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Reevaluation of The Phylogeny and Taxonomy of The Asian Fossil Hippopotamuses

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Abstract

The Phylogeny of *Hexaprotodon* (Mammalia, Artiodactyla, Hippopotamidae) was reevaluated by using parsimony analysis. *Hex iravaticus* is the most primitive lineage of the Asian hippos, situated at the base of *Hexaprotodon* clade. *Hex sivalensis* and small-sized *Hex. palaeindicus* of Myanmar remained in the primitive morphological stages which are quite distinct from Indian and Javan forms. The cladistic analyses strongly suggest that the size variation seen in south Asian and Southern Asian taxa is interpreted as an interspecies variation rather than interspecific difference.

Key words: Asia, *Hexaprotodon*, Myanmar, phylogeny

Introduction

The origin of Asian hippopotamus, *Hexaprotodon*, was most probably in Africa during the Late Miocene (Boisserie *et al.*, 2005). They probably migrated into Asia during the latest Miocene. In Asia, their remains have been discovered from the various Mio-Pleistocene paleontological sites of South and Southeast Asia (Figure 1) (Falconer & Cautley, 1836, 1847; Lydekker, 1884; Colbert, 1938; Hooijer, 1950). In Asia, the latest Miocene to Late Pliocene fossil localities are restricted only for inland South and Southeast Asia (Siwalik, Myanmar), while, the Pleistocene sites are more widely distributed, continental Central India (Narbada) to insular Java.

Hippo remains from Siwalik, Narbada and Java have been described on many skulls, mandibles, and isolated teeth (e.g., Falconer & Cautley, 1847; Falconer, 1868; Lydekker, 1884; Colbert, 1938, 1943; Hooijer, 1950). Boisserie (2005) revised the phylogeny and taxonomy of family Hippopotamidae, mainly Hippopotaminae, by using the craniodental characters. In that analysis, only *Hexaprotodonsivalensis* and *Hex.palaeindicus* were adopted for Asian species, and *Hex.iravaticus* of Myanmar was not included because of lack of well-preserved skull and

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dental remains. Boissierie described that, in Asia, there are ten different forms recognized by Hooijer (1950). Hooijer's discussion on the fossil Hippopotamidae of Asia was done by using well-known skull and dental specimens, most of which are the Pleistocene Javan hippos. Boissierie (2005) followed Hooijer's idea that all small-sized Javan *Hexaprotodon* spp. are the sub species of *Hex. sivalensis*, but he did not use Hooijer's specimens and taxa in his description. However, he concluded that a comprehensive revision on the phylogeny of insular Indonesian hippos should be done. The variations on the morphology of skull and dentition among the continental Indian species and insular Javanese species are large. In previous, there was no information about the intermediate form in Myanmar, the midway between South Asia and peninsular Southeast Asia, and it was difficult to correlate the Indian forms and Javanese species.

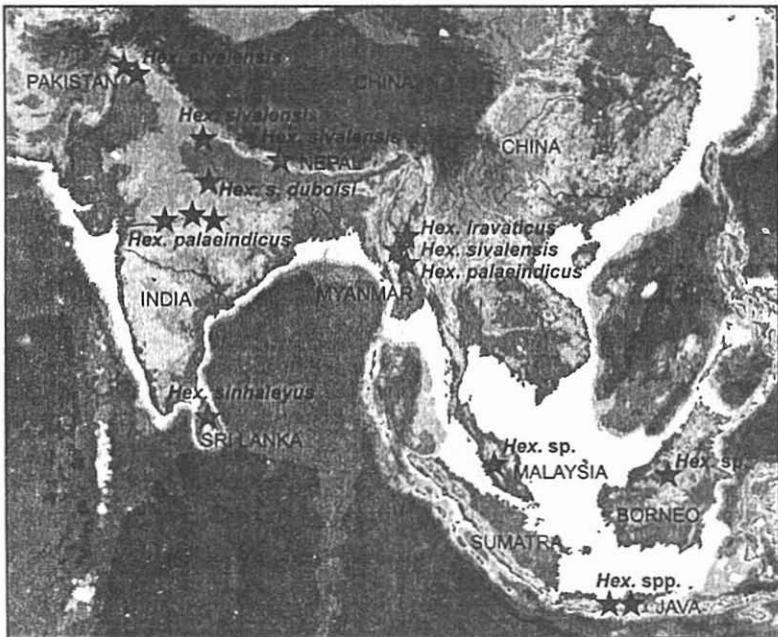


Figure 1. Fossil hippopotamuse localities in south and Southeast Asia.

Newly discovered hippo remains from Myanmar include *Hex. sivalensis* and *Hex. palaeindicus*, which are identified from the partial skulls and dentitions. The antecedent research data for the known species of Siwalik and Javan hippos have been described by previous workers (Hooijer,

1950; Boisserie, 2005), and new data for the skull and dental morphological characters of Myanmar species prompted to analyze the phylogenetic and taxonomic relationships between Myanmar and other Asian *Hexaprotodon*. In this study, the phylogeny of Asian *Hexaprotodon* together with African species is reevaluated by the parsimony analysis using morphological characters of fossil skull and dentition.

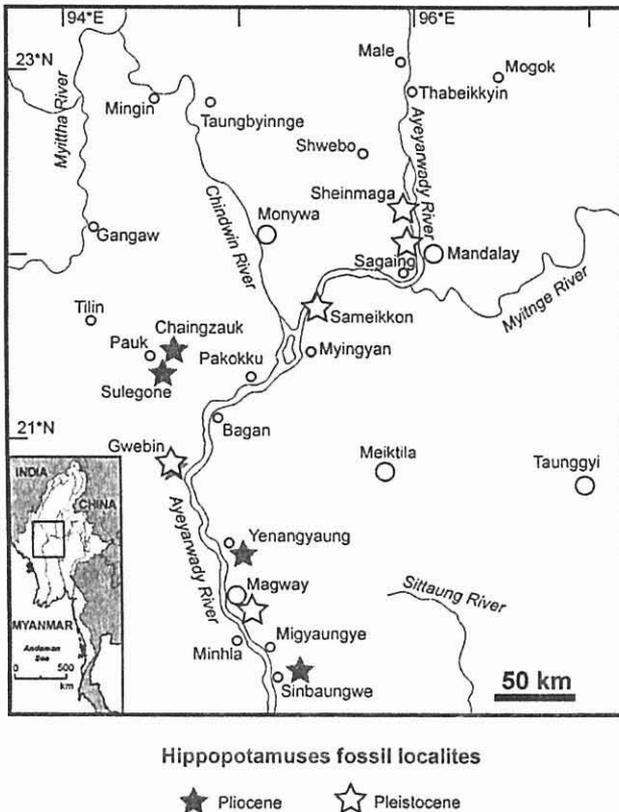


Figure 2. Hippopotamuses fossil localities in central Myanmar.

Previous studies on Asian fossil hippopotamuses

In Asia, there are three well known representative species, *Hex. sivalensis*, *Hex. palaeindicus* and *Hex. iravaticus*, and several poorly known subspecies, such as *Hex. namadicus*, *Hex. sivalensisduboisii*, *Hex. sinhaleyus*, *Hex. sivalensissivajavanicus*, *Hex. s. koenigswaldi* and *Hex. s. soloensis*. These subspecies were neglected in Boisserie's discussion on the

taxonomy and phylogeny of Hippopotamidae (Boisserie, 2005), probably because Hooijer (1950) placed them as the synonym or subspecies of *Hex. sivalensis*.

Koenigswald (1939) suggested that the intermediate-sized *Hex. namadicus* of Siwalik probably evolved from the small-sized Javanese hippos after their re-entering into India rather than directly from large-sized *Hex. sivalensis* of Siwalik. On the contrary, Hooijer (1950) revised Koenigswald's idea that Asian hippos, except for *Hex. iravaticus*, are single species, *Hex. sivalensis*, and skull and dental morphological variations among Siwalik and Javan species are intraspecies variations. He also described that "there is a Lower Pleistocene stages with low orbits, elongated post dental portion, long and low symphysis, and low horizontal ramus, and a stage with high orbits, shortened post-dental portion, and a short and high symphysis and horizontal ramus that appears higher up in the geological time scale and that prevails toward the close of the Pleistocene". Hooijer's (1950) idea was mainly based on the Pleistocene appearance of *Hex. sivalensis* in Siwalik, and his suggestion on the evolutionary trend in Asian hippos meant for the gradual changes from Siwalik *Hex. sivalensis* to Siwalik *Hex. palaeindicus* and from *Hex. sivalensis* to *Hex. s. soloensis* via *Hex. s. koenigswaldi*.

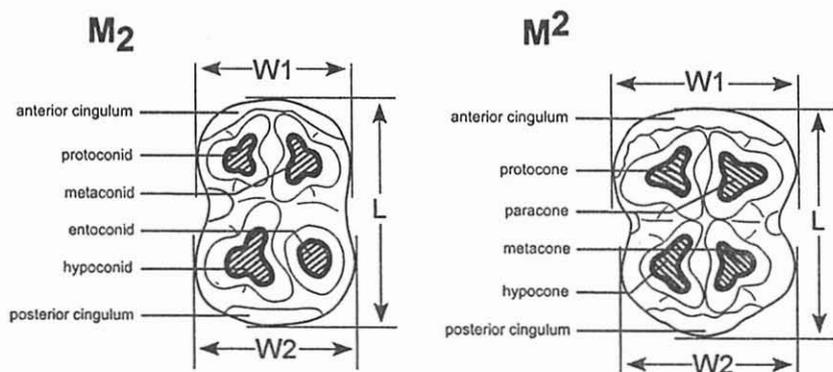


Figure 3. Dental terminology and measurement method of Hippopotamidae. All are left cheek teeth.

Recently, the first and last appearances of *Hex. sivalensis* in northern Pakistan were revised, latest Miocene to Late Pliocene, by the

results of radiometric and paleomagnetic dating (Barry *et al.*, 2002). According to the Hooijer's hypothesis, there would be the largest *Hex. sivalensis* of Siwalik which shows more primitive character stages than Javanese hippos: such as, in having much lower orbit, shorter molar row compare to premolar row, longer and lower symphysis, and lower horizontal ramus (Hooijer, 1950). However, Siwalik *Hex. sivalensis* is definitely larger in size and more derived than Javanese hippos. It appears difficult to explain that the phylogenetic and taxonomic relationship between larger, primitive and geochronologically older Siwalik *Hex. sivalensis* and smaller, progressive and geochronologically younger Javanese hippos. There is a large morphological and size gap between Siwalik and Javanese species, requiring an "intermediate form" between the Siwalik and Javanese forms in the "intermediate place", such as Myanmar (Hooijer, 1950).

Material and method

Three partial skulls and more than 55 dentognathic materials of fossil hippopotamuses were newly recorded from Myanmar during the present study (Table 1). 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 (Figure 2) and housed in Department of Archaeology and Museum (Yangon). Dental terminology and measurement method are according to Thenius (1989) (Figure 3). Dental measurements of some Myanmar specimens are listed in the Table 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). The cranial and mandible dimensions for the adult *Hexaprotodon* of Myanmar are described in the Table 3.

Skull and dental measurements of Asian hippos are taken mostly from well-known research data of the previous publications (Hooijer, 1950; Weston, 2003; Boisserie, 2005) and some from specimens housed in the National Science Museum, Tokyo, Japan. Foreign specimens are housed in the following museums and institution: Leiden Museum, Netherland; National Museum of Ethiopia, Addis Ababa, Ethiopia; Centre National d'Appui à la Recherche, Ndjamena, Chad; National Science Museum, Tokyo,

Japan; BMNH, London, UK. A parsimony analysis was performed to determine the position of Myanmar species within the *Hexaprotodon*. List of the taxa considered in this study are described in Table 4. Some not well-known Taxa, *Hex. sivalenssinhaleys* and *Hex. palaeindicus* (Myanmar, large), are extracted from cladistic analysis because they are known only for dental fragments.

Cladistic analysis

Outgroup

Among the Hippopotamidae, *Archaeopotamusharvardi*, Coryndon, 1977, is the oldest well known taxa (Weston, 2003). *Archaeopotamusharvardi* and *Hexaprotodongaryam* are contemporaneous in the Lower Nawata Formation (6.54 – 7.44 Ma), and the former is also discovered in the Upper Nawata Formation of Lothahgam (5.0 - 6.5 Ma) (McDougall and Feibel, 2003), southwest of Lake Turkana, Kenya. *A. harvardi* is well documented by numerous skulls and dental specimens and regarded as forerunner of all post-Miocene species except for the Liberian hippo, *Choeropsisliberensis* (Boisserie *et al.*, 2005). In this analysis, *A. harvardi* was taken as an out group of *Hexaprotodon* lineage. The morphological data of *A. harvardi* are taken from Weston (2003) and Boisserie (2005).

Characters

Only distinct morphological features are taken for the character. The total 28 cranial and dental features of adult specimens are described in the Appendix. All characters seen in *Archaeopotamusharvardi* are placed for state (0).

The character matrix includes 28 characters and 13 taxa (Table 5). The missing data percentage for the character matrix is 23.6%. All characters are type of unordered and unweighted. All characters are parsimony-informative.

Analysis

The analysis was performed in PAUP* v4.0β10 (Swofford, 1998). A maximum parsimony analysis was performed by bootstrap method. The stability of clades was evaluated by using 1000 replications of branch-and-bound search option (Felsenstein, 1985; Hills and Bull, 1993). Bootstrap value is used in order to examine the robustness of the various

clades revealed in the consensus tree clades (Felsenstein, 1985). Consensus trees with mean bootstrap values of <50% were rejected. According to Hills and Bull (1993), bootstrap values above the 70% has 95% confidence for related taxa. A strict consensus of the minimum length maximum parsimony trees was calculated. Tree length, consistency index (CI), and retention index (RI) were calculated. Consistency index measures the level of support for each tree. Consistency index will equal one when a data set explains the tree as well as possible. Retention index measures the congruency of the characters to each other and the tree. Retention index will equal one when the characters in a data set are totally congruent with each other and the tree.

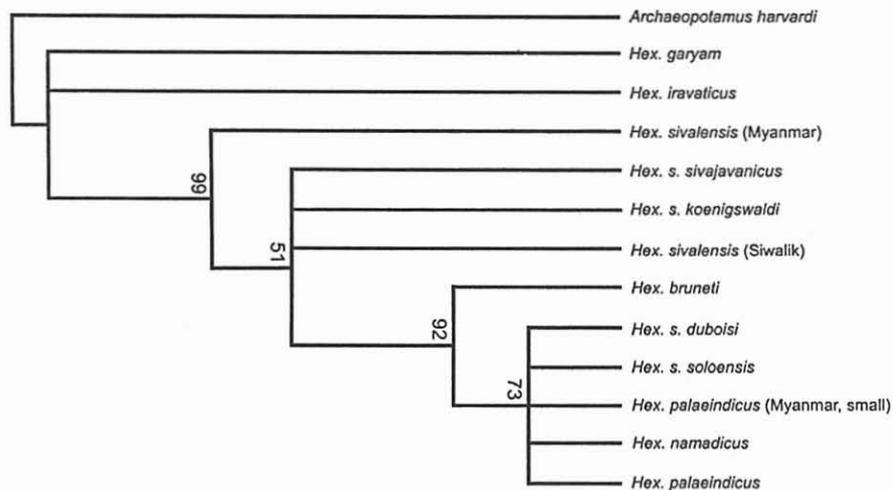


Figure 4. The most parsimonious tree of Hexaprotodon obtain from the cladistic analysis (length = 66, CI = 0.830, RI = 0.8219). Bootstrap results are given as an indication of clade robustness.

Results

The most parsimonious phylogenetic tree was obtained, and the length of the tree is 66 steps. The consistency index (CI) of the tree is 0.803. The retention index (RI) of the tree is 0.829. The most parsimonious tree with the results of the bootstrap analysis for an estimate of the node robustness is described in Figure 4. The character state changes of each node

(Accelerated transformation: ACCTRAN) for the most parsimonious tree is shown in Figure 5. 5 nodes for a monophyletic clade containing 12 taxa can be seen in the most parsimonious tree. A detail discussion for the case of each node is described in the following.

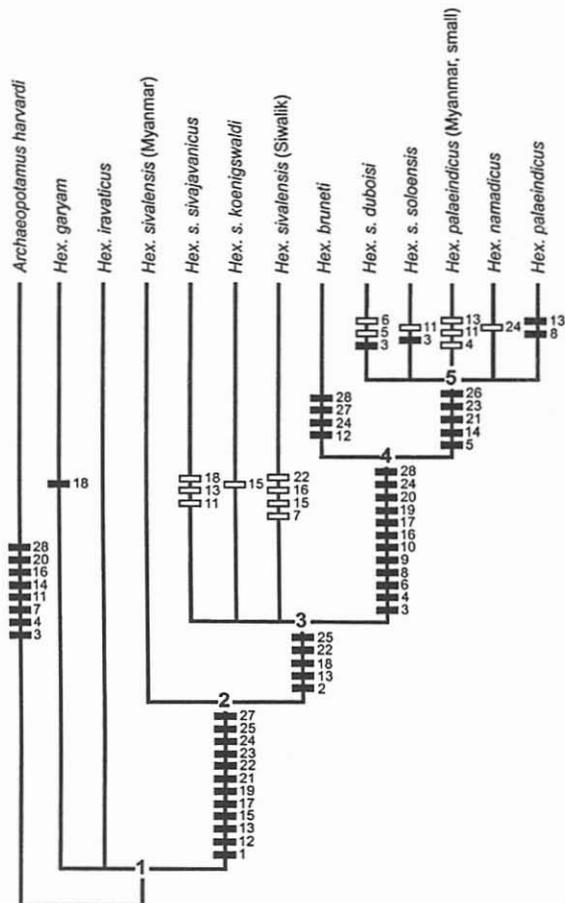


Figure 5. The most parsimonious trees of *Hexaprotodon* with nodes and character stages. The bold numbers indicate the nodes. The number boxes indicate the ACCTRAN character state changes (white boxes indicate reversion and convergences).

Node 1

Node 1 separates *Hexaprotodon* clade from outgroup, *Archaeopotamusharvadi*. The monophyletic genus *Hexaprotodon* is well supported by eight synapomorphic features: height of the orbits (character 3, state 1); outline of the orbits (character 4, state 1); outline of the glenoidarticular area (glenoid fossa) (character 7, state 1); frontal height index (character 11, state 2), degree of the inclination of the mandibular symphysis (character 14, state 1); symphysis height-length –index (character 16, state 1); distolingual heel for P² and P³ (character, 20, state 1); arrangement of the alveolus of the lower incisors (character 28, state 1).

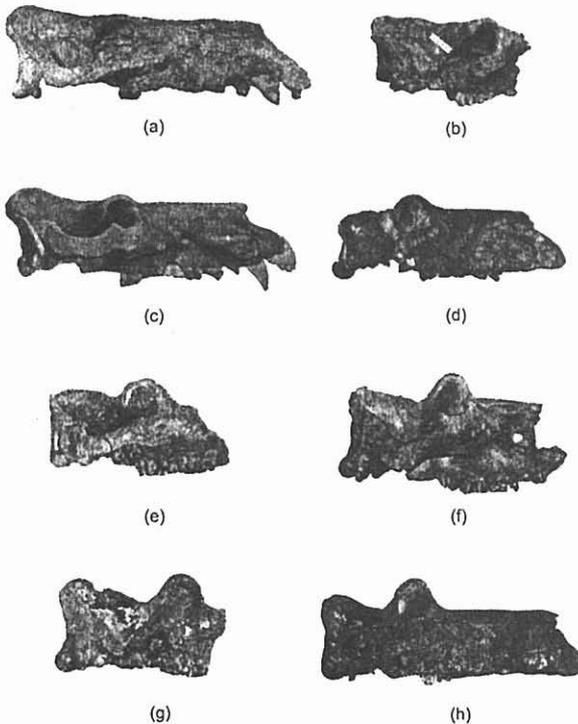


Figure 6. Right lateral view of hippopotamus skulls arranged in geochronologically older to younger. (a) *Archaeopotamusharvadi*; (b) *Hexaprotodonsivalensis* sp. nov.; (c) *Hex. s. sivalensis*; (d) *Hex. s. sivajavanicus*; (e) *Hex. s. koenigswaldi*; (f) *Hex. palaeindicus palaeindicus*; (g) *Hex. p. duboisi*; (h) *Hex. p. soloensis*.

However, character state changes of 3, 4 and 7 between *A. harvadi* and two primitive *Hexaprotodon*, *Hex. iravaticus* and *Hex. harvadi* are unknown because of the missing data.

Node 2

Node 2 separates the group consisting of *Hex. iravaticus* and *Hex. garyam* from the other 10 taxa of *Hexaprotodon*. These two groups can be separated distinctly by the 12 synapomorphic features: post-canine constriction of the muzzle (character 1, state 1); proportion of the largest width of the muzzle relative to the narrowest width of the post canine constriction of the muzzle (character 12, state 1); general skull size (character 13, state 1); Symphysis length-width index (character 15, state 3); ramus length-height index (character 17, state 1); outline of ramus (character 19, state 1); occlusal area of P³ and P⁴ (character 21, state 1); P⁴ morphology (character 22, state 1); occlusal outline of the cusp of upper molars (character 23, state 1); Size of the I₃ relative to the I₁ (character 24, state 1); P₄ morphology (character 25, state 1); the upper margin of the lower canine (character 27, state 1).

Hex. iravaticus and *Hex. harvadi* are the most primitive taxa within *Hexaprotodon*, and can be taken as the sister taxa of the remaining *Hexaprotodon*. Only one synapomorphy unifies *Hex. iravaticus* and *Hex. garyam*: lateral outline of the mandible (character 8). *Hex. garyam* show more derived in character state (state 2, mesially higher mandible) than the *Hex. iravaticus*. Boissieriet al. (2005) emphasized this character as a diagnosis of this species to differentiate from the Asian primitive type *Hexaprotodon*, *Hex. sivalensis*. *Hex. iravaticus* Falconer & Cautley, 1847, is firstly identified under the diagnosis of small size (character 13) and narrow and long mandibular symphysis (character 15) and has been suggested as the most primitive form of *Hexaprotodon* in Asia (Lydekker, 1884). The additional distinct characters between *Hex. iravaticus* and other Asian species strongly support the valid taxonomic status *Hex. iravaticus* among Asian hippos.

Node 3

Node 3 separates *Hex. sivalensis* (Myanmar) from the group of the remaining species except for *Hex. iravaticus* and *Hex. garyam*. They are differentiated by the five synapomorphic features: position of the anterior border of the orbit (character 2, state 1); general skull size (character 13,

state 2); lateral outline of the mandible (character 18, state 1); P⁴ morphology (character 22, state 2); P₄ morphology (character 25, state 2). However, some character states changes which are used to separate *Hex. sivalensis* (Myanmar) from others in node 3 are appeared again as the homoplastic character states (reversion and convergence) in *Hex. sivalensis* (Siwalik), *Hex. s.sivajavanicus* and *Hex. s. koenigswaldi* of node 3. As a result, this clade is only weakly supported (51% bootstrap result).

Node 3 associates two groups, Node 4 group (the association of the African Pliocene *Hex. bruneti* and five *palaeindicus* type taxa (*Hex. s. soloensis*, *Hex. palaeindicus* (Myanmar, small), *Hex. s. duboisi*, *Hex. palaeindicus* and *Hex. namadicus*) and the group of *sivalensis* type taxa (*Hex. sivalensis*, *Hex. s.sivajavanicus* and *Hex. s. koenigswaldi*). Among the three species of the group of *sivalensis* type taxa, it can be seen that they are supported separately by the different homoplastic characters states: *Hex. s. sivajavanicus* by character 11 (state 0), character 13 (state 1) and character 18 (state 0); *Hex. s. koenigswaldi* by character 15 (state 2); *Hex. sivalensis* by character 7 (state 0), character 15 (state 1), character 16 (state 0) and character 22 (state 1).

Node 4

Node 4 is strongly supported (92% bootstrap result). It separates two groups of node 3 (node 4 group and group of *sivalensis* type taxa). There are 12 synapomorphic features which separate these two groups (see Figure 40). Within the node 4 group, the African Pliocene *Hex. bruneti* Boissier & White, 2004, and *Hex. palaeindicus* (a species of *palaeindicus* type taxa) has been suggested as the sister taxa, both of which are evolved from *Hex. sivalensis* of Siwalik (Boissier, 2005). It is not surprising that this node 4 is strongly supported to separate the *sivalensis* type taxa and *palaeindicus* type taxa.

Hex. bruneti is unified by the 4 synapomorphic features: proportion of the largest width of the muzzle relative to the narrowest width of the post canine constriction (character 12, state 2), size of the I₃ relative to the I₁ (character 24, state 3), the upper margin of the lower canine (character 27, state 2), arrangement of the alveolus of the lower incisors (character 28, state 3). These features are taken as the diagnosis of this species, and that is why *Hex. bruneti* is separated from the remaining species by well supported node 5.

Node 5

Node 5 is well supported by the 73% bootstrap result. It associates the Asian species which possesses the dental and skull features of *Hex. palaeindicus*. It consists *Hex. palaeindicus*, *Hex. namadicus*, *Hex. palaeindicus* (Myanmar, small) *Hex. sivalensisduboisii*, and *Hex. s. soloensis*.

Hex. sivalensis soloensis of Java and *Hex. s. duboisii* of India are unified by the same states of synapomorphic character, height of the orbit (character 3, state 3); however, the remaining homoplastic features which support these two species are quite different, character 6 (state 0) and character 5 (state 0) in *Hex. s. duboisii* and character 11 (state 1) in *Hex. s. soloensis*. These differences have been used to separate these two subspecies (Hooijer, 1950).

The remaining three species of this node are unified by separate synapomorphic and homoplastic features. Two synapomorphies unify *Hex. palaeindicus*: general skull size (character 13, state 3) and posterior border of the plate (character 8, state 2). Single homoplastic feature unifies *Hex. namadicus*: size of the I₃ relative to the I₁ (character 24, state 1). Small-sized Myanmar *Hex. palaeindicus* is unified by three homoplastic features: outline of the orbit (character 4, state 1), frontal height index (character 11, state 0) and general skull size (character 13, state 1).

Discussion

The result of the parsimony analysis indicates a distinct monophyletic tree including all species of *Hexaprotodon*. High RI and CI values for this most parsimonious tree indicate the high reliability of this phylogenetic tree. The taxonomic statuses of two African species, *Hex. garyam* and *Hex. bruneti* are same as the results of previous works, where *Hex. garyam* is situated at the base of the clade, and *Hex. bruneti* and *Hex. palaeindicus* are sister taxa (Boisserie and White, 2004; Boisserie, 2005; Boisserie et al., 2005). The character states of *Hex. garyam* and *Hex. iravaticus* are very similar to each other, with only one character separating them in this analysis. The progressive stage for the lateral outline of the mandible in *Hex. garyam* suggests this species might be a close relative of *Hex. iravaticus* rather than an ancestor.

The relatively low bootstrap value between *Hex. sivalensis* of Myanmar and others suggests that Myanmar specimen may not represent a

new species. Within the parsimonious tree, three subspecies of *Hex.sivalensis* from Java are clearly separated by the two phylogenetic steps, *Hex. sivalensis* and *Hex. palaeindicus*. *Hex. sivajavanicus* and *Hex. koenigswaldi* lie within the morphology stage of *Hex. sivalensis*, whereas *Hex. s. soloensis* falls within the morphology stage of *Hex. palaeindicus*, suggesting that taxonomic status of *Hex. s. soloensis* may be close to *Hex. palaeindicus* rather than to *Hex. sivalensis*.

Hooijer (1950) insisted the elevation of the orbit above the frontal bone is an evolutionary trend of *Hexaprotodon*. Three convergence homoplastic character states of relatively low elevation of orbit, smaller sized and lower in frontal height index for the small-sized *Hex. palaeindicus* of Myanmar suggests that it is more primitive than other taxa of *Hex. palaeindicus* lineage. The phylogenetic position of *Hex.namadicus* is still uncertain, because most of the characters of this species is missing, and the most of known materials of *Hex. namadicus* and *Hex. palaeindicus* (Myanmar, small) are mostly different parts of the skull. However, the two separated localities of them, Narbada of India and central Myanmar, suggest the different subspecies or species status for them.

Phylogenetic context and evolutionary trends in Asian hippopotamuses

The result of the present parsimony analysis for the phylogenetic relationships within *Hexaprotodon* lineage is mostly similar to the result of previous works (Boisserie & White, 2004; Boisserie, 2005; Boissier *et al.*, 2005). The origin of *Hexaprotodon* might be Africa. At present, *Hex. garyam* is considered the oldest taxa (ca 7.0 Ma), and its first appearance is very close to the oldest Late Miocene taxa of Hippopotaminae, such as *Archaeopotamusharvadi* (ca. 5.0 – 7.44 Ma). The poorly differentiated hexaprotodont incisors, uninterrupted cingulum on upper molars and strong accessory cusps and bicuspidate P⁴ of *Hex. garyam* has been suggested clear primitive features of Hippopotaminae clade (Boissier *et al.*, 2005). *Hex. garyam* would be the first representative of the “Asian” hippopotamuses which were recovered after 6 Ma (Boissier *et al.*, 2005).

In Asia, on the other hand the oldest well known species is *Hex.sivalensis* of Siwalik in northern Pakistan (5.9 Ma for first occurrence and 6.1 Ma for inferred first appearance: Barry *et al.*, 2002). However, *Hex. garyam* is similar to *Hex. iravaticus* rather than to *Hex. sivalensis*. The significant size and morphological differences between *Hex.garyam* and *Hex. iravaticus* are very small, the latter also shows primitive characters of

hippopotamuses (poorly differentiated hexaprotodont incisors, uninterrupted cingulum on upper molar, strong accessory cusps and bicuspidate P⁴). These two small-sized *Hexaprotodon* are described based on the partial cranial and mandibular fragments. There may be some unknown distinct characters differentiating these two species. At present, they can be differentiated only by the overall morphology of the mandibular corpus, which may be related with substantial difference of their diets. Anteriorly tapering mandible of *Hex. iravaticus* is considered the most primitive state seen in the oldest hippopotamuses, such as *Archaeopotamusharvadi*, so that *Hex. garyam* may be the sister taxon of *Hex. iravaticus* rather than an ancestor.

According to the recent publications, *Hex. sivalensissivalensis*, a large-sized *Hexaprotodon*, is the well-dated oldest species of Asia. It was recorded as the Pleistocene Upper Siwalik fauna in old literatures (e.g., Colbert, 1935). Barry *et al.* (1995) revised the first appearance date of *Hex. sivalensis* to 5.7 Ma based upon the radiometric and paleomagnetic data, and he furthermore inferred first appearance of *Hex. sivalensis* to 6.1 Ma (Barry *et al.*; 2002), without giving any reason for his identification (Gentry, 1999).

On the other hand, there are some records for the discoveries of *Hex. iravaticus*-sized hippo remains from the Middle Siwalik, DhokPathan equivalent sediments (Lydekker, 1884; Pilgrim, 1910). The latest Miocene and the Pliocene *Hexaprotodon* in Asia may be a small-sized species, became *Hex. iravaticus* and small-sized *Hex. sivalensis* subsp. nov. has been discovered from the Early Pliocene in Myanmar. It suggested a small-sized *Hexaprotodon* have arrived in Asia during the latest Miocene, and later, some forms such as the Siwalik *Hex. sivalensis* (*Hex. s. sivalensis*) became larger in size.

In Myanmar, both Pliocene *Hex. sivalensis* (*Hex. sivalensis* subsp. nov.) and *Hex. iravaticus* do not show large body size variations, whereas in Java, *Hex. sivalensiskoenigswaldi* is quite smaller than *Hex. sivalensissivajavanicus*. The first appearance of the former is younger than the latter (Koenigswald, 1933, 1934) and there can be seen the reverse progressive trend compare to Siwalik species which progress small to large-sized taxa. The late Pliocene and Pleistocene *Hex. palaeindicus* in Siwalik shows large size variation, *Hex. palaeindicusnamadicus*, *Hex. p. duboisi* and *Hex. p. palaeindicus*. In Southeast Asia, Middle Pleistocene Javanese form (*Hex. p. soloensis*) is only slightly larger than the Late

Pliocene Myanmar form (*Hex. palaeindicussubsp. nov.*) and smaller than the Early Pleistocene Myanmar form (*Hex. p. cf. palaeindicus*). It suggests that large size variation among *Hexaprotodon* species is the intraspecies geographical variation rather than evolutionary trends.

Compared to size variations, the gradual elevation of the orbits can be seen in younger species, without any relation of body size enlargement. The position of the orbits in the latest Miocene to the Late Pliocene large-sized *Hexaprotodonsivalensissivalensis* is distinctly lower than that of the latest Pliocene or Early Pleistocene Javanese *Hex. s. sivajavanicus* and *Hex. s. koenigswaldi*. The position of the orbits in the Early Pleistocene large-sized *Hex. palaeindicuspalaeindicus* much lower than that of Middle to Late Pleistocene Javanese *Hex. p. soloensis* (Figure 6). Thus, the elevation of the orbits can be seen as the evolutionary trend in the *Hexaprotodon* lineages. Hooijer (1950) described that Middle to Late Pleistocene forms have high positioned orbits, shorter and higher in mandibular symphysis, shorter in post-dental portion and higher in the height of mandibular corpus than those of the Early Pleistocene forms. He also suggested that these transformations have certainly been accomplished in several collateral lines of the Hippopotamidae.

Boisserie (2005) also described the evolutionary trends of *Hexaprotodon* as follows: increase in diameter of the I₃ diameter relative to that of the other incisors; the increasing elevation of the orbits; and increasing height of the molar crown.

The present analysis, demonstrate some evolutionary changes within *Hexaprotodon* lineages: reduction of protocone in P⁴, reduction of distolingual heel in P³, reduction of metaconid and linguo-distal cusplets in P₄; gradually expanded cusps in upper molars, gradual change from poor tri-foliate outline with wide grooves to sometimes tetra-foliate outline with narrow grooves in cusps of the upper molars, backward shift in the position of the posterior border of the palate; and dorsally shifted I₂.

As discuss in above Javanese *Hex. sivalensissubsp.* probably evolved from small-sized *Hex. sivalensissubsp. nov.* of Myanmar. However, the morphological feature and result of parsimony analysis indicate that *Hex. s. soloensis*) might be closely related to *Hex. palaeindicus* and likely evolved from *Hex. palaeindicus subsp. nov.* of Myanmar rather than directly from Javanese *Hex. sivalensis*.

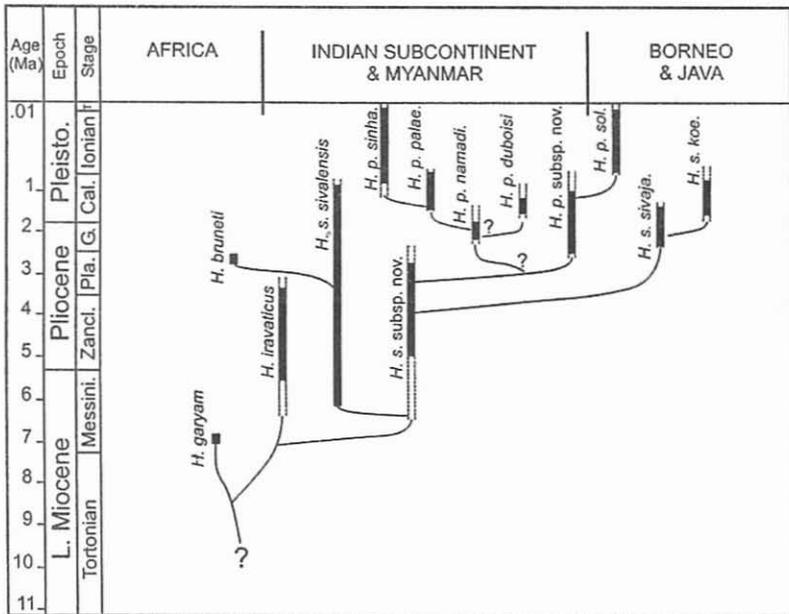


Figure 7. Probable new phylogeny for *Hexaprotodon*: geographical distribution.

According to the results of parsimony analysis, the revised phylogeny and evolutionary trend for the *Hexaprotodon* is newly described (Figure 7). Most of *Hexaprotodon* species are highly diversified in South and Southeast Asia after they migrated from Africa. Only *Hex. bruneti* is the exceptional which constitutes a presumptive migrant of the lineage into Africa during Pliocene (Boisserie & White, 2004). In Asian hippopotamuses, the morphology and size of the skull and dentition of *Hex. iravaticus* do not exhibit significant variation. In *Hex. sivalensis* and *Hex. palaeindicus*, there are several changes in evolutionary and geographical. Compared to *Hex. sivalensis*, the phylogenetic relationship among *Hex. palaeindicus* subspecies is quite problematic. The data contained in the present study do not permit to identify more precisely on the phylogenetic relationship among *Hexaprotodon* spp. However, the discovery of intermediate forms in Myanmar, together with well informative skull and dental fragments, greatly supports to reconstruct the phylogeny of the Asian hippos.

Conclusion

Three distinct species of *Hexaprotodon* are recovered from the central Myanmar. The cladistic analysis of Asian hippos suggested that *Hex. iravaticus* is a primitive in Asian hippos and the sister taxon of others. *Hex. sivalensis* of Myanmar represent a new subspecies, and shows primitive in character than the other species of *Hex. sivalensis*. A small-sized *Hex. palaeindicus* from Myanmar is placed to new subspecies, and it is primitive than others *Hex. palaeindicus*. The analyses suggest that *Hexaprotodon* species are highly diversified in South and Southeast Asia after they migrated from Africa. The discovery of intermediate forms in Myanmar, together with well informative skull and dental fragments, greatly supports to reconstruct the phylogeny of the Asian hippos, and the size variation seen in south Asian and Southern Asian taxa is interpreted as an interspecies variation rather than interspecific difference.

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Table 1. List of the hippo specimens of Myanmar which have been studied in this work

| Subfamily | Taxa | NMMP-KU number | NMM number | Locality | Material |
|----------------|---|----------------|------------|---|---|
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0006 | | Gbn1 | canine fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0015 | | Gbn2 | canine fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0023 | | Gbn1 | molar fragment |
| Hippopotaminae | <i>Hexaprotodon sivalensis.</i> | IR 0046 | | Gbn2 | partial skull fragment with right upper P3-M3 and left upper P4-M3 |
| Hippopotaminae | <i>Hexaprotodon sivalensis</i> | IR 0067 | | Gbn2 | right upper P4 |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0070 | | Gbn2 | molar fragment |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0080 | | Gbn1 | right upper P1 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0124 | | near Chaingzauk Village, Pauk TS., Magway Div. | right upper M1 or M2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0125 | | near Chaingzauk Village, Pauk TS., Magway Div. | right lower canine |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0177 | | near Chaingzauk Village, Pauk TS., Magway Div. | fragment of mandibular symphysis with roots of right i1-c, and alveolus of p1-p2; roots of left i1-c and alveolus of p1-p2 |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0184 | | CHZ14 | root of upper P3 or P4 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0191 | | CHZ20 | right mandibular fragment with p4-m3 and root of p3 |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0210 | | CHZ15 | mandibular fragment with root of a molar |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0229 | | Gbn1 | molar fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0281 | | near Chaingzauk Village, Pauk TS., Magway Div. | right astragalus |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0302 | | near Chaingzauk Village, Pauk TS., Magway Div. | right mandibular fragment with mesial half of m2 and roots of p4-m1 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0326 | | near Chaingzauk Village, Pauk TS., Magway Div. | right mandibular fragment m3 |
| Hippopotaminae | <i>Hexaprotodon sivalensis</i> | IR 0436 | HBG-19 | near Tabingyaung Village, Seikpyu TS, Magway Div. | right mandibular fragment with m2 |
| Hippopotaminae | <i>Hexaprotodon palaeindicus subsp.</i> | IR 0437 | HBG-20 | near Tabingyaung Village, Seikpyu TS, Magway Div. | left mandibular fragment with m2-m3 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0438 | IAH-1 | Yebyu-Letma area, Yaw Chaung, Magway Div. | maxillary fragment with right P4-M3, and roots of P2-P3; left P3-M3, and roots of P2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0449 | | Yebyu-Letma area, Yaw Chaung, Magway Div. | mandibular fragment with right m1-m3, roots of i3, c, p2-p4, and alveolus of i1-i2, p1; left roots of c, p2-p3, and alveolus of i1-i3, p1 |
| Hippopotaminae | <i>Hexaprotodon sivalensis</i> | IR 0458 | GPN 55 | near Gwebin Village, Seikphyu TS., Magwe Div. | left upper canine fragment |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0459 | GPN 56 | near Gwebin Village, Seikphyu TS., Magwe Div. | right upper m3 |
| Hippopotaminae | <i>Hexaprotodon sivalensis</i> | IR 0460 | GPN 54 | near Gwebin Village, Seikphyu TS., Magwe Div. | left upper canine fragment |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0461 | GPN 53 | near Gwebin Village, Seikphyu TS., Magwe Div. | left lower canine fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0487 | | CHZ (157) | premolar fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0492 | | CHZ (163) | premolar fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0519 | | SLG 4 | canine fragment |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0529 | | CHZ 172 | right upper M2 |

Table 1 (continue). List of the hippo specimens of Myanmar which have been studied in this work.

| | | | | |
|----------------|--------------------------------|-----------|--|------------------------------------|
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0530 | CHZ 171 | molar fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0543 | CHZ 182 | molar fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0545 | CHZ 186 | canine fragment |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0547 | near Chaingzauk Village, Pawk TS., Magway Div. | distal fragment of right lower m2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0548-1 | near Chaingzauk Village, Pawk TS., Magway Div. | left lower p4 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0546-2 | near Chaingzauk-Village, Pawk TS., Magway Div. | right lower p3 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0546-3 | near Chaingzauk Village, Pawk TS., Magway Div. | mesial fragment of right upper M2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0550 | near Chaingzauk Village, Pawk TS., Magway Div. | right upper M1 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0551-1 | CHZ 183 | left upper P4 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0551-2 | CHZ 183 | mesial fragment of left lower m3 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0555 | near Chaingzauk Village, Pawk TS., Magway Div. | right upper DP4 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0556 | near Chaingzauk Village, Pawk TS., Magway Div. | lingual fragment of right upper M2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0557 | near Chaingzauk Village, Pawk TS., Magway Div. | left lower m2 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0560 | CHZ 172 | canine fragment |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0565 | CHZ 185 | molar fragments (two pieces) |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0566 | CHZ 185 | right mesial fragment of dp4 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0567 | CHZ 185 | right lower m3 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | IR 0570 | near Chaingzauk Village, Pawk TS., Magway Div. | left upper P2 |
| Hippopotaminae | <i>Hexaprotodon sp.</i> | IR 0674 | CHZ 180 | molar fragment |

| Subfamily | Taxa | NMMP-KU number | MGW number | Locality | Material |
|----------------|--------------------------------|----------------|------------|--|---|
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | - | 1 | near Suptayan Village, Thityakauk TS., Magway Div. | left mandibular fragment with p4-m2, and alveolus of p3, m3 |
| Hippopotaminae | <i>Hexaprotodon iravaticus</i> | - | 55 | unknown locality, Magway Div. | proximal of mandibular symphysis with right I1-I3; left I1-I2 |

| Subfamily | Taxa | NMMP-KU number | MUOG-V number | Locality | Material |
|----------------|--|----------------|---------------|--|--|
| Hippopotaminae | <i>Hexaprotodon palaeindicus</i> subsp. nov. | - | 1001 | E bank of Ayeayawady River, Sameikkon City, Mandalay | partial skull fragment with right M3; proximal part of skull is broken |
| Hippopotaminae | <i>Hexaprotodon palaeindicus</i> subsp. nov. | - | 1002 | near Sheinmaga Village, Saseing Div. (from Plateau Gravel) | right maxillary fragment with M1-M3 |
| Hippopotaminae | <i>Hexaprotodon svaleris</i> | - | 1003 | near Payeayo Village, Magway Div. (between Natmauk & Magway) | left mandibular fragment with m2-m3; m2 frontal is broken |

List of Suidae (Mammalia, Artiodactyla) with Magway University-Geology Museum specimen no. (MGW)

MGW = Magway University

storage location: Geology Museum, Department of Geology, Magway University, Magway, Myanmar

List of Suidae (Mammalia, Artiodactyla) with University of Mandalay-Geology Museum specimen no. (MUOG-V)

MUOG-V = Mandalay University Department of Geology-Vertebrate

storage location: Geology Museum, Department of Geology, University of Mandalay Mandalay, Myanmar

Table 3. Measurements (mm) of the skulls of Myanmar *Hexaprotodon*.Cranial dimension of adult *Hexaprotodon* of Myanmar

| Specimen | NMM IAH 1 | NMMP-KU-IR 0046 | MUDG-V 1001 |
|---|------------------------|-------------------------------------|--|
| Taxa | <i>Hex. iravaticus</i> | <i>Hex. sivalensis</i> (Myanmar) | <i>Hex. palaeindicus</i> (Myanmar, small) |
| Zygomatic width | | >250 mm | 308 mm |
| Width of the brain case | | 82 mm | 102.8 mm |
| Maximum horizontal diameter of the orbit | - | 52.58 mm | 64.78 mm |
| Maximum vertical diameter of the orbit | - | 59.14 mm | >70 mm |
| Height of the orbit above the frontal bone | - | 12 mm | *30 mm |
| Index of the height of the orbit | | 20 | 43 |
| Length of the sagittal crest | - | 122 mm | 66 mm |
| Smallest width of sagittal crest | - | 17 mm | 5 mm |
| Height of the occiput | - | >163 mm | >150 mm |
| Width of the occiput | - | >210 mm | 227 mm |
| Occiput height- width index | | 77.2 | 66 |
| Height of the frontal to M3 | - | 126 mm | 115 mm |
| Width of the plate at M1 | 41.4 mm | 44.4 mm | *55 mm |
| Frontal height index | - | 35 | 48 mm |
| Largest width of the muzzle | 187 mm | - | - |
| Narrowest width of the post canine constriction | 101 mm | - | - |

Mandible dimension of adult *Hexaprotodon* of Myanmar

| Specimen | NMMP-KU-IR 0449 |
|--|------------------------|
| Taxa | <i>Hex. iravaticus</i> |
| Degree of the inclination of the symphysis | 46 |
| Length of symphysis | 147 mm |
| Height of the symphysis | 88 mm |
| Symphysis height-length index | 59.8 |
| Interval between lower canines | 140 mm |
| Symphysis length-width index | 105 |
| Length from front to M3 | 307 mm |
| Height of ramus at M2 | 86.6 mm |
| Ramus length-height index | 354.5 |

Table 4. The examined and studied *Hexaprotodon* spp. in this work and their geographical distribution.

| Taxa | Occurences | References |
|---|---|--|
| <i>Hex. iravaticus</i> | Myanmar (Plio.) | Falconer & Cautley, 1847; Colbert, 1938; Hooijer, 1950; present work |
| <i>Hex. sivalensis</i> (Myanmar) | Myanmar (M. Plio.) | Colbert, 1938; Chit-Sein, 2006; present work |
| <i>Hex. palaeindicus</i> (Myanmar, small) | Myanmar (U. Plio.) | present work |
| <i>Hex. palaeindicus</i> (Myanmar, large) | Myanmar (L. Pleisto.) | Colbert, 1938; Hooijer, 1950 |
| <i>Hex. garyam</i> | Djurab, Chad (U. Mio.) | Boisserie <i>et al.</i> , 2005a |
| <i>Hex. sivalensis</i> (Siwalik) | Siwalik, India, Pakistan, Nepal (U. Mio. - L. Pleisto.) | Falconer & Cautley, 1836; Colbert, 1935b; Hooijer, 1950 |
| <i>Hex. palaeindicus</i> | Narbada Valley, central India (Pleisto.) | Falconer & Cautley, 1847; Hooijer, 1950 |
| <i>Hex. namadicus</i> | Narbada Valley, central India (Pleisto.) | Falconer & Cautley, 1847; Hooijer, 1950 |
| <i>Hex. sinhaleysus</i> | Ratnapura, Sri Lanka (L. Pleisto.) | Deraniyagala, 1936; Hooijer, 1950 |
| <i>Hex. bruneti</i> | Bouri, Ethiopia (U. Plio.) | Boisserie & White, 2004 |
| <i>Hex. sivalensis sivalavanicus</i> | Western and central Java, Indonesia (L. Pleisto.) | Hooijer, 1950 |
| <i>Hex. sivalensis koenigswaldi</i> | Java, Indonesia (L. Pleisto.) | Hooijer, 1950 |
| <i>Hex. sivalensis duboisi</i> | Punjab, India (Pleisto.) | Hooijer, 1950 |
| <i>Hex. sivalensis soloensis</i> | Central and eastern Java, Indonesia (M. - U. Pleisto.) | Hooijer, 1950 |

Table 5.Character matrix of *Hexaprotodon*. Missing data are indicated by ?

| Characters | 1 | | | | | 1 1 1 1 1 | | | | | 1 1 1 1 2 | | | | | 2 2 2 2 2 | | | | | 2 2 2 | | | | | | | | |
|---|---|---|---|---|---|-----------|---|---|---|---|-----------|---|---|---|---|-----------|---|---|---|---|-------|---|---|---|---|---|---|---|---|
| Taxa | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | |
| <i>Archaeopotamus harvardi</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>Hex. iravaticus</i> | 0 | 0 | ? | ? | ? | 0 | ? | 0 | 0 | 0 | ? | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | |
| <i>Hex. sivalensis</i> (Siwalik) | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | |
| <i>Hex. sivalensis</i> (Myanmar) | ? | 0 | 1 | 1 | 0 | 0 | ? | 0 | 0 | 0 | 2 | ? | 1 | ? | ? | ? | ? | 0 | 1 | 1 | 1 | 1 | ? | ? | 1 | 0 | ? | ? | |
| <i>Hex. s. sivajavanicus</i> | ? | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 1 | 1 | 3 | ? | ? | 0 | 1 | 1 | 1 | 2 | 1 | 1 | ? | 0 | ? | ? | |
| <i>Hex. s. koenigswaldi</i> | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | ? | 1 | 1 | 2 | 0 | 1 | 1 | |
| <i>Hex. palaeindicus</i> | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 3 | 2 | 3 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | |
| <i>Hex. namadicus</i> | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | 2 | 3 | 2 | ? | 1 | 2 | ? | ? | ? | ? | ? | 1 | 2 | 1 | 1 | 2 |
| <i>Hex. palaeindicus</i> (Myanmar, small) | ? | 1 | 2 | 1 | 1 | 1 | 1 | ? | 1 | 1 | 0 | ? | 1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | ? | ? | 1 | ? | ? | |
| <i>Hex. s. soloensis</i> | 1 | 1 | 3 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 2 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 2 | |
| <i>Hex. s. duboisi</i> | ? | 1 | 3 | 2 | 0 | 0 | ? | 1 | ? | 1 | ? | ? | 2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | ? | ? | 1 | ? | ? | |
| <i>Hex. bruneti</i> | 1 | ? | ? | ? | ? | 1 | ? | ? | ? | 1 | ? | 2 | 2 | 1 | 3 | 2 | 2 | 1 | 2 | 2 | 1 | 2 | 1 | 3 | 2 | 0 | 2 | 3 | |
| <i>Hex. garyam</i> | 0 | ? | ? | ? | ? | 0 | ? | ? | 0 | 0 | ? | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | |

Appendix

The characters: description and comments

Skull (cranium)

1. *Post-canine constriction of the muzzle*: (0) weak constriction in comparison to the lateral extension of the skull canine apophyses; (1) deep constriction in comparison to the lateral extension of the skull canine apophyses.
2. *Position of the anterior border of the orbit* (in lateral view): (0) anterior to the middle of M^2 ; (1) posterior to the middle of M^2 .
3. *Height of the orbits* (100 x elevation of the orbit above the frontal / vertical diameter of the orbit): (0) orbital summit at the level of the cranial roof; (1) orbital summit poorly elevated above the cranial roof (<40); (2) orbital summit elevated well above the cranial roof (40~65); (3) orbital summit strongly elevated above the cranial roof (>70).
4. *Outline of the orbits* (lateral view): (0) maximum horizontal diameter is larger than maximum vertical diameter; (1) vertical diameter is quite larger than horizontal diameter; (2) vertical diameter is distinctly larger than horizontal diameter.
5. *Sagittal crest*: (0) strong; (1) weak.
6. *Brain case morphology* (dorsal view): (0) elongated; (1) short.
7. *Outline of the glenoidarticular area* (in ventral view): (0) an elongated shape with laterally convergent anterior and posterior borders; (1) laterally divergent anterior and posterior borders.
8. *Posterior border of the plate*: (0) more backward than the distal end of M^3 ; (1) sub-parallel with the distal end of M^3 ; (2) M^3 extends more backward.
9. *Anterior border of the palato-maxillary suture*: (0) anterior (or) same level to the mesial border of M^2 ; (1) posterior to the middle of M^2 .
10. *Occiput height-width index* (100 x height of the occiput / width of the occiput); (0) high (>70); (1) low (<70).
11. *Frontal height index* (100 x width of the palate at M^1 / height of the frontal to M^3 alveolus): (0) low (>45); (1) high (45~40); (2) very high (<40).
12. *Proportion of the largest width of the muzzle relative to the narrowest width of the post canine constriction of the muzzle*: (0) small (<200%); (1) medium (200~250%); (2) large (>250%).
13. *General skull size*: (0) small; (1) medium; (2) large; (3) very large.

Mandible

14. *Degree of the inclination of symphysis*: (0) low angle (<45°); (1) moderate angle (45°~65°); (2) high angle (>65°).
15. *Symphysis length-width index* (100 x length of symphysis / interval between canines): (0) > 100; (1) 95~85; (2) 80~70; (3) <70.
16. *Symphysis height-length index* (100 x height of symphysis / length of symphysis): (0) <50; (1) 50~60; (2) >60.
17. *Ramus length-height index* (100 x length from front to M₃ / height of the ramus at M₂): (0) high (>300); (1) moderate (300~250); (2) low (<250).
18. *Lateral outline of the mandible*: (0) anteriorly tapered; (1) sub-parallel; (2) anteriorly higher.
19. *Outline of ramus*: (0) low and nearly upright ramus; (1) ramus become higher and robust; (2) ramus extremely high and distinctly inclined toward the medial.

Dentition

20. *Distolingual heel for P² and P³*: (0) weakly present; (1) strong at least on P³; (2) lost.
21. *Occlusal area of P³ and P⁴*: (0) nearly same; (1) P³ > P⁴; (2) P⁴ > P³.
22. *P⁴ morphology*: (0) bicuspidate: protocone is smaller than paracone; (1) bicuspidate, protocone is nearly same size with paracone, and minor cusplets are mostly present at the mesial of protocone; (2) single-cuspidated tooth (protocone confluent with paracone).
23. *Occlusal outline of the cusp of upper molars*: (0) weak trifoliate outline with wide grooves; (1) trifoliate outline with moderately wide grooves; (2) tetrafoliate outline in paracone with narrow grooves, posterior lobe of the paracone extends buccally beyond the anterior lobe of the metacone.
24. *Size of the I₃ relative to the I₁*: (0) nearly same; (1) small; (2) large; (3) very large.
25. *P₄ morphology*: (0) presence of a large metaconid in the centrolingual, with one or several minor cusplets in linguo-distal; (1) relatively longer in length with no minor cusplet in linguo-distal; (2) metaconid distally shifted, low and reduced.
26. *Molar hypsodonty*: (0) low-crowned teeth with hypsodonty index (100 x crown height / width) inferior or equal to 125 (lower molars) or 100 (upper molars); (1) high-crowned teeth with hypsodonty index superior to 125 (lower molars) or 100 (upper molars).
27. *The upper margin of the lower canine*: (0) distinctly higher than that of I₃; (1) around the upper half of I₃; (2) lower than the middle of I₃.
28. *Arrangement of the alveolus of the lower incisors*: (0) all are nearly same size and nearly straight alignment; (1) I₂ is quite smaller than others and shifted dorsally; (2) I₂ is distinctly smaller than others and shifted more dorsally, the lower margin of I₂ lies within the upper half of I₁ and I₃; (3) I₂ is tiny and lies above the upper margin of I₁ and I₃.