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An early diverging crocodylid from the Middle Miocene of Thailand highlights the role of SE Asia for the radiation of the Crocodyloidea

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ABSTRACT

The Neogene period witnessed the radiation of modern crocodylian genera, as evidenced from their fossil record in intertropical zones. Despite its recognition as a modern biodiversity hotspot, South East Asia remains undersampled for that age bin. Here, we describe a new crocodylian from northern Thailand, *Antecrocodylus chiangmuanensis* n. gen. n. sp. from the Middle Miocene lignite seams of Chiang Muan and refer to it other specimens from the nearby lignite seams of Mae Moh. The holotype specimen preserves the posterior half of the skull and mandible. Anatomical observations are aided by medical computed tomography. A phylogenetic analysis places the new taxon in a basal position relative to Crocodylidae. This discovery highlights the underrated fossil record of Neogene crocodyloids in Asia compared to Africa or Australia and allows us to reconsider palaeobiogeographic relationships between supposed endemic clades.

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Crocodylia; Crocodylidae;
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Introduction

Modern crocodylians include three lineages: Alligatoroidea, Crocodyloidea and Gavialoidea that split during the Cretaceous according to morphological and molecular studies (Brochu 2003; Oaks 2011). Today, the most speciose is the genus *Crocodylus* with a pan-tropical distribution. Crocodyloidea also includes the African genera *Mecistops* and *Osteolaemus*, making Africa the place hosting maximum phylogenetic diversity. Yet, whether this distribution is recent or ancient is poorly appraised. Genomic data regarding crocodylines indicate dispersal scenarios from mainland Africa or from Australasia to the Neotropics (Oaks 2011; Meredith et al. 2011), the former being supported by the fossil record of the Libyan *Crocodylus checchiai* (Delfino et al. 2020). Oaks (2011) refuted the out-of-Africa origin of *Crocodylus*, supporting instead an Australasia to Africa dispersal model. Yet, the fossil record of *Crocodylus* in Australasia is poor and includes a handful of late Neogene species such as *Crocodylus palaeindicus* from India possibly related to the extant *Crocodylus palustris* (Mook 1933; Rio and Mannion 2021), the Quaternary *Crocodylus ossifragus* from Java, which is thought to be related to the extant *Crocodylus siamensis* (Delfino and De Vos 2010), and an unnamed species of *Crocodylus* from the Plio-Pleistocene of the Tirari Desert of Australia (Yates and Pledge 2017; Lee and Yates 2018; Hekkala et al. 2021). This suggests that the radiation of *Crocodylus* and its arrival in Asia is a recent event. It is, however, difficult to estimate how recent the presence of *Crocodylus* has been in SE Asia, which starts only to be unveiled with Pleistocene records from Java, Thailand, and Myanmar (Delfino and De Vos 2010; Lauprasert et al. 2019; Iijima et al. 2020). Finally, the Asian fossil record may also challenge

earlier radiation events within Crocodylia, with the origin and position of Mekosuchinae, a group traditionally viewed as a member of the Crocodyloidea and rooted in the Eocene with a fossil record from Australasia (Salisbury and Willis 1996), but recently found to include the Orientalosuchins (Ristevski et al. 2023), represented by short-snouted semi-aquatic forms traditionally grouped in Alligatoroidea (Martin and Lauprasert 2010; Massonne et al. 2019).

The Miocene Asian fossil record thus represents a key area to untangle these problematic evolutionary questions. In addition, the Miocene record of freshwater crocodylians is relatively well sampled in other parts of the world where it is dominated by alligatoroids in North America and Europe (e.g. Brochu 2003; Martin et al. 2014), by osteolaemines in Africa (e.g. Cossette et al. 2020) and by mekosuchines in Australia (Ristevski et al. 2023). Despite a rich fossil record for mammals and being located in the subtropical belt, the Miocene fossil record of crocodylians in Asia remains poor, preventing a proper sampling of the fossil record in this part of the world. Here, we describe a new crocodyloid specimen from a Miocene freshwater deposit in northern Thailand and explore its phylogenetic affinities, identifying important directions of research to understand the role of Asia in the evolution of the group.

Geological settings

Northern Thailand is tectonically active and is crossed by strike-slip faults associated with grabens filled with non-marine sediments of the Neogene (Morley et al. 2001). Two of these basins south east of

the city of Chiang Mai, namely the Chiang Muan and Mae Moh basins, have produced vertebrate remains that were discovered thanks to industrial mining of the lignite deposits. The vertebrate assemblage from Chiang Muan and Mae Moh includes fishes, crocodiles, birds, mammals, snakes and turtles (Nakaya et al. 2002; Naksri et al. 2013; Suraprasit et al. 2014). The material studied here comes from the lower bed of the Chiang Muan mine and from the K coal seam from Mae Moh.

Former datation of the lignite beds in the Chiang Muan basin were conducted by biostratigraphic comparisons and were disputed among authors (e.g., Chaimanee et al. 2003; Pickford et al. 2004), later palaeomagnetic studies were indicating a late Middle Miocene age for the Sa Tai Member and a terminal Middle Miocene age for the Kon Member, so a Serravallian age for the series (Suganuma et al. 2006; Coster et al. 2010). The new crocodylian described here was discovered below the layer that produced the turtle *Cuora chiangmuanensis* (Naksri et al. 2013) and comes close to the contact between the calcareous sandstone at the base of the formation and the LS layer. Its age is necessarily older than the cinerite level found in Chiang Muan (Coster et al. 2010) but cannot yet be clearly associated with a magnetic chron. A magnetostratigraphic study of the Mae Moh lignite deposits indicates a similar age (Coster et al. 2010) for the K coal zone layer of the Na Khaem Formation of Mae Moh.

Material and methods

Specimens

CMMC22 was recovered from the Chiang Muan pit in 1999 by Mr. Nikorn Wongchai, a former staff of the mine. This specimen



Figure 1. The holotype skull (CMMC22) of *Antecrocodylus chiangmuanensis* n. gen. n. sp. from the lignite seams of Chiang Muan, as preserved under natural light. Abbreviations: an, angular; art, articular; boc, basioccipital; den, dentary; ec, ectopterygoid; emf, external mandibular fenestra; exo, exoccipital; fa, foramen aereum; ltf, lower temporal fenestra; pht, pharyngotympanic foramina; or, orbit; p, parietal; pa, palatine; pt, pterygoid; q, quadrate; qj, quadratojugal; ra, retroarticular process; san, surangular; sq, squamosal; stf, supratemporal fenestra.

(Figure 1) was borrowed in December 2010 and examined first-hand by JEM, WN and KL. It was scanned in a medical CT at Mahasarakham University Hospital on the 21st of March 2011 (Toshiba Aquilion, slice thickness = 0.5 mm, X-ray tube current of 150kV, and a voxel size of 415 microns) and the file is available on demand from the authors. The resulting file has the following dimensions: x = 512, y = 512, z = 1581. Further observations of the specimen were obtained from digital slices, and where relevant, cranial and mandibular bones were segmented (Figure 2). The character states that could be documented for this specimen were coded in the matrix of Brochu and Storrs (2012) for 53 taxa and 189 characters. Additional specimens from the Mae Moh mine were prepared and examined by all of us in April 2023 and are illustrated in the present work (Figure 3).

Phylogenetic analysis

A phylogenetic exploration of the position of *Antecrocodylus chiangmuanensis* was conducted using the data matrix of Brochu and Storrs (2012), updated with the six additional characters described by Brochu et al. (2022), which, in final contains 195 characters and 53 taxa. As in Brochu et al. (2022), we did not include *Quinkana* sp. because it is a composite terminal unit. In addition, we scored the six additional characters on 12 taxa that were used by Brochu and Storrs (2012) but not included in the study of Brochu et al. (2022). The characters were treated as unordered in all analyses. The data matrix is available as supplemental material of this article.

A set of parsimony analyses was performed using or without a molecular backbone based on the recent literature (Pan et al. 2021; Hekkala et al. 2021) to constrain the tree (supplemental material). Nodes that were not resolved at 100% were left unresolved in that constraint. Both analyses were run under PAUP 4.0a169 (Swofford 2002) using random addition sequence and the tree bisection – reconnection branch swapping algorithm across 250 replicates and were eventually stopped once 500,000 most parsimonious trees were found, setting the rearrangement limit to 10,000,000.

Institutional abbreviations

CMMC, Chiang Muan Mining Company Ltd. Museum; LM, Fossil, Geology, and Natural Science Museum, Lampang Province; MMCR, Mae Moh Crab, Mae Moh Museum.

Systematic Palaeontology

Crocodylia Gmelin (1789)

Crocodyloidea Fitzinger (1826)

Family incertae sedis

Antecrocodylus new genus

Derivation of name

The genus name refers to its phylogenetic position just outside Crocodylidae.

Antecrocodylus chiangmuanensis new species

Figs. 1–2

Derivation of name

The species name refers to the Chiang Muan lignite mine, which produced the holotype skull.

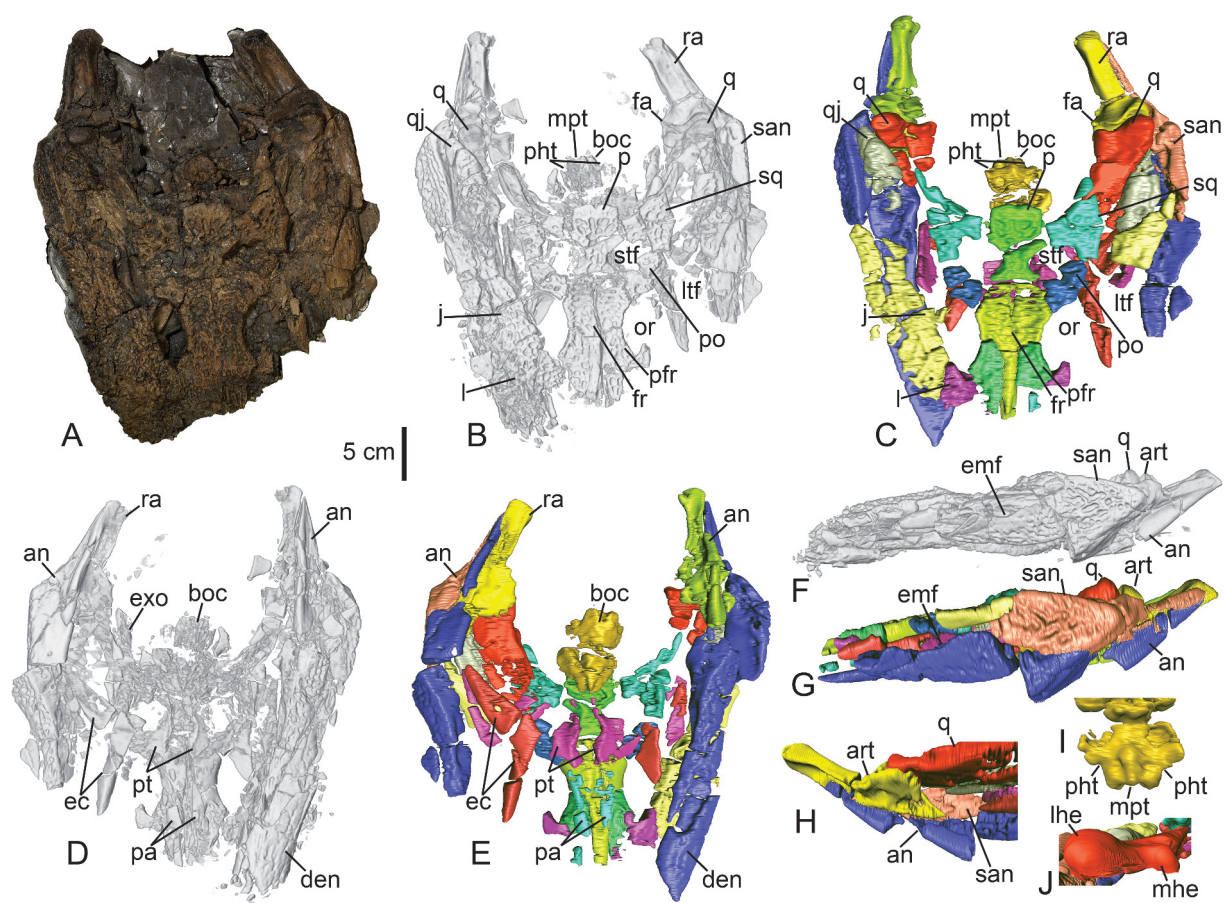


Figure 2. The holotype skull (CMMC22) of *Antecrocodylus chiangmuanensis* n. gen. n. sp. from the lignite seams of Chiang Muan. Comparative views of different renderings allow various aspects of its morphology to be assessed. Dorsal views of the holotype: A, photograph using natural light; B, general digital rendering based on medical CT data; C, digital rendering displaying manually segmented bones. Ventral views of the holotype: D, general digital rendering based on medical CT data; E, digital rendering displaying manually segmented bones. Lateral view of the holotype: F, general digital rendering based on medical CT data; G, digital rendering displaying manually segmented bones. Selected areas of the holotype (not to scale) showing H, the left posterior mandibular ramus in medial view; I, the basioccipital plate in posterior view; J, the left quadrate in posterior view. Abbreviations: an, angular; art, articular; boc, basioccipital; den, dentary; ec, ectopterygoid; emf, external mandibular fenestra; exo, exoccipital; fa, foramen aereum; ltf, lower temporal fenestra; pht, pharyngotympanic foramina; mpt, median pharyngeal tube; or, orbit; p, parietal; pa, palatine; pt, pterygoid; q, quadrate; qj, quadratojugal; ra, retroarticular process; san, surangular; sq, squamosal; stf, supratemporal fenestra.

Holotype. CMMC22, the posterior part of a skull including the periorbital region and the corresponding section of the mandibles in occlusion.

Provenance and age

Chiang Muan mine, just below the lowest lignite seam (LS), Serravallian, Middle Miocene (Suganuma et al. 2006; Coster et al. 2010).

Referred specimens

MMCR-1, a right quadratojugal-jugal bone; LM2023-1-034, a left scapula; LM2023-1-35 to LM2023-1-40, a set of dorsal vertebrae. The K coal zone layer of the Na Khaem Formation of Mae Moh, Serravallian (Coster et al. 2010).

Diagnosis

Antecrocodylus chiangmuanensis is characterised by the combined presence of the following traits: wide interorbital distance; shallow knob at the frontal-postorbital suture just medial to orbital margin; small circular supratemporal fenestrae; unaligned pharyngotympanic foramina; posterodorsally elongate and projecting retroarticular processes; quadrate-quadratojugal suture located at the

posteroventral corner of lower temporal fenestra; absence of ridge on the dorsal surface of frontal; autapomorphies include a straight jugal-quadratojugal outer margin of the lower temporal bar.

Description of CMMC22

When no mention is given, the following description contains references to character codings following the data matrix of Brochu and Storrs (2012). Characters coded in the data matrix of Rio and Mannion (2021) are also indicated, when relevant.

Orbital area (Figures 1, 2A–C)

The margins of the orbits are delimited by a shallow ridge (137–1). Preorbital ridges were not observed even if the skull is broken off just anterior to the orbits. Anterior to the right orbit, the frontal, prefrontal and lacrimal are still preserved and offer a glimpse as to the absence of ornamentation or crest in the antorbital surface of the skull (97–0). The orbit ventral rim is circular (138–0). The frontal sends an anterior process that separates the prefrontals (129–0). The median orbital margin is made of the prefrontal and frontal and is delineated by a shallow ridge. A protuberance is present in the frontal-postorbital suture at the orbital margin (71–1 in Rio and

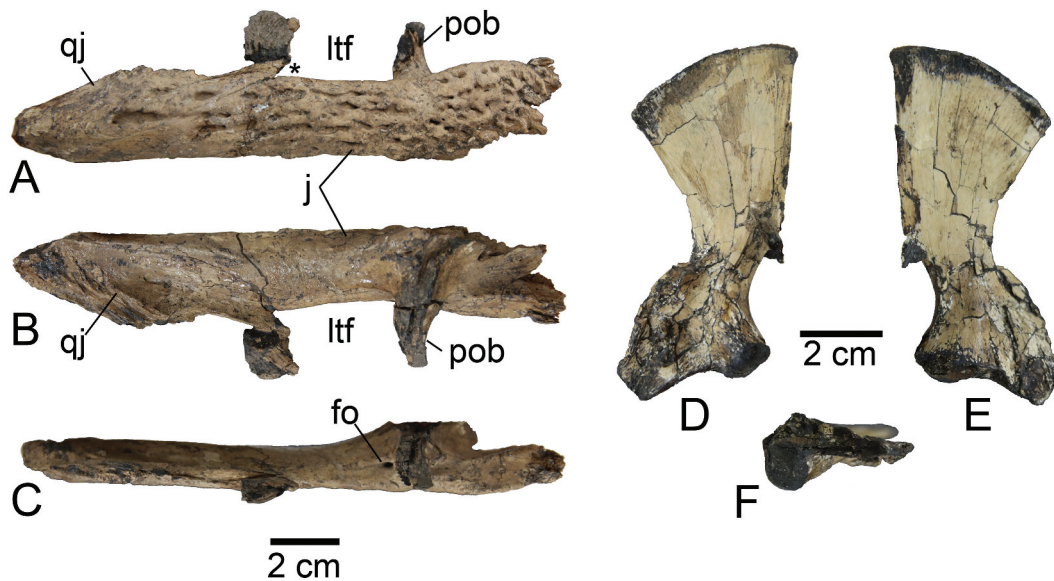


Figure 3. Crocodylid remains from the lignite seam of Mae Moh and referred to *Antrocodylus chiangmuanensis* n. gen. n. sp. Right temporal bar (MMCR-1) in A, dorsal; B, ventral and C, dorsal views; left scapula (LM2023-1-034) in D, lateral, E, medial and F, proximal views. Abbreviations: fo, foramen; fr, frontal; j, jugal; l, lacrimal; ltf, lower temporal fenestra; pfr, prefrontal; po, postorbital; pob, postorbital bar; qj, quadratojugal. The asterisks indicates the position of the jugal-quadratojugal suture.

Mannion 2021; not coded in: Brochu and Storrs 2012) as in *Crocodylus siamensis* or more variably as in other *Crocodylus* species. The prefrontal shows no outgrowth or knob on its dorsal surface (107–0). The prefrontal pillar morphology cannot be observed due to dorsoventral crushing in this area. The postorbital bar can be seen on the right side, where it is crushed and preserves a contact with the jugal. The post-orbital bar is inset from the lateral surface (135–1) of the jugal and is slender (133–1) as in other crocodylids. The post-orbital bar is inset from the skull table too (136–1).

Skull table (Figures 1, 2A–C). The skull table is planar (156–1) and does not possess any outgrowth or horns on its lateral margins (157–0). The presence of a quadratojugal spine cannot be assessed. The quadratojugal-jugal suture is best seen on the right side and sits at the posteroventral corner of the lower temporal fenestra. The jugal forms a straight outer margin for the lower temporal bar. As seen on the right side, the rims of the squamosal groove are parallel (147–0). The squamosal-quadratojugal suture is fully closed behind the otic aperture (148–0). The frontoparietal suture lies entirely on the skull table and the postorbital and parietal have a sutural contact near the anterolateral corner of the supratemporal fenestrae (150–2). Although partly damaged, the anteromedial corner of the parietal forms part of the supratemporal fossa. The supratemporal fossa is small but without overhang of surrounding dermal bones (152–0). The posterior wall of the supratemporal fenestrae is too damaged to yield any information about the dorsal contribution of the quadrate. The squamosal prongs project far posteriorly beyond the posterior margin of the skull table (158–1), as in *Crocodylus* species but not as extensively as in longirostrine taxa. There is no prominent boss on the paroccipital process (174–1). Contrary to *Crocodylus siamensis*, there is no sagittal interorbital ridge of the frontal (188–0). The supraoccipital exposure on the skull table is very limited (160–0,1) as indicated by the morphology of the posterior margin of the parietal.

Palate

Most of the bones of the palate and basicranium are heavily crushed, but some palatal bones allow some information to be

gathered (Figure 2D, E, I, J). The pterygoids are partly preserved. Along their medial suture, they are disarticulated and displaced for a short distance. The choanal opening is not preserved, the posterior area of the pterygoids being crushed. However, the morphology of the median pterygoid suture (Figure 2C) indicates that the choanae were opening in a posterior position within the pterygoidean palate (121–1). The palatine is mostly destroyed near its contact with the pterygoid. Here, the pterygoid forms the posterior corner of the suborbital fenestra. As seen on the right side of the posterior corner of the suborbital fenestra, the pterygoid-ectopterygoid suture is straight (119–0) unlike in modern *Crocodylus* where it is bowed. Here, the pterygoid-ectopterygoid suture shows no flexure (126–0). As observed on the right side, the ectopterygoid reaches the posterior tip of the pterygoid (127–0). The ectopterygoid extends well along the medial face of the post-orbital bar (132–0). The ventral portion of the basioccipital plate is preserved but has been displaced and is no longer connected to the pterygoid, so it is not possible to assess the ventral extent of the basisphenoid here. However, here, the ventral exit foramina of the pharyngotympanic sinuses are visible where the pharyngotympanic foramina are dorsally positioned relative to the median pharyngeal tube foramen (175–0) unlike in extant *Crocodylus* species, but similar to the extant *Mecistops* (Brochu 2000) or basal crocodyloids such as *Asiatosuchus*. Although the foramen aereum is visible on the articular, it could not be examined on the quadrate. The quadrate condyles are best preserved on the left side with the lateral hemicondyle being larger than the medial one. As in *Crocodylus* and unlike Mekosuchinae, the medial hemicondyle is tall (181–3).

Mandible (Figure 2)

Both posterior mandibular rami are preserved and are broken off in the middle of the angular and surangular bones. A small but well-formed external mandibular fenestra with a concavity on the angular dorsal surface is visible on both sides. Posterior to it, the position of the surangular-angular suture is difficult to assess as both bones are dorsoventrally displaced. Yet, on the left side, the suture seems visible and appears to display a derived state, passing broadly along the ventral margin of the external mandibular fenestra as in modern

species of *Crocodylus* (60–1). The surangular-angular suture meets the articular at its ventral tip (66–0) as seen medially on the left side. On the lateral wall of the glenoid fossa, the surangular ascending process is similar in morphology to that of *Crocodylus niloticus*, being truncated dorsally (67–1) and the suture between the surangular and articular bones is bowed laterally (73–1). The position of the angular and articular relative to the foramen intermandibular caudalis could not be assessed, the foramen not being located during the segmentation. The surangular reaches the posterior tip of the elongated retroarticular process (72–0), which is projecting posterodorsally as a long process (71–1). On the articular, the foramen aereum is located on the medial margin (70–0). Large foramina are visible on the medial surface of the angular.

Description of referred specimens from Mae Moh

Pending the description of more complete specimens from this locality, the below-described postcranial specimens are provisionally referred to as *Antecrocodylus chiangmuanensis* because Mae Moh and Chiang Muan localities are equivalent in age.

Jugal and quadratojugal (Figure 3)

MMCR-1 is a right part of a quadratojugal and jugal in connection, which fits with the description of CMMC22 notably in sharing the diagnostic straight outer margin of the lower temporal bar. It measures 3.7 cm between the posterior level of the lower temporal fenestra and the posterior margin of the postorbital bar, and therefore matches the dimensions of CMMC22. A small foramen is located behind the jugal pillar of the postorbital bar (93–0 in Rio and Mannion 2021). There is no posterior process of the ectopterygoid suture, as observed medially (181–2 in Rio and Mannion 2021). The postorbital bar is inset from the medial surface. The quadratojugal, not the jugal, contributes to the posterior margin of the lower temporal fenestra unlike in modern species of *Crocodylus*; the suture is located at the posterolateral level (142–2). The ventral part of the jugal is straight. There is no anterior process of the quadratojugal (144–1). The jugal goes far posteriorly but is not hiding the quadratojugal in lateral view. The post-orbital bar is cylindrical and slender (133–1). The dorsal profile of the posteroventral margin of the jugal is straight and acute in the dorsal edge (94–0 in Rio and Mannion 2021). The posterior margin of the ventral part of the skull is rather straight, whereas it is more curved in extant crocodylians.

Scapula (Figure 3)

LM2023-1-034 is a left scapula possessing a thin acromion process that is not characteristic of *Alligator* (24–0). This area is not concave but is straight but is a convex outline of the anterior part of the scapula. This is not seen in other extant crocodylians (e.g. figure 125 in Rio and Mannion 2021). The scapulocoracoid facet is uniformly narrow (26–0).

Vertebrae

A number of isolated dorsal vertebrae are also known from Mae Moh. Their centrum is procoelous as is typically observed in eusuchians.

Phylogenetic results

The general topology obtained when no molecular backbone is given (Figure 4B) is consistent with previous studies that used the

same data matrix (Brochu and Storrs 2012; Cossette et al. 2020; Brochu et al. 2022). The resulting consensus was obtained from 1728 equally optimal trees with a length of 340 steps (CI = 0.4676, RI = 0.7241; CI excluding uninformative characters = 0.4217). Fifty-nine bipartitions were found, and 36 nodes were fully resolved. *Antecrocodylus chiangmuanensis* is placed in a more derived position relative to Crocodylidae than the monophyletic Mekosuchinae but stays outside of a monophyletic osteolaemine lineage; Crocodylinae are recovered and *Mecistops* is basal relative to all species of *Crocodylus sensu stricto*. *Crocodylus palaeindicus* and modern day *Crocodylus* are monophyletic. The position of *Crocodylus palaeindicus* relative to Americano-African *Crocodylus* or Australasian *Crocodylus* is not resolved. *C. chechchai* from Turkana, *C. thorbjarnarsoni*, and *C. anthropophagus* form together the sister clade of all modern *Crocodylus*. On the other hand, *Voay* is in a sister position to *Osteolaemus*. The monophyly of Mekosuchinae as inclusive of *Australosuchus*, *Kambara*, and *Trilophosuchus* is found and is supported by a unique non-exclusive synapomorphy (character 181 (state 1), also seen in *Leidyosuchus canadensis*).

The analysis using a molecular constraint provided 216 equal trees of 349 steps (CI = 0.4556; RI = 0.7104; CI excluding uninformative characters 0.4099). Sixty bipartitions were found, and 41 nodes were fully resolved.

As above, the analyses using a molecular constraint recover *Antecrocodylus chiangmuanensis* immediately basal to Crocodylidae but outside of the family (Figure 4). The obtained trees differ from nine steps and Adams consensus (Figure 4A) or strict consensus (supplemental material) are nearly identical, with the important exception of the phylogenetic position of *Mecistops* and *Voay robustus*, which, respectively, move in Osteolaeminae and in Crocodylinae. The Adams consensus tree is represented in Figure 4A. Osteolaeminae includes *Osteolaemus*, *Mecistops*, *Euthecodon*, *Rimasuchus* and *Brochuchus*, while Crocodylinae includes *Crocodylus*, *Voay*, and *Crocodylus chechchai* from Turkana.

Discussion

Affinities of *Antecrocodylus chiangmuanensis*

Despite its preservation, CMMC22 reveals several features that allow its phylogenetic affinities to be established. The skull is superficially similar to any eusuchian that displays semi-aquatic adaptations in harbouring a sculpted dorsal surface with ovoid pits, dorsally facing orbits, posterodorsally expanded retroarticular processes and an overall dorsoventrally compressed morphology. The ventral margin of the jugal arch is straight (Figure 4A, B), whereas it is usually concave in most crocodylians except longirostrine forms such as *Gavialis*, *Eosuchus*, *Piscogavialis* and *Tomistoma* (Jouve et al. 2008; Rio and Mannion 2021). As that shape is similar between the holotype and the referred material, deformation is unlikely to have generated it. This character may be interpreted as an autapomorphy within Crocodylidae and allows to associate the material from Chiang Muan and Mae Moh with few doubts. An attribution to a longirostrine form such as a tomistomine or a gavialid is discarded on the basis of the relative position of the lateral margin of the orbit with the rest of the rostrum (character 74 in Rio and Mannion 2021). Moreover, the absence of an acute indentation at the level of the posterior margin of the skull table discards any close affinities with a tomistomine (character 82 in Rio and Mannion 2021). The phylogenetic analysis fails to underline other obvious autapomorphies for the Chiang Muan taxon, which is otherwise diagnosed by a combination of characters (see above in diagnosis).

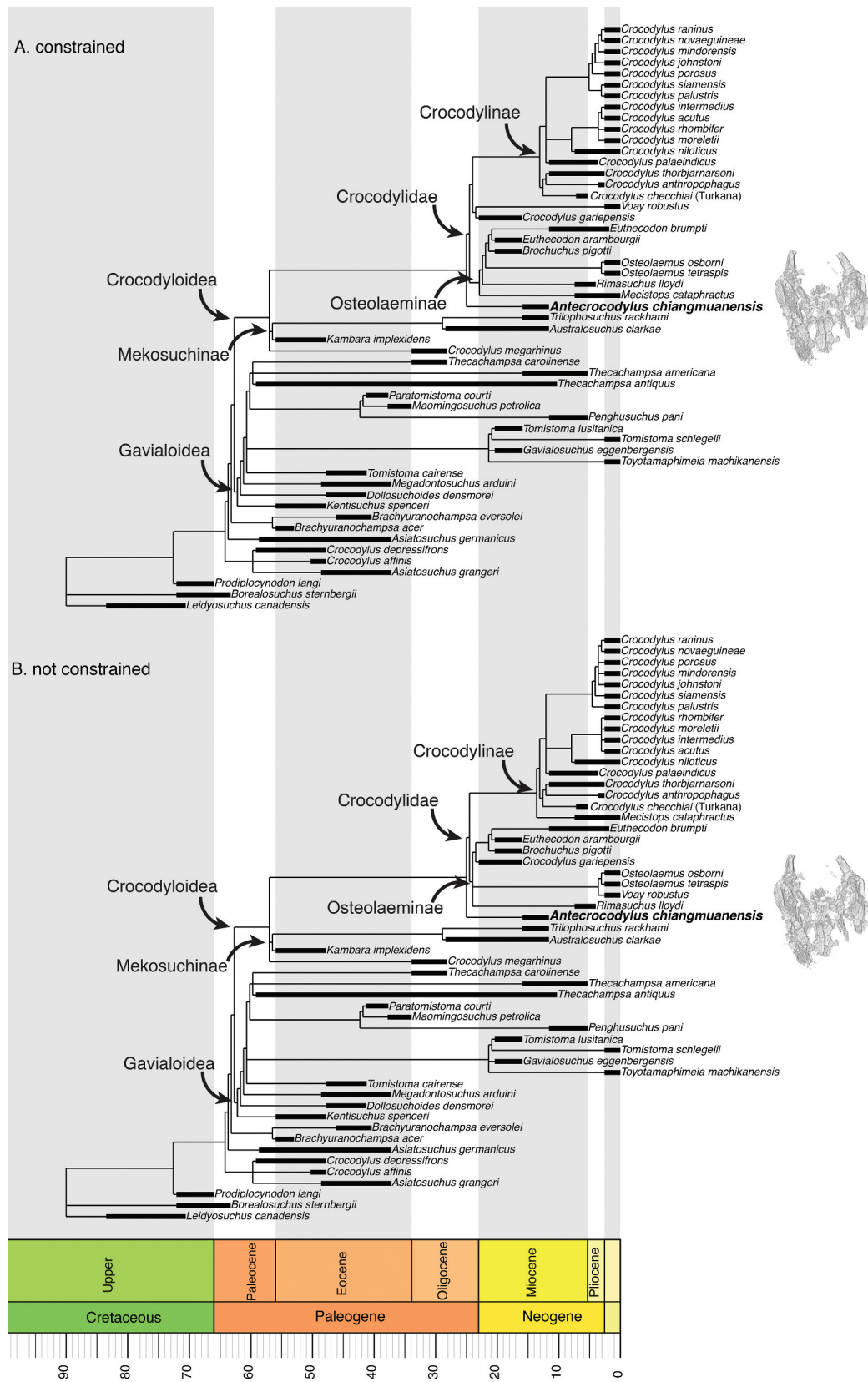


Figure 4. Phylogenetic position of *Antecrocodylus chiangmuanensis* n. gen. n. sp. as part of basal crocodylidae. Adams consensus tree obtained with the data matrix of Brochu and Stors (2012) with a molecular constraint (A) and without a molecular constraint (B).

The phylogenetic analysis recovers *Antecrocodylus chiangmuanensis* as a basal crocodylid that falls outside osteolaemines and crocodylines. *Antecrocodylus chiangmuanensis* also displays a quadratojugal-jugal suture that lies at the posterior angle of the infratemporal fenestra, whereas it is made exclusively of the jugal in all modern *Crocodylus* species and osteolaemines (character 142).

In CMMC22, the position of the foramen aereum and the general morphology of the retroarticular process allow us to discard a referral to the genus *Diplocynodon* (e.g. Martin et al. 2014).

Among the Mae Moh specimens examined by our team, the right part of a quadratojugal-jugal arch is completely consistent with that of CMMC22 from Chiang Muan. Identical characters include the position of the quadratojugal-jugal suture at the posterior corner of the lower temporal fenestra and the rather straight profile of the lower temporal bar. For this reason, the Mae Moh specimen (MMCR-1) is also attributed to *Antecrocodylus chiangmuanensis*. Attributing the scapula (LM2023-1-034) to the same species is more difficult and could be challenged with discoveries of material in connection. In addition, the shape of the scapulocoracoid facet is narrow in LM2023-1-034, whereas it is broad in other derived crocodylids (character 26) and would therefore also lend support to its attribution to *Antecrocodylus chiangmuanensis*.

Osteolaeminae include a number of extinct genera, exclusively recovered from Africa, characterised by three unambiguous synapomorphies according to Cossette et al. (2020). Although the morphology of the choanal neck is not preserved in *Antecrocodylus chiangmuanensis*, the absence of preorbital ridges seems to exclude any affinity of *Antecrocodylus chiangmuanensis* with this African lineage.

Mekosuchines consist of a disparate crocodylian lineages of debated affinities that span the Palaeogene, Neogene and Holocene record of Australasia (see review in Ristevski et al. 2023). Whether they transpired outside their known biogeographic province is a pending question and it would make sense to recover members in the neighbouring SE Asia. Nevertheless, the group includes both altirostral (e.g. *Mekosuchus inexpectatus* Balouet and Buffetaut 1987) and platyrostral forms (the genus *Kambara*, Salisbury and Willis 1996) and their monophyly is weakly supported. *Antecrocodylus chiangmuanensis* is found to be more derived than this assemblage and closer to Crocodylidae in our phylogenetic analysis. The only potential non-exclusive synapomorphy for Mekosuchines is the shape of the medial quadratohemicondyle, which could be shared with Orientalosuchina (but that is also present in *Leidyosuchus canadensis*). In that respect, *Antecrocodylus chiangmuanensis* can be excluded from the Mekosuchinae.

Eocene Vietnamese and Thai orientalosuchins (Martin and Lauprasert 2010; Massonne et al. 2019) are brevirostrines and display alligatoroid characters according to previous works (Martin and Lauprasert 2010). Therefore, they are not comparable in morphology to *Antecrocodylus chiangmuanensis*. However, Orientalosuchina as defined by Massonne et al. (2019) and now incorporating some platyrostral forms from the Palaeogene and Late Cretaceous of China (Li et al. 2019; Shan et al. 2021) could challenge the basal phylogenetic relationship, especially if with Mekosuchinae they became their close relatives. Basal crocodyloids with a Eurasian distribution include the genus *Asiatosuchus*; however, their fossil record is restricted to the Palaeogene (e.g. Delfino et al. 2017) and their occurrence in the Miocene of SE Asia would represent an extensive ghost range of nearly 30 myr. On morphological grounds, *Antecrocodylus chiangmuanensis* is distinguished from *Asiatosuchus*-like taxa (compare with data from Delfino and Smith 2009; Delfino et al. 2017) by a small medial foramen of the

jugal (Figure 4B, C), by an absence of contribution of the supraoccipital onto the dorsal surface of the skull table (Figure 3A) and by a longer retroarticular process (Figure 3D, E).

Although the new Thai crocodylid superficially resembles a modern *Crocodylus* species or other semi-aquatic crocodyloid morphotypes (e.g. *Asiatosuchus*, some Mekosuchinae), the phylogenetic results indicate that *Antecrocodylus chiangmuanensis* occupies a basal position within Crocodylidae but can be distinguished from the genus *Crocodylus*, notably in the configuration of the ventral exit foramina of the pharyngotympanic sinuses.

Crocodylus palaeindicus is allied with the living species of *Crocodylus*. Its position relative to the Afro-American or to the Australasian group could not be clarified in our analyses and leaves the geographic origin of *Crocodylus* open. In the case of an African origin for Crocodylidae, at least two independent groups could have invaded Asia. One before the end of the Middle Miocene and a second one before the Quaternary.

The untapped fossil record of Neogene crocodyloids in Asia and paleobiogeographic implications

Nowadays, Asia hosts all the modern representatives of Crocodylia, including *Gavialis gangeticus* inhabiting the Himalayan drainage systems, the false gharial *Tomistoma schlegelii* mostly distributed in SE Asia, *Alligator sinensis* restricted to the Yangtze river Basin and seven species of *Crocodylus* distributed from India to northern Australia. Close allies of these modern forms are indeed already documented from various localities in Asia during the Pliocene (e.g. Delfino and De Vos 2010; Claude et al. 2011; Martin et al. 2019; Iijima et al. 2020; Ristevski et al. 2023; Darlim et al. 2023), the oldest occurrences of the modern genera being Late Miocene in age according to molecular estimates (Oaks 2011). While the origin and distribution of modern species and closely allied forms is largely underevaluated and poses several questions about their past distribution (e.g. Claude et al. 2011), the origin and evolution of modern groups during the Miocene in Asia is equally scarcely understood.

Our current understanding of Australasian lineages during the Neogene is dominated by the fossil record of Mekosuchinae in Australia and surrounding islands (see review in Ristevski et al. 2023). Mio-Pliocene crocodylian occurrences in continental Asia do exist but discussion about their historical biogeography is hampered by a lack of stratigraphical resolution (e.g. Claude et al. 2011). Miocene crocodylians include the tomistomine *Penghusuchus pani* and the alligatorid *Alligator* sp. from Taiwan (Hsi-Yin et al. 2013). Crocodyloids are nearly absent from the Neogene picture with the earliest report of a basal form, *Astorgosuchus bugtiensis*, from the early Oligocene or Oligo-Miocene of Pakistan (Martin et al. 2019). The next oldest Neogene crocodyloid from Asia is *Crocodylus palaeindicus* from the Late Miocene of the Siwalik Hills (Lydekker 1886; Mook 1933), hence most of the Miocene record in Asia is devoid of fossil occurrences.

The present description of a form immediately basal to Crocodylidae from the Middle Miocene of Thailand fills an important gap of the crocodylian fossil record in Asia. Further detailed studies of more complete specimens will certainly reveal important traits to refine their phylogenetic placement. Yet, our analyses indicate that *Antecrocodylus chiangmuanensis* is ancestral to both osteolaemines and crocodylines and may be distantly related to mekosuchines. The earliest mekosuchines are Eocene in age with the genus *Kambara* from Australia (Salisbury and Willis 1996). Future studies will have to investigate whether mekosuchines evolved from an Asian ancestor or

were later also capable to re-disperse from Australia to continental Asia. One key taxon to answer such question may be *Orientalosuchina*. Although the Eocene *Orientalosuchina* are traditionally viewed as members of the Alligatorinae on the basis of specimens from Thailand and Vietnam (Martin and Lauprasert 2010; Massonne et al. 2019), recent phylogenetic hypotheses yielded conflicting results, placing them into Mekosuchinae, i.e. among Crocodyloidea (Ristevski et al. 2023), although it was also questioned whether Mekosuchinae could be positioned outside Crocodyloidea (Lee and Yates 2018; Ristevski et al. 2023, 2023). Such challenges are equally rooted in the Late Cretaceous of China with forms such as *Jiangxisuchus nankangensis* originally recovered as one of the earliest crocodyloids (Li et al. 2019) but recently resolved as a member of the *Orientalosuchina* as part of Alligatoroidea (Shan et al. 2021). Updates in such new taxon descriptions and character codings may help clarify these issues but not only because such lability in phylogenetic results indicates a lack of robustness and resolution when using traditional morphological character matrices. Indeed, the addition of new taxa from the Neogene of Asia such as those described in this work represent an important key to untangle such problematic relationships. Regarding character states used in the present phylogeny, it is noteworthy that they are rarely listed in an ascending way (making their use as ordered characters complicated). Such definitions might have been designed to stabilise some nodes. There is therefore an important need in the future to rework character/taxon definitions and test for their homology using molecular consensus. In parallel, exploitation of overlooked endocranial characters may prove to be a source of additional taxonomic and phylogenetic information (e.g. Burke and Mannion 2023; Perrichon et al. 2023).

Here, with the description of *Antecrocodylus chiangmuanensis* n. gen. n. sp., this work demonstrates that Asia hosts an under-evaluated fossil record for basal crocodylids during the Miocene. At the same epoch, Europe was dominated in freshwater ecosystems by the basal alligatoroid *Diplocynodon* (e.g. Martin et al. 2014; Kuzmin and Zvonok 2021), which later became replaced shortly in time by *Crocodylus* sp. following its regional extinction (Delfino et al. 2007). There is no obvious major biogeographic barrier between Western Europe and continental Asia during the Miocene and one may be expecting freshwater ecosystems of SE Asia to also host *Diplocynodon*. But according to the present report, this is not the case, and our lack of knowledge of the crocodylian fossil record in the Middle East during the early Neogene illustrates how poorly we can interpret biogeographic scenarios involving crocodylians in this part of the world. North America is dominated by alligatorines during the Miocene, but those forms are unrelated to *Diplocynodon*, suggesting that biogeographic exchanges with Europe interrupted before the Neogene. The presence of *Alligator sinensis* and allied forms during the Miocene in Asia (Shan et al. 2013) indicates that a preferred biogeographic link persisted between North America and Asia during the Neogene, but this did not involve crocodylids, the latter having colonised North America later during the Pliocene through a trans-Atlantic route (Oaks 2011; Delfino et al. 2020). That Western Europe and Asia had less to do with each other than Asia and North America is puzzling and invites future sampling efforts in Palaeogene and Neogene deposits of the middle East (e.g. Buffetaut and Thomas 1981; Martin et al. 2019). This will also be key to understand any potential links between crocodylian faunas from Asia and those from the Neogene of Africa (Cossette et al. 2020). Here, in all phylogenetic topologies

obtained, modern Crocodylinae are monophyletic and are in a sister-group relation to Osteolaeminae. This clade forms, with Mekosuchinae and with some ancient forms, a monophyletic group, their origin being rooted with the Oligocene African *Crocodylus megarhinus*. If we consider that we know the Eurasian record well, this suggests that African and Australian forms certainly had a common ancestor (possibly in the Palaeocene). Depending on the origin of salt excretion, transoceanic dispersal may explain this biogeographic distribution. The presence of a taxon basal and closely related to Crocodylidae in the Miocene of Thailand may indicate an independent migration from Africa to Asia that may have occurred in the Oligocene or in the Early Miocene. Under this scenario, the arrival of the genus *Crocodylus* in SE Asia can only be considered as a later dispersal event. An alternative scenario would be to consider that the fossil record is indeed not well enough documented in the Oligocene or Early Miocene in Asia and may correspond to the geographic origin of African taxa. Finally, as discussed above, the unsettled intra- and inter-relationships of Mekosuchinae and *Orientalosuchina* are to be investigated through the lens of the yet untouched fossil records of the Middle East and of South East Asia.

Conclusions

A plethora of crocodylian taxa are recognised in the Neogene fossil record of several continents but Asia remains under-represented, despite being a possible hotspot of biodiversity at the origin of modern crocodylian clades according to molecular studies (e.g. Oaks 2011). Here, we have described a new crocodylid taxon, *Antecrocodylus chiangmuanensis*, from the Middle Miocene of northern Thailand. Although preliminary, this discovery highlights the importance of Asia for deciphering relationships among modern lineages and explaining their past distribution in the tropics.

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No potential conflict of interest was reported by the author(s).

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