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A new Middle Miocene tarsier from Thailand and the reconstruction of its orbital morphology using a geometric–morphometric method

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Tarsius is an extant genus of primates endemic to the islands of Southeast Asia that is characterized by enormously enlarged orbits reflecting its nocturnal activity pattern. Tarsiers play a pivotal role in reconstructing primate phylogeny, because they appear to comprise, along with Anthropoidea, one of only two extant haplorhine clades. Their fossils are extremely rare. Here, we describe a new species of *Tarsius* from the Middle Miocene of Thailand. We reconstructed aspects of its orbital morphology using a geometric–morphometric method. The result shows that the new species of *Tarsius* had a very large orbit (falling within the range of variation of modern *Tarsius*) with a high degree of frontation and a low degree of convergence. Its relatively divergent lower premolar roots suggest a longer mesial tooth row and therefore a longer muzzle than in extant species. The new species documents a previous unknown Miocene group of *Tarsius*, indicating greater taxonomic diversity and morphological complexity during tarsier evolution. The current restriction of tarsiers to offshore islands in Southeast Asia appears to be a relatively recent phenomenon.

Keywords: *Tarsius*; Tarsiidae; morphometrics; Miocene; orbit; Thailand

1. INTRODUCTION

The fossil record of Tarsiidae is very scant, consisting of only two genera, *Xanthorhysis* and *Tarsius*, that were apparently restricted to Asia. The oldest tarsiid ever discovered, Middle Eocene *Xanthorhysis tabrumi* from the Heti Formation, Shanxi Province, China, is documented by a dentary with P_3–M_3 and alveoli for C_1 and P_2 [1]. *Tarsius eocaenus*, from the Shanghuang fissure-fillings, Jiangsu Province, China, was initially represented by five isolated teeth [2]. More recently, a facial fragment with the crown of P^3 and complete or partial alveoli for I^2, C^1, P^2 and the mesial roots of P^4 was described [3]. It demonstrates that the large orbit characteristic of living *Tarsius* was already present in the Middle Eocene and that *T. eocaenus* also possessed a haplorhine oronasal configuration. *Tarsius* has often been considered a living fossil, displaying no evolutionary changes in the orbit and dentition since the Eocene [4]. A Middle Miocene tarsiid, *Tarsius thailandicus* [1,5,6], is documented by six isolated teeth from the Li Basin, northern Thailand. It corresponds to a small-sized species showing modern dental characters. *Afrotarsius chatrathi* from the Oligocene of Fayum, Egypt, which consists of a lower jaw with part of P_3–P_4 and M_1–M_3 [7], has been described as an African tarsiiform primate. Its tarsiid affinities have been widely challenged, and *Afrotarsius* is more plausibly interpreted as a basal anthropoid primate [1,5,8]. A tibiofibula specimen attributed to *A. chatrathi* by Rasmussen *et al.* [9] was considered as probably not belonging to a primate [10].

Here we describe a new species of Middle Miocene *Tarsius* from northern Thailand. The new species is represented by a maxillary fragment preserving the partial orbital floor with P^3, P^4 and M^1, 17 mandibular fragments and two isolated molars. As a result, this Miocene species of *Tarsius* is now the best-documented fossil tarsier currently known. Its orbit is poorly preserved, but the morphology of this region can be reconstructed using a geometric–morphometric method. Our main objective is to compare the orbital morphology of the new Miocene tarsier with that of extant *Tarsius* in order to assess the antiquity of the peculiarly enlarged orbits of living species of *Tarsius*. If our results confirm the antiquity of modern tarsier orbital morphology (and their secondarily nocturnal adaptations), this will support the proposal that haplorhines were primitively diurnal, a condition retained in early anthropoids. Alternatively, these distinctive adaptations to nocturnal life may have originated relatively recently during the course of tarsier evolutionary history. The peculiar dental characters displayed by the new species will also permit an assessment of its phylogenetic relationships with extant species of *Tarsius*, which are considered to cluster into two distinct groups. This also

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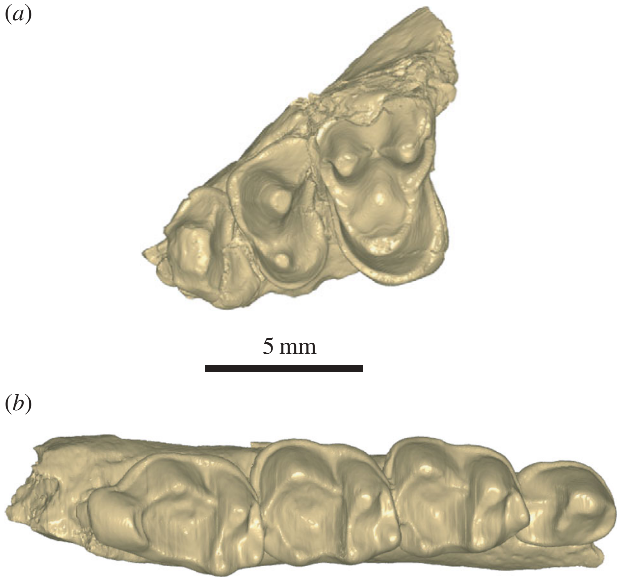

Figure 1. Occlusal view of *Tarsius sirindhornae* n. sp. (*a*) Maxillar fragment with P^3–M^1 holotype (TF 6260); (*b*) lower jaw with P_4–M_3 (TF 6247).

raises questions about the diversity of *Tarsius* during the Miocene.

2. GEOLOGICAL BACKGROUND

The new *Tarsius* specimens were recovered from the Q and K coal zones of the Na Khaem Formation, Mae Moh coal mine, Mae Moh District, Lampang Province, northern Thailand. The Na Khaem Formation is composed of the main lignite-bearing units, interbedded with lacustrine mudstones and minor sandstones, indicating sedimentation under the alternation of freshwater lake and swamp/marsh in a calcium-rich lacustrine environment [11]. The Q and K coal zones, the main coal-producing layers, range in thickness from 10 to 30 m and 15 to 30 m, respectively. The new *Tarsius* species was discovered through surface survey, and it is associated with a diversified vertebrate fauna including bony fishes, snakes, turtles, crocodilians and a variety of other mammals such as *Stegolophodon* [12,13], *Gomphotherium* cf. *browni* [14], *Gaindatherium* [15], *Siamogale thailandica* [16], *Maemohcyon potisati* [17], *Neocometes* cf. *orientalis*, *Prokanisamys benjavuni* [18] and *Siamoadapis maemohensis* [19].

The age of the Q and K coal zones of the Na Khaem Formation is conventionally considered as Middle Miocene and magnetostratigraphic data correlate these strata with chron C5Aar, between 13.3 and 13.1 Ma [20,21].

3. SYSTEMATIC PALAEONTOLOGY

Primates Linnaeus, 1758: Haplorhini Pocock, 1918, Tarsiiformes Gregory, 1915, Tarsiidae Gray, 1825, *Tarsius* Storr, 1870.

***Tarsius sirindhornae* sp. nov.**

Holotype. TF 6260 (Department of Mineral Resources, Bangkok), left maxilla preserving partial orbit floor with P^3–M^1 (figures 1*a*, 2*i*–*l*).

Etymology. In honour of Her Royal Highness Princess Maha Chakri Sirindhorn, who has repeatedly demonstrated her great interest in the palaeontological richness of her country.

Type series. TF 6244, right mandible with P_3–M_3 (figure 3*e*); TF 6245, left mandible with P_4–M_2; TF 6246, right mandible with P_4 (figure 3*d*); TF 6247, left mandible with P_4–M_3 (figures 1*b* and 3*c*); TF 6248 right mandible with M_1–M_3; TF 6249, right mandible with P_4–M_1; TF 6250, left mandible with fragment of P_3–P_4 and M_1–M_3; TF 6251, right mandible with M_1–M_3; TF 6252, right mandible with M_1-M_3; TF 6253, left mandible with fragment of M_1–M_2 and M_3; TF 6254, left mandible with M_2 and fragment of M_3; TF 6255, right mandible with fragment of M_2 and M_3; TF 6256, right mandible with M_1–M_2 and fragment of M_3; TF 6257, left mandible with P_4–M_1; TF 6258, left mandible with fragment of M_2 and M_3; TF 6259, left mandible with P_4–M_3; TF 6261, left mandible with fragment of M_2 and M_3; TF 6262, right M_2; TF 6263, right M_3. All specimens are from the same locality as the holotype. Tooth dimensions are given in table 1.

Type locality and age. Q and K coal layers of the Na Khaem Formation, Mae Moh coal mine, Mae Moh District, Lampang Province, northern Thailand; Middle Miocene (13.3–13.1 Myr ago).

Diagnosis. Differs from extant species of *Tarsius* by its anteriorly less expanded orbit, less elevated molar cusps, P_4 with variably developed metaconid, more robust protoconid and hypoconid on M_1 and M_2, and larger hypoconulid on M_3; P_3 and P_4 roots well separated, as in *Tarsius spectrum*, not fused or appressed as in *Tarsius bancanus*. Mesial root of P_3 vertical, not procumbent as in extant species. Less reduced $P^3/_3$ and $P^4/_4 \cdot P^3$ nearly the size of P^4 and P^4 roots significantly longer than those of M^1. Differs from *T. thailandicus* by its larger size, less elevated cusps and divergent and non-appressed P_3 and P_4 roots. Differs from other fossil *Tarsius* and *Xanthorhysis* by it larger size, less elevated cusps, better defined hypoconulid, less developed protocristid, shallower trigonid basin and more mesial position of entoconid relative to hypoconid.

Measurements. All measurements of *T. sirindhornae* and extant *Tarsius* are given in table 1 and electronic supplementary material, table S1.

Description and comparisons. TF 6260 is a left maxillary fragment with P^3–M^1 and a preserved partial orbital floor. P^3 and P^4 generally resemble those of extant species but display larger paracone on P^3 and stronger protocone on P^4. The antero-buccal corner of P^3 is damaged, but the crown is less reduced than that of extant species. The paracone of P^4 is inclined more lingually and located more mesially than is the case in extant species of *Tarsius*. The preparacrista of P^4 is better developed among extant species, in which it is strongly connected to the parastyle. This crest is absent on the fossil. M^1 is significantly larger than P^4. It differs from M^1 in other species of *Tarsius* in having a distal margin with a more waisted outline and a stronger metastyle. The postprotocrista splits into two crests, a premetaconule crista joining the mesiolingual slope of the metacone and a postmetaconule crista connecting the metastyle, but among extant *Tarsius* conules are generally less well expressed and the metaconule cristae are reduced, especially the distal ones. Horizontal wear facets can be observed on the paracone, metacone, protocone, paraconule and metaconule. Cingula

Table 1. Dental measurements (mm) in MD (mesiodistal) × BL (buccolingual) of *T. sirindhornae* n. sp. compared with other Tarsiidae. (Numbers in parentheses are BL of talonid.)

taxa	P_3	P_4	M_1	M_2	M_3	estimated body weight (g)
T. sirindhornae						
TF 6244	1.62 × 1.66	2.06 × 1.92	2.67 × 2.46	2.82 × 2.66	3.44 × 2.15	119
TF 6245		2.42 × 1.88	2.98 × 2.60	3.19 × 2.92		153
TF 6246		2.30 × 1.77				
TF 6247		2.09 × 1.66	2.94 × 2.40	2.99 × 2.60	3.81 × 2.52	133
TF 6248			2.77 × 2.42	3.00 × 2.55	3.73 × 2.50	123
TF 6249		2.48 × 1.99	3.21 × 2.74			185
TF 6250			— × 2.64	3.25 × 2.62	3.83 × 2.42	
TF 6251			3.20 × 2.33	3.06 × 2.42	3.53 × 2.10	144
TF 6252			2.92 × 2.48	2.89 × 2.59	3.54 × 2.30	138
TF 6253			— × 2.73	— × 2.92	3.70 × 2.37	
TF 6254				3.27 × 2.50	3.63 × 2.32	
TF 6255				— × 2.47	3.50 × 2.27	
TF 6256			2.62 × 2.11	2.67 × 2.16		92
TF 6257		2.17 × 1.93	3.14 × 2.48			154
TF 6258				— × 2.51	3.48 × 2.25	
TF 6259		2.18 × 1.90	2.75 × 2.47	2.98 × 2.59	3.52 × 2.39	130
TF 6261				— × 2.77	3.57 × 2.39	
TF 6262				3.35 × 2.71		
TF 6263					3.83 × 2.56	
T. thailandicus[a]						
T Li43	1.25 × 1.27					
T Li44		1.27 × 1.35				
T Li45			2.43 × 1.83 (0.89)			66
T Li46				2.52 × 2.10 (1.02)		
T Li47				2.58 × 1.83 (0.89)		
T. eocaenus[b]						29
IVPP V11030			1.65 × 1.55			
X. tabrumi[c]						
IVPP V12063	1.55 × 1.20	2.10 × 1.55	2.25 × 1.85	2.20 × 1.80	2.35 × 1.60	60
T. bancanus[d]			2.97 × 2.67	2.72 × 2.90		158
T. syrichta[d]			2.59 × 2.47	2.44 × 2.62		114
T. spectrum[d]			2.18 × 2.20	2.17 × 2.33		74
T. pumilus[d]			2.00 × 1.85			50

taxa	P^2	P^3	P^4	M^1
T. sirindhornae				
TF 6260 (holotype)		1.77 × 2.58	2.11 × 3.17	3.19 × 4.15
T. thailandicus[a]				
T Li42	1.06 × 0.93			
T. eocaenus[e]				
IVPP V14563		1.39 × 1.63		
T. bancanus[d]				2.73 × 4.42
T. syrichta[d]				2.52 × 3.83
T. spectrum[d]				2.26 × 3.44
T. pumilus[d]				1.85 × 2.90

[a] Mein & Ginsburg [6].
[b] Beard *et al.* [2].
[c] Beard [1].
[d] M. Dagosto 2008, personal communication.
[e] Rossie *et al.* [3].

surround the entire perimeter of the crown's base, but the lingual cingulum is remarkably developed.

The teeth described above are part of a maxillary fragment that includes the floor of the orbital cavity (figure 2*i*–*l*). In the lateral view, a small area in its uppermost mesial part corresponds to the lower edge of the infra-orbital foramen. The three root apices of M^1 pierce the floor of the orbital cavity as in modern *Tarsius*. Such is not the case for the three roots of P^4, which are much longer than those of M^1, indicating that the floor of the orbital cavity rises at the level of the distal roots of P^4. Therefore, the great length of the P^4 roots indicates that the orbit extended less anteriorly in TF 6260 than in any extant species. Among modern species of *Tarsius*, the

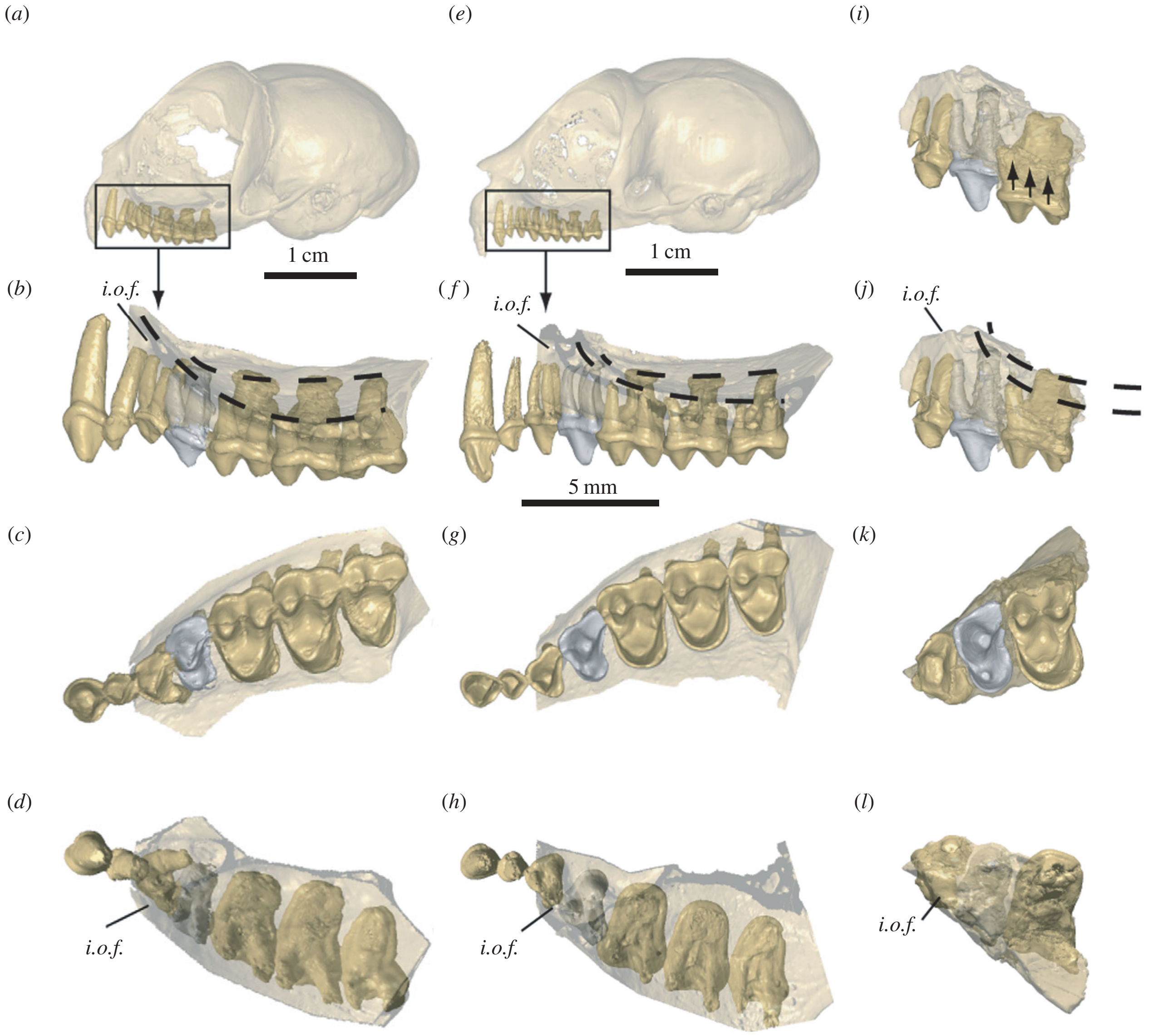

Figure 2. Micro-CT scan views of the orbital floors and premolar and molar root patterns in extant *Tarsius* (*a–h*) compared with those of *T. sirindhornae* n. sp. (*i–l*). The two dashed lines join the tips of the lingual roots and of the labial roots in the orbital floor. P^4 is represented in a grey colour. i.o.f., infraorbital foramen. (*a–d*) *Tarsius bancanus* skull (PAL-44), with orbital floor expanding until above P^3 root. (*e–h*) *Tarsius spectrum* skull (AS 1821), with P^2 and P^3 roots excluded from orbital floor. (*i–l*) Maxillary fragment image of *T. sirindhornae* n. sp. holotype (TF 6260) in its original configuration (*i*), then with the M^1 lifted upwards to bring its labial cingulum in line with that of P^4 as in extant *Tarsius* (*j*), suggesting that according to the long roots of P^4, the orbital floor must have raised abruptly in front of M^1, indicating a less anteriorly expanded orbit compared with those of extant *Tarsius*. (*b,f,j*) Labial view. (*c,g,k*) Occlusal view. (*d,h,l*) Apical view of the orbital floor.

roots of the posterior upper cheek teeth, including P^4, are always in contact with the floor of the orbital cavity (figure 2*b*,*f*). As the size and morphology of the orbital cavity constrain the imprints of the root apices on the orbital floor, we hypothesize that the dimension and orientation of the orbital contour can be partially inferred from the length and position of the roots of P^3, P^4 and M^1.

The dentary of the new species resembles those of extant species of *Tarsius* (figure 3*a*,*b*), differing chiefly in being more robust. A single *foramen mentale* can be observed on one specimen (TF 6246) under the mesial root of P_3, but there are two such foramina in *Xanthorhysis*, beneath the mesial part of the alveolus of P_2 and the mesial root of P_3, and also in extant *Tarsius* (beneath P_3 and P_4). Images produced by micro computed tomography (micro-CT) scans image show that *T. sirindhornae* has only one lower incisor (figure 3*d*), documented by a partial alveolus located mesial to the canine alveolus. It is tiny and rather procumbent, being inclined about 55° relative to the tooth row. The diameter of C (figure 3*d*) can be estimated on the basis of a partial alveolus in TF 6246. It shows an estimated mesiodistal dimension of 1.47 mm. The canine root is massive and procumbent, oriented about 60° relative to the tooth row. P_2 is represented only by a partial alveolus (TF 6246) and a micro-CT scan image confirms that it is single-rooted and inclined like the incisor and canine (figure 3*d*). P_3 is double-rooted with vertical and well-separated roots. Its crown displays a large protoconid (figure 3*e*). Mandible ramus depth beneath P_3 measures 4.38 mm on TF 6244 and 3.53 mm on TF 6246, similar to extant *Tarsius* (3.66–4.23 mm). P_4 shows a variably

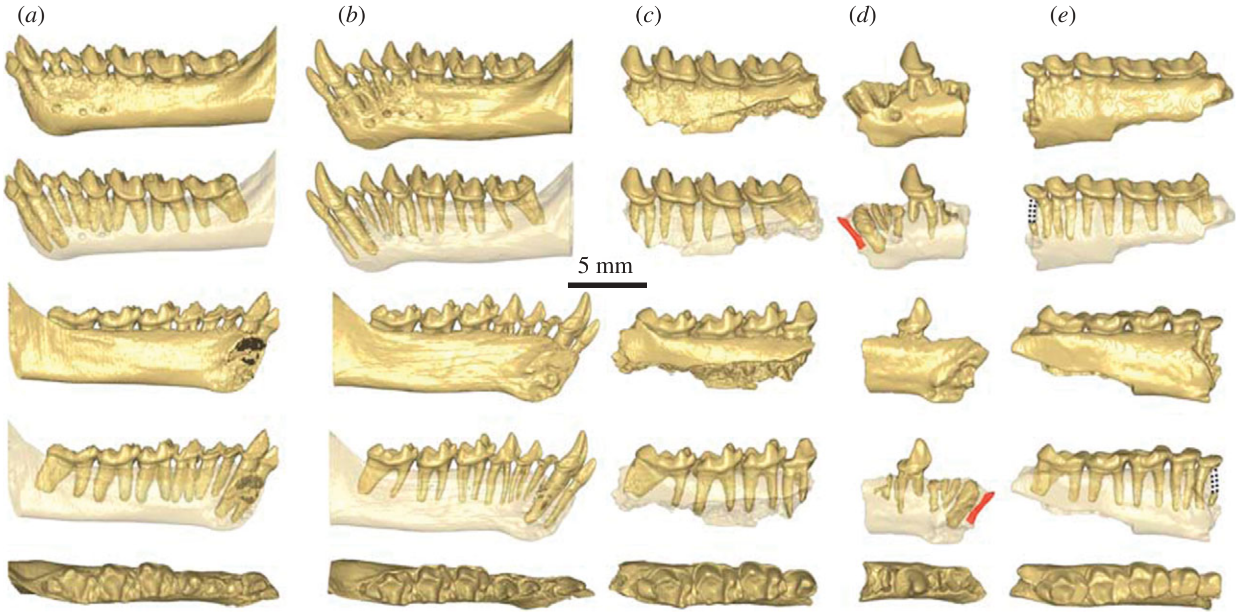

Figure 3. Micro-CT scan views of the lower jaws of extant *Tarsius* (*a*,*b*) compared with those of fossil *T. sirindhornae* n. sp. (*c*–*e*). Lower jaws of fossil fragments are represented from top to bottom in respective buccal, buccal transparent, lingual, lingual transparent and occlusal views. (*a*) *Tarsius bancanus* (PAL-44) left lower jaw, (*b*) *T. spectrum* (AS 1821) left lower jaw, (*c*) *T. sirindhornae* n. sp. left lower jaw fragment with P_4–M_1 (TF 6247), (*d*) mirror image of the right lower jaw fragment of *T. sirindhornae* n. sp. with crown of P_4 and roots of I (in red), C, P_2 and P_3 (TF 6246), (*e*) mirror image of the right lower jaw fragment of *T. sirindhornae* n. sp. with P_3–M_3 (TF 6244) displaying unreduced premolars and vertical, parallel and not appressed roots of P_3 (mesial root completed with dotted lines) and P_4.

developed metaconid and is double-rooted as in *T. spectrum* but in contrast to *T. bancanus*, the P_4 of which has a single root or two closely appressed roots (figure 3*c*–*e*). The lower molars of *T. sirindhornae* are similar to those of extant *Tarsius*, with the exception of their less elevated cusps and the notably enlarged $M_{3,}$ which bears a larger hypoconulid than in extant *Tarsius*. The talonid of M_1 is broad and bears an enlarged hypoconid and a smaller entoconid as in all extant *Tarsius*, differing also from the Eocene *Tarsius* that shows equal size of these two cusps. The paraconid of M_2 is more lingually situated than on $M_{1,}$ yielding a longer paracristid and a wider trigonid than on M_1. Its entoconid is more reduced than on M_1. M_3 is mesiodistally longer than those of any extant species of *Tarsius*. The entoconid, located at the same level as the hypoconid, is tiny to absent. This cusp is usually more strongly expressed in extant *Tarsius*, as it is in *Xanthorhysis*. The symphysis was unfused and its surface is notable for the depth of the pit for the genioglossus muscle (figure 3*d*). The coronoid process rises from the occlusal surface of the molars at an angle of 55°. Its lateral side bears a strong anterior masseteric ridge. A retromolar space is present. The angular region shows a slight downward inclination, starting at the level posterior to the beginning of the vertical branch.

4. METHOD AND RESULTS

(a) *Methods*

We used geometric–morphometric methods to estimate the root and orbital morphology of *T. sirindhornae*. The comparative sample consists of 12 crania of extant *Tarsius* (*T. bancanus*: $n = 4$; *T. syrichta*: $n = 4$; *T. spectrum*: $n = 1$; *T. sp.* indet.: $n = 3$), nine of which are adults, the three remaining ones being subadults exhibiting relatively smaller orbits, with P^4 and M^1 erupted and a P^3 almost fully erupted (see the electronic supplementary material, table S2, for a list of the specimens). Though limited in size, the comparative sample was chosen to be representative of modern *Tarsius* variability, with the aim to build a satisfactorily model of *Tarsius* orbital morphology. The analysis protocol involved 10 landmarks corresponding to the centre of the root apices of P^3, P^4 and M^1 and to the floor of the infraorbital foramen, which were digitized on the reconstruction of *T. sirindhornae* TF 6260 and on the left maxillae of extant specimens (see the electronic supplementary material, figure S1*a*). Patterns of radicular shape variation were analysed using principal components (PC) analysis of shape in linearized Procrustes space [22].

Owing to the small number of specimens, we could not predict accurately orbital parameters such as diameter, convergence and frontation directly from Procrustes coordinates. As such, in order to estimate the orbital morphology of *T. sirindhornae*, we first reduced the dimensionality of the system describing shape variation. We only considered the components of shape variation that relate the best to orbital diameter, convergence and frontation. To do so, we performed multivariate regressions of root apex shape against orbital diameter, the degree of frontation and the degree of convergence on the extant specimen sample, following the protocol described by Frost *et al.* [23]. In extant *Tarsius*, the centroid size of the landmark configuration was found to be only weakly and insignificantly correlated with orbital diameter ($r^2 = 0.25$; $p = 0.11$). This is the reason why the estimation of the orbital diameter of *T. sirindhornae* was derived from a measure of shape, and not size. This procedure yielded regression shape vectors of orbital diameter (*RSVb*), frontation (*RSVf*) and convergence (*RSVc*). Variation in orbital diameter and in the degrees of frontation and convergence accounted for substantial parts of radicular apex shape variation (23.44, 19.57 and 21.09%, respectively), confirming the hypothesis that jugal teeth root morphology and the position of the infraorbital foramen of extant *Tarsius* are correlated with the orbital geometry. *RSVo*, *RSVf* and *RSVc* projecting scores of extant specimens were well correlated with their measured orbital diameters ($r^2 = 0.89$; $p < 0.0001$), degrees of frontation ($r^2 = 0.69$, $p = 0.0008$) and convergence ($r^2 = 0.72$, $p = 0.0005$). This allowed for estimations of orbital diameter, frontation and convergence for *T. sirindhornae* derived from its *RSVo*, *RSVf* and *RSVc* projecting scores, as well as 95% confidence and prediction intervals (see the electronic supplementary material, figure S2). We used MORPHOTOOLS [24,25] to perform the geometric–morphometric analysis and the multivariate regressions, and *R* [26] to predict orbital diameter, frontation and convergence.

(b) *Results*

Visualizing patterns of root apices shape variation in morphospace permits characterization of taxon-specific morphologies (see the electronic supplementary material, figure S3*a*). PC1 describes the curvature of the dental root arch, the lingual root apex line being more curved lingually for high PC1 values (see the electronic supplementary material, figure S3*b*). Specimens with low PC1 scores, such as *T. spectrum*, exhibit a less compressed mesial tooth row and a more laterally and posteriorly placed infraorbital foramen. PC2 reflects mainly differences in P^3 root apex shape (see the electronic supplementary material, figure S3*b*). Specimens with high PC2 scores (the three subadults) exhibit a lingual root apex of P^3 placed more lingually, and an infraorbital foramen placed in a relatively lower and more lateral position. *Tarsius sirindhornae* exhibits a curved dental root arch and lies inside the morphological variation of extant adult *Tarsius* and resembles more *T. bancanus* and *T. syrichta* than *T. spectrum*. The position of *T. sirindhornae* within PC1–PC2 subspace gives further support to the hypothesis that extant *Tarsius* is an adequate model to estimate the orbital morphology of this fossil.

Tarsius sirindhornae orbit lies within the extant sample range variation and exhibits a high degree of frontation (64.5°; 95% confidence intervals (CI): 63.5–65.4°; 95% pred. int.: 60.97–67.98°) and a low degree of convergence (50.6°; 95% CI: 49.2–52.0°; 95% pred. int.: 45.65–55.59°) and a large diameter (18.3 mm; 95% CI: 17.9–18.6 mm; 95% pred. int.: 17.06–19.46 mm) (see the electronic supplementary material, figure S2 and table S2). But the orbit of *T. sirindhornae* was relatively less expanded anteriorly than what can be observed in extant *Tarsius*.

5. DISCUSSION AND CONCLUSION

Tarsiers are among the smallest haplorhine primates (80–150 g), and their diet is based on insects and other small animal prey [27]. *Tarsius sirindhornae* was a large species of *Tarsius*, as large as or possibly larger than *T. bancanus*, the largest extant *Tarsius*. We used the regression equation of the M_1 area against body weight proposed by Gingerich [28] for *Tarsius* and obtained an estimated body weight of *T. sirindhornae* of 90–180 g. Its body mass places it below 'Kay's threshold' of 500 g, below which primates cannot be obligate folivores owing to fundamental metabolic constraints [29]. Some specimens of *T. sirindhornae* display a high degree of premolar and molar wear with horizontal wear facets, suggesting a dietary difference from most other tarsiers. Its large premolars and molars, with enlarged M_3 and low and less acute molar cusps, also point towards a less insectivorous and carnivorous diet than the extant and fossil *Tarsius* and even other fossil Tarsiidae. The meaning of such an odd wear pattern has previously been discussed concerning *Tarsius pumilus* without conclusive evidence [30], gum feeding observed for that species being incapable of producing such a peculiar wear pattern and the small body weight of both species making it unlikely to have included significant amounts of plant food [31]. The diet of *T. sirindhornae* (like that of *T. pumilus*) must nevertheless have included some kind of food with an abrasive component. Microwear analysis may deliver additional information concerning the diet of this peculiar *Tarsius* species.

Fragmentary cranial remains of *T. eocaenus* demonstrate that tarsiers already possessed greatly enlarged orbits during the Middle Eocene [3]. The new species from Thailand confirms that the very large orbits which are associated with the nocturnal activity pattern of modern *Tarsius* were already developed 13 Ma. This extreme orbital enlargement is considered to be the consequence of a secondary shift to nocturnality from a diurnal ancestor [32]. The most primitive known primates, including basal haplorrhines, had relatively small orbits, suggesting a diurnal activity pattern [33]. Indeed, most primitive anthropoids for which orbit anatomy is partially known, including *Bahinia* [34] and *Phenacopithecus* [35], display small orbits, corresponding to a diurnal activity pattern. However, *Biretia* from the oldest Fayum locality BQ2, Egypt, displays greatly enlarged orbits, which are interpreted as a derived feature [36]. This indicates that orbital enlargement occurred several times during the evolution of haplorhines. *Tarsius* apparently displays exceptionally stable craniodental anatomy over tens of millions of years. Such stasis is exceptional among eutherian mammals over such a long time interval.

Tarsius sirindhornae is the second recorded species of fossil *Tarsius* found in the Miocene strata of Thailand. *Tarsius thailandicus*, a Middle Miocene fossil from the Li Basin of northern Thailand, is significantly smaller but similar in age [18] to *T. sirindhornae*. It displays appressed roots on its P_4 and probably on P_3, which further distinguishes it from *T. sirindhornae* and brings it closer to the extant species of *Tarsius*. This shows the occurrence of at least two distinct Miocene groups of *Tarsius* in Thailand. We compared the possible relationships of *T. sirindhornae* with the two morphological groups of extant tarsiers: a Philippine-Western group (from the Philippines and the Greater Sunda Islands) and an Eastern group (from Sulawesi) [37]. The Philippine-Western group shows extremely enlarged orbits, enlarged molars (especially the third molar), narrow molar talonids and prominent cingula around maxillary incisors and canines. P_3 is one rooted and roots of P_4 are strongly appressed. No metaconid seems present on the P_4. The Eastern group shows relatively smaller orbits, a shorter tooth row, reduced third molars, broad molar talonids and poor development of cingula on maxillary incisors and canines. P_3 and P_4 have two well-separated roots as in *T. sirindhornae*. By its unreduced lower premolar roots, interpreted here as a plesiomorphic character, *T. sirindhornae* appears to be closer to the Eastern group. But other derived characters, such as the enlarged M_3 and the large orbit, are shared with the other group. Recent discoveries of new extant species of *Tarsius* have increased the number of taxa, thereby complicating their phylogenetic relationships [37–39]. The preliminary genetic analysis published by Shekelle [40] suggested an unresolved trichotomy among the Philippine, Western and Eastern tarsiers, with a divergence possibly dating to the Middle Miocene. Shekelle [41] also proposed that the small size of *T. pumilus* represents a primitive character and that the large size of some island species is the consequence of an island effect. The large size of our Miocene tarsier does not support this interpretation.

Tarsius sirindhornae displays several autapomorphic characters, such as less elevated molar cusps, enlarged M_3 hypoconulid, robust lower jaw, in addition to its peculiar orbit. It also displays some primitive characters, such as retention of a strong postmetacrista and postmetaconule crista on upper molars and the divergent roots of premolars and molars that suggest a less mesio-distally compressed lower mesial tooth row. This unusual combination of primitive and derived characters indicates that it belongs to a distinct group of Miocene *Tarsius* that is probably not specially related to any of the extant ones. This suggests a higher diversification of *Tarsius* clades during the Miocene and its reduction through time. The same is true for their geographical range. During the Middle Eocene, their distribution reached as far north as central China. In the Miocene, they are only recorded in Thailand and remain undocumented in China, even in nearby Yunnan Province. They disappeared from Thailand prior to the Plio-Pleistocene, because no trace of fossil *Tarsius* was found in the rich Plio-Pleistocene micromammal assemblages collected in caves and fissure-fillings across Thailand [42]. At that time, they probably had reached their present refuge distribution.

To conclude, *T. sirindhornae* represents a new species and also the largest known fossil assemblage of *Tarsius*. It significantly expands the taxonomic and anatomical diversity of this intriguing primate. Its unique combination of primitive and derived dental characters excludes *T. sirindhornae* from the two main clusters of extant *Tarsius*, supporting that it belongs to an extinct Miocene group. This fossil evidence therefore suggests a reduction in taxonomic diversity that accompanied the contraction of the geographical range of *Tarsius* during its Neogene evolutionary history in Southeast Asia. A geometric–morphometric analysis demonstrates that the new fossil tarsier had an enlarged orbit, a high degree of frontation and a low degree of convergence, similar to that shown by modern species of *Tarsius*. However, according to the great length of its P^4 roots, the orbit of the new species was less expanded anteriorly than those of extant *Tarsius*, and its muzzle was longer, documenting morphological differences from the extant forms. Nevertheless, the modern orbit characters associated with a nocturnal activity pattern are still present, confirming the great antiquity and stability of these characters during *Tarsius* evolution within the last 45 Ma. This, in turn, supports the inference that haplorhines are primitively diurnal and that this condition was retained in early anthropoids.

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