



HAL
open science

An Eocene tomistomine from peninsular Thailand

Jérémy Martin, Komsorn Lauprasert, Haiyan Tong, Varavudh Suteethorn,
Eric Buffetaut

► **To cite this version:**

Jérémy Martin, Komsorn Lauprasert, Haiyan Tong, Varavudh Suteethorn, Eric Buffetaut. An Eocene tomistomine from peninsular Thailand. *Annales de Paléontologie*, 2019, 10.1016/j.annpal.2019.03.002 . hal-02121886

HAL Id: hal-02121886

<https://hal.science/hal-02121886v1>

Submitted on 6 May 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

An Eocene tomistomine from peninsular Thailand

Un tomistominé éocène de la péninsule Thaïlandaise

Jeremy E. Martin¹, Komsorn Lauprasert², Haiyan Tong², Varavudh Suteethorn² and Eric Buffetaut³

¹Laboratoire de Géologie de Lyon: Terre, Planète et Environnement, UMR CNRS 5276 (CNRS, ENS, Université Lyon 1), Ecole Normale Supérieure de Lyon, 69364 Lyon Cedex 07, France, email: jeremy.martin@ens-lyon.fr

²Palaeontological Research and Education Centre, Mahasarakham University, Khamrieng, 44150 Thailand

³Laboratoire de Géologie de l'Ecole Normale Supérieure, CNRS (UMR 8538), 24 rue Lhomond, Paris Cedex 05, 75231, France

Abstract

Skull and mandibular elements of a tomistomine crocodylian are described from the late Eocene to early Oligocene lignite seams of Krabi, peninsular Thailand. The Thai tomistomine is a longirostrine form characterized by a rostrum/skull ratio of about 0.6; a mandibular symphysis reaching the level of the eleventh alveolus; a deep participation of the splenial in the symphysis to the level of ninth alveolus; an enlarged fifth maxillary alveolus; long nasals reaching the premaxillae at the level of the fifth maxillary alveolus but not contributing to the external nares; undivided posterior processes of premaxillae; a short prefrontal, excluded by a longer lacrimal from the posteromedial margin of maxillae; vomers visible on the palate. A phylogenetic analysis recovers the Thai specimen among derived tomistomines, on the stem lineage of the extant *Tomistoma schlegelii*, as a close ally of *Maomingosuchus petrolica*, a late Eocene tomistomine from southern China. The present recognition of *Maomingosuchus*

sp. in late Eocene Thai deposits expands the distribution of Eocene tomistomines from southern China to the tropics. The origin of Tomistominae in Asia is briefly discussed.

Résumé

Des éléments crâniens et mandibulaires d'un crocodylien tomistominé sont décrits en provenance de niveaux à lignite de l'Eocène supérieur à Oligocène inférieur de Krabi sur la péninsule Thaïlandaise. Le tomistominé Thaïlandais est caractérisé par un crâne de type longirostre présentant un ratio rostre/crâne d'environ 0.6 ; une symphyse mandibulaire qui atteint le niveau du onzième alvéole ; une participation profonde du splénial dans la symphyse mandibulaire au niveau du neuvième alvéole ; un cinquième alvéole maxillaire élargi ; les os du nasal qui atteignent les prémaxillaires au niveau du cinquième alvéole maxillaire mais ne participant pas aux narines externes ; des processus postérieurs des prémaxillaires non-divisés ; un préfrontal court, exclu de la marge postéromédiale des maxillaires par un lacrymal plus long ; un vomer visible sur le palais. Une analyse phylogénétique place le spécimen Thaïlandais au sein des tomistominés dérivés, au sein de la lignée de l'actuel *Tomistoma schlegelii*, et proche de *Maomingosuchus petrolica*, un taxon de la fin de l'Eocène connu en Chine du sud. La présente découverte de *Maomingosuchus* sp. dans l'Eocène tardif de Thaïlande étend l'aire de répartition des tomistominés eocènes depuis la Chine du sud jusqu'aux tropiques. L'origine des Tomistominae en Asie est brièvement discutée.

Keywords: Tomistomine, Eocene, Oligocene, Thailand

Mots clés: Tomistominés, Eocène, Oligocène, Thaïlande

1. Introduction

Tomistoma schlegelii, or the false gharial, is the only living representative of the tomistomine lineage and nowadays inhabits freshwater habitats in Indonesia and Malaysia. Although other extant crocodylians such as *Gavialis* or *Crocodylus* are known in the SE Asian fossil record (Claude et al., 2011; Martin et al., 2012; Delfino and De Vos, 2010), the genus *Tomistoma* has never been reported from Plio-Pleistocene deposits. The only known Pleistocene tomistomine from Asia is *Toyotamaphimeia machikanensis* but recent phylogenetic analyses indicate it is distantly related to *Tomistoma schlegelii* (e.g. Jouve et al., 2015; Shan et al., 2018) and this may indicate that the extant species diverged from a much older stock of tomistomines, perhaps during the Paleogene when the oldest tomistomines are known (Brochu, 2007; Jouve et al., 2015).

Reports of Paleogene herpetofaunas from SE Asia remain scarce. Few Paleogene localities are known from Burma (Ciochon et al., 1985; Ducrocq et al., 1992), Southern (late Eocene – early Oligocene of Krabi; Suteethorn et al., 1988), Western Thailand (late Oligocene of Nong Ya Plong; Marivaux et al., 2004), Northern Vietnam (late Eocene or early Oligocene of Na Duong, Cao Bang and Hang Mon basins; Böhme et al., 2011; Ducrocq et al., 2015) and South China (late Eocene of Maoming Basin; Shan et al., 2017). Here and additionally to one previous study (Martin and Lauprasert, 2010), we report crocodylian remains from the late Eocene – early Oligocene lignite mines of Krabi, peninsular Thailand. This locality was discovered in the late 1980s (Suteethorn et al., 1988) and has yielded a rich mammalian fauna (Ducrocq et al., 1992). The herpetofauna includes snakes (Ducrocq et al., 1992; Rage et al., 1992), turtles (Claude et al., 2007) and alligatorine crocodiles (Martin and Lauprasert, 2010). A detailed paleomagnetic study reinforces the late Eocene – early Oligocene age of the locality (Bennami et al., 2001; Claude et al., 2007), previously based on

the mammal assemblage. The present description of a tomistomine expands the geographical range of tomistomines, so far known in Southern China and Vietnam for the same epoch.

Institutional abbreviations. IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; PRC: Palaeontological Research and Education Centre, Mahasarakham University, Mahasarakham, Thailand; ZH: collection Zhang He, Shenzhen Museum, Shenzhen, China.

2. Systematic palaeontology

Eusuchia Huxley, 1875

Gavialoidea Hay 1930

Tomistominae Kälin, 1955

Maomingosuchus Shan, Wu, Chen and Sato, 2017

***Maomingosuchus* sp.**

Referred specimens. PRC-1121, a skull comprising the skull table and most of the rostrum (Fig. 1); PRC-1122, an almost complete left mandible (Fig. 2); PRC-1123, a right dentary with portion of the splenial (Fig. 2).

Provenance and age. late Eocene – early Oligocene of Wai Lek, Krabi Province, Thailand (see Martin and Lauprasert, 2010 and Claude et al., 2007 for geological information).

3. Description

Preservation and general shape. The skull (PRC-1121, Fig. 1) is incomplete and suffered from overall dorsoventral compression. The anterior portions of the premaxillae are missing. The jugal arches, quadrate rami, the braincase and the posterior palatal area were not recovered. Sutural patterns are nevertheless well discernible on the remaining bones. Discarding the effects of compression, the skull is clearly longirostrine with an approximate skull/snout ratio of about 0.6. Skull and mandibular measurements are recorded in table 1. The pattern of ornamentation is dominated by furrows on the rostrum and large ovoid pits on the skull table. Lacrimal and prefrontal distinguish themselves from other bones of the rostrum in having a similar ornamentation as those bones of the skull table. Elements of the lower jaw are relatively well preserved and underwent minor deformation. The mandible is a delicate and elongate structure bearing an extensive mandibular symphysis. A left mandible (PRC-1122) is almost complete, lacking only its anteriormost tip. Another specimen consists of a right mandible (PRC-1123) that preserves the entire dentary and the anterior extension of the splenial. All other elements are missing. The lateral and ventral surfaces of the dentaries are ornamented with small and shallow furrows. The ornamentation on the angular and surangular is made of pits. The mandible is a delicate and elongate element bearing an extensive mandibular symphysis. The external mandibular fenestra is small and consists of longer than deep slit.

Cranial bones. Most of the anterior portion of the premaxillae, including the external nares is not preserved. Dorsally, the premaxilla preserves the sutural contact with the maxilla. This suture is oblique in lateral view. Posteriorly, the premaxilla wedges between the maxilla and the anteriormost process of the nasal. This is especially obvious on the left side but less clear on the right side due to compression. In ventral view, no alveoli are visible. The sutural pattern between premaxillae and maxillae is unclear. The maxillae are elongated. Their posteriormost lateral margins are not preserved but judging from the morphology of the left

maxilla, this area almost reaches the anterior orbital level. The anterior nasal extension prevents any medial contact between the maxillae. The suture with the jugal is unknown. The maxillary toothrow is most complete on the left side but the very last alveoli are not preserved. Here, thirteen alveoli are fully preserved, the fourteenth being damaged but preserving a part of the alveolus in section. The fifth alveolus is the largest of the maxillary tooth row (see table 2 for measures). Each alveolus is clearly separated from another by a pit, the depth of which increases toward the rear of the row. The premaxillo-maxillary suture does not present any pit but it is notched. Pits begin to occur behind the second maxillary alveolus and the last pit occurs behind the eleventh alveolus. The anterior palatine process projects between the maxillae and reaches the level of the tenth maxillary alveolus, i.e. further anteriorly than the anterior level of the suborbital fenestra, which is not preserved here. The vomer is visible on the palate and occurs at the level of the palatine processes – median maxillary suture.

The lacrimal is a long bone, which sends an extensive anterior projection along the lateral margin of the nasal. The lacrimal prevents the short prefrontal from meeting with the maxilla. The lacrimal builds the anteriormost and anterolateral orbital margin. Its orbital margin is not vertical but concave. This margin also contrasts with its heavily ornamented dorsal surface in being smooth. Here, the anteriormost wall of the orbit is pierced by two series of foramina. This region connects to the dorsal margin of the bone through a smooth sulcus that extends anteriorly for nearly one centimetre. The prefrontal is restricted to the anteromedial margin of the orbit, where it projects above the orbital wall. This wall is pierced by a foramen. The prefrontal pillars are barely discernible because they are crushed. The nasals are very long, extending for most of the rostrum length. The nasals are thin all along but are slightly expanded around the level of the eighth maxillary alveolus. They reach the premaxilla anteriorly but do not attain the external nares. Posteriorly, the nasals contact the

frontal in the vicinity of the orbits. The anterior frontal process is short, triangular and smooth. It does not divide the nasals and reaches slightly anterior to the orbital level. The mediolaterally oriented and nearly linear frontoparietal suture is excluded from the supratemporal fenestrae. Only the postorbital and parietal participate in the anterior rim of this fenestra and exclude the frontal. The frontal-postorbital suture is straight. The postorbital has a rounded anterolateral corner. Here, the base of the postorbital bar originates from and appears continuous with the skull table. The main shaft of the postorbital bar is unknown. The postorbital-squamosal suture is oblique and directed ventrally. The contact between the squamosal and postorbital near the bar is broken but the squamosal is possibly contacting the bar as indicated by the suture on the postorbital. On the other hand, the quadrate does not reach the postorbital bar and supports only the ventral area of the squamosal. The squamosal builds the posterolateral corner of the supratemporal fenestra. The shape of the squamosal gives to the skull table a curved outline. Its smooth prong greatly expands both laterally and posteriorly. Although incomplete in its anterior region, the parietal occupies the posteromedial corner of the supratemporal fenestra. The parietal was not greatly expanded between the fenestrae. The posterior margin shows a sutural notch that accommodates the supraoccipital. The supraoccipital may therefore participate in the posteriormost margin of the skull table.

Lower jaw. The right dentary preserves eighteen alveoli, the last being broken off. The left dentary preserves 15 alveoli but the anteriormost portion of the bone and the associated alveoli are missing. Nevertheless, based on close proportions of the two dentaries, we estimate a total of eighteen dentary alveoli (Fig. 2). Dentary alveoli are homogenous in size (Table 2). Each alveolus is well separated from each other by a diastema, delineating the contour of the bone for occluding teeth. On both dentaries, the eighth and the ninth alveoli are smaller than other alveoli and are arranged in couplets. Behind the tenth alveolus, pits for

reception of maxillary teeth occur between each alveolus. The dentary participates in the anterior and dorsal border of the external mandibular fenestra, almost reaching the posteriormost corner of the fenestra. On the lateral surface, the dentary displays a long groove, which runs along the last alveoli. The dentary builds the medial alveolar wall up to the level of the fourteenth alveolus included. The dentary symphysis is long and extends to the level of the eighth alveolus.

The splenial contribution to the mandibular symphysis is shorter than that of the dentary and takes part between the eighth and the twelfth alveoli, preventing the dentary to face medially. In dorsal view, the splenial symphysis is V-shaped and extends along the medial surface of the mandible to participate in the dorsal margin of the foramen intermandibularis caudalis. Its relationship to the coronoid is unknown but it is clearly excluded from the anterior margin of the mandibular adductor fossa. The splenial builds the medial wall of the tooth row from the fifteenth to the last alveolus. Here, the surangular wedges between the splenial and dentary. No foramina were detected on the medial surface of the splenial but the posteriormost region of this bone bears several fractures.

The angular builds the entire ventral margin of the external mandibular fenestra. The angular-surangular suture sits just below the corner of the fenestra and runs all the way to the tip of the retroarticular process. In this lateral region, the angular is smooth and corresponds to the attachment of the well-developed pterygoideus posterior muscle. The angular builds all the ventral and anterior margins of the mandibular adductor fossa as well as its medial wall. Anterior to this fossa, the angular sends a process, which precludes any participation of the splenial in this fossa. The angular also builds the posterior and ventral margins of the small foramen intermandibularis caudalis.

The surangular is longer than the angular and also reaches the posteriormost tip of the retroarticular process by sending a thin process. The surangular contacts the posterodorsal

corner of the external mandibular fenestra only. Its unsculptured dorsal surface for attachment of adductor mandibulae externus superficialis and medius muscles is well delimited from the lateral surface of the bone by a slightly elevated rim. A medial projecting process is present near the anteromedial end of this surface. The surangular takes part in the medial wall of the glenoid fossa. Below this level, a small foramen pierces the medial wall of the surangular.

The articular bears a posterodorsally projecting retroarticular process. The retroarticular process is long and deeply concave from a medial view. It bears a fine median ridge on its dorsal surface. Its medial margin is broken. The glenoid fossa is divided in two unequal parts. The lateral articular hemi-fossa is roughly rectangular being wider than long. The smaller medial articular hemi-fossa is longer than wide. In dorsal view, the posterior wall of the glenoid fossa is convex at the level of the lateral hemi-fossa and concave at the level of the medial hemi-fossa. The foramen aereum is located at the medialmost margin of this wall and faces an embayment at the junction between the glenoid fossa and the retroarticular process.

Dentition. Teeth are preserved in first, fifth, eighth, tenth, eleventh and twelfth maxillary alveoli but are incomplete, except one replacement tooth in the eleventh that is low crown and triangular. The right dentary preserves complete teeth (second and ninth alveoli) and fragments (fourth, sixth, tenth, eleventh, twelfth and thirteenth). According to information preserved in the right dentary, anterior teeth are subcircular in cross section and bear two well-developed carinae. The labial and lingual surfaces of the enamel show several longitudinal ridges that do not meet the carinae but remain 'parallel' to them (Fig. 3A, B). The morphology of the posterior dentition is shown by the eleventh maxillary tooth (Fig. 3C), which is low-crown, triangular and somehow blunt. Its lingual and labial surfaces bear several fine wrinkles of the enamel. The carinae are crenulated (Fig. 3C).

4. Phylogenetic analysis

The specimen from Krabi is incomplete and could be coded for less than 30% in the dataset of Jouve et al. (2015), which was built to explore the affinities of *Morccosuchus zenaroi* with other tomistomines. *Maomingosuchus petrolica* was coded by Shan et al. (2017) in the same matrix and was included as well in our analysis. Therefore, the dataset includes a total number of 68 taxa including 16 tomistomines coded for 238 characters. Replicates of 1000 random addition sequences (Wagner trees) were treated under TNT (Goloboff et al. 2003). Character codings and the datamatrix are available in the supplementary information.

The phylogenetic analysis recovered 40 most parsimonious trees (best tree length = 880; CI = 0.359; RI = 0.712, Fig. 4) with a topology similar to that recovered in Jouve et al. (2015) or Shan et al. (2018). Here, the Krabi specimen is recovered as a derived tomistomine being the sister taxon to *Maomingosuchus petrolica*. Both the Krabi specimen and *M. petrolica* are closely related to *T. schlegelii* and successively close to other tomistomines from the Miocene of Europe (*Tomistoma lusitanica* + *Gavialosuchus eggenburgensis*). This clade is more derived than African tomistomines (*Tomistoma coppensi* + *Paratomistoma courti* then *T. cairensis*). Noteworthy is the fact that the Krabi specimen and *M. petrolica* are not closely related to more recent, extinct tomistomines from Asia, *Penghusuchus pani* and *Toyotamaphimeia machikanensis*, which possess an enlarged 7th maxillary alveolus. This topology contrasts with the results of Shan et al. (2009) who recovered these two Asian taxa as closely related to *Maomingosuchus petrolica*, albeit previous to a revision of this taxon (Shan et al., 2017).

5. Comparison and affinities

Although fragmentary and missing many characters of the basicranium, the specimen from Krabi preserves two unambiguous synapomorphies of the Tomistominae as recovered from this analysis and originally presented in Jouve et al. (2015): participation of the splenial in the symphysis over the length of two to five teeth (43-3) and palatine process in the form of a thin wedge (118-1). Although a tomistomine synapomorphy, the maxilla sending a short process in the lacrimal (93-1) is not a character observed in the Krabi specimen (93-0). Additionally in the Krabi specimen, the presence of an enlarged fifth maxillary tooth is interpreted as a tomistomine character (Brochu, 1997) with the exception of *Toyotamaphimeia machikanensis* and *Penghusuchus pani*, which display an enlarged seventh maxillary alveolus (Kobayashi et al., 2006; Shan et al., 2009). Among Asian tomistomines, the Krabi specimen, an undescribed late Eocene–early Oligocene Vietnamese specimen (Böhme et al. 2011) and *Maomingosuchus petrolica* differ from *Penghusuchus pani* and *Toyotamaphimeia machikanensis* in the position of the largest maxillary alveolus. *Tomistoma* (?) *taiwanicus* is too incomplete (Shikama, 1972; Shan et al. 2009) for comparison, but recent reports of tomistomine remains from Taiwan seem to indicate the presence of *Toyotamaphimeia* in the Pleistocene of Taiwan (Ito et al., 2018).

The Thai specimen from Krabi here described resembles *Maomingosuchus petrolica*, known from the late Eocene of China (Shan et al., 2017). Both share similar size proportions of the skull table, of the supratemporal fenestrae, of the orbits; and have a similar interorbital and inter-supratemporal width, a similar shape of the squamosal prong (projecting posteriorly and being wavy on its lateral margin), the same morphology of the posterior maxillary teeth bearing wrinkles on the crown surface and presenting crenulated carinae. They also share the canalized dorsal surface of the lacrimal, the prefrontal that slightly overhangs the orbital margin, a lacrimal longer than prefrontal and excluding a contact between prefrontal and maxilla and a linear frontoparietal suture excluded from the supratemporal fenestrae.

Nevertheless, minor morphological differences are noted and involve the frontal and prefrontal anterior tips, which project further anteriorly from the orbits in *M. petrolica* than in the Krabi specimen; and the dentary alveolar count of 19 in *M. petrolica* versus 18 in the Thai specimen. Further comparisons are rendered challenging (e.g. shape and extent of external mandibular fenestra) by the compression of the Thai specimen and the minor differences noted above could be part of intraspecific variability, which is not possible to assess because of the absence of multiple individuals in the type locality. Therefore, in view of the little differences noted between the Krabi specimen and *Maomingosuchus petrolica* from China, we refer the material here described to *Maomingosuchus* sp.

The Krabi and Chinese tomistomines are recovered in a sister taxon position with the extant *Tomistoma schlegelii*. They share the same dentary alveolus count (18-19), the posteriorly elongated, narrow and adjoining premaxillae that reach the nasals at the level of the largest maxillary alveolus and the presence of vomer on the palate. All other fossil tomistomines have their posterior premaxillary processes bifurcated by the anterior extension of the nasals. Although the tomistomine from Krabi and *Maomingosuchus petrolica* superficially resemble *Tomistoma schlegelii*, they can nevertheless be differentiated from the extant species by the following characters: the angular-surangular suture contacting the external mandibular fenestra at the posterior angle (47-0); the surangular-dentary suture intersecting the external mandibular fenestra at its posterior corner (65-1); the absence of a posterior process of the maxilla in the lacrimal (93-0), the palatine process extending beyond the anterior end of the suborbital fenestra (110-0); the frontal ending at the same level to the anterior extension of the prefrontal (171-1); a shorter symphysis extending posteriorly less than the level of the thirteenth alveolus (176-0); and a prefrontal that does not send a process within the nasal (226-0).

The tomistomine from Krabi and *M. petrolica* can be differentiated from all known fossil tomistomines by the premaxillary sutural configuration with the nasals (see above). The supratemporal fenestrae of the specimen from Krabi and *M. petrolica* are not as enlarged as in some tomistomine species such as *Toyotamaphimeia machikanensis*, *Megadontosuchus arduini*, *Kentisuchus spenceri*, *Dollosuchoides densmorei*, *Thecachampsa* (*Gavialosuchus*) *americanus*, *Gavialosuchus eggenburgensis*, *Paratomistoma courti* or *Tomistoma cairensis*, but they are most similar to the smaller and longer than wide ones of some derived forms such as those of *Tomistoma schlegelii*, *Penghusuchus pani*, *Tomistoma lusitanica*. Furthermore, the Krabi tomistomine and *M. petrolica* can be differentiated from *Morrocosuchus zennaroii* by the rather straight snout profile and the more extensive mandibular symphysis (incorporating only 9 alveoli in *M. zennaroii*; fig. 4 in Jouve et al., 2015), from *Kentisuchus spenceri* and *Dollosuchoides densmorei* by the shorter prefrontal relative to the lacrimal and the extent of the nasals (figs. 2 and 3 in Brochu, 2007), excluded from the narial border in the Krabi specimen and *M. petrolica*; from *Megadontosuchus arduini* by the absence of a marked undulation of the rostrum at the level of the largest maxillary alveolus (fig. 1 in Piras et al., 2007); from *Thecachampsa* (*Gavialosuchus*) *americanus* by having longer than wide supratemporal fenestrae (plate V in Mook, 1921); from *Tomistoma cairensis* (plate 2 in Müller, 1927) and *Paratomistoma courti* (fig. 2 in Brochu and Gingerich, 2000) by the lack of distinctly upturned margins of the orbits and supratemporal fenestrae; from *Tomistoma coppensi* by a dentary symphysis reaching the level of the 11th and 12th alveoli (whereas it extends to the level of the 7th and 8th alveoli in *T. coppensi*; plate IV in Pickford, 1994); from *Gavialosuchus eggenburgensis* (plate 1 in Toula and Kail, 1885) in the maxilla not sending a posterior process within the lacrimal; from *Tomistoma lusitanica* by a longer mandibular symphysis that incorporates 12 alveoli versus 10 alveoli in *T. lusitanica* (fig. 21 in Antunes, 1961).

In conclusion, the Krabi specimen is interpreted as a derived tomistomine, closely related to *Maomingosuchus petrolica* from the late Eocene of China and to the extant *T. schlegelii*. Other putative tomistomines such as *Tomistoma tandoni* Sahni and Mishra, 1975 are too poorly preserved to be compared (see Piras et al. 2007 for a list and distribution) or are currently undergoing a revision (e.g. *Tomistoma calaritanum* Capellini 1890 (Zoboli et al., in press) or *Ramphosuchus crassidens*, Falconer and Cautley, 1840 – identified as a tomistomine by Head, 2001). Some taxa are too fragmentary or need revisions. As such, the Siwalik Hills of India and Pakistan contains several taxa previously considered as belonging to the genus *Gavialis* but instead sharing similarities with tomistomines (Martin, 2018). Also, *Ferganosuchus planus* was first considered a tomistomine by Efimov (1982) but Jouve (2004) emitted doubt about this identification. Although not observed first-hand, *Tomistoma coppensi* Pickford, 1994 from the Pliocene of Uganda shows a short symphysis (that incorporates the first 7 alveoli) and possesses 15 dentary alveoli, a count substantially lower than any Neogene tomistomines but identical to that of the extant *Mecistops cataphractus*, inviting for a critical reevaluation of this taxon. *Tomistoma dowsoni* (Fourtau, 1920) may be known from a complete skull according to Jouve et al. (2014). Moreover, a critical reevaluation of North African tomistomines is desirable. In that sense, the relatively complete specimens of *Tomistoma caireense* reported by Müller (1927) should be redescribed together with Miocene specimens from Malta (Lydekker, 1886) that deserve attention. Altogether, these specimens have the potential to shuffle the tomistomine topology recovered in the present study. Interestingly, a recent study using both DNA and morphological datasets recovered Tomistominae and Gavialoidea as closely related (Lee and Yates, 2018), a hypothesis already reached by Buffetaut (1985) and currently being re-tested using morphological data (e.g. Ijima and Kobayashi, 2019). Feeding fossil data in such datasets will certainly allow a better resolution of phylogenetic relationships among longirostrine taxa. It

should also be noted that our results imply a late Eocene minimum divergence for the *Gavialis* and *Tomistoma* lineages, which is somewhat older than the Oligo-Miocene molecular divergence estimates of Oaks (2011).

6. Distribution and origin of Asian tomistomines

The present report from Thailand expands the distribution of late Eocene – early Oligocene tomistomines to southern latitudes in South East Asia. Tomistomines have been originally recovered from late Eocene lignite seams near Maoming, southern China and were named by Yeh (1958) as *Tomistoma petrolica*. Other remains from this locality have been subsequently reported (Li, 1975) and many more served to reevaluate the anatomy and relationships of *T. petrolica*, which has been renamed *Maomingosuchus petrolica* by Shan et al. (2017). Böhme et al. (2011) briefly reported remains of longirostrine crocodylians as cf. Tomistominae from late Eocene–early Oligocene coal and lignite seams of northern Vietnam at the same latitude as the Chinese locality of Maoming (22°N). The specimen figured by Böhme et al. (2011) is an anterior region of the rostrum, which, in addition to the longirostrine nature of the skull, presents several similarities with the Thai tomistomine (PRC-1121) and with *M. petrolica* including an enlarged fifth maxillary alveolus, well-spaced maxillary alveoli and a notched premaxillary-maxillary suture.

The type of environment from which the late Eocene-early Oligocene Chinese, Vietnamese and Thai fossils have been recovered, namely coal seam mines, corresponds to freshwater peat swamps. In their geological analysis of such depositional environment, Böhme et al. (2011) interpreted lignite seams to be deposited in a shallow aquatic environment with extremely low oxygenation such as a swamp. This is in agreement with the habitat of the extant *Tomistoma schlegelii*, which mainly inhabits the swamp peat forests of

peninsular Malaysia, Indonesia and Borneo (Bezuijen et al., 2010). Such modern tropical forests are characterized by the accumulation of plant remains under waterlogged conditions, thus under extreme low oxygen conditions favoring peat production. It is therefore conceivable that these types of environments spread relatively far north during the late Eocene – early Oligocene in what is today southern China, above the limit of the extant northern tropical belt. Vegetation such as that from swamp peat forests requires warm continental air temperatures year-round that were prevailing during most of the Eocene (see discussion on paleoclimate in Böhme et al., 2011). Important requirement of this type of vegetation suggests prevailing humid context in these areas during the late Eocene. At that time, peat swamp forests may have occupied a larger range than today, encompassing peninsular Thailand and lowland plains of continental southeast Asia.

Our knowledge of tomistomine evolution in Asia is limited from the Oligocene-middle Miocene interval. Aside the early Oligocene Vietnamese occurrence (Böhme et al., 2011), SE Asia does not offer a record for tomistomines. Early Miocene tomistomines might be represented by taxa related to *Rhamphosuchus crassidens* from the Siwalik Hills of India and Pakistan (Falconer and Cautley, 1840; Head, 2001; Martin, 2018) but their precise stratigraphic distribution and paleoenvironmental context will have to be reevaluated.

Although the type of environment where the late Miocene *Penghusuchus pani* from Taiwan originates was not reported (Shan et al., 2009), that of *Toyotamaphimeia machikanensis* from the Pleistocene of Japan (Kobayashi et al., 2006) contrasts with the peat swamp forests-type of habitat of *Maomingosuchus petrolica* and *T. schlegelii*. The original specimen of *Toyotamaphimeia machikanensis* was recovered from a freshwater horizon together with plant remains indicative of a moderate temperate climate and the proximity of an evergreen forest; this freshwater horizon is an alternation of sand and silts and lies just one meter below a marine clay deposit (Kobayashi et al., 2006), indicating a close proximity to

the shore. A recent reexamination of the fossil record of the genus *Toyotamaphimeia* in Japan allowed to characterize its thermal preferences and indicates a continuous presence for about 3 million years (Ijima et al., 2018). From the current data at hand, it cannot be ascertained whether *Toyotamaphimeia machikanensis* strictly inhabited the freshwater environment or whether it also foraged in the nearby marine environment, but Ijima et al. (2018) hypothesized repeated dispersals of this genus from mainland Asia into Japan either thanks to a temporary land bridge or through coasting. Other Miocene tomistomines are recovered in estuarine environments with *Thecachampsa (Gavialosuchus) americanus* from the phosphates of Florida (Mook, 1921), *Gavialosuchus eggenburgensis* from Austria (Toula and Kail, 1885) or *Tomistoma lusitanica* (Antunes, 1961) from Portugal (see also Whiting et al., 2016).

Several hypotheses have been discussed about the origin and dispersal of tomistomines (Antunes, 1994; Brochu and Gingerich, 2000; Kotsakis et al., 2004; Piras et al., 2007; Jouve et al., 2015), recognizing that marine dispersal may have played a significant role. Among derived tomistomines, the presently recovered phylogenetic hypothesis implies the existence of two tomistomine radiations in Asia (Fig. 4), supporting the result of Jouve et al. (2015): a Mio-Pleistocene stock (*P. pani* + *T. machikanensis*) related to the North American Mio-Pliocene *Thecachampsa*; a second stock with African forms (*P. courti*, *T. coppensi* and *T. cairensis*) basal to an Eurasian stock comprised of *G. eggenburgensis* and *T. lusitanica* on the one hand and of the Thai tomistomine, *M. petrolica* and *T. schlegelii* on the other hand. This phylogenetic hypothesis would be compatible with a dispersal of tomistomines outside Africa during the Eocene into Eurasia, with the *Tomistoma* lineage being established in Asia since the Eocene. Rather than being long established since the Eocene in Asia, *P. pani* and *T. machikanensis* could be interpreted as more recent arrivals of tomistomines from a marine dispersal from North America, as testified by the close relationships with the *Thecachampsa* lineage and the proximity of marine environment for *T. machikanensis* and perhaps for *P.*

pani (Jouve et al., 2015). Finally, the close relationships of the Thai tomistomine and *T. schlegelii* with the Miocene European taxa *T. lusitanica* and *G. eggenburgensis* would be in agreement with a previous hypothesis that the European taxa would originate from Asia (Antunes, 1961). Alternatively, *Tomistoma lusitanica* has been viewed as possibly congeneric with the North American genus *Thecachampsa* (Vianna and Moraes, 1945; Myrick, 2001). Ultimately, this has consequences for the affinity of *Gavialosuchus eggenburgensis*, which under the present hypothesis, is viewed as closely related to *Tomistoma lusitanica*. The origin and dispersal scenarios of tomistomines, not only requires the study of new taxa from Asia, but is in want of a revision of several members from the Europe, Asia and from Africa.

Acknowledgments

X-C. Wu provided information on '*T.*' *petrolica* from Maoming, F. Zheng and Y. Wang (Beijing) provided access to '*T.*' *petrolica* specimens housed in IVPP collection. This research is supported by the project PalBioDivASE under a 'Groupe de Recherche International' (GDRI) grant from CNRS. K. Lauprasert thanks the Faculty of Science, Mahasarakham University. We thank the two reviewers, M. Rabi and M. Delfino, as well as the editor J. Claude, who provided comments that helped improve the initial version of this work.

References

- Antunes, M.T. (1961). *Tomistoma lusitanica*, crocodilien du Miocène du Portugal. Revista da faculdade de Ciências de Lisboa. Série IIc 9: 5-88.
- Benammi, M., Chaimanee, Y., Jaeger, J-J., Suteethorn, V., Ducrocq, S. (2001).

- Eocene Krabi Basin (southern Thailand): paleontology and magnetostratigraphy. Bulletin of the Geological Society of America. 113: 265-273.
- Bezuijen, M.R., Shwedick, B.M., Sommerlad, R., Stevenson, C. Steubing, R.B. (2010). *Tomistoma Tomistoma schlegelii*. pp. 133-138 in Crocodiles. Status Survey and Conservation Action Plan. Third Edition, ed. By S.C. Manolis and C. Stevenson. Crocodile Specialist Group: Darwin.
- Böhme, M., Prieto, J., Schneider, S., Hung, N. V., Quang, D.D. Tran, D.N. (2011). The Cenozoic on-shore basins of Northern Vietnam: biostratigraphy, vertebrate and invertebrate faunas. Journal of Asian Earth Sciences. 40: 672-687.
- Brochu, C.A. (2007). Systematics and taxonomy of Eocene tomistomine crocodylians from Britain and Northern Europe. Palaeontology. 50: 917-928.
- Brochu, C.A., Gingerich, P.D. (2000). New tomistomine crocodylian from the middle Eocene (Bartonian) of Wadi Hitán, Fayum Province, Egypt. Contributions to Museum of Paleontology, University of Michigan. 30: 251-268.
- Buffetaut, E. (1985). The place of *Gavialis* and *Tomistoma* in eusuchian evolution: a reconciliation of palaeontological and biochemical data. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte. 12: 707-716.
- Capellini, G. (1890). Sul coccodrilliano gavialoide (*Tomistoma calaritanus*) scoperto nella collina di Cagliari nel 1868. Rendiconti della Reale Accademia dei Lincei. 4: 149-151.
- Ciochon, R.I., Savage, D.E., Tint, T. Maw, B. (1985). Anthropoid origins in Asia? New discovery of *Amphipithecus* from the Eocene of Burma. Science. 229: 756-759.
- Claude, J., Suteethorn, V., Tong, H. (2007). Turtles from the Late Eocene-early Oligocene of the Krabi Basin (Thailand). Bulletin de la Société géologique de France. 178: 305-316.
- Claude, J., Naksri, W., Boonchai, N., Buffetaut, E., Duangkayom, J., Laojumpon, C.,

- Jintasakul, P., Lauprasert, K., Martin, J., Suteethorn, V., Tong, H. (2011). Neogene reptiles of northeastern Thailand and their paleogeographical significance. *Annales de Paléontologie*. 97: 113-131.
- Delfino, M., De Vos, J. (2010). A revision of the Dubois crocodylians, *Gavialis bengawanicus* and *Crocodylus ossifragus*, from the Pleistocene *Homo erectus* beds of Java. *Journal of Vertebrate Paleontology*. 30: 427-441.
- Ducrocq, S., Buffetaut, E., Buffetaut-Tong, H., Helmcke-Ingavat, R., Jaeger, J-J., Jongkanjanasontorn, Y., Suteethorn, V. (1992). A lower Tertiary vertebrate fauna from Krabi (South Thailand). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*. 184: 101-122.
- Ducrocq, S., Benammi, M., Chavasseau, O., Chaimanee, Y., Suraprasit, K., Pha, P.D., Phuong, V.L., Phach, P.V., Jaeger, J-J. (2015). New anthracotheres (Cetartiodactyla, Mammalia) from the Paleogene of northeastern Vietnam: biochronological implications. *Journal of Vertebrate Paleontology*. e929139.
- Falconer, H., Cautley, P.T. (1840). Notice on the remains of a fossil monkey from the Tertiary strata of the Siwalik Hills in the North of Hindoostan. *Transactions of the Geological Society of London*. 2: 499-504.
- Fourtau, R. (1920). *Contribution à l'étude des vertébrés miocènes de l'Égypte*. Government Press.
- Hall, R. (1997). Cenozoic plate tectonic reconstructions of SE Asia. In Fraser, A.J., Matthews, S.J. and Murphy, R.W. (eds.) *petroleum geology of Southeast Asia*. Geological Society of London Special Publication. 126: 11-23.
- Hay, O.P. (1930). *Second bibliography and catalogue of the fossil Vertebrata of North America*. Carnegie Institut, Washington Publications. 390: 1-1074.
- Head, J.J. (2001). Systematics and body size of the gigantic, enigmatic crocodyloid

- Rhamphosuchus crassidens*, and the faunal history of Siwalik Group (Miocene) crocodylians. *Journal of Vertebrate Paleontology*. 21: 59A.
- Iijima, M., Momohara, A., Kobayashi, Y., Hayashi, S., Ikeda, T., Taruno, H., Watanabe, K., Tanimoto, M., Furui, S. (2018). *Toyotamaphimeia* cf. *machikanensis* (Crocodylia, Tomistominae) from the Middle Pleistocene of Osaka, Japan, and crocodylian survivorship through the Pliocene-Pleistocene climatic oscillations. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 496: 346-360.
- Iijima, M., Kobayashi, Y. (2019). Mosaic nature in the skeleton of East Asian crocodylians fills the morphological gap between “Tomistominae” and Gavialinae. *Cladistics*. doi: 10.1111/cla.12372.
- Ito, A., Aoki, R., Hirayama, R., Yoshida, M., Kon, H., Endo, H. (2018). The rediscovery and taxonomical reexamination of the longirostrine crocodylian from the Pleistocene of Taiwan. *Paleontological Research*. 22: 150-155.
- Jonet, S., Wouters, G. (1977). *Maroccosuchus zennaroi*, crocodylien eusuchien nouveau des phosphates du Maroc. *Notes et mémoires du service géologique du Maroc* 38: 177-202.
- Jouve, S. (2004). Etude des crocodyliiformes fini Crétacé-Paléogène du Bassin de Oulad Abdoun (Maroc) et comparaison avec les faunes africaines contemporaines : systématique, phylogénie et paléobiogéographie. Ph.D. thesis. Muséum National d'histoire Naturelle de Paris, Paris. 652 p.
- Jouve, S., Bouya, B., Amaghaz, M. Meslouh, S. (2015). *Maroccosuchus zennaroi* (Crocodylia: Tomistominae) from the Eocene of Morocco: phylogenetic and palaeobiogeographical implications of the basalmost tomistomine. *Journal of Systematic Palaeontology*. 13: 421-445.
- Kotsakis, T., Delfino, M., Piras, P. (2004). Italian Cenozoic crocodylians: taxa, timing and

- biogeographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 210: 67-87.
- Kobayashi, Y., Tomida, Y., Kamei, T., Eguchi, T. (2006). Anatomy of a Japanese tomistomine crocodylian, *Toyotamaphimeia machikanensis* (Kamei et Matsuto, 1965), from the middle Pleistocene of Osaka Prefecture: the reassessment of its phylogenetic status within Crocodylia. *National Science Museum Monographs*. 35: 1-121.
- Lee, M.S.Y., Yates, A.M. (2018). Tip-dating and homoplasy: reconciling the shallow molecular divergences of modern gharials with their long fossil record. *Proceedings of the Royal Society, B*. 285: 20181071.
- Li, J-L. (1975). New material of *Tomistoma petrolica* from Maoming, Guangdong. *Vertebrata Palasiatica*. 13: 190-194.
- Lydekker, R. (1886). On the occurrence of the crocodylian genus *Tomistoma* in the Miocene of the Maltese islands. *Quarterly Journal of the Geological Society*. 42: 20-22.
- Marivaux, L., Chaimanee, Y., Yamee, C., Srisuk, P., Jaeger, J-J. (2004). Discovery of *Fallomus ladakhensis* Nanda and Sahni, 1998 (Mammalia, Rodentia, Diatomyidae) in the lignites of Nong Ya Plong (Phetchaburi Province, Thailand): systematic, biochronological and paleoenvironmental implications. *Geodiversitas*. 26: 493-507.
- Markwick, P.J. (1998). Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology*. 24: 470-497.
- Martin, J.E. (2018). The taxonomic content of the genus *Gavialis* from the Siwalik Hills of India and Pakistan. *Papers in Palaeontology*. doi: 10.1002/spp2.1247
- Martin, J.E., Lauprasert, K. (2010). A new primitive alligatorine from the Eocene of Thailand : relevance of Asiatic members to the radiation of the group. *Zoological Journal of the Linnean Society of London*. 158: 608-628.
- Martin, J.E., Buffetaut, E., Naksri, W., Lauprasert, K., Claude, J. (2012). *Gavialis* from the

- Pleistocene of Thailand and its relevance for drainage connections from India to Java. PLoS ONE. 7: e44541.
- Myrick, A.C. (2001). *Thecachampsa antiqua* (Leidy, 1852) (Crocodylidae, Thoracosaurinae) from fossil marine deposits at Lee Creek Mine, Aurora, North Carolina, USA. Smithsonian Contributions in Paleobiology. 90: 219-225.
- Müller, L. (1927). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere : 1. Beiträge zur Kenntnis der Krokodilier des ägyptischen Tertiär. Abhandlungen der Bayerischen Akademie der Wissenschaften. 31: 1-97.
- Oaks, J.R. (2011). A time-calibrated species tree of Crocodylia reveals a recent radiation of the true crocodiles. Evolution. 65: 3285-3297.
- Pickford, M. (1994). Late Cenozoic crocodiles (Reptilia : Crocodylidae) from the Western Rift, Uganda. In B. Senut, M. Pickford (eds.). Geology of the Albertine Rift Valley, Uganda-Zaire. M. CIFEG, Publication Occasionnelle, Orléans. Vol. II. Palaeontology, pp. 137-155.
- Piras, P., Delfino, M., Del Favero, L., Kotsakis, T. (2007). Phylogenetic position of the crocodylian *Megadontosuchus arduini* and tomistomine palaeobiogeography. Acta Palaeontologica Polonica. 52: 315-328.
- Rage, J.-C., Buffetaut, E., Buffetaut-Tong, H., Chaimanee, Y., Ducrocq, S., Jaeger, J.-J., Suteethorn, V. (1992). A colubrid snake in the late Eocene of Thailand: the oldest known Colubridae (Reptilia, Serpentes). Comptes Rendus de l'Académie des Sciences, Série 2 314: 1085-1089.
- Sahni, A., Mishra, V.P. (1975). Lower Tertiary vertebrates from western India. Monographs of the Palaeontological Society of India. 3: 1-48.
- Sellard, E.H. (1915). A new gavial from the Late Tertiary of Florida. American Journal of

- Sciences. 4: 135-138.
- Shan, H-Y., Wu, X-C., Cheng, Y-N., Sato, T. (2010). A new tomistomine (Crocodylia) from the Miocene of Taiwan. *Canadian Journal of Earth Sciences*. 46: 529-555.
- Shan, H.Y., Wu, X.C., Cheng, Y.N., Sato, T. (2017). *Maomingosuchus petrolica*, a restudy of 'Tomistoma' petrolica Yeh, 1958. *Palaeoworld*. 26: 672-690.
- Shikama, T. (1972). Fossil Crocodylia from Tsochin, southwestern Taiwan. *Science Report of Yokohama National university: Biological and Geological Sciences*. 19: 125-131.
- Suteethorn, V., Buffetaut, E., Helmcke-Ingavat, E., Jaeger, J-J., Jongkanjanasontorn, Y. (1988). Oldest known Tertiary mammals from South-East Asia: middle Eocene primate and anthracotheres from Thailand. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*. 9: 563-570.
- Toula, F., Kail, J. A. (1885). Über einen Krokodil-Schädel aus den Tertiärlagerungen von Eggenburg in Niederösterreich. Eine paläontologische studie. *Denkschriften der Kaiserlichen Akademie der Wissenschaften von Wien. Mathematisch-naturwissenschaftliche Klasse*. 50: 299-355.
- Vélez-Juarbe, J., Brochu, C.A., Santos, H. (2007). A gharial from the Oligocene of Puerto Rico: transoceanic dispersal in the history of a non-marine reptile. *Proceedings of the Royal Society B*. 274: 1245-1254.
- Vianna, A., Moraes, A. (1945). Sur un crâne de crocodile fossile découvert dans le Miocène de Lisbonne. *Boletim de la Sociedade Geológica de Portugal*. 4: 161-170.
- Whiting, E.T., Steadman, D.W., Krigbaum, J. (2016). Paleocology of Miocene crocodylians in Florida: insights from stable isotope analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 451: 23-34.
- Yeh, H-K. (1958). A new crocodile from Maoming, Kwangtung. *Vertebrata palasiatica*. 2: 237-242.

Zhao, K.-T., Zong, Y., Ma, J.-F. (1986). On the ancient crocodiles of Guangdong Province.

Acta Herpetologica Sinica. 5: 161-165.

Zoboli, D., Sanciù, L., Pillola, G.L., Delfino, M. (2019). An overview of the crocodylian fossil record from Sardinia (Italy), Annales de Paléontologie.

Figure 1. The skull of *Maomingosuchus* sp. from the late Eocene–early Oligocene of Krabi, Thailand and associated line drawings in A, dorsal and B, ventral views. Abbreviations: fr, frontal; j, jugal; l, lacrimal; lg, lacrimal groove; mx, maxilla; n, nasal; or, orbit; p, parietal; pa, palatine; pfr, prefrontal; pfr.p.: prefrontal pillars; po, postorbital; pob, postorbital bar; pmx, premaxilla; stf, supratemporal fenestra; sq, squamosal; t, tooth; vo, vomer. Scale bar = 1 cm.

Figure 1. Le crâne de *Maomingosuchus* sp. de l’Eocène tardif–Oligocène basal de Krabi, Thaïlande et les illustrations au trait associées en vues A, dorsales et B, ventrales.

Abréviations : fr, frontal; j, jugal; l, lacrimale; lg, gouttière lacrimale; mx, maxillaire; n, nasal; or, orbite; p, pariétal; pa, palatin; pfr, préfrontal; pfr.p.: piliers préfrontaux; po, postorbitaire; pob, barre postorbitaire; pmx, prémaxillaire; stf, fenêtre supratemporale; sq, squamosal; t, dent; vo, vomer. Echelle = 1 cm.

Figure 2. The lower jaw of *Maomingosuchus* sp. from the late Eocene–early Oligocene of Krabi, Thailand (PRC-1122 and 1123) in A, occlusal, B, ventral views, C, left lateral and D, medial views. Abbreviations: an, angular; ar, articular; den, dentary; emf, external mandibular fenestra; fa, foramen aereum; fio, foramen intermandibularis oralis; san, surangular; sp, splenial; sym, symphysis. Scale bar = 1 cm.

Figure 2. La mandibule de *Maomingosuchus* sp. de l’Eocène tardif–Oligocène basal de Krabi, Thaïlande (PRC-1122 et 1123) en vues A, occlusales, B, ventrales, C, latérales gauches

et D, médiales. Abréviations: an, angulaire; ar, articulaire; den, dentaire; emf, fenêtre externe mandibulaire; fa, foramen aereum; fio, foramen intermandibularis oralis; san, surangulaire; sp, splénial; sym, symphyse. Echelle = 1 cm.

Figure 3. Details of the dentition of *Maomingosuchus* sp. from the late Eocene–early Oligocene of Krabi, Thailand. A, anterior tooth of PRC-1122 in mesial view, presenting ridges on the surface of the crown; B, close-up of a posterior tooth (PRC-1121) showing the low crown morphotype and crenulation of the enamel.

Figure 3. Détails de la dentition de *Maomingosuchus* sp. de l’Eocène tardif–Oligocène basal de Krabi, Thaïlande. A, Dent antérieure de PRC-1122 en vue mésiale, présentant des rides sur la surface de la couronne; B, agrandissement d’une dent postérieure (PRC-1121) présentant le morphotype de couronne basse et la crénulation de l’émail.

Figure 4. Strict consensus of the phylogenetic analysis focusing on the relationships of tomistomines, as discussed in this work.

Figure 4. Consensus strict de l’analyse phylogénétique se focalisant sur les relations de parenté des tomistominés, tel que discuté dans ce travail.

Table 1. Dimensions of the skull and mandible of *Maomingosuchus* sp. from the late Eocene–early Oligocene of Krabi, Thailand (cm).

Table 1. Dimensions du crâne et de la mandibule de *Maomingosuchus* sp. de l’Eocène tardif–Oligocène basal de Krabi, Thaïlande (cm).

Table 2. Dimensions (in mm) of the alveoli of *Maomingosuchus* sp. from the late Eocene–early Oligocene of Krabi, Thailand. ‘a’ indicates alveolar width while ‘b’ indicates alveolar

length. Absence of scores in the 'b' rows indicate that alveoli are circular. Grey shaded scores referred to the alveolar couplets.

Table 2. Dimensions (en mm) des alvéoles de *Maomingosuchus* sp. de l'Eocène tardif–Oligocène basal de Krabi, Thaïlande. 'a' indique la largeur de l'alvéole tandis que 'b' indique sa longueur. L'absence of mesures dans la rangée 'b' indique que l'alvéole est circulaire. Les mesures en grisé font référence aux alvéoles en couplets.

Supplementary data. Data matrix used in the phylogenetic analysis.

Données supplémentaires. Données matricielles utilisées pour l'analyse phylogénétique.

xread

238 68

Bernissartia_fagesii

??11?1210?010????00??0?0000?000010101000?0????0100??????110?0?00000100?2?00
00001011003020301?00?00110100100?000?000?0???0?????0?00??0100000010?00001???
????00?0000?0?0001000?0?0?0?00?0100001?0000000?0101000003?00?00000??01??00?1
?000

Iharkutosuchus_makadii

??
001120600?201?00?00?0?000000?00??0100??1000??1??0?0???00000100?1000????????
0??00110000220001?01?1??0?0?11010141?0100010200210????0?011010001??10?1001
?

Hylaeochampsa_vectiana

??
01100600120??0?000100?0000?00??0101??0?000?1000000?0100?00?100?000?????????
?0?001??000?21?0?00??1??00001??0???0011?????0?210?????????1101??0????10?1?0?0

Allodaposuchus_precedens

??
0110?2?00??1?0??000100?00000?0??00011?000010?1?0010??110000001??0001?????????
?0?000000?0?0?0?000????010100?0?000000010?0110?????0?0000?0200?????0?100?0

Borealosuchus_formidabilis

00000101001100??01?000000000100010000?200030000?020010?001001200000001200?0?
02000000110030110020000001000000000000?021100?100000??010?1010111000000?1000
2??????000?0100110?000000100000110001010012000000011200000123000?00000120???
?00?10000

Borealosuchus_wilsoni

??????10??0??1??0000001??10000?20??10?0000?0010?0??011?000000120000102
00100?11003011002?00000100000?00?00000211??01??0??01001?1?111??0??1000???
??0000?0??01??0??0?10?????????10000020000?00?120?00?????0?0000012????00?10?
?0

Borealosuchus_sternbergii

?0001?10?110000?1100000000010001000??000300?0001001??00?002000000012000010
100000010013011012?00000100000000000?00011001000000101011?1?111000000010001
0?????000?010011000?000010000011000100000000000001200000??00?000001200??
00?10000

Leidyosuchus_canadensis

????????????????1??????1?01??0111??110?300?011110?????????2?00000012000010000
000010013021011?00000200100000010100001010100000?101?10?1?111000010?10001??
??0000?0?001100000000000?00010001001011000010010201000??3?00?0000112010??00?
10010

Thoracosaurus_macrorhynchus

?11?1?1??0?????11?????0??0??000??0??400??00?11??????0?100000201200?010210
0101110050?1003??00001100000000000?1010?000000?0?0?1000?0?111000100?10012????
??000?1001100?00110100?10?00001110023000000021300001??3?00?000001202??00?1
1000

Eogavialis_africanum

????1?????0????11????????????0?????060??10?1111?????1?2?00002002000010210
110110005001002?020001200000000000000100000100?0?001000000101000100?101030??
??000?10010000000101201?11000011110023000011021300001????00?000001202????0?
110?0

Gryposuchus_colombianus

?1?0????00????1????000?????????????0?060000001111100??00202000200200101021
0110101005011103?02000120000000?010000100000100000001000??321000100?10103??
????000?100?10[12]0100111311?11001111010023010111021300001????00100000??021??
10?110?0

Siwalik_Gavialis

?????????0?????????????????????????????60??0?????????????2?0000200200?01?2?0?1
01??00?01??04??20?012000?000?010??000001?000??01000??311????00?10102??????0
00?1001?021110?11311?11001111001023010111021300001????00?000001202??10?11000

Gavialis_gangeticus

0211010110000000011000000010010000?0003000600000011110000100020000020020000
102101101110050111040020001200000000010000100000100000001000000311000100010
102000000000001001202111021131111100111100102301011102130000102310010000012
0200010011000

Boverisuchus_vorax

?000101??01??0?10??00000111??00010??100001?0??1?11?????????2?00000?1200?0100
00200010003001001?00000110000000020?0000100?1000?1?102010????111001000?10001?

?????00?0?1100110001000100?0011000100011?000000010200000?23?10?00001010????0
0?1?0?0

Diplocynodon_darwini

100000?0000101000101?000?1141?0011011210010100111101?000?1?2?00000112?0?01
10000000110131?1002?00000200000000?101?000101?1000?0??12?10??111000010?10001
??????000?011001?????0000000?0110??1000011000000010?0?000123100?00001?20????0
0?100?0

Stangerochampsia_mccabei

?00?1?00?010????11??000?11010000101??110100?001??111???????12?011001121010210
1010000001212101?00?002000000?00101?0001?1?1300???????10??111000110?1?010??
?????000?01100100201000100?011000110101110010001020000012?100?0000101010??
0?10010

Brachychampsia_montana

10001?00111?10001?10?00011010000?10311110100?0111111??00?112?00?00112101021
010130000011121201?000002000001000101000010101300000112110?1?111000110?10010
??????000?01100100201?001000?011000110101110011001020100012?100?0000101010??
00?10010

Alligator_mississippiensis

100011000101010011011110111110000111213111201001111111000011130000001121010
210102200010121212000001002100100000101101010101000000122110110111100010010
02101100110011011001000000000000011000100100010010001020100012310000000001
0000000010010

Caiman_crocodylus

10001100011001011101110111111000011112211122011110110100111020001101121010
211112400001121211010000002111010000101010010101000000122110110211000010010
21[1 2]011101100110110010000100000000011000100[0 1]002000[0
1]00010200000123100000000010000000010010

Mecistops_cataphractus

100001000?001100?101010011121200011111311011101001011100100?020000000120011
0021120101001100100200100021001001003000000101011000111101010111011000000110
002101010101010110011010000010000011000100001200000002120000112310000000111
0010000013010

Crocodylus_niloticus

101001001110100011010100111212000111123110111010010111001001121000000120011
002112010100110010010010002100100100300000001011000111101010111011000001110
00110101010101011001001000001000001100010000020000000020100112310000000011
0010100012010

Crocodylus_porosus

111001101100100011010100011212000111123110111010010111001001120000000120011
002112010100110010010010002100100100300000001011000111101010111011001001110
00110101010101011001001000001000001100010000020000000020100112310000000011
0010100012010

Crocodylus_rhombifer

001001001110100011010100111112000111123110111010010111001001120000000120211
002112010100110010010010012100100100300000001011000111101010111011000001110
0011010101010101100100000000100?001100010000020000001021100012310000000011
00?0100012010

Crocodylus_palaeindicus

????????????1????1????????????????1?????1011?0100?111?0?0112000000012001100211
2210100110?1001?0100021001?0100300?00001001000111101010111011000001?10001??
????010?0?1001??0??001??00?1000100000?000?00000?0100?????0?0000011?0??00?1
2?10

Osteolaemus_tetraspis

?1001100100100?1101010011111201011111110111000010111001001120100001120211
002102010111110010101110002101000010300000011011000111101010111111001000011
0011010101011101100100000000000000110001000102000000010200000123100?0000101
0011100112010

Voay_robustus

????????????1????10????????111??101?????11011100011011100?011200000011202110021
1221010111001011?0100021001000103000000010?1000111101010111011001000011001??
????011101100100000000000000110001000012000000010211000?23100?0000001001??
0?12010

Rimasuchus_lloydi

??1?????????????????????0????0120?1100211201
0?00?1?011?1?0100021000?0000300?00?1011000?11101?10111011001000??10?1??????
0?0?1?001?0????001????0?00?100?01200000001020100?????00?0000?11?0??00?12??0

Crocodylus_megarhinus

?????????0????????1????????????????????????101??000?011?????112?000000120002?02112
?101?013001?01?01000210000000?300000001011000?11?01010??011000000?1000?????
??010?011001?0????00100??01?000100?0?000?00000?0100?????00?0000011?0??00?120
10

Euthecodon_arambourgi

??4????????????????????1?????1????100211201
0?10?50?1?03?0?00021000?0000301??00?10?1100?1?101010111011001100??1003??????0
??0?110?1?000?000?0?0?0????101?023000000001?0000?????0?000001201??00?110?0

Tomistoma_schlegelii

021001001100100011010000111111000110133110300010010110000000020000120120000
102102210110010111020110002100000010300000101011101111101010111011000100010
0031010101010101100100000100000000110001110020000011121300000123100000000?2
1011100111010

Tomistoma_lusitanica

????????????????1????????????????10???1??[3
5]?0?000101?????????2?0000201200001021122?1110010?1002?0100021000000003000001

01?013?01?01?00??02000?0001130?00?01?01100001?1???10?10011000?00?10001??????0
?0?011001?00??00100?00?1000100?0??000?00000201000??0?0000?12?0??00?12010

Australosuchus_clarkae

?????1?0?????????1?????????1??1???0?10???110111?000?011??????112?0000001????200211
2210?00?1?11001?0?00021000?0000100?00101011000?11102010?1?0110001000100?11???
??010????001000000001?00?0?????100?002000000010?0?0?????0?0000?1100??00?12?
?0

Gavialosuchus_eggenburgensis

?????????????????1???0?????120?0?021?2??
11?0020?1302??000?100??0?0?0??001????10?0??1???0?011100010??0??3??????0??
?0110011?000?00200??0?0001?100??02?0?1121?1000?????0??00?001200??00?11??1

Kambara

?????????????????1?????????1?11??00110???110111?0001011??????112?0000001201120021
1201010001011001?0100121000000100000001011000111100020?010101?011001010011??
??010?000110011000000010??001100010000??000000010?00??????00?000001100????0?
120?0

Thoracosaurus_neocesariensis

??1?1?1????0??11??????01?0??0000??0??40??01?11?????????1?00?0201200001021?
0101100050?1003?0000011000000000000?010?00000000000?000?0?111000100?1001?????
??000?100??0?000?1?10??1?000?1??002300001?0?1?00001?23?00?0?000??2??00?110
?0

Paratomistoma

??00?0?010??????0?2?00?0??1??0?1?2??20?
1?00??10????000?10?0????0?0?0????0??10100?????1??11??0?00?00?0??0??0??10?
1?1??2?00??00??1?0001??0??0??1????0??????0????00?0?0??0?0??0??0??0

Argochampsia_krebsi

??11?????0??00??10?????0?????????0?????[4
6]?????????11??????????2??2?1200?000210110??10?5??1003?0??001100?00?000??01???
00000??0?1010?1?10100010??01?0??????0?0?1001200?000?0?111?10?01111100023000
01002130000??2??0??0?0010002??00?110?0

Piscogavialis_jugaliperforatus

??0????6????0??11????????[1
2]??2??2?1200?000211210110005011?03?12?00?100?0000?00?001?00001000?001000???
12100010??10103??????0?0?1001202111?2013?1?11?01?11110023000010021300001??3?
0??000000002??10?11000

Ikanogavialis_gameroi

??60??00??11?????0?2?20?02?120??020?21
0??10?501?0?3?02?00?20??0?0?00??010?0?01??0?0?00??321000100??01?3??????0
0??0?020?101020?3?????0?111110023010010021?00??1????0??0000?202??10?110?0

Dollosuchoides

0010?1?00111?????1?????011????0010??????3??00?1111??????02?00??2?0200?0?021?

20?110001001102?11?00?000001?0?3???0011?0?1000??????10???011000100?100?2?????
??010?01100100000000300?011000101001200001102020000012?100?00001?200???00?1
3001

Harpacochampsia

??
?????01?0?12?0211211
??0?1?1???1?01???2?????????000?0?0?0?100?1????201????0010?0?0?00?2??????0?0?
?1?0?1?0?????0100?10?0000?00?0?000?00000?0?00?????0?000??11?????????1?0?0

Eothoracosaurus

?????????????????1????000?????00?00???0?40???0011?1?????0?0?0???2?1200?01021?0
0?1100050?1?03?00?00100000000000???01000?0?0?????1?00???111000100?1?00??????
?00??1001102?010110000??010000100?0230000?0021?0000?????00?0000002?2???00?11??
0

Ocepesuchus

??
?10?5?00?????00?0?0??????????2???1?0??????????0???11?00?????00?????????????1?
0???0??0?0?1??????0001??????00??????0?0??????0?????00?0?0?????0?????

Eosuchus minor

??1?1?????0?????11?00?0?100??000000?0?0400000011110?0?00?2?00?02?1200?01021
0200110005011002?00000?00000000030???010000000?0?1010020?0111000100?1?1?3???
????000?10100?00000?0?100???10000101002300101?0?1?00000?2?00?00000?02????00?1
10?0

Eosuchus lerichei

??0?1??????????1??????1??????0??????4??????11?????????0???201200?0?021?2?
0110005011002?00?00?000?00000300?001000?0000???010?2?0?11100010??10113?????
0?0?110100?0000010?100???000010100230010?0021200000?2?100?000010202???00?110
00

Siquisiquesuchus

?????????????????1?????????????0?????????60?0?0?0?110?0??????2???2??2??0?021??1
?1?0?50?1?0??02??01200??000?0?????10?0?0???0?????00??321000100??1?????????00
??1?0?20??1??20?3?????0000?111?02301?11?0?1?00?0?????0?????00????2?????0?11??0

Maroccosuchus

?????????????????1?????????????1????00110???1??30??00?1011??????112?00?0000201?000211
2210100010?1101?01?0021000010013?0?0011?0?1000????001010?1?01100010??10002????
??0010?011?011?0000001000?01?0001000012000?10020200000?3?0?0?000011001?00?1
3010

Toyotamaphimeia

001100001111?1?0010?010111111000000???100500?10?10?????00?02?00?02?020??0?00
1?2?1?1?007011?02?01?002100000000300??000???100?0?0?0?10????011000101?10?03???
????00?0?1001000001003000001100011100?20000?0021300001123100?0000?11?1???00?
10?00

Megadontosuchus

????????????????1????????????????1????????[3
5]????1?0??11??????0?2?00??0?0??0?021?20?0?10?1??1??1????00?1??????????????1????
10??????1?0??201100010????1?????????0??0?1?012??010?1????0?????1?1?0??0?010
0?0?0??0?2??0????00110????0?1??0

Aktiogavialis

??0??????0?1??????11??
?10????1????2??120??0????1????0??00????0001????????????????????1?????????????????
0????????????10??????0011??????0??1????0??1????????????????????????????1??0

Planocrania_datagensis

??11??????????0?????12?????000?00?
0?00?30?1?01?0?00210????00????0??1?00????0??0????10001?0??????????????0??
0?1?0????0100010????1?0?0?11002??0000000?0?00??????1??0?001??????00?12??0

Planocrania_Hengdongensis

??0????01?11????????[1
2]0????0?12????010??0?0100030?1?01????002000????01????????1????????10??0????11
????00?0????????00?0?000????0010??11?00?1??0211000000010?0000?????1?0000
01?1????0?1??0

Penghusuchus

00100?101000?01101?10?10111111?00000??110501?0001?1????00??2?00?02?0201????2
??2??1??0701?10??1100?1?000000030??0210?1?1??0?0?0?010111011?00?00?1000?????
????01?011?0100000100?0??00110001??0010?000?0?0?300001123100??0001??11??00110
10?

Thecachampsia_carolinensis

??001?01??1000?10??0?01??????00100??1?0531?00?011??????002?00?02?0200?0?021
?22?110001001?02?01?00?10010?00030?0010??10??????????0??11000100?1003?????
??01??0110012?0?000??01?00?0000101001?0020?000130000112?100??0000200??00?1?
100

Euthecodon_brumpti

????????????????????????????????????10??1?0411?000?021??????002110?02?12021100211
1010110150?1003?01?00210010010030?00001011100?11101010??011001100011003????
??011?0111111?0?0200000?00?0000111002300000000120000?????0?000001202??00?1
1010

Tomistoma_coppensi

??3?????1?11????????2?0??2?12????021?201
010001??1[0 1
3]2?0??0021?00??0?3??00??0?0??0??????10??01100010??00?3??????0??0110010
00?0000000?00?10?010?001?0000?1121?0000??????00000120????0?11??0

Xaymacachampsia

????????????????1????????????????????3????????11????????????0????????2?????
????????????????????3????????0????????????????1????00?0?0?????????????1?
????????0??0????000????01????????????0????0????????????????

Maomingosuchus_petrolica

??10?0?00?10?000?111?000?1??1??00110??111030000001011000??000200101200202?210
210201011001001002?01?00200000000?3000001000?1000??101010??011000100?00002
01????211?101001[0,1]1000000001000100001000010000010121200000?23?00?00010110
00??00?11000

Krabi_tomistomine

??30??0?01011?????002?01012????????02??2?
?0?10?1??10?2????0020??0?0?0?????01????1?0??????????????1??001??????????????1??
????0?1??0000????0??1????1??01000????1?1?0????????0?????0?00????0??1??0

;

Table 1. Dimensions of the skull and mandible of *Maomingosuchus* sp. from Krabi, Thailand (cm)

Characteristics	
Length of skull from tip of snout to posterior edge of cranial table	48+?
Maximal width of skull, across quadratojugals	?
Length of snout	34.5+?
Length of post-snout region, from anterior border of orbit to posterior edge of cranial table	13.5
Maximal width of snout	8
Maximal length of naris	?
Maximal width of naris	?
Maximal length of orbit	5.3
Maximal width of orbit	4?
Interorbital width	3
Length of cranial table, through center of supratemporal fenestrae	8.2
Width of cranial table, across centers of supratemporal fenestrae	11.5
Maximal length of supratemporal fenestra	4
Maximal width of supratemporal fenestra	3.6
Interfenestral width	1.5
Length of ventral border of infratemporal fenestra	?
Length of incisive foramen	?
Width of incisive foramen	?
Length of long axis of suborbital fenestra	?
Length of short axis of suborbital fenestra	?
Interfenestral width of palatines	?
Width of choanae	?
Width across pterygoid flanges	?

Table 2. Dimensions (in mm) of the alveoli of *Maomingosuchus* sp. from the late Eocene of Krabi. ‘*a*’ indicates alveolar width while ‘*b*’ indicates alveolar length. Absence of scores in the ‘*b*’ rows indicate that alveoli are circular. Grey shaded scores referred to the alveolar couplets.

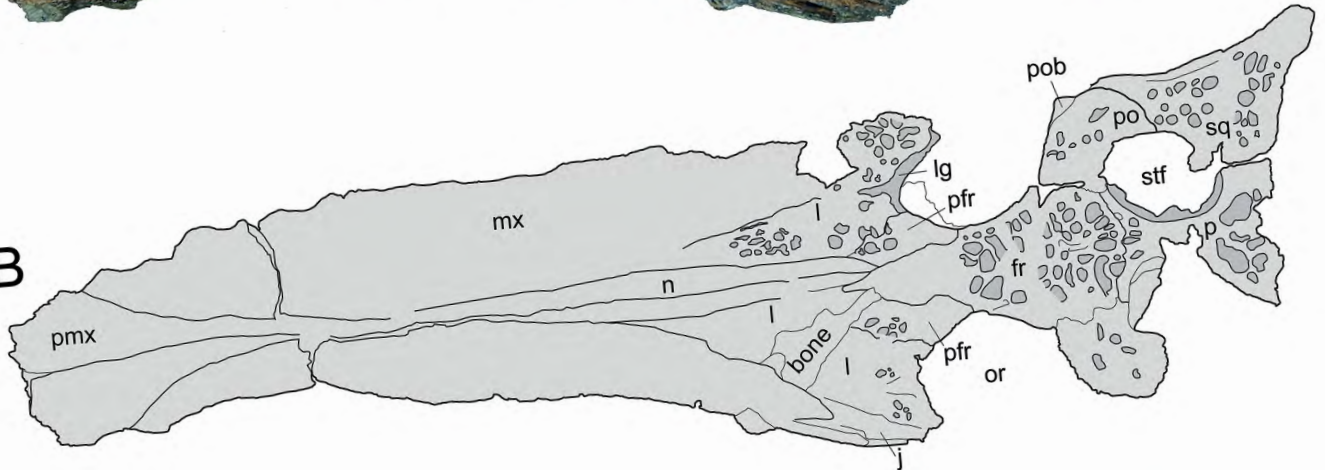
Curation number	alveoli count and measurements																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
PRC-1121	<i>a</i>	8*	8	11	10?	16	11?	10?	10?	10?	12?	?							
PRC-1122	<i>a</i>	?	?	?	?	6	6	6	?	6	6	5	7	6	6	6	5	4	4
	<i>b</i>												10	9	9	9	7	6	?
PRC-1123	<i>a</i>	8	?	?	9	6	5	5	6	6	5	5	7	7	7	7	6	6	?
	<i>b</i>												10	10	9	9	7	7	?

2 cm

A



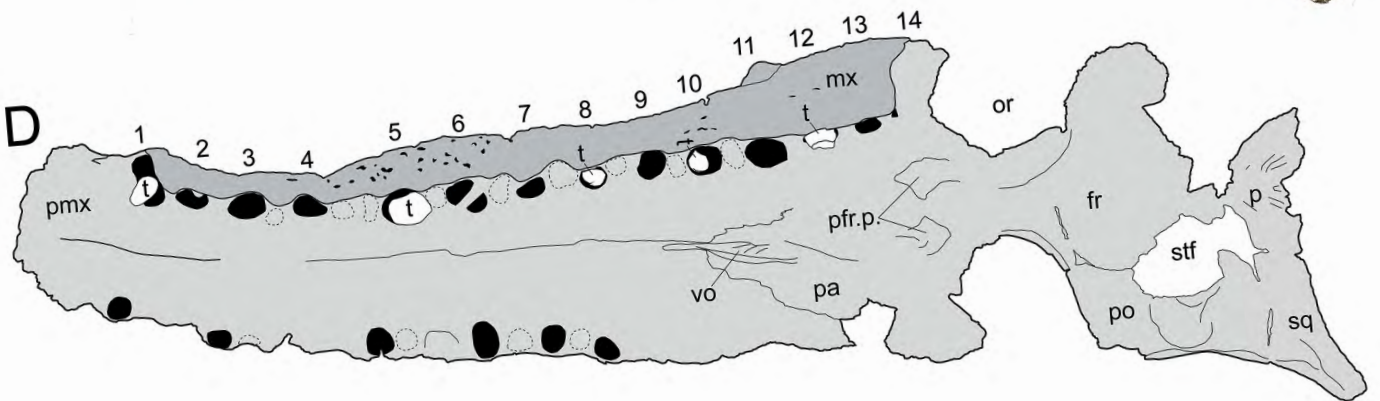
B

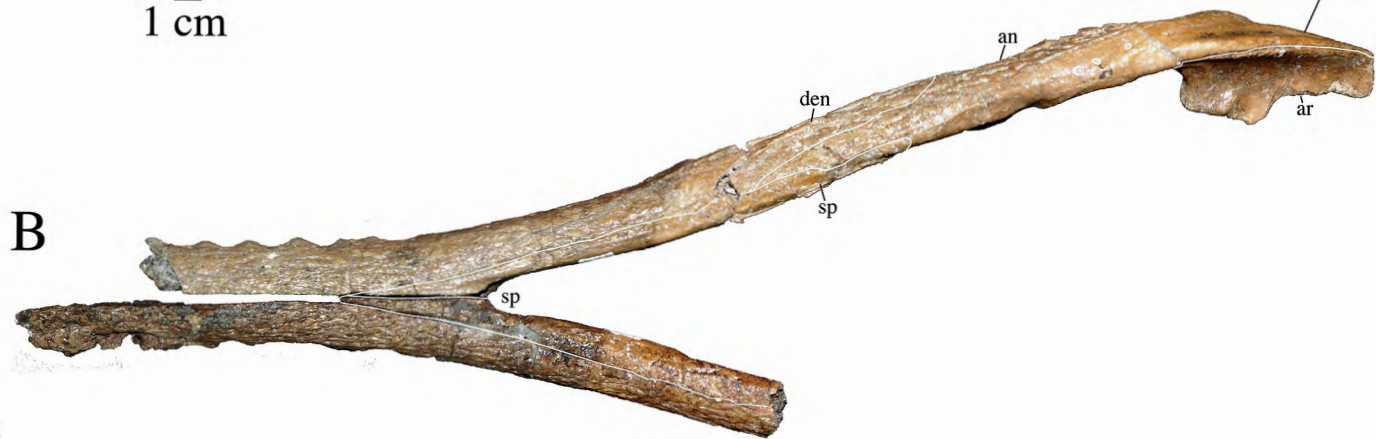
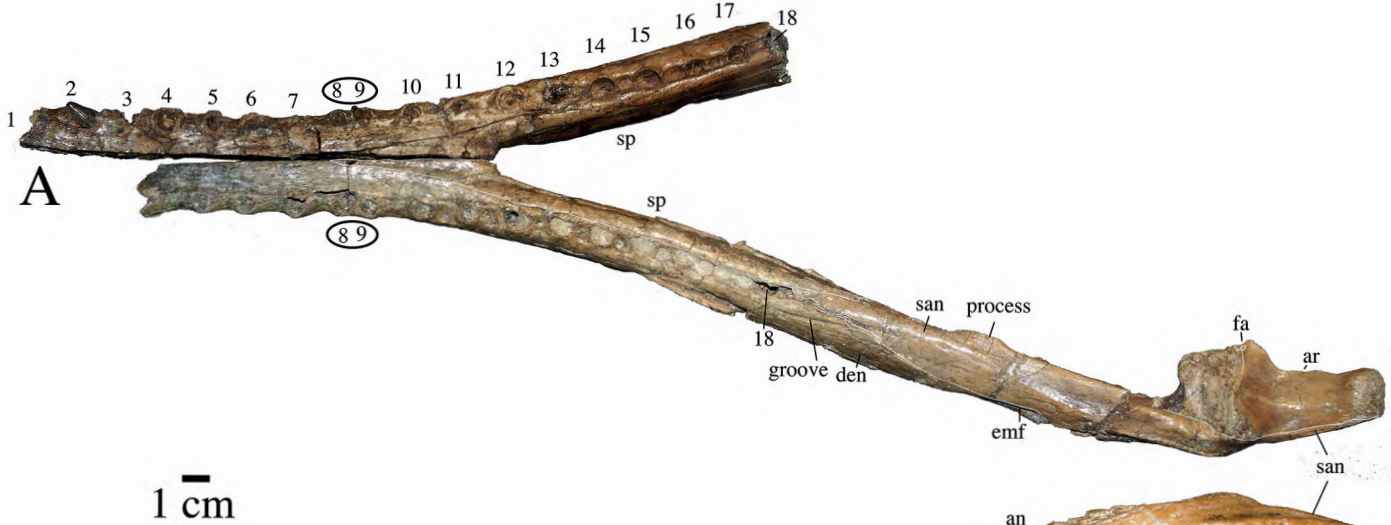


C

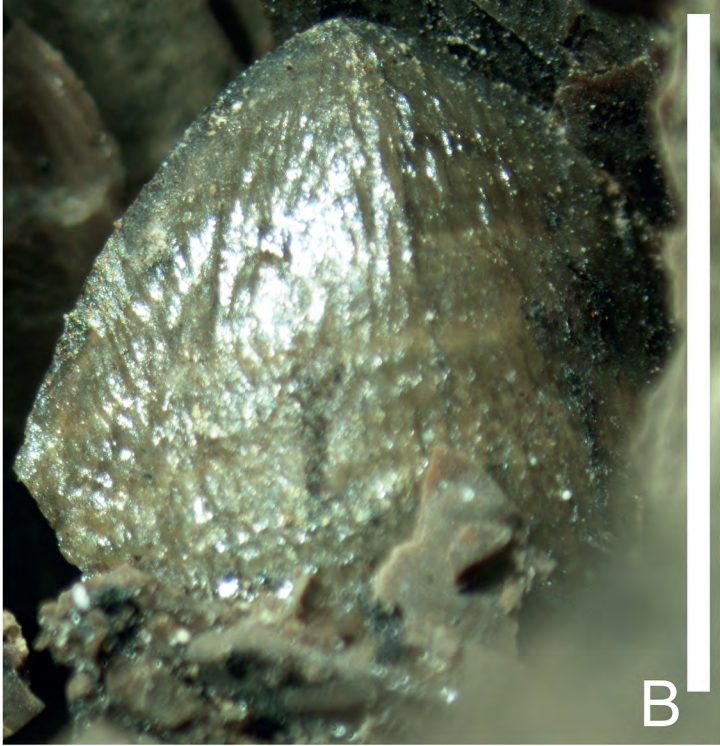


D





5 mm



5 mm

B

