most of the fossil hippopotamuses of Asia have been recorded from the Middle and Upper Siwalik Group of India/ Pakistan and the Pleistocene deposits of Java, and some from the Plio-Pleistocene deposits of Nepal, Sri Lanka, Myanmar, Borneo, and Malay Peninsular (Falconer, 1836, 1868; Falconer & Cautley, 1847; Lydekker, 1884, Dubios, 1908; Colbert, 1935a, 1935b, 1938; Deraniyagala, 1937; Hooijer, 1950; Cranbrook *et al.*, 2000; Corvinus & Rimal, 2001).

Previously, Asian hippopotamuses were described under the generic name of *Hippopotamus* and *Hexaprotodon*. Recently, however, Boisserie (2005) revised the phylogeny and taxonomy of Hippopotamidae, placing all Asian fossil hippopotamuses under a single genus, *Hexaprotodon*. Although the term *Hexaprotodon* is given for its total six incisors in lower jaw, however, most of the primitive hippopotamuses have this character not only for *Hexaprotodon* (e.g., Coryndon, 1977, 1978). Among the fossil hippopotamuses, *Hexaprotodon* is well known for its high, robust and strongly inclined mandibular symphysis. As fossil

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materials, *Hexaprotodon* have also been discovered also from Africa, such as the Late Miocene of Chad and the Pliocene of Ethiopia, it has been suggested that *Hexaprotodon* evolved in Africa during the Late Miocene (Boisserie & White, 2004; Boisserie, 2005; Boisserie *et al*., 2005a).

In Myanmar, fossils of extinct hippopotamuses have been frequently discovered from the Pliocene to Pleistocene localities of the Irrawaddy Formation and Terrace Deposits (Figure 1). However, most of them are poorly known and detailed paleontological works have not yet been done. To date, three forms of *Hexaprotodon* have been known from Myanmar: *Hex. iravaticus* Falconer & Cautley, 1847, *Hex*. cf. *sivalensis* and *Hex*. cf. *palaeindicus* (Colbert, 1943; Hooijer, 1950). Among the Asian *Hexaprotodon*, *Hex. iravaticus* of Myanmar has been interested for its smaller size and narrow and long mandibular symphysis, and regarded as a primitive Asian hippopotamuses. However, its known fossil materials are very few and most of these are fragmentary. Fossil hippopotamuses can not be identified only from cheek teeth, so well-preserved skull and dental materials are necessary to analyze and discuss the evolution and phylogeny of Asian *Hexaprotodon*.

No additional taxon has been described for the fossil hippopotamuses of Myanmar after Hooijer (1950), who reviewed the specimens of Colbert (1938) and Falconer & Cautley (1847). Recently, the taxonomic status of *Hex. iravaticus* was suspected by some workers (e.g., Boisserie, 2005) because of its rare and poorly preserved specimens. Some additional partial skulls and dental materials are discovered from the Pliocene of Myanmar during the present study. Most of these are good in preservation. In this work, the taxonomic status of *Hex. iravaticus* among the Asian and African *Hexaprotodon* is revised and discussed.

Previous works and problems on the fossil hippopotamuses of Myanmar

The first description on the fossil hippopotamuses of Myanmar was done by Clift (1828) and the name *Hippopotamus* was used. Falconer & Cautley (1847) firstly described *Hex. iravaticus* by illustrations under the name of *Hippopotamus* (*Hexaprotodon*) *iravaticus*. The descriptions and discussions on *Hex. iravaticus* have mostly been done during the earlier part of 20th Century (Lydekker, 1882, 1884, 1885; Pilgrim, 1910b; Matthew, 1929; Maarel, 1932; Colbert, 1935a, 1938, 1943; Hooijer, 1950).

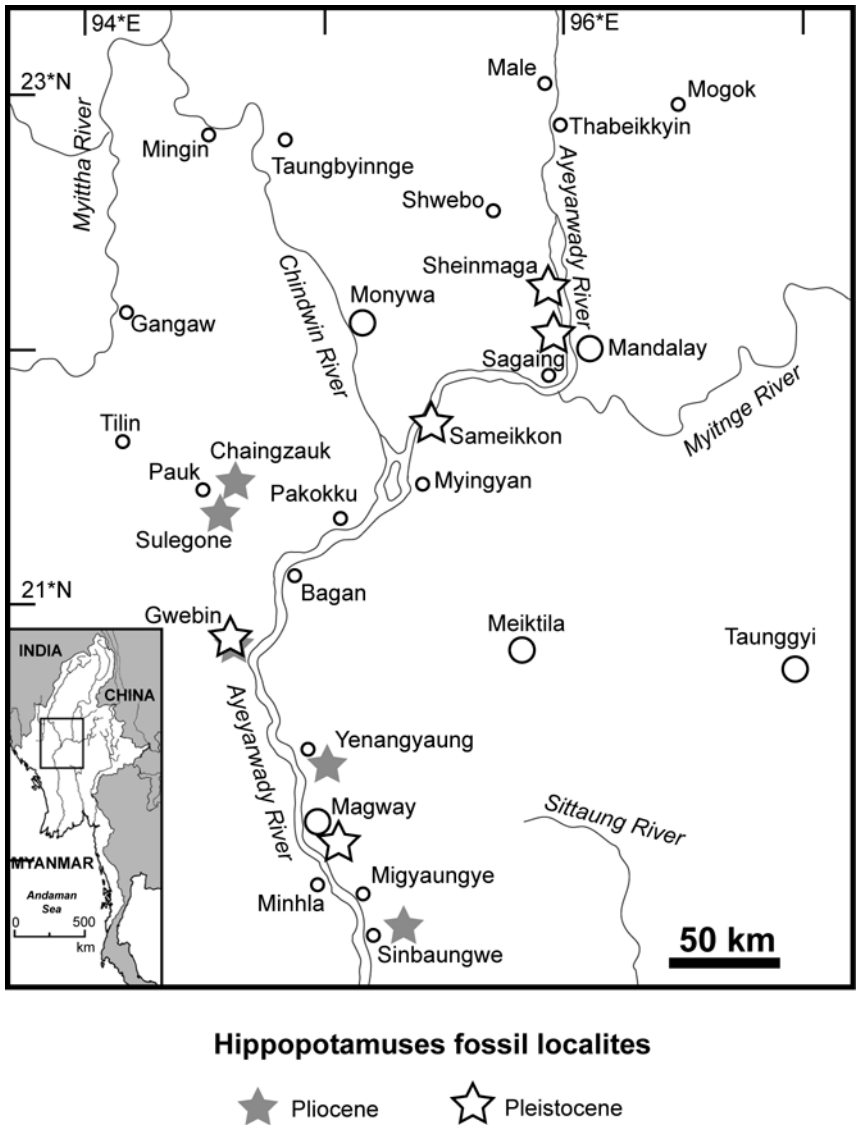

Figure 1. Hippopotamuses fossil localities in central Myanmar.

Many workers have been interested in *Hexaprotodon iravaticus* for its smaller size and narrow symphysis, which are the characters of the primitive Late Miocene African hippopotamuses, and placed *Hex. iravaticus* at the base of the Asian hippopotamuses (Lydekker, 1884). However, the geological age of *Hex. iravaticus* had been considered for the Late Pliocene or Pleistocene by previous workers, very much younger than the Siwalik large-sized *Hex. sivalensis*, which has been discovered from the latest Miocene to Late Pliocene in Northern Pakistan (Barry *et al.*, 2002). However, the smaller size has been marked for the primitive Mio-Pliocene African and Eurasian hippos compared to younger Pleistocene forms, some workers suggested that among the Asian *Hexaprotodon* the smaller but chronologically younger *Hex. iravaticus* is specialized taxa of Myanmar. *Hex. iravaticus* has been neglected from the phylogenetic analysis and discussion of Asian Hippopotamidae.

Hex. iravaticus was firstly described from a partial symphysis of sub-adult individual (BMNH 14771) (Falconer & Cautley, 1847), and very long symphysis relative to its width is used as a diagnosis of this species (Lydekker, 1884). Gentery (1999) applied the term "narrow muzzled" for *Hex. iravaticus* to distinguish it from other Asian hippopotamuses, and it was widely accepted by later researchers. Boisserie (2005), however, stated that the lectotype of *Hex. iravaticus* is not an adult but a juvenile specimen by using the hypothesis of Laws (1968), where P/2 is not fully erupted. He mentioned that a fully adult mandible from Myanmar, housed in BMNH (NHM) shows appreciably laterally extended mandibular symphysis, and the "narrow muzzled" feature for the juvenile lectotype of *Hex. iravaticus* is ill-founded and the lectotype should not be informative for the species definition. In his revision on the phylogeny of Hippopotamidae, taxonomic status of *Hex. iravaticus* has revised to *Hexaprotodon* sp. (Boisserie, 2005).

Most of the previously discovered skull and dental remains of the fossil hippopotamuses of Myanmar are smaller than those of Siwalik, it had been generally accepted that only small-sized *Hexaprotodon*, *Hex. iravaticus* is discovered in Myanmar.

Material and Method

More than 29 partial skull and dental fragments of *Hex. iravaticus* were newly recorded from Myanmar during the present study. All specimens were recovered from the central part of Myanmar: some of them are formerly housed in the National Museum, Yangon, Geology Museum, Mandalay University, Mandalay, and Geology Museum, Magway University, Magway, others were newly collected near Chaingzauk and Sulegone Villages, Pauk Township, and Gwebin Village, Seikpyu Township, Myanmar. Dental terminology and measurement method are according to Thenius (1989) (Figure 2).

The identification on the hippopotamuses has done not only by the dentition but also by the skull morphology. Measuring style on the skull materials is based mainly on Hooijer (1950), partly on Weston (2003) and Lihoreau *et al.* (2007). It is difficult to use the length of first molar as the size indicator in hippopotamuses. The position of the true length in the molar of hippopotamuses is slightly higher than the base of the crown because of protuberances of the anterior and posterior cingula. Most of the first and second molars, especially first molar, are worn out before fully eruption of the third molar, and it is difficult to measure the true length of first molar. In hippopotamuses, the talon and talonid of third molar is very simple. Compared to M/3, the structure of M3/ is more stable preserving four main cusps and less

prominent anterior and posterior cingula. Here, the size of M3/ is used to figure the size differences among Asian *Hexaprotodon*.

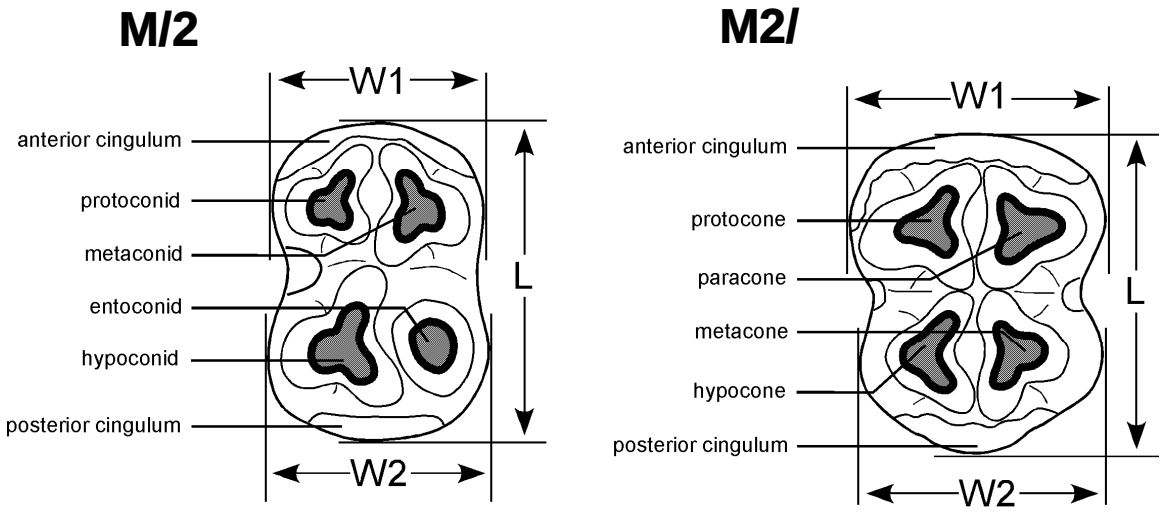

Figure 2. Dental terminology and measurement method of Hippopotamidae. All are left cheek teeth.

Abbreviations

NMM, National Museum, Yangon, Myanmar; NMMP–KU–IR, National Museum, Myanmar, Paleontology–Kyoto University–Irrawaddy; BMNH, British Museum of Natural History; I, incisor; P, premolar; M, molar; P1/, upper first premolar; P/1, lower first premolar.

Systematic Paleontology

Order Artiodactyla Owen, 1848

Family Hippopotamidae Gray, 1821

Subfamily Hippopotaminae Gray, 1821

Diagnosis.—Common subfamily for the extinct and extant hippopotamus. Main cusps of molars show tri-foliate outline in occlusal both for the upper and lower.

Genus ***Hexaprotodon*** Falconer & Cautley, 1836

Type species.—Hexaprotodon sivalensis Falconer & Cautley, 1836.

Other included species.—Hexaprotodon iravaticus Falconer & Cautley, 1847; *Hexaprotodon palaeindicus* Falconer & Cautley, 1847; *Hexaprotodon namadicus* Falconer & Cautley, 1847; *Hexaprotodon bruneti* Boisserie & White, 2004; *Hexaprotodon garyam* Boisserie *et al*., 2005.

Diagnosis.—Boisserie (2005) revised the phylogeny and taxonomy of Hippopotamidae, separating the hexaprotodont European fossil hippopotamuses from genus *Hexaprotodon*, and placed all of the Asian fossil hippopotamuses in to the genus *Hexaprotodon*. He revised the diagnosis of *Hexaprotodon* as follows; "hexaprotodont"; characterized by a very high robust mandibular symphysis, relatively short in spite of its canine processes, which are not particularly extended laterally; dorsal plane of symphysis very inclined anteriorly; thick incisor alveolar process, frontally projected; some relatively small differences between the incisor diameters, the I/2 being usually the smallest; laterally everted but not hook-like gonial angle; orbit having a well developed supra-orbital process, and a deep but narrow notch at its anterior border; thick zygomatic arches; elevated sagittal crest on a transversally compressed braincase. Some constant features of this genus appear to be primitive: the strong double-rooted P1/, the quadrangular lacrimal separated from the nasal bone by a long maxillary process of the frontal.

Hexaprotodon iravaticus Falconer & Cautley, 1847

Figure 3, 4

? *Hippopotamus*, Clift, 1828, p. 373, pl. 40, figs. 3-4, pl. 41, figs. 19-20.

Hippopotamus (*Hexaprotodon*) *iravaticus* Falconer & Cautley, 1847, pl. 57, figs. 10-11.

Hippopotamus iravaticus, Lydekker, 1882, p. 31; Lydekker, 1883, pp 83 and 91; Lydekker, 1884, pp. 42 and 137; Lydekker, 1885a; p. 309; Schlosser, 1903, p.207; Pilgrim, 1910a, pp. 196 and 203; Matthew, 1929, p. 449; Maarel, 1932, p. 91. Hooijer, 1950, p. 34.

Hexaprotodon iravaticus, Falconer, 1868, p. 407; Colbert, 1935b, p. 280.

Lectotype.—BMNH 14771, a mandibular symphysis with left and right roots of I1-P2, illustrated by Falconer & Cautley (1847: plate 57, figures 10).

Type locality.—Irrawaddy (Ayeyarwady) River valley, Myanmar.

Type horizon and age.—Middle and upper part of Irrawaddy deposits, Pliocene.

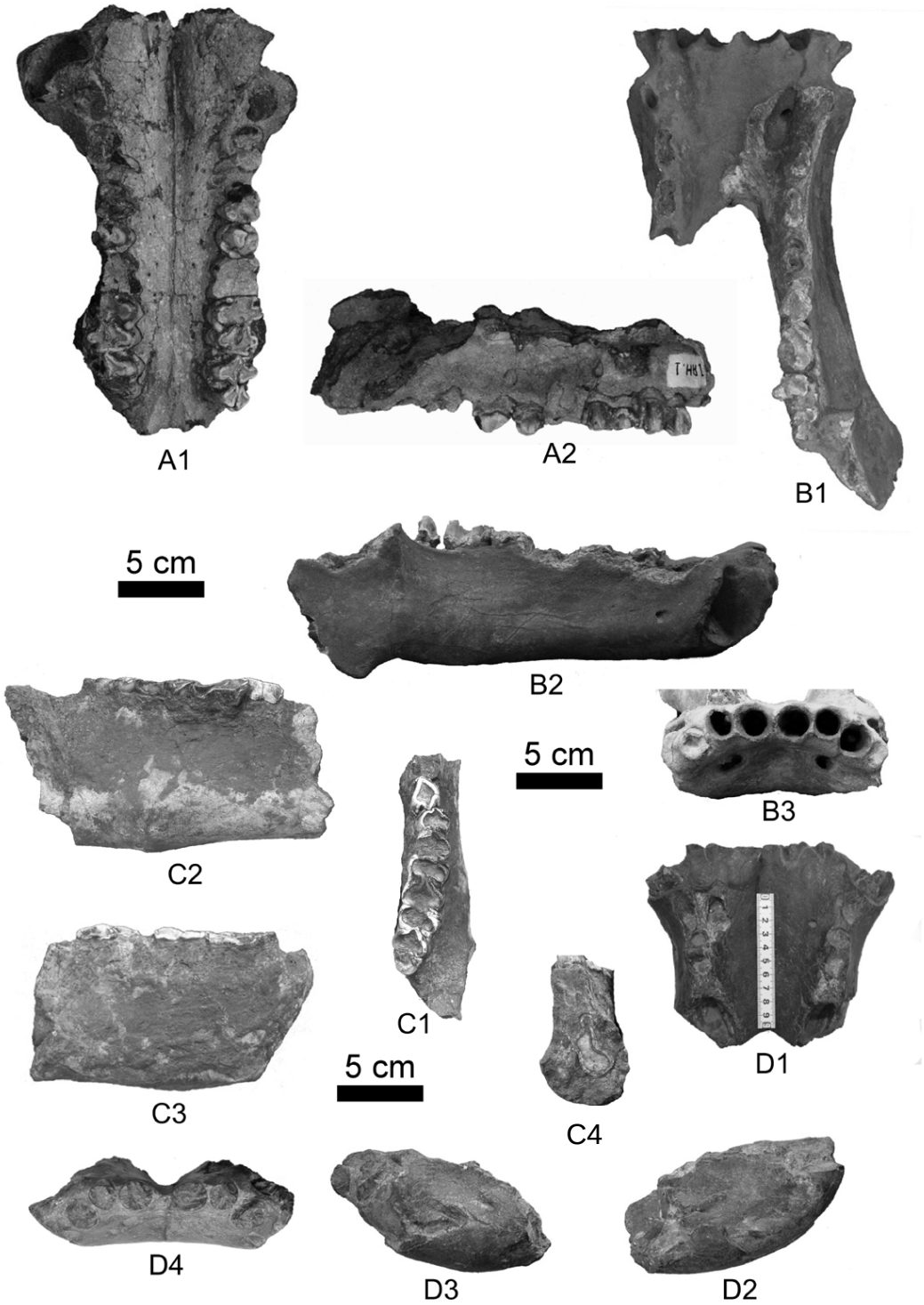

Figure 3. A-D, *Hexaprotodon iravaticus*. A, NMM IAH 1, maxillary fragment with right P4/-M3/, and roots of P2/-3/; left P3/-M3/, and roots of P2/: A1, palate view; A2, left lateral view. B, NMMP-KU-IR 0449, mandibular fragment with right M/1-/3, roots of I/3, C, P/2-/4, and alveolus of I/1-/2, P/1; left roots of C, P/2-/3, and alveolus of I/1-/3, P/1: B1, dorsal view; B2, right lateral view; B3, anterior view. C, NMMP-KU-IR 0191, right mandibular fragment with P/4-M/3 and root of P/3: C1, occlusal view; C2, buccal view; C3, lingual view; C4, anterior view. D, NMMP-KU-IR 0177, fragment of mandibular symphysis with roots of right I/1-C, and alveolus of P/1-/2; roots of left I/1-C and alveolus of P/1-/2: D1, dorsal view; D2, right lateral view; D3, left lateral view; D4, anterior view.

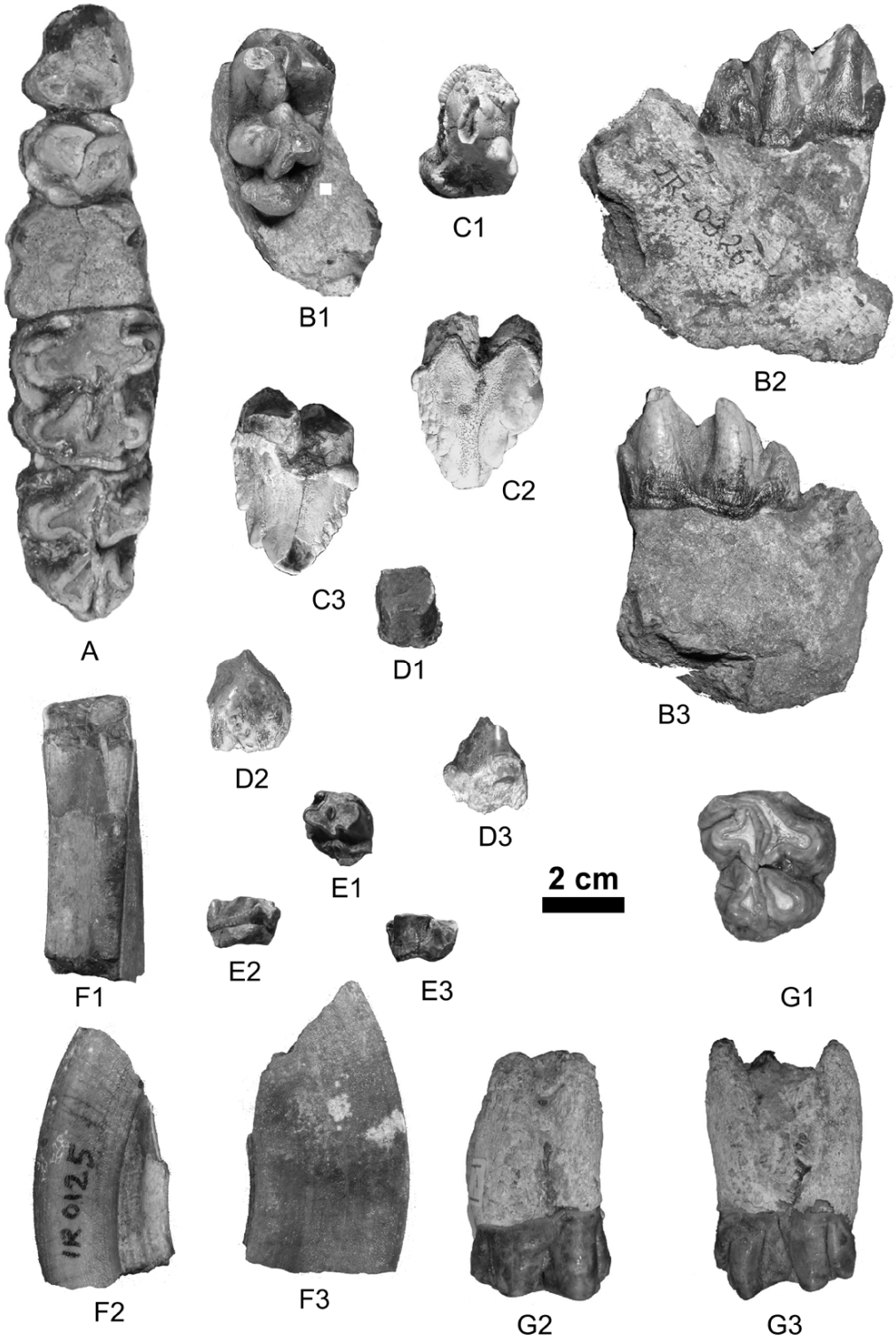

Figure 4. A-G, *Hexaprotodon iravaticus*. A, left P3/-M3/ of NMM IAH 1: occlusal view. B, NMMP-KU-IR 0326, right mandibular fragment with M/3: B1, occlusal view; B2, buccal view; B3, lingual view. C, NMMP-KU-IR 0570, left upper P2/: C1, occlusal view; C2, buccal view; C3, lingual view. D, NMMP-KU-IR 0080, right upper P1/: D1, occlusal view; D2, buccal view; D3, lingual view. E, NMMP-KU-IR 0566, right mesial fragment of DP/4: E1, occlusal view; E2, buccal view; E3, lingual view. F, NMMP-KU-IR 0125, left lower canine: F1, distal view; F2, buccal view; F3, lingual view. G. NMM GPN 56, right M3/: G1, occlusal view; G2, buccal view; G3, lingual view.

Emended diagnosis.—A smallest *Hexaprotodon* of the Asiatic species; narrow and long mandibular symphysis; anteriorly tapered mandible; P3/ with a distinct distolingual heel; P3/ and P4/ are nearly same in size; protocone is distinctly smaller and lower than paracone in P4/; no minor cuspule at the mesial of P4; P2 is distinctly larger than P3; main cusps of the upper molars are simple, tri-foliate and less expanded; bi-foliated hypocone in M3/; degree of inclination of the symphysis is about 50°; anterior border of palato-maxilla suture reach the mesial of M2/.

Differential diagnosis.—Generally, *Hexaprotodon iravaticus* differs from all Asian *Hexaprotodon* by its distinctly smaller size (Figure 5). It differs from *Hex. sivalensis* in having narrow and long mandibular symphysis, nearly same size in P3/ and P4/, no minor cuspule at the mesial of the protocone of P4/, shorter P/4 with one or several minor cusplets in distolingual part, less expanded but tri-foliated cusps in molars, lesser development of cingulum, anteriorly tapered mandible, smaller in inclination degree of mandibular symphysis, the lower canine distinctly higher than I/3, and weak post-canine constriction of the muzzle. It differs from *Hex. namadicus* in having narrow and long symphysis, poorly dorsally shifted and not much smaller I/2, and shallower mandibular corpus. It differs from *Hex. palaeindicus* like in those of *Hex. sivalensis* and *Hex. namadicus*, additionally, in having more backward posterior border of palate than that of M3/ and anterior border of palato-maxilla suture, which is more anterior than the mesial of M2/. It differs from *Hex. bruneti* like in those of *Hex. sivalensis*, additionally, in having not much smaller and poorly dorsally shifted I/2. It differs from *Hex. garyam* in having anteriorly tapered mandible.

Associated fauna.—*Sivachoerus prior*, *Merycopotamus dissimilis*, *Propotamochoerus hysudricus*, *Hexaprotodon sivalensis*, cf. *Hemibos* sp., *Stegolophodon* sp., *Stegodon* sp., *Agriotherium* sp., *Sinomastodon* sp., *Rhinoceros sivalensis*, *Selenoportax* sp.

Locality of the material.—Near Chaingzauk Village, Pauk Township; near Supyitsan Village, Magway Township; near Gwebin and Tabingyaung villages, Seikpyu Township.

Horizon and age of the material.— the upper part of the Lower Irrawaddy Formation, Pliocene.

Description.—A craniomaxillary fragment, a juvenile mandibular symphysis, partial and fragmental mandibles and well-preserved upper and lower cheek teeth are associated in the newly discovered materials of *Hexaprotodon iravaticus*. Here, additional morphology of skull and dentition are described in detail.

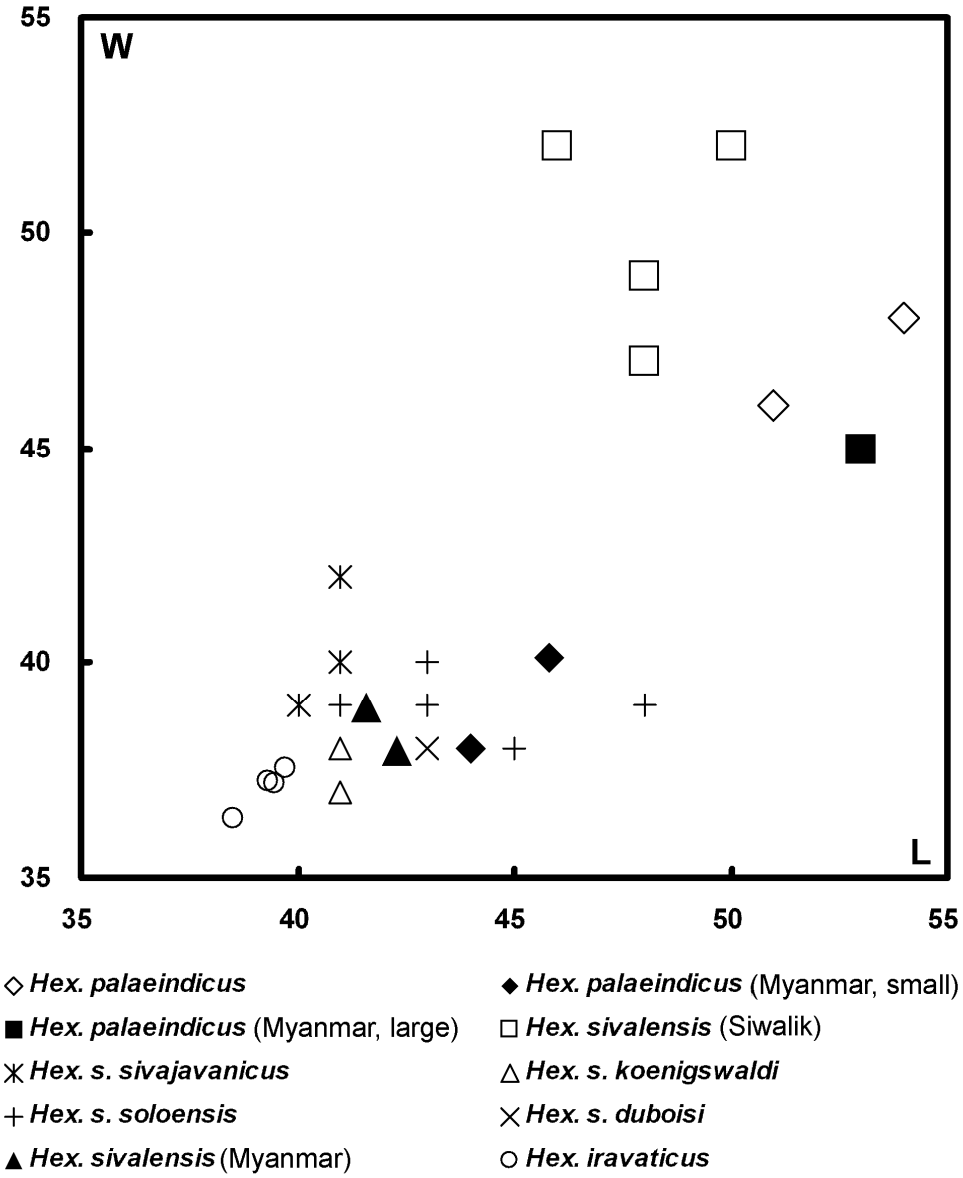

Figure 5. Sizes of M3/ in Asian *Hexaprotodon*. L = mesiodistal length. W = buccolingual width. Measurements data area in mm.

Cranium: A maxillary fragment is characterized by a narrow muzzle compared to the length of the maxilla and post canine constriction. Medial border of the canine aligned closely to the buccal margin of the molars. Roots of I1/-3/ can be traced from the broken remain of proximal part. The anterior border of the palato-maxilla suture reaches the mesial end of the M2/. Root of canine reaches up to mesial above of P3/. The posterior border of the palate is more posterior than that of M3/. The row of premolars is longer than row of molars, and slightly diverges anteriorly on the either side.

Mandible: NMMP-KU-IR 0177 is a fragment of juvenile mandibular symphysis very similar to the lectotype (BMNH 14771). The symphysis of juvenile specimen is less inclined in position than that of adult specimen (NMMP-KU-IR 0449) (Figure 6). Narrow and long symphysis can also be seen in adult specimen. The adult mandibular symphysis is high and robust. The mandibular corpus is high (Figure 3), especially highest below M/2, and tapered anteriorly. The ventral and dorsal surfaces of the symphysis are concave and convex, respectively. The mandibular ramus is nearly upright in position. A distinct mental foramen is located under P/2. The posterior part of mandible is broken in the present specimens and morphology of coronoid and condyloid processes cannot be seen, however, laterally everted feature for the gonial part of mandible can be traced.

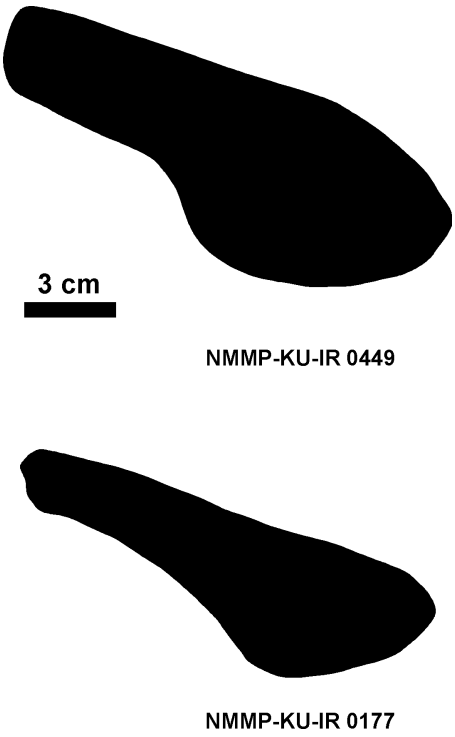

Figure 6. Dorsal plane of mandibular symphysis in *Hexaprotodon iravaticus*.

Dentition: The incisors are thick, long, cylindrical and frontally projected. The cheek teeth are hypsodont. The enamel is gradually thicker in the posterior teeth. The crowns of the incisors are unknown and roots of incisors are known only for the lower. I/1 has nearly rounded outline, larger than I/2 and quite smaller than I/3. I/2 is quite smaller than both I/1 and I/3. It is shifted dorsally, and slightly higher in position than I/1. I/3 is mesiodistally compressed in juvenile specimen (Figure 3) but nearly rounded in adult specimen. Upper canine has a deep posterior groove and bilobate outline in occlusal view. Enamel striations are

very distinct both in upper and in lower canines except for the medial surface. The occlusal outline of lower canine is nearly rectangular but slightly narrower in buccolingual side. The superior border of the lower canine is distinctly higher than that of I/3.

P1/ is well developed, double-rooted, and monocuspid by paracone. A small disto-lingual heel is distinct. Enamel is thick and weakly wrinkled. Buccal cingulum is present.

P2/ is extremely larger than P1/ and distinctly larger than P3/. It is the larger version of P1/ but the posterior root is slightly bifurcated in distal surface. Numerous small lobes can be seen along the precrista and posterior sagittal ridge in the unworn stage. Anterior and posterior cingula are more distinct than in P1/.

P3/ is nearly piriform in occlusal outline. The crown surface is usually worn out. The center of the crown is probably a monocuspid by paracone. The distolingual heel is distinct. A poorly developed cingulum can be seen around the base of the crown.

P4/ is usually rounded in occlusal outline, and slightly wider and shorter than P3/. P4/ is bicuspidate with the large paracone and small but distinct protocone. Anterior and posterior cingula are stronger than lingual and buccal ones (Figure 4).

M1/ is nearly rectangular in outline, and distinct by simple tri-foliated four main cusps (paracone, protocone, metacone, and hypocone). The occlusal area of each cusp varies due to the wear stages. The whole crown is surrounded by the strong basal cingulum. The top of the posterior cingulum is higher than anterior one. The lobes/ridges of the cusps are poorly expanded. The posterior lobes of paracone and protocone are opposed to the anterior lobes of metacone and hypocone. M2/ is the larger version of M1/. M1/<M2/.

M3/ is smaller than M2/, and narrower posterior. Outlines of main cusps are similar to those of M2/ except for hypocone which is not tri-foliate but bi-foliate in occlusal outline (Figure 4, G1). The buccal and lingual cingula are poorly developed.

P/1 and P/2 are known only for roots. P/1 is distinctly smaller than P/2. Both P/1 and P/2 are rounded in occlusal outline, and single-rooted. P/2 has distinctly separated two roots.

P/3 is elliptical in occlusal outline, and mesiodistally long. The protoconid is highest and situated at the center of the crown. Metaconid is distinct at in the centrolingual surface forming a ridge on the lingual wall. Precristid and posterior sagittal ridge are distinct. Anterior prestylid and posterior cingulum are distinct.

P/4 is similar to but slightly smaller than P/3. The metaconid is more distinct than that in P/3. Some minor cusplets are often occurring at distolingual corner.

M/1 is highly worn and rectangular in occlusal outline. M/2 is the larger version of M/1. It has four main cusps (protoconid, metaconid, hypoconid and entoconid). Main cusps are tri-foliate, except for the rounded entoconid. Anterior and posterior cingula are well developed. Posterior cingulum is narrow but higher than the anterior one. There are small minor cusplet at the buccal edge of the medium valley. The hypoconid is always larger than other main cups. The posterior lobe of metaconid is opposed to the anterior lobe of the hypoconid.

M/3 is the longest and the widest among cheek teeth. The morphology of four main cusps is similar to M/2. The posterior cingulum is very strong, forming a distinct talonid cuspid.

DP/4 has the same morphology as but distinctly smaller than M/1. Enamel is thinner than in M/1. DP/4 is known only for the mesial part. It has distinct cingulum. Paraconid and primoconid can be seen but heavily worn out, and it is impossible to trace their morphology.

Comparison.—The narrow and long mandibular symphysis seen in the present specimen is the diagnosis of *Hexaprotodon iravaticus*. NMMP-KU-IR 0177, a juvenile mandibular symphysis, is very similar to the lectotype of *Hex. iravaticus*. Sizes of the skull and dental materials in the present specimens are distinctly smaller than those of the other *Hexaprotodon* except for the *Hex. garyam* from Africa. However, anteriorly tapered mandible for *Hex. iravaticus* is distinct from the anteriorly higher mandible of *Hex. garyam*. The degree of inclination for the mandibular symphysis is lower (50°) than that of other *Hexaprotodon* species, but higher than that of other African and European Mio-Pliocene hippopotamuses.

Discussion

Among the fossil hippopotamuses, the Asian fossil hippopotamuses have a long research history (e.g., Clift, 1828; Falconer & Cautley, 1836). During the 19th Century they were placed in a single genus, *Hippopotamus*. The name *Hexaprotodon*, which means total six incisors in lower jaw, was only used for subgenus to differentiate from extant hippopotamuses, common hippopotamus (*Hippopotamus amphibious* Linnaeus, 1758) and pygmy hippopotamus (*Choeropsis liberiensis* Morton, 1844). These two extant hippopotamuses were known as tetraprotodont for *Hippopotamus* in having total 4 incisors in lower jaw and diprotodont for *Choeropsis* in having total two incisors in lower Jaw. The taxonomic status of *Hexaprotodon* was revised several times, some time it became genus, and some times it was taken as a

synonym of *Hippopotamus* (e.g., Lydekker, 1884, Colbert, 1935b; Hooijer, 1950). Many researchers did not prefer to separate *Hippopotamus* and *Hexaprotodon*. *Hexaprotodon* had been used in Mio-Pliocene African and European fossil hippopotamuses also having total six incisors. These extinct *Hexaprotodon* species are similar to Asian species only for six incisors and tri-foliated cusps in molars. They are greatly different in skull and premolar morphology from Asian forms. Most researchers accept a hypothesis that *Hexaprotodon* is a paraphylitic group.

Boisserie (2005) revised the subfamily Hippopotaminae, introducing five distinct genera, *Hippopotamus*, *Hexaprotodon*, *Choeropsis*, *Archaeopotamus*, and *Saotherium*, and placed some indistinct North African and European taxa under the name incertae sedis. Bosserie's classification was very useful to discuss the phylogeny of hippopotamus, and has been cited by many researchers. In his revision, the taxonomic status of *Hex. iravaticus* has been discussed as *Hex.* sp. indet. because the lectotype was a juvenile specimen. He described that a full adult mandible from Myanmar, which was discovered in later, shows laterally expanded mandibular symphysis and did not mentioned the possibility that there may be another species in Myanmar (Colbert, 1943; Hooijer, 1950).

The present discovery of *Hex. iravaticus* specimens prove that the adult mandible of *Hex. iravaticus* also has the "narrow-muzzled" character compared to *Hex. sivalensis* of Siwalik. The newly discovered juvenile mandibular symphysis (NMMP-KU-IR 0177) is mostly identical to the lectotype of *Hex. iravaticus,* and the locality is associated with adult hippo specimens. Only one taxa of *Hexaprotodon* has been discovered from the locality of that new juvenile symphysis, suggesting that the adult and juvenile symphysis belong to the same taxa, *Hex. iravaticus*. The contemporaneous mammalian fauna of *Hex. iravaticus* include the typical Pliocene forms (*Sivachoerus prior*, *Agriotherium* sp., *Stegolophodon* sp., *Sinomastodon* sp.) suggesting the first appearance of *Hex. iravaticus* in Myanmar is not younger than the Pliocene.

Recently described *Hex. garyam* from Chad, Africa, shows similar dental morphology to *Hex. iravaticus*: bicuspidated P4/ with no minor cusplet; bi-foliated hypocone in M3/; similar size for P3/ and P4/; presence of accessory cuspids in disto-lingual corner of P/4; and similar dental and skull sizes. They can be differentiated only by the morphology of the mandibular corpus: in *Hex. iravaticus* the mandible is tapered anterior whereas vice versa in *Hex. garyam*. *Hex. garyam* is discovered form latest Miocene deposits (ca. 7.0 ma) and *Hex. iravaticus* has now been discovered form the Pliocene deposits of Myanmar. In general,

anteriorly tapered mandible is considered the primitive character for the artiodactyl which is obvious also in the Late Miocene African hippopotamuses. Therefore, *Hex. iravaticus* with primitive mandibular outline has not likely evolved directly from *Hex. garyam*, probably from same ancestor during the Late Miocene at Africa, and migrated and entered Myanmar during the Pliocene.

Conclusion

Three forms of *Hexaprotodon* have been discovered from Myanmar: *Hex. iravaticus*, *Hex.* cf. *sivalensis* and *Hex.* cf. *palaeindicus*. Among *Hexaprotodon*, *Hex. iravaticus* is the smallest and interested for its primitive characters, smaller size and narrow mandibular symphysis. The present study elucidates that the adult mandible of *Hex. iravaticus* has the "narrow-muzzled" character, and its juvenile mandibular symphysis is identical to the lectotype of *Hex. iravaticus*. It suggests that *Hex. iravaticus* is a definite taxa not an ill-founded one of Boisserie (2005), and migrated and entered Myanmar during the Pliocene.

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