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Asian Miocene Great Apes: Searching for Orangutan Ancestors

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ABSTRACT.– Pongids are represented today by the genus *Pongo* (orangutan), with three species that live on islands of Southeast Asia. However, orangutans were much more widely distributed during the Pleistocene. The changes in their geographical distribution and taxonomy are discussed here since the first appearance of this genus in the early Pleistocene (~2.2 million years ago) in South China. During the Pleistocene, orangutans coexisted with *Gigantopithecus* in South China, sharing their food and environment. Between the middle and late Miocene (12.5–5.4 million years ago), four distinct large apes were evolving in South and Southeast Asia. Each genus has been proposed as a potential ancestor of extant orangutans. However, *Lufengpithecus*, from South China is excluded from the pongids and is interpreted as having Eurasian dryopithecines ancestors. *Sivapithecus*, from India-Pakistan, exhibits orangutan skull characters but its dentition is more primitive, and its postcranial skeleton is specialized in another locomotory repertoire. *Indopithecus* appears to be the closest relative of *Sivapithecus* and is considered a potential ancestor of *Gigantopithecus*. *Khoratpithecus*, from Thailand and Myanmar, is recognized as the closest sister taxon of extant orangutans because both genera share characters such as the symphysis structure, teeth and jaw morphology, the absence of anterior digastric muscles of the mandible, and the organization of the nasoalveolar clivus. However, the absence of Pliocene large apes in Southeast Asia prevents us from documenting the evolutionary transition between *Khoratpithecus* and orangutans.

KEYWORDS: evolution, hominoids, *Khoratpithecus*, orangutans, pongids, Southeast Asia

INTRODUCTION

Today, great apes and humans are classified under the same family, Hominidae which is further divided into two subfamilies. The first is the Asian Ponginae, which includes orangutans (*Pongo*), and the second is the African Homininae, which consists of chimpanzees (*Pan*), gorillas (*Gorilla*), and humans (*Homo*). The African origin of *Homo* is widely accepted (Dennell and Roebroeks, 2005). Based on the molecular clock analysis of their DNA, both subfamilies share a common ancestor estimated to have diverged approximately 18.3 (16.3–20.8) million years ago (Ma) (Steiper and Young, 2006). These findings suggest that a group of primitive hominids migrated to Asia during that time period. The oldest known fossil apes discovered in South Asia can be traced back to the middle Miocene period, especially the Siwaliks region in Pakistan and India, as well as Chiangmuan in Thailand. These fossils have been dated to around 12.5 Ma (Kappelman et al., 1991; Coster et al., 2010). Despite having a substantial paleontological record in this area, no older great ape fossils have been discovered, confirming therefore a dispersal scenario from Eurasia to East Asia shortly before 12.5 Ma. There are two possible dispersal routes: one through South Asia and then into Southeast Asia for the *Pongo* clade, and another via the northern route between Eastern Eurasia and South China for the ancestors of *Lufengpithecus* (Kelley and Gao, 2012). Several Miocene apes have documented this scenario, indicating that the evolutionary history of the great apes and humans was more complex than what can be inferred solely from DNA analyses of the few extant species.

We try to summarize here our knowledge concerning the history of the Asian branch of great apes, demonstrating that it was significantly more diverse and complex than initially believed. We recognize hereby six genera of Asian great apes, including both extant and extinct species. These genera are *Pongo*, *Gigantopithecus*, *Sivapithecus*, *Indopithecus*, *Khoratpithecus*, and *Lufengpithecus* (Table 1). Notably, *Ankarapithecus*, previously considered a member of the great ape and human clade, is now regarded as a stem taxon (Alpagut et al., 1996). However, Begun and Güleç (1998) suggest that *Ankarapithecus* may be related to *Sivapithecus*, either as a sister clade of the *Sivapithecus*-*Pongo* clade or by sharing a common ancestor. With the exception of *Gigantopithecus* and *Indopithecus*, all these extinct taxa have been proposed as ancestors of orangutans. Nevertheless, the absence of fossil evidence of great apes during the Pliocene (5.4–2.4 Ma) in this region makes it difficult to fully understand this crucial evolutionary transition.

Orangutans

Orangutans (*Pongo*) are currently represented by three species: *Pongo abelii* and *P. tapanuliensis* from North Sumatra, and *P. pygmaeus* from Borneo (Nater et al., 2017). The molecular phylogeny established for these three species indicates a relatively recent divergence. *P. tapanulliensis* separated from the other two species during the Pliocene period (3.38 Ma),

TABLE 1. Systematic of fossil and extant Asian great apes.

- Order Primates Linnaeus, 1758
  - Superfamily Hominoidea Gray, 1825
    - Family Hominidae Gray, 1825
      - Subfamily Ponginae Elliot, 1913
        - Genus *Sivapithecus* Pilgrim, 1910
          - †*Sivapithecus sivalensis* (Lydekker, 1879)
          - †*Sivapithecus indicus* Pilgrim, 1910
          - †*Sivapithecus parvada* Kelley, 1988
        - Genus *Indopithecus* von Koenigswald, 1949
          - †*Indopithecus giganteus* (Pilgrim, 1915)
        - Genus *Khoratpithecus* Chaimanee et al., 2004
          - †*Khoratpithecus chiangmuanensis* (Chaimanee et al., 2003)
          - †*Khoratpithecus piriyai* Chaimanee et al., 2004
          - †*Khorapithecus ayeyarwadyensis* Jaeger et al., 2011
          - †*Khoratpithecus magnus* Chaimanee et al., 2022
        - Genus *Gigantopithecus* von Koenigswald, 1935
          - †*Gigantopithecus blacki* von Koenigswald, 1935
        - Genus *Pongo* Lacépède, 1799
          - †*Pongo weidenreichi* Hooijer, 1948
          - *Pongo pygmaeus* (Linnaeus, 1760)
          - *Pongo abelii* Lesson, 1827
          - *Pongo tapanuliensis* Nurcahyo et al., 2017
      - Subfamily Homininae Gray, 1825
        - Genus *Lufengpithecus* Wu, 1987
          - †*Lufengpithecus lufengensis* (Xu et al., 1978)
          - †*Lufengpithecus keiyuanensis* (Woo, 1957)
          - †*Lufengpithecus hudienensis* (Zhang et al., 1987)

while the two other species, *P. pygmaeus* and *P. abelii*, diverged during the mid-Pleistocene (674,000 years ago) (Nater et al., 2017). Orangutans are the largest arboreal hominoids that spend the majority of their time in trees (Hunt, 2016). Adult males can weigh between 60–90 kg, while females typically weigh around 40–50 kg (MacDonald and Norris, 2001). They have developed a unique and specialized mode of positional behavior, which is evident in their postcranial skeleton (Hunt, 2016). The dental characteristics of *Pongo* are distinct. The upper incisors are heteromorphic, with I^2 being much narrower than I^1. Additionally, both upper and lower canines exhibit sexual dimorphism, and the upper and lower molars display intricate and complex wrinkles on the occlusal surface (Swindler and Olshan, 1988). Orangutans are primarily fruit-eaters, consuming a diet that included leaves, bark, honey, bird eggs, insects, and small vertebrates (MacDonald and Norris, 2001). Their current distribution in the tropical rainforest of Borneo and Sumatra is considered relictual. Throughout the Quaternary period, their geographic range expanded significantly in Southeast Asia (Fig. 1). This expansion occurred from the early Pleistocene in South China, where they reached as far north as the Yangtze River (~27°N) to the late Pleistocene-Holocene in Borneo and Java (~10°S) (Harrison et al., 2006; Liao et al., 2022). It should be noted that distribution maps indicating a concentration of fossil localities during the early Pleistocene in China are misleading due to the scarcity of early Pleistocene localities in Southeast Asia. Outside China, the only documented late early Pleistocene orangutans in mainland Southeast Asia come from Pah Bong locality in Mae Hong Son Province, northern Thailand (Bocherens et al., 2017). During the middle and late Pleistocene, orangutans were widely distributed across South China, mainland Southeast Asia (including Laos, Vietnam, Cambodia, Thailand, and Malaysia), and Southeast Asian islands (Borneo, Sumatra, and Java). Fossil orangutans have predominantly been discovered in cave deposits and karst fissure fillings. Typically, their remains are brought into caves by porcupines, which collect various bones from their surrounding and gnaw on them. The porcupines consume most of the bones, leaving behind only the enamel-capped teeth, which are more resistant. This unique phenomenon is specific to Southeast Asia and explains why the majority of these caves or karst fissure fillings contain very few bones. Consequently, the fossil record of orangutans is incomplete, with isolated teeth being the most commonly found remains. While teeth are valuable for taxonomic indication, skulls, lower jaws, and postcranial bones are also essential in distinguishing fossil species.

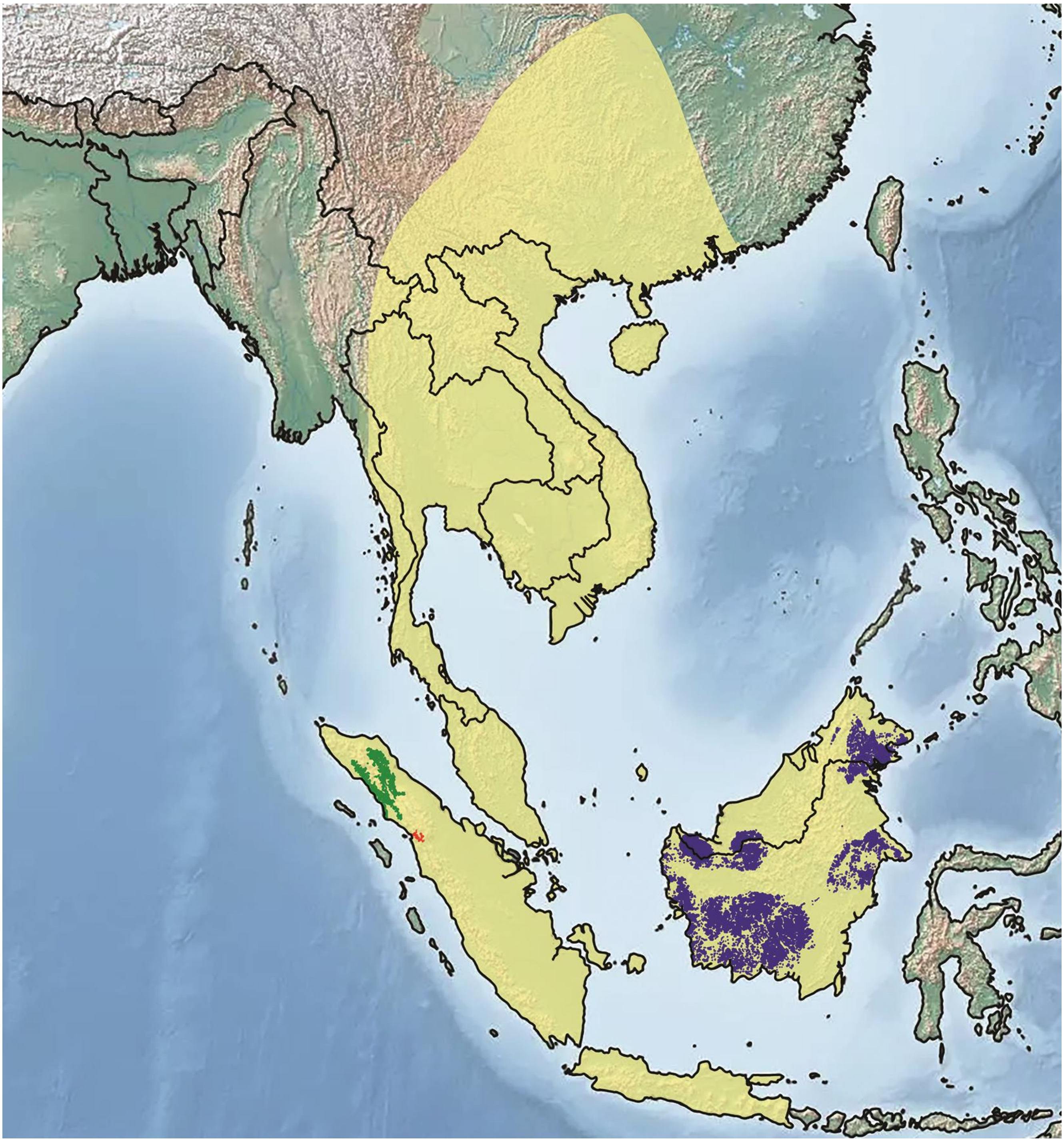

FIGURE 1. Distribution map of orangutans, Bornean orangutan (*Pongo pygmaeus*, in violet), Sumatran orangutan (*Pongo abelii*, in green), Tapanuli orangutan (*Pongo tapanuliensis*, in red), and fossil orangutans (*Pongo* spp., in yellow).

Harrison et al. (2014) identified five distinct extinct species of fossil *Pongo*. These include *P. weidenreichi* from the early and middle Pleistocene of China and the middle Pleistocene of Vietnam, *P. devosi* from the middle to late Pleistocene of China and Vietnam, *P. palaeosumatrensis* and *P. duboisi* from the late Pleistocene of Sumatra, and *P. javaensis* from the late Pleistocene of Java. However, this classification is currently considered provisional, as the distinctions are not based on distinct morphological characteristics but rather on a combination of size and geographic origins. Therefore, it is recommended not to use these species names until they become more precisely defined, with the exception of *P. weidenreichi*. This species, known from the early Pleistocene caves (~2.2 Ma) in South China, had significantly larger teeth than those of the extant species (Harrison et al., 2014). It appears that *P. weidenreichi* was eventually replaced by a smallertoothed species during the middle Pleistocene, *P. devosi*. However, it remains uncertain whether this event represents a taxonomic replacement or a local size evolution within a single lineage. The size of the dentition in fossil *Pongo* exhibits a reduction over time. The early Pleistocene *Pongo* had teeth that were 38.1 % larger than those of the extant *P. pygmaeus*, while the middle and late Pleistocene specimens had teeth that were 25.2 % and 18.9 % larger, respectively (Harrison et al., 2021). Estimates of body masses, based on the occlusal area of the lower first molar, suggest that the early Pleistocene *Pongo* individuals reached approximately 95.9 kg (Harrison et al., 2021). In their recent analysis, Liao et al. (2022) concluded that there is a single continuous morphocline of size decrease in Pleistocene *Pongo*. They suggest that all the Chinese and Vietnamese Pleistocene *Pongo* populations should be considered as belonging to the same species, *P. weidenreichi*. The most recent representatives of this species were still larger than the extant ones but became extinct in South China approximately 110,000 years ago while surviving in northern Vietnam until around 30,000 years ago (Bacon and Long, 2001; Liao et al., 2022). Carbon stable isotope data indicate that the reduction in dental size in *Pongo* is associated with environmental changes. These morphological changes in *Pongo* seem to align with the expansion of savannah biomes and the contraction of forested habitats from the middle Pleistocene onward (Liao et al., 2022). The reasons for the extinction of this large ape from mainland Southeast Asia are still unknown. Reduction of forests during glacial periods or human hunting pressure are working hypotheses in this regard (Louys et al., 2021).

Gigantopithecus

*Gigantopithecu*s is considered the largest extinct ape to have ever lived. Its estimated body mass, based on dental and mandible dimensions is approximately 200–300 kg (Zhang and Harrison, 2017). The first remains of *Gigantopithecus* were discovered in a drugstore in Hong Kong, and the initial description of this species was based on an isolated lower molar, named *Gigantopithecus blacki* by von Koenigswald in 1935. Since then, *Gigantopithecus* fossils have been found alongside *Pongo* in caves from the early and middle Pleistocene in southern China, dating back from approximately 2.0 Ma to nearly 300,000 years ago (Zhang and Harrison, 2017). *Gigantopithecus* displays a relatively high level of sexual dimorphism. Similar to *Pongo*, the fossil remains of *Gigantopithecus* are primarily represented by isolated teeth, as their bones were also destroyed by porcupines. However, unlike *Pongo*, there is evidence of a progressive increase in dental size from the early to middle Pleistocene in *Gigantopithecus*, along with a possible shift toward greater complexity of the cheek teeth (Zhang and Harrison, 2017). The situation is similar to that of orangutans with no cranial or post-cranial elements remaining in *Gigantopithecus*. However, four mandibles have been discovered, revealing some notable differences from orangutans. These differences include reduced canines and incisor area, molarization of premolars, a waisting of lower molars, enlarged premolar and molar surfaces, thick enamel, high crown elevation, and distinct enamel wrinkling (Woo, 1962; Zhang et al., 2016b). Some of these features suggest a diet consisting of hard food, and some researchers have proposed that *Gigantopithecus* primarily consumed bamboo shoots (Ciochon et al., 1990). However, carbon stable isotope analysis of *Gigantopithecus* tooth enamel has shown that their diet was similar to that of orangutans sharing the same environment (Bocherens et al., 2017). Carbon isotope analysis of *G. blacki* and associated mammal fauna indicates that they inhabited closed subtropical monsoon forests (Nelson, 2014). However, according to their large body size, it is likely that their arboreal life was somewhat restricted, and they probably spent more time collecting food on the forest floor. Jaw and tooth characteristics of *Gigantopithecus* exhibit several similarities with orangutans, including the low elevation of dentine horns in molars, unlike African apes (Olejniczak et al., 2008). Therefore, their classification as pongines (a subfamily that includes orangutans) is widely accepted, although it is not definitively established based on skull, jaw, and postcranial characters.

Recently, researchers have been able to extract proteins bound to the enamel of *Gigantopithecus* teeth for study, and the finding suggested similarities with orangutans (Welker et al, 2019). Most *Gigantopithecus* teeth have been discovered in early Pleistocene caves of South China, with two exceptions found outside of China, one in Vietnam (Ciochon et al., 1996) and one in Northern Thailand (Bocherens et al., 2017) (Fig. 2). However, the Vietnamese specimens previously identified as *G. blacki* have now been recognized as belonging to *Pongo weidenreichi* (Zhang and Harrison, 2017). In South China, *Gigantopithecus* appears to have gone extinct around 300,000 years ago, during the late middle Pleistocene, possibly due to the reduction of forests caused by increasing glacial events. Its phylogenetic relationships between *Gigantopithecus* and orangutans remain unclear due to the lack of fossil records from the Pliocene. Apart from size and teeth, anatomical differences have been observed between these two apes. One significant difference is the anterior digastric muscle scars under the symphysis of

FIGURE 2. Distribution map of *Gigantopithecus* (in blue).

Gigantopithecus jaws, which have disappeared in orangutans (Zhang and Harrison, 2017). These muscles are used by most mammals to open their mouths but are absent in orangutans due to the extensive development of their vocal poaches (Brown and Ward, 1988).

Therefore, it seems that if *Gigantopithecus* belongs to the pongines, it would have diverged from the ancestors of orangutans before the disappearance of these muscles in the orangutan lineage. However, considering the significant amount of homoplasy observed during the evolution of great apes, caution is needed before attributing *Gigantopithecus* to the pongines. It is crucial to have decisive cranial characteristics to confirm that hypothesis. Recently, Noerwidi et al. (2016) described mandibular fragments with lower molars from a Plio- Pleistocene locality in Java, which belonged to a giant ape of similar size and

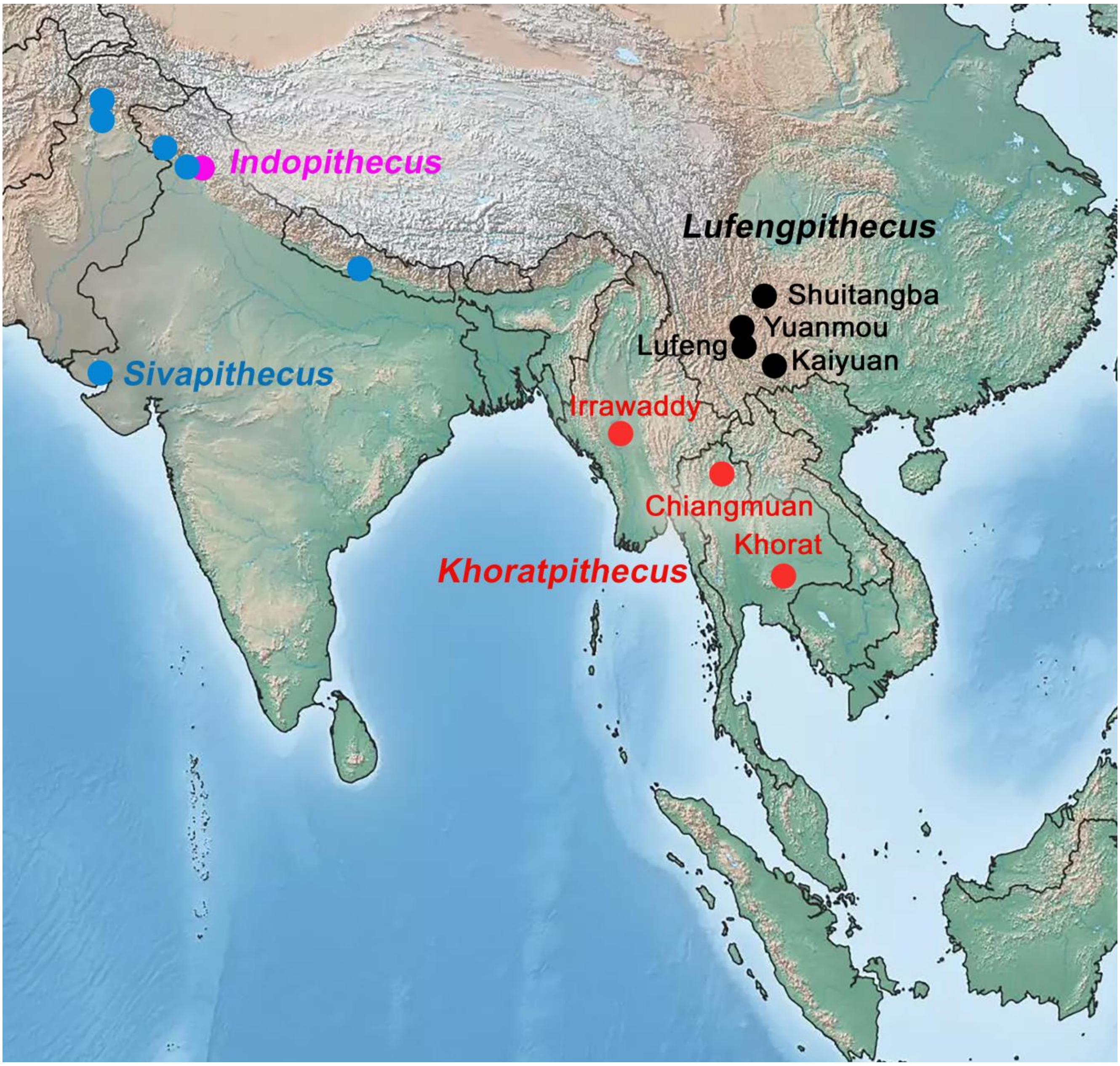

FIGURE 3. Distribution map of Asian Miocene great apes.

morphology to *G. blacki*. If this taxonomic identification is validated, it would significantly expand the geographical range of this species. Alternatively, it could also indicate the existence of a new species of gigantic ape. Further discoveries and detailed analyses are needed to clarify this matter in the future.

Sivapithecus

The search for potential ancestors of orangutans and *Gigantopithecus* required an investigation into the Miocene fossil apes. In South Asia, several fossil apes dating from 12.7–8.5 Ma have been discovered (Kelley, 2005), previously attributed to pongines. Among them, the most extensively studied and well-known fossil large ape is *Sivapithecus*, found in the Siwaliks region of the Himalayan foothills in Pakistan, India, and Nepal (Fig. 3). *Sivapithecus* is represented by a facial fragment, numerous jaw fragments, isolated teeth, and a substantial number of postcranial elements (Pilbeam, 1982; Pilbeam et al., 1980; 1990). Currently, three species of *Sivapithecus* have been identified: *S. indicus*, the oldest (12.7–11.4 Ma), which is the smallest and less specialized, *S. sivalensis* (11–8.5 Ma), which is larger and exhibits slightly more derived dental features, and *S. parvada*, a very large species with wide anterior dentition found in a single locality dated to approximately 10.1 Ma (Kelley, 1988). These three species show significant sexual dimorphism,

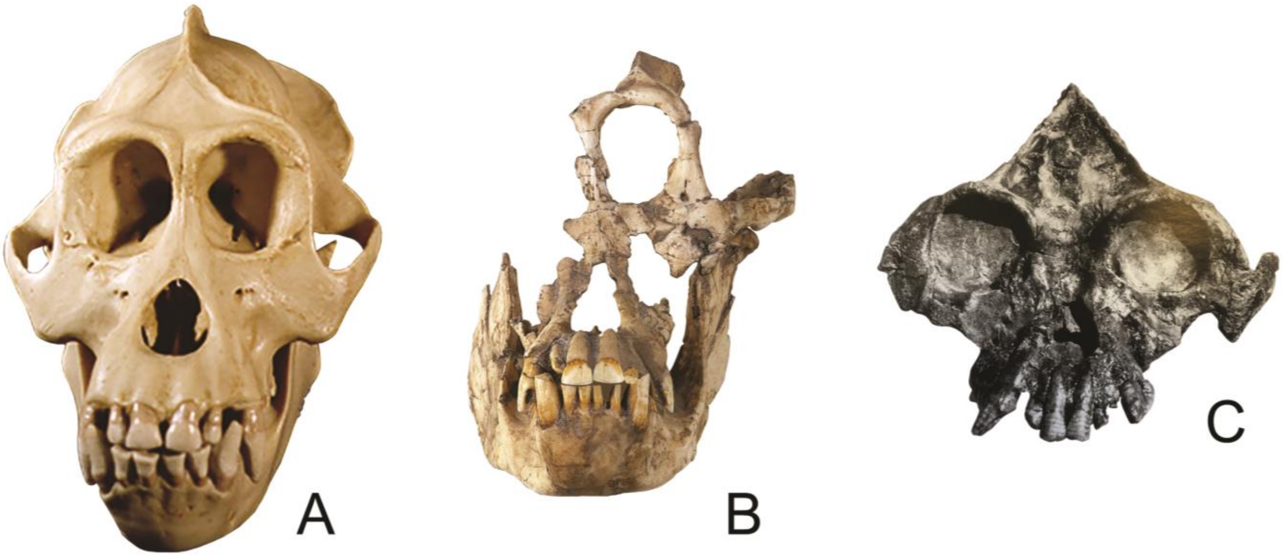

FIGURE 4. Comparison of skulls and face structures of **A)** *Pongo*, **B)** *Sivapithecus indicus* (GSP 15000), and **C)** *Lufengpithecus lufengensis* (PA644) from Xu and Lu (2008) in frontal view. Not to scale.

similar to what is observed in extant apes (Plavcan, 2001). The estimated body weights for *S. indicus* and *S. sivalensis* based on postcranial evidence range from 30–50 kg for males and 20–24 kg for females (DeSilva et al., 2010). For *S. parvada*, the estimates are 68–75 kg for males and 30–45 kg for females for (Kelley, 1988).

One particularly informative fossil, GSP 15000 of *S. indicus*, preserves both the face and mandible and shares several characteristics with orangutans (Fig. 4). The face of GSP 15000 is concave and oriented upwards (known as airorynchy), whereas, in African apes and humans, it is oriented downwards (known as klinorynchy). The orbital outlines are oval and narrow, the supraorbital torus is absent, the interorbital distance is very narrow and the nasoalveolar clivus is similar to that of modern *Pongo*. These features make it difficult to dismiss some phylogenetic relationships with orangutans (Pilbeam, 1982). However, the teeth and jaws do not indicate a close relationship with the orangutans. The jaws of *Sivapithecus* are more robust, and the anterior dentition is less enlarged compared to the extant genus. The inferred locomotion of *Sivapithecus* remains a matter of debate. Its humerus is curved, similar to that of a quadrupedal baboon, rather than straight like the arboreal great apes such as orangutans or chimpanzees (Pilbeam et al., 1990). However, evidence from the femoral head and proximal femur had been interpreted as indicating a climbing and suspensory behavior, rather than quadrupedalism (Maclatchy and Bossert, 1996). Other postcranial elements such as the distal femur, navicular, and phalanges, suggest that *Sivapithecus* was primarily engaged in pronograde locomotion, vertical climbing, and clambering activities, and did not exhibit suspensory behavior like extant primates (Madar et al, 2002). The hand phalanges of *Sivapithecus* were not strongly curved like those of orangutans. The anatomy of the hand bones suggests that they were knuckle-walking apes, a specialized form of quadrupedalism also independently developed by chimpanzees and gorillas (Begun and Kivell., 2011). Therefore, their postcranial anatomy is not primitive but specialized for specific locomotory behavior. In this context, *Sivapithecus* would appear as an early specialized stem group of pongines, already displaying orangutan characteristics on its face but not yet on its jaws, teeth, and postcranial elements. Modern orangutans have developed a remarkable set of adaptations for suspensory locomotion, resulting in significant modification to their postcranial skeleton. They are considered the most specialized great apes adapted to climbing and suspensory locomotion. For instance, while all primates possess a ligament called the *ligamentum capitis* that attaches to the femoral head, creating a depression called the *fovea capitis*, orangutans lack this ligament, which allows for highly mobile hips and complex locomotion (Georgiou et al., 2019). In addition, like other suspensory adapted primates, they also developed strongly curved phalanges that allow their hands to better hang their body on branches, and their humerus is straight like other suspensory modern apes, not curved as in *Sivapithecus* and quadrupedal primates. The timing of when orangutan ancestors developed these adaptations remains unknown. The last known representatives of *Sivapithecus* disappeared from the Siwaliks around 8.5 Ma, coinciding with the progressive disappearance of evergreen forests in the region, which were replaced by more open vegetation dominated by C_4 plants, primarily grasses (Nelson, 2003).

Indopithecus

The late Miocene giant ape from northern India-Pakistan, *Indopithecus giganteus*, has been recovered from deposits dating back to 8.85–8.6 Ma (Pilgrim, 1915; Simons and Chopra, 1969; Pillans et al., 2005) (Fig. 3). Its estimated body weight is about 150 kg (Fleagle, 2013). The remains consist of a nearly complete lower jaw, one isolated third lower molar, and one upper second molar. These findings indicate that *Sivapithecus* was not the only great ape present in South Asia at that time. Stable carbon and oxygen isotope analysis of dental enamel suggests that *Indopithecus* had a C_3 based diet, likely including nuts, seeds, and fruits with hard shells, and it inhabited a seasonal forest characterized by long dry and wet seasons (Patnaik et al., 2014). Due to its large size, with large molars, molarized premolars, a massive jaw, and reduced anterior dentition, it bears resemblance to the Chinese Pleistocene *Gigantopithecus*, leading some authors to propose it as a potential ancestor of the Pleistocene Chinese giant apes. In a comprehensive analysis, Kelley (1988) demonstrated that *I. giganteus* shared many characters with other *Sivapithecus* species, suggesting a close evolutionary relationship. Therefore, Cameron (2001) proposed distinguishing it under the name *I. giganteus*.

Two main arguments can be proposed to understand the phylogenetic position of these two taxa. Firstly, the two fossil-rich geographic areas, South China and northern India, are geographically distant and also separated by a time gap of more than 6 Ma. Based on what we have observed in Asia, the evolution of these great apes was highly localized, with only monophyletic clusters of species recorded so far. For instance, *Lufengpithecus* in South China, *Khoratpithecus* in Southeast Asia, and *Sivapithecu*s + *Indopithecus* in Siwaliks regions (India, Pakistan, and Nepal). The presence of large rivers originating from the Himalayan mountains and the Tibetan plateau likely acted as dispersal barriers for these apes, as no migration event has been documented between these provinces. In the present day, the Congo River acts as a barrier between the two chimpanzee species, *Pan paniscus* and *Pan troglodytes* (Almécija et al., 2021). In nearly every South Asian ape province, the appearance of large species coincided with climatic and vegetation changes that began around 8 Ma. This is evident in the case of *Indopithecus* in the Siwaliks, *Khoratpithecus magnus* in Southeast Asia, and likely the unknown ancestor of *Gigantopithecus* in South China, which was the only one to survive until the late Pleistocene period. However, during the period when large apes become extinct in the Siwaliks, this climatic change was delayed until 6 Ma in more eastern regions such as South China and Southeast Asia, allowing populations of fossil apes to survive longer duration. This is exemplified by the presence of the South Chinese *Lufengpithecus*, another large ape that was once considered a potential ancestor of orangutans.

Lufengpithecus

Lufengpithecus is a late Miocene ape that has been found in four areas in Yunnan Province, South China (Fig. 3). Currently, three species have been identified: *L. keiyuanensis*, which is the oldest, followed by *L. hudiensis*, and *L. lufengensis* the youngest. Their estimated body weights were approximately 54.9 kg, 47.4 kg, and 67.6 kg, respectively (Liu et al., 2002). *Lufengpithecus keiyuanensis* (Woo, 1957) is the oldest known hominoid discovered in the Xiaolongtan coal mine in Kaiyuan. Paleomagnetic dating indicates an age range of 12.5–11.7 Ma for the fossil hominoid layer (Zhang et al., 2019). Pollen evidence suggests that the deposit environment corresponds to a subtropical evergreen broad-leaved forest (Zhang et al., 2019). *Lufengpithecus hudiensis* (Zhang et al., 1987) originates from the Leilao and Xiaohe areas in Yuanmou (Qi et al., 2006) and the paleomagnetic dating of the localities indicates an age range of 8.2–7.2 Ma (Yue and Zhang, 2006). *Lufengpithecus lufengensis* (Wu, 1987) is the youngest ape discovered in the Shihuiba lignite mine in Lufeng (Xu et al., 1978). The paleomagnetic analysis of the sediments indicated an age of 6.9–6.2 Ma (Yue and Zhang, 2006). This species is the most abundant Asian fossil hominoid, represented by hundreds of isolated teeth, several skulls, mandibles, and postcranial elements (Xu and Lu, 2008). Two juvenile crania attributed to *Lufengpithecus* have been recovered. The first skull, found in Shuitangba, Zhaotang basin, has been assigned to *L.* cf. *lufengensis* (Ji et al., 2013). Paleomagnetic data suggest a terminal Miocene age of 6.5–6.0 Ma for this specimen (Ji et al., 2013). Based on paleoenvironmental data, the area may be a mildly warm and humid lacustrine or swampy forested environment with grasses in the understory or at the woodland edge. The region experienced warm and wet summers along with cool and dry winters (Chang et al., 2015; Zhang et al., 2016a; Huang et al., 2017; Lu et al., 2017; Li et al., 2019). The second juvenile cranium attributed to *L. hudiensis*, was discovered in Yuanmou. However, it does not exhibit affinities to orangutans and appears to be closer to dryopithecids, which are stem members of the hominids (great ape and human) (Kelley and Gao, 2012). Xu and Lu (2008) described several jaws, skull fragments, and postcranial elements of *L. lufengensis*. Unfortunately, these fossils have been heavily crushed during diagenesis in their coal layers, making some detailed anatomical characters difficult to discern. However, the dentition of *L. lufengensis* is well-preserved and shows significant sexual dimorphism (Kelley and Xu, 1991). The species exhibits several specializations, including narrow, elevated, and acute lower incisors, sharp canines, and distinctive premolar and molar structures. One particularly character of *L. lufengensis* molars is the development of fine enamel wrinkles that closely resemble those observed in orangutan molars. Therefore, based on its geographic origins, several authors have considered *Lufengpithecus* as a possible ancestor of orangutans, despite the observed differences in jaw structure, orbit shape, interorbital distance, symphysis section, nasoalveolar clivus organization, and anterior dentition. However, when comparing its skull to those of orangutans and *Sivapithecus*, this interpretation can be challenged. Despite the significant crushing affecting the *Lufengpithecus* skulls, it is evident that the square orbital shape and large interorbital distance of *Lufengpithecus* bear no resemblance to those of orangutans and *Sivapithecus* (Fig. 4). Similarly, the nasoalveolar clivus of *Lufengpithecus* is more similar to that of Miocene dryopithecids and African apes than to pongines. In fact, the skull of *Lufengpithecus* differed from pongines and shows similarities to Eurasian Miocene apes (Begun, 2015). *Lufengpithecus* did not develop the facial characteristics observed in pongines, which are already present in the earlier genus *Sivapithecus*. However, it could be suggested that *Lufengpithecus* retained mostly primitive characters in its skull, along with some unique derived dental characters. The postcranial bones indicate that *Lufengpithecus* was an arboreal ape specialized for climbing with forelimb suspension similar to *Pongo* (Xu and Lu, 2008; Zhang et al., 2020). The question remains whether its specialized postcranial characters represent synapomorphies (shared derived characters) that link *Lufengpithecus* with *Pongo*, or if highly curved phalanges evolved independently in multiple hominoid lineages associated with convergent positional behaviors, as suspected by some authors. Paleoenvironmental data indicate that *Lufengpithecus* lived in humid subtropical evergreen and deciduous broad-leafed forests (Sun and Wu, 1980; Badgley et al., 1988; Qi, 1993; Cheng et al., 2014; Chang et al., 2015).

The phylogenetic relationships of *Lufengpithecus* are disputed. This genus has been interpreted either as a primitive hominid (sister taxon of Ponginae + Homininae) (Schwartz, 1997; Kelley and Gao, 2012), more closely related to Eurasian dryopithecines than to *Pongo* and *Sivapithecus* (Begun, 2015; Nengo et al., 2017; Gilbert et al., 2020), or as a primitive sister taxon of Ponginae (Harrison et al., 2002). More recently, a detailed cladistic analysis (Pugh, 2022; Gilbert et al., 2020) concluded that it corresponds to a paraphyletic genus and that only *L. lufengensis* should be considered as a basal pongid. This led Urciuoli and Alba, (2023) to attribute the two oldest taxa to an *incertae sedis* tribe and to rename them *Sinopithecus*. However, the fossil record testifies to a 6 Ma evolution in isolation for these late Miocene apes in the South Chinese evergreen forests. The terminal Miocene cooling episodes within the prevailing warm and humid climate, and associated changes in vegetation, may have been factors responsible for the disappearance of hominoids from this region (Li et al., 2020).

Two hypothetical interpretations can be proposed to explain the *Lufengpithecus* dilemma. Firstly, *Lufengpithecus* could be a survivor from the earliest wave of great ape colonization of South Asia, which did not develop orangutan characteristics except for locomotory adaptations. This would indicate its ancestral status as one of the first apes that dispersed to South Asia from Eurasia. However, such a long stasis of anatomical characters is highly unlikely and has no other analogue, except for *Oreopithecus*, which evolved on an island separated from the European and African continents with no competitors and no predators (Azzaroli et al., 1986). This kind of isolated situation did not exist in South China, which was open to the dispersal of many fossil mammal groups. Another hypothesis is to consider *Lufengpithecus* as a member of the European dryopithecids (Begun, 2015) that originated from a distinct immigration wave compared to the ancestors of the pongines. This immigration might occur through a forest corridor between Eastern Europe and South China, as suggested by some of the fossil rodents co-occurring with *Lufengpithecus* (*Hansdebruijna*, *Kowalskia*, Platacanthomyines, and Eomyids) (Qiu and Li, 2003). In any case, *Lufengpithecus* appears to have become extinct without any known descendant. In other regions of southern China, another genus of large ape, *Khoratpithecus*, evolved during a similar period in Myanmar and Thailand, between 12.5 and 9–7 Ma.

Khoratpithecus

This genus represents the only Miocene fossil hominoid found in Southeast Asia. It is supported by the discovery of *K. ayeyarwadyensis* in the late Miocene (10.4–8.8 Ma) Irrawaddy Formation in Central Myanmar, (Jaeger et al., 2011; Takai et al., 2021). Additionally, three species have been identified in Thailand: *K. chiangmuanensis* from the middle Miocene (12.4–12.2 Ma) in the Chiang Muan coal mine in northern Thailand (Chaimanee et al., 2003; Coster et al., 2010), and *K. piriyai* and *K. magnus* from the late Miocene (9–7 Ma) in the Khorat sandpits in northeastern Thailand (Chaimanee et al., 2004; 2006; 2019; 2022) (Fig. 3). *Khoratpithecus* is characterized as a large-bodied ape, with an average body mass of 45 kg for the male of *K. ayeyarwadyensis*, 29 kg for the female and 45 kg for male of *K. chiangmuanensis*, 52 kg for males of *K. piriyai*, and 77 kg for *K. magnus*. This suggests that *Khoratpithecus* displayed significant sexual dimorphism, similar to other Asian fossils and extant great apes (Chaimanee et al., 2022). *Khoratpithecus chiangmuanensis* is documented only by a dozen of isolated teeth, which bear a striking resemblance to those of extant orangutans. This resemblance is particularly evident in the wide upper central incisors with their spatulate crown, as well as the molar structure. The holotype of *K. piriyai* consists of a nearly complete mandible that exhibits a more robust corpus and less wrinkled enamel on the molar occlusal surface compared to orangutans. More recently, three mandibles and two maxillae of *K. piriyai*, one mandible of *K. magnu*s, and one toothless mandible of *Khoratpithecus* sp. have been discovered (Chaimanee et al., 2019; 2022). These findings were associated with a diverse assemblage of large mammals that bears similarities to mammalian faunas described in the Siwaliks of India and Pakistan (Chaimanee et al., 2006). Interestingly, it appears that large apes were more geographically restricted than their associated large mammals, such as pigs, anthracotheriids, proboscideans, giraffids, and bovids, with several species being common to both areas. Studies on dental topography, microwear texture analysis, and dental root apical morphology suggest that the diet of *Khoratpithecus* primarily consisted of fruits, particularly soft ones (Merceron et al., 2006; Hamon et al., 2012a). The carbon isotopes extracted from the dental enamel of *K. ayeyarwadyensis* indicate that its diet was predominantly composed of C_3 vegetation, suggesting a canopy forest habitat, similar to that of *Sivapithecus* (Habinger et al., 2022). Paleobotanical evidence also supports the notion that *Khoratpithecus* inhibited a tropical riverine forest environment (Sépulchre et al., 2010).

There are three notable characteristics shared by *Khoratpithecus* and orangutans. Firstly, their symphysis exhibits a distinct section outline and a low inclination, setting them apart from *Sivapithecus*, *Indopithecus*, *Gigantopithecus*, and *Lufengpithecus* (Jaeger et al., 2011*)*. Secondly, a unique feature found only in *Khoratpithecus* and orangutans is the absence of anterior digastric muscles (Chaimanee et al., 2004). The disappearance of these muscles is believed to be connected to the development of large oral pouches, which enable orangutans, characterized by less social interaction, to communicate over distances with scattered individuals in the forest (Brown and Ward, 1988; Wall et al., 1994). This particular characteristic is observed not only in the three known mandibles of *K. piriyai* from Thailand but also in *K. ayeyarwadyensis* from Myanmar (Chaimanee et al., 2004; 2022; Jaeger et al., 2011; Takai et al., 2021) (Fig. 5). The third shared derived character relates to the structure and organization of the nasoalveolar clivus, as well as the relationship between the premaxillary and palatine bones of the maxilla (Chaimanee et al., 2019).

In orangutans, the premaxilla bone is strongly curved and overlaps the palatine bone, which develops a narrow nasopalatine canal that slants forward. This characteristic is also observed in *Sivapithecus* and is considered a pongid trait (Ward and Kimbel, 1983). In contrast, African apes and *Lufengpithecus* have a nearly vertical premaxilla bone and a large nasoalveolar canal. The four mandibles of *K. piriyai* exhibit significant variations in morphological features such as inter-canine distance, dental arcade shape, and M_3 size.

Khoratpithecus magnus, found in the same locality as *K. piriyai*, is larger in size and displays several differences in the premolar and molar characters, including higher crown elevation and thicker enamel. Its symphysis exhibits a thicker superior transverse torus with a deep genioglossal fossa. This occurrence of two great apes of different sizes in the same area is reminiscent of the situation observed in the Siwaliks where *Sivapithecus* coexisted with a closely related but larger species, *Indopithecus* (Pilbeam et al., 1977). It is also possible to hypothesize that during the same period, a large ape in southern China, likely an ancestor of the Pleistocene *Gigantopithecus*, was undergoing evolutionary changes. The appearance of these very large fossil apes in three distinct geographic areas can be seen as an adaptation to a changing environment. This led to the development of larger ape species that were better suited to a mosaic environment of savannah and forest, less dependent on arboreal locomotion, and capable of consuming harder and more abrasive food.

The confirmation of the hypothesis regarding orangutan locomotion evolution would greatly benefit from the recovery of postcranial bones in the fossil records of Southeast Asian great apes. However, the absence of such bones currently limits our understanding in this regard. It remains unclear whether the Miocene *Khoratpithecus* already exhibited arboreal

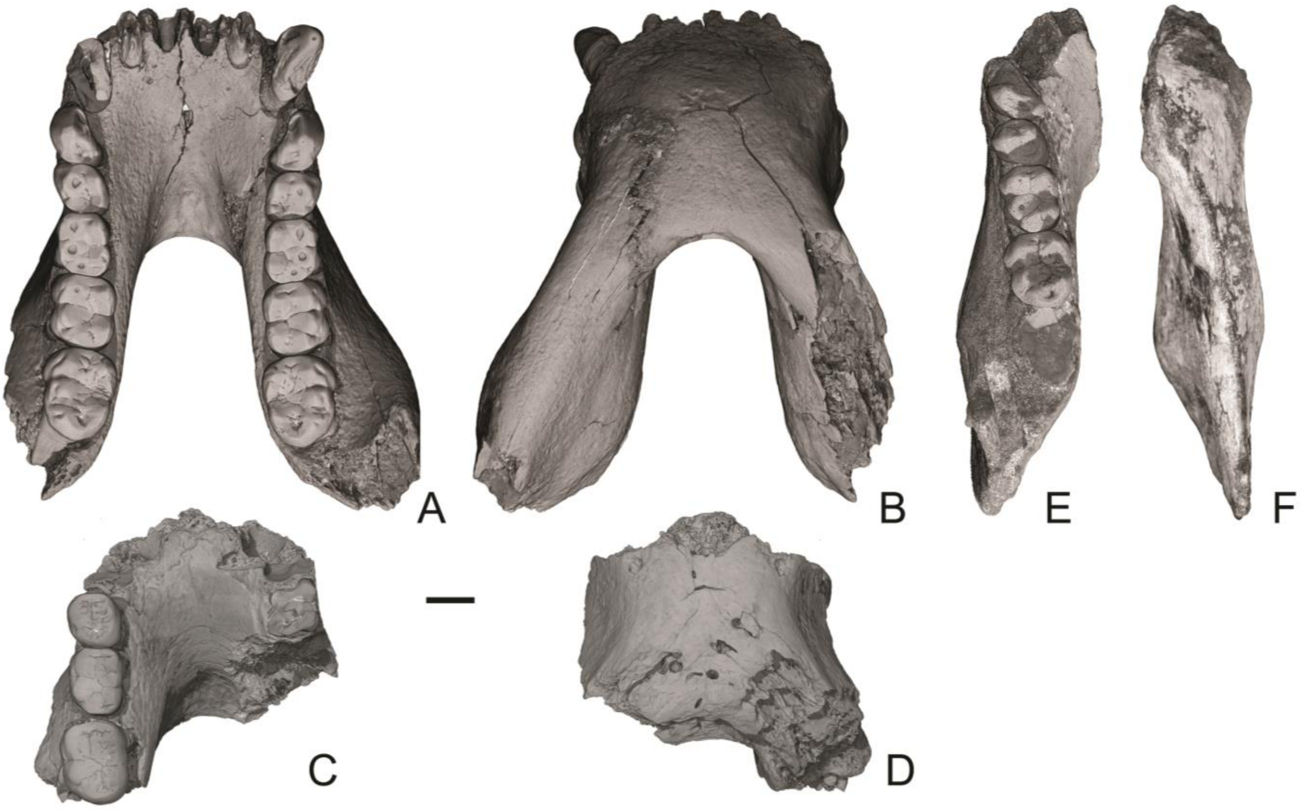

FIGURE 5. Comparison of mandibles of *Khoratpithecus piriyai* (TF 6233) in occlusal (**A**), and inferior (**B**) views, *K. magnus* (MFT-K178) in occlusal (**C**), and inferior (**D**) views, and *K. ayeyarwadyensis* (MFI-K171) in occlusal (**E**), and inferior (**F**) views, scale bar 1 cm.

adaptations similar to those seen in extant orangutans or if the extreme specialization for arboreal life and locomotion arose more recently. Bridging the approximately 5 Ma gap between *Khoratpithecus* and the earliest orangutans is a task that requires further investigation in the near future. Regarding the phylogenetic relationships of *Khoratpithecus*, there is a broad consensus that considers this genus as the closest sister group to orangutans (Urciuoli and Alba, 2023). However, a recent comprehensive phylogenetic analysis by Pugh (2022) restricts this sister-group relationship with orangutans to *K. ayeyarwadyensis*, which is not the most well-documented species. It should be noted that this restriction may stem from the limitations of cladistics analysis, which can be influenced by high levels of homoplasy and a considerable number of characters that may not be genetically independent as required by principles of cladistics. Based on the numerous shared derived characters among the three species, it is not appropriate to consider *Khoratpithecus* as a paraphyletic taxon.

DISCUSSION

Considering all available information provided by the fossil record of Asian apes, it is possible to propose a phylogenetic scenario that can be tested by future discoveries. Apes originated in Africa during the late Oligocene and underwent significant diversification in the early and middle Miocene (Begun, 2015). A climatic optimum occurred during the middle Miocene, bringing a tropical climate and associated vegetation to extend to northern latitudes (Hamon et al., 2012b; Morley, 2018). Apes might have dispersed to Europe, Central Asia, and South and Southeast Asia during this time. This last event is supposed to have occurred slightly before 12.5 Ma, the date of the first occurrence of *Sivapithecus*, *Lufengpithecus*, and *Khoratpithecus* in their respective provinces. Whether the dispersal routes of the pongines ancestors (*Sivapithecus* and *Khoratpithecus*) and of *Lufengpithecus* were similar or distinct is presently unknown. But as in Europe, taxonomic diversification was extremely rapid, and when first documented, these apes had already accumulated many anatomical differences. Regarding *Lufengpithecus*, data are slowly accumulating and related to another primitive branch of apes, also documented in Eastern Europe, but not related to pongids. Instead, it is more closely related to a stem group of hominids, the dryopithecids. If further discoveries demonstrate that it is, nevertheless, a basal pongids that retained its primitive characteristics until the late Miocene, we would have to reconsider several accepted evolutionary rules. However, according to the fossil record, the pongines skull characters (such as the absence of supraorbital torus, airorynchy, narrow interorbital distance, oval orbits shape, nasoalveolar clivus) appeared early, before the postcranial features as observed in *Sivapithecus*. The *Sivapithecus* clade further retained primitive symphysis and dental characters and still exhibited anterior digastric muscles.

The *Khoratpithecus* clade appears to have taken a step closer to orangutans in terms of its teeth, symphysis, and lack of anterior digastric muscles. This implies that it also shared skull characteristics such as orbit shape, airorynchy, and narrow interorbital distance with *Sivapithecus* and orangutan. Although there is no documentation regarding the facial anatomy of *Khoratpithecus*, the presence of several critical pongids characters strongly supports this interpretation. Therefore, based on current data, *Khoratpithecus* appears to be the closest sister group of orangutans. However, the new material recently described of *K. piriyai* (Chaimanee et al., 2022) indicates a species that was already adapted to a more diversified diet than that of extant orangutans. It was also more adapted to hard and abrasive food. This suggests that the extant orangutan branch originated from an older and less specialized *Khoratpithecus* species, such as *K. chiang-muanensis*, which dated from 12.4 to 12.2 Ma. This possible scenario indicated a rapid initial diversification shortly after the dispersal of an ancestral population of early pongines in Southeast Asia. However, the anatomical characters of this ancestral population are still unknown. Nevertheless, the 5 Ma gap between the last recorded *Khoratpithecus* and the first documented orangutans corresponds to the Pliocene period (5.4–2.4 Ma). This period is characterized by the spread of C_4 savannahs and the reduction of rainforests, followed by the onset of glacial periods. The absence of fossil deposits, especially those containing ape fossils in Southeast Asia during this long period makes it challenging to reconstruct the history of orangutans in more detail. It is likely that rain forests refuges existed, allowing the ancestors of orangutans to evolve and survive until they became restricted to their present refuge areas on the islands of Southeast Asia.

By extrapolating the anatomical characters of early pongines common ancestors of *Sivapithecus* and *Khoratpithecus*, it becomes possible to explore other Old-World fossil apes to find their potential sister group. West of the pongines territory, most of the Eurasian fossil apes, except *Ouranopithecus*, are more or less closely related to a group named dryopithecids. These dryopithecids are considered as potential ancestors for African hominins (Almécija et al., 2021). They are generally represented by arboreal middle-sized apes with relatively thin dental enamel, klino-rhynchid skulls with a developed supraorbital torus, and primitive nasoalveolar clivus. They diversified in the tropical forests of western and eastern Europe between 13 and 9 Ma but eventually become extinct due to drastic climatic changes that significantly reduced their forest habitats. In more eastern European areas, such as Greece, Turkey, and Iran, they survived longer, until 7–6 Ma, as they adapted to a more diversified environment and developed jaw and dental adaptations to feed on harder and more abrasive food. While some of these Eurasian taxa may have developed isolated orangutan-like features, none of them acquired a set of characteristics that would identify them as pongines. There is a strong likelihood that the African great apes and early humans such as *Sahelanthropus* (Brunet et al., 2002), *Orrorin* (Senut et al., 2001), and *Ardipithecus* (White et al., 2009) are descendants of these Eurasian apes. This has led some authors to consider the Eurasian origin of hominins (Begun et al., 2012).

Among these numerous taxa, only one has been considered as a possible ancestor of pongines. It was described under the name *Ankarapithecus* because it was found in the late Miocene deposits near the Turkish capital. Two partial skulls and mandibles have been documented and attributed to a male and a female individual, with the latter remains being more complete. Both samples display an interesting combination of pongines and dryopithecines characters. Among the pongines characters, the wide central upper incisors and the nasoalveolar clivus are considered to display a more primitive state than that of *Sivapithecus*, *Khoratpithecus*, and the orangutans. However, the shape of the orbits, the presence of a large frontal sinus, the symphysis, and the supraorbital torus do not correspond to those of a pongine ancestor. As a result, authors have diverged in their opinions regarding the phylogenetic affinities of *Ankarapithecus*, with some considering it as a primitive pongine (Begun, 2015) and others as a dryopithecine related to the origins of African apes (Alpagut et al., 1996; Kappelman et al., 2003). It is important to note that the geological age of *Ankarapithecus* is estimated around 10 Ma, a period when some Asian apes had already accumulated several significant pongines features. Therefore, the earliest pongids are not yet documented in the fossil record.

CONCLUSIONS

Several conclusions can be drawn from these data. First, all preserved anatomical characters designate *Khoratpithecus* as the closest sister taxon of orangutans because it shares more specialized characters with orangutans than *Sivapithecus* does, even if the face of *Khoratpithecus* is unknown. A second point concerns the question of the transition between *Khoratpithecus* and *Pongo,* which are separated by a time gap of 5 Ma. This transition probably occurred in Southeast Asia, in some geographic refuge areas where rain forests persisted despite the numerous glacial events that began during the late Pliocene and became increasingly stronger until the last glaciation. Finally, the ancestral population that dispersed to South and Southeast Asia is still unidentified, but undoubtedly, it arose from a Eurasian geographical area during the Mid-Miocene climatic optimum between 18 and 14 Ma. The evolution of the locomotor system of orangutans, the best-adapted large ape for tree climbing and suspensory locomotion, remains largely undocumented and constitutes a significant challenge for future research.

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