
Cynocephalid dermopterans from the Palaeogene of South Asia (Thailand, Myanmar and Pakistan): systematic, evolutionary and palaeobiogeographic implications

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Cynocephalid dermopterans (flying lemurs) are represented by only two living genera (*Cynocephalus* and *Galeopterus*), which inhabit tropical rainforests of South-East Asia. Despite their very poor diversity and their limited distribution, dermopterans play a critical role in higher-level eutherian phylogeny inasmuch as they represent together with Scandentia (tree-shrew) the sister group of the Primates clade (Plesiadapiformes + Euprimates). However, unlike primates, for which the fossil record extends back to the early Palaeogene on all Holarctic continents and in Africa, the evolutionary history of the order Dermoptera *sensu stricto* (Cynocephalidae) has so far remained undocumented, with the exception of a badly preserved fragment of mandible from the late Eocene of Thailand (*Dermotherium major*). In this paper, we described newly discovered fossil dermopterans (essentially dental remains) from different regions of South Asia (Thailand, Myanmar, and Pakistan) ranging from the late middle Eocene to the late Oligocene. We performed microtomographic examinations at the European Synchrotron Radiation Facility (ESRF, Grenoble, France) to analyse different morphological aspects of the fossilized jaws. The abundant material from the late Oligocene of Thailand (Nong Ya Plong coal mine) allows us to emend the diagnosis of the genus *Dermotherium* and to describe a new species: *Dermotherium chimaera* sp. n. This species exhibits an interesting mosaic of plesiomorphic cynocephalid characters shared with *Cynocephalus* and *Galeopterus*, and as such, it probably documents a form close to the ancestral morphotype from which the two extant forms are derived (supported by cladistic assessment of the dental evidence). The discovery of Palaeogene cynocephalids is particularly significant since it attests to the great antiquity of the order Dermoptera in Asia, and besides, it provides the first spatio-temporal glimpse into the evolutionary history of that enigmatic mammal group. In that respect, these fossils testify to a long history of endemism in South Asia for dermopterans, and demonstrate that their modern geographic restriction in south-eastern Asia is clearly a relictual distribution. Cynocephalids had a more widespread distribution during the Palaeogene, which extended from the Indian subcontinent (the rafting Greater India) to South-East Asia. Their subsequent extinction on the Indian subcontinent was probably mediated by the major palaeogeographic and geomorphologic events related to the India-Eurasia collision (retreat of the Paratethys Sea, formation of orogenic highlands) that have strongly affected the climate of South Asia at the end of the Oligocene. Laurent Marivaux, Jean-Jacques Jaeger, Bernard Marandat & Jean-Loup Welcomme, Laboratoire de Paléontologie, Institut des Sciences de l'Évolution (ISE-M, UMR-CNRS 5554), c.c. 064, Université Montpellier II, Place Eugène Bataillon, F-34095 Montpellier Cedex 05, France. E-mails: marivaux@isem.univ-montp2.fr; jaeger@isem.univ-montp2.fr; marandat@isem.univ-montp2.fr; jl@welcomme.org

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Introduction

Dermopterans are an enigmatic group of nocturnal gliding mammals that live exclusively in tropical rainforests of South-East Asia. This group is represented by only one family, the Cynocephalidae, which includes two parapatric species (following Stafford & Szalay 2000): *Galeopterus variegatus* and *Cynocephalus volans*, the Sundaic and Philippine dermopterans, respectively. In South-East Asia, cynocephalids are more commonly known by the name ‘colugo’ (original Malaysian word for the animal) or ‘kagwang’ (original Filipino word). Because of their gliding adaptation and their lemur-like face, cynocephalids are also dubbed ‘flying lemurs’ (*Lemur volans* Linnaeus 1758). However, it must be specified that these animals have not achieved real flight as bats have. Moreover, they are not phylogenetically linked to the living strepsirrhine primates. In fact, the phylogenetic position of living dermopterans among eutherians is uncertain since there is no real consensus deriving from neontological data (morphological vs. molecular phylogenies). On the one hand, some morphologists consider living dermopterans to be closely related to chiropterans (Volitantia; e.g. Szalay & Drawhorn 1980; Novacek & Wyss 1986; Simmons 1993, 1995; Stafford & Thorington 1998; Bloch & Silcox 2001; Sargis 2002a; Silcox *et al.* 2005) among the archontan mammals (Dermoptera, Chiroptera, Scandentia, Primates; e.g. Gregory 1910; Novacek 1992). On the other hand, molecular biologists consider that Dermoptera have nothing to do with Chiroptera and are closely — and exclusively — related to Scandentia (the Sundatheria according to Olson *et al.* 2005), and that both are related to Primates (Euarchonta; e.g. Liu & Miyamoto 1999; Waddell *et al.* 1999; Murphy *et al.* 2001a; Springer *et al.* 2003, 2004; but also Sarich & Cronin 1976). For some other molecular biologists, cynocephalids are definitely primates, and more precisely the sister group of the Anthropeidea (Murphy *et al.* 2001b; Arnason *et al.* 2002; but see Schmitz *et al.* 2002 for a contrary opinion). From a palaeontological point of view, this phylogenetic issue is somewhat more complex, especially because of the ambiguity related to the definition of the taxon ‘Dermoptera’, which is used to cover several different combinations of eutherians. Many of these complications arise from the conflicting views regarding the phylogenetic position of some Palaeogene taxa, such as the plagiomenids (e.g. Matthew 1918; Simpson 1945; Rose 1973, 1975; Rose & Simons 1977) and paromomyid plesiadapiforms (Beard 1989, 1990, 1993a,b; Kay *et al.* 1990, 1992; McKenna & Bell 1997), for which affinities with extant cynocephalids have long been advanced. However, these possible plagiomenid–cynocephalid and paromomyid–cynocephalid links have recently been re-evaluated and challenged by new palaeontological evidence. The Plagiomenidae are now considered as *incertae sedis* within Eutheria (after MacPhee *et al.* 1989; but see the works of Silcox 2001, which still support the traditional alliance of

plagiomenids with cynocephalids), while the Paromomyidae are likely to be more closely related to other Palaeogene Plesiadapiformes and Eocene Euprimates than to extant dermopterans (Bloch & Silcox 2001; Silcox 2001; Sargis 2002a). As a result, the family Cynocephalidae alone would compose the entire order Dermoptera (as suggested by Ducrocq *et al.* 1992). Considering this specific systematic context, it is important to note that the evolutionary history of the Dermoptera *sensu stricto* therefore remains virtually unknown inasmuch as the fossil record of cynocephalids is practically non-existent. Indeed, despite their current relative abundance in south-eastern Asia, fossils of flying lemurs are extremely rare. Until recently, only one very worn fossil fragment of mandible belonging to a large species (*Dermotherium major* Ducrocq, Buffetaut, Buffetaut-Tong, Jaeger, Jongkanjana-soontorn & Suteethorn, 1992) was reported from the late Eocene Krabi coal mine in Peninsular Thailand (Fig. 1). However, according to Stafford & Szalay (2000), the dermopteran affinities of this specimen remain uncertain because of its poor stage of preservation (but see Silcox *et al.* 2005, for a contrary opinion).

Recent collaborative field expeditions in Peninsular Thailand [Thai–French team: Department of Mineral Resources (DMR), Bangkok–‘Institut des Sciences de l’Évolution’, Montpellier (ISE-M)], in central Pakistan [Pakistani–French team: Earth Sciences Division of the Pakistan Museum of Natural History (PMNH), Islamabad–‘Mission Paléontologique Française au Balouchistan’ (MPFB)–ISE-M], and in central Myanmar (Myanmar–French team: Geology Department of the Yangon University–ISE-M) have led to the recovery of several dermopteran fossils of different ages through the Palaeogene. The material consists of fragments of mandibles and isolated teeth (upper and lower) that have been collected by surface findings, excavations, or by screen-washing operations of the excavated residues. Most of specimens described in this paper come from the Cha Prong pit of the Nong Ya Plong coal mine in Thailand (Phetchaburi Province; Fig. 1), which is late Oligocene in age (Marivaux *et al.* 2004). In Myanmar, fossils come from Paukkaung Kyitchaung no. 2 (PK2; Fig. 1) in the Pondaung Formation, which is late middle Eocene in age (Benammi *et al.* 2002; Soe *et al.* 2002; Tsubamoto *et al.* 2002). Finally, the material from Pakistan (eastern Balochistan) has been recovered from the lower Chitarwata Formation (Bugti Member) in the Bugti Hills (Paali Nala, DBC₂), which is early Oligocene in age (Marivaux *et al.* 1999; Welcomme *et al.* 2001). The abundant fossil material from Nong Ya Plong (SHM-CP 363, 368, 374, TF 6183, TF 6184) allows us to describe here a new species of the genus *Dermotherium*: *D. chimaera* sp. n. The specimen from Pakistan is referred to this new taxon, while those from Myanmar remain indeterminate because of the paucity of the fossil material and due to their unusual dermopteran dental

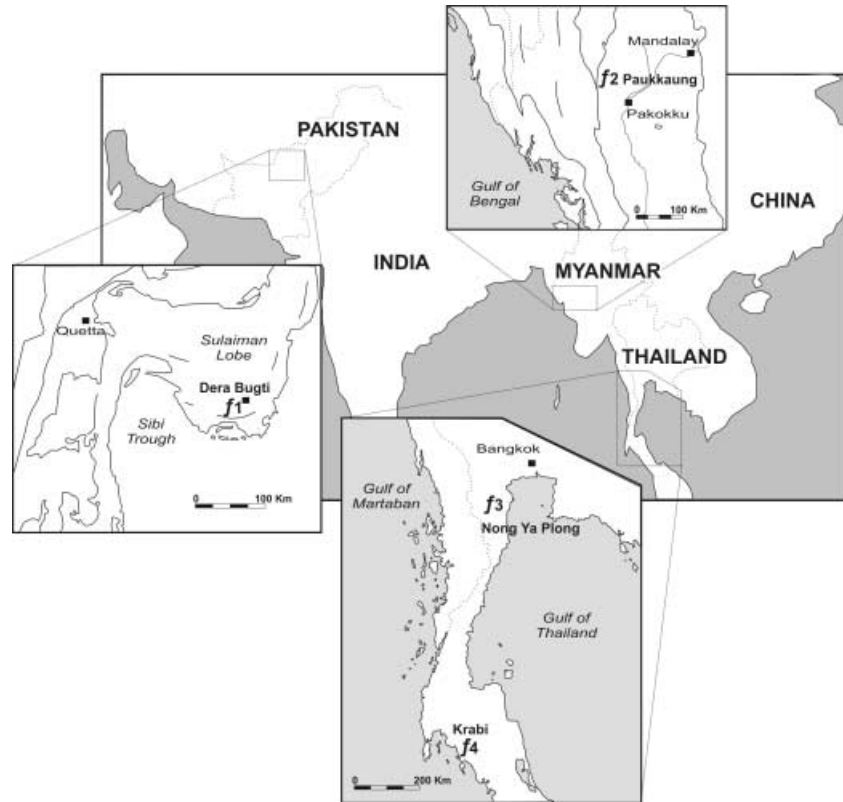


Fig. 1 Map of South Asia showing the geographic location of the Palaeogene fossiliferous localities (denoted by the symbol ‘f’) situated in Pakistan, Myanmar and Thailand, which have yielded dental remains of dermopterans. *f1*, Paali Nala level C₂ (DBC₂), Bugti Hills, Gandoi syncline, southern part of the Sulaiman Lobe, Pakistan (Balochistan); *f2*, Paukkaung Kyitchaung locus no. 2 (PK2), north of the village of Paukkaung, Pondaung area, central Myanmar; *f3*, Cha Prong pit, Nong Ya Plong coal mine, Phetchaburi Province, Peninsular Thailand; *f4*, Wai Lek pit, Changwat Krabi coal mine (type locality of *Dermotherium major*), Peninsular Thailand.

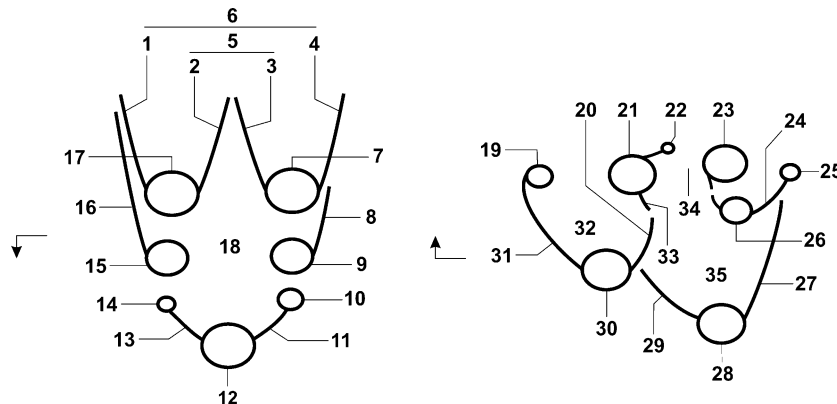


Fig. 2 Occlusal dental morphology of upper and lower teeth of dermopterans and related nomenclature (modified after Stafford & Szalay 2000). Upper teeth: —1. preparacrista; —2. postparacrista; —3. premetacrista; —4. postmetacrista; —5. centrocrista; —6. eocrista; —7. metacone; —8. postmetaconule crista; —9. metaconule; —10. protostyle β; —11. postprotocrista; —12. protocone; —13. preprotocrista; —14. protostyle α; —15. paraconule; —16. preparaconule crista; —17. paracone; —18. trigon basin. Lower teeth: —19. paraconid; —20. protocristid; —21. metaconid; —22. postmetacristid (+ metastylid); —23. entoconid; —24. post-hypoconulid cristid; —25. distocuspid; —26. hypoconulid; —27. posteristid; —28. hypoconid; —29. cristid obliqua; —30. protoconid; —31. paracristid; —32. trigonid basin; —33. hypometacristid; —34. lingual talonid notch; —35. talonid basin.

morphology. Given the important gap in the fossil record of Dermoptera, these discoveries significantly improve our knowledge of the evolutionary history of that enigmatic and fascinating group. We will discuss these fossils with

special emphases on palaeobiogeographic and palaeoenvironmental implications. The dental terminology (Fig. 2) used for describing the new material is adapted from Stafford & Szalay (2000).

The following are abbreviations used in this paper. AMNH-VP, American Museum of Natural History (Vertebrate Palaeontology); DBC, Dera Bugti locus C; Pkg, Paukaung Kyitchaung; SHM-CP, Srisuk House Museum, Cha Prong; TF, Thai Fossil; UMC, Université Montpellier II Collection; USNM, United States National Museum of Natural History; YPM-PU, Yale Peabody Museum (Princeton University collections).

Methods

X-ray synchrotron microtomography analyses

In order to be able to study two of the fossils described hereafter (SHM-CP 368 and SHM-CP 374), we used X-ray synchrotron microtomography (SR- μ CT) on the beamline ID19 at the European Synchrotron Radiation Facility (ESRF, Grenoble, France). Thanks to the particular properties of the X-ray beams used at the ESRF for SR- μ CT (monochromaticity, nearly parallel geometry and high flux), reconstructed slices are free of beam-hardening and geometric artefacts (Salvo *et al.* 2003). High-quality pictures can be rapidly obtained, especially on fossils (Chaimanee *et al.* 2003; Tafforeau 2004; Brunet *et al.* 2005; Tafforeau *et al.* 2006; Marivaux *et al.* in press).

For the investigations of the SHM-CP 363 specimen (Fig. 3A,B), we used an optical system linked to a CCD FreLoN camera (Fast Read-out Low Noise) giving a pixel size of 10.13 microns for a 1024*1024 pixels field of view. We used a 40 keV monochromatic beam. Three scans were performed (900 projections of 1 s each on a half rotation) to image the complete fossil. After a conversion of the original 32 bits data into 8 bits slices, the reconstructed volumes were aligned and concatenated in order to obtain a single volume of the whole sample. The sample was then separated from the background on each slice using a script developed with Photoshop 5.5 (Adobe System, Inc., San Jose, CA, USA) for automatic processing of SR- μ CT slices.

On this dataset, we observed four unerupted teeth germs. As their enamel exhibited higher X-ray absorption values than the surrounding bone dentin and matrix, we performed a segmentation using 3D region growing of all the germs, represented by their enamel cap (Fig. 3C,D). A specific volume was defined for each tooth in order to be able to study them separately with specific orientations (Fig. 4).

This peculiar fossil exhibited a lot of small pyrite crystals on its jugal side and around the tooth germs that prevented us from observing the unerupted germs using classical radiographs. Pyrite crystals were segmented and removed from the volume by thresholding and series of dilatation/erosions. Figure 3C is then a pseudo-radiograph that was generated from the microtomographic data after the removal of the pyrite crystals and the segmentation of the teeth. It allowed us to enhance the germs inside the dentary as if there were no pyrite and as if the absorption contrast between enamel and the rest of the fossil is stronger than the present one.

For the SHM-CP 374 sample (Fig. 5), we used a pixel size of 30 microns on the ID19 beamline of the ESRF. The energy was this time 50 keV. We used such a high energy because this fossil was scanned with the other samples. Regarding also its bad preservation state, we considered a 30- μ m resolution to be sufficient. The dentary bone of this fossil was surrounded by a lignite matrix. As the lignite X-ray absorption was much lower than that of the bone, dentin or enamel, the matrix was virtually removed during the 3D processing by a simple thresholding.

All the pictures derived from SR- μ CT dataset presented here were generated using the software VGStudioMax 1.1 (Volume Graphics, Heidelberg, Germany).

Phylogenetic analyses

In order to formalize the phylogenetic position of the new cynocephalid species described hereafter with respect to the extant cynocephalid forms, we have conducted a cladistic assessment of the dental evidence. Dermopterans were examined within a context of higher-level phylogeny (Euarchonta), together with Scandentia, Primates (Plesiadapiformes + Euprimates) and Plagiomenidae (Eutheria *incertae sedis*, after MacPhee *et al.* 1989). Primates and the genus *Plagiomene* (plagiomenid) were designated as outgroups. The description of selected characters and the data matrix are presented in Appendices 1 and 2, respectively. Data were managed by MacClade 3.04 (Maddison & Maddison 1992). Phylogenetic reconstructions were performed by PAUP* 4.0 beta 10 Win (Swofford 2002) using a Branch and Bound algorithm of search. The degree of sample error for particular nodes was evaluated with the Decay index (DI) by AutoDecay 3.0.3 (Erikson 1997), using Branch and Bound searches retaining suboptimal trees ('topological constraints enforced' in PAUP). The clade robustness was also measured by the Bootstrap percentages (BP) in equally weighted maximum parsimony (after 1000 iterations).

Systematic palaeontology

Order Dermoptera Illiger, 1811

Family Cynocephalidae Simpson, 1945

Genus *Dermotherium* Ducrocq, Buffetaut, Buffetaut-Tong, Jaeger, Jongkanjanasontorn & Suteethorn, 1992

Type species. *Dermotherium major* Ducrocq *et al.* (1992). (Fig. 9A)

Included species. *Dermotherium chimaera* sp. n. (Figs 3–7 and 9B,C)

Emended diagnosis. Large-bodied cynocephalids, slightly larger than the megadont *Cynocephalus volans*. Differs from *Galeopterus* and *Cynocephalus* in having lower molars with stronger and cuspidate paraconids, well-developed metastylids,

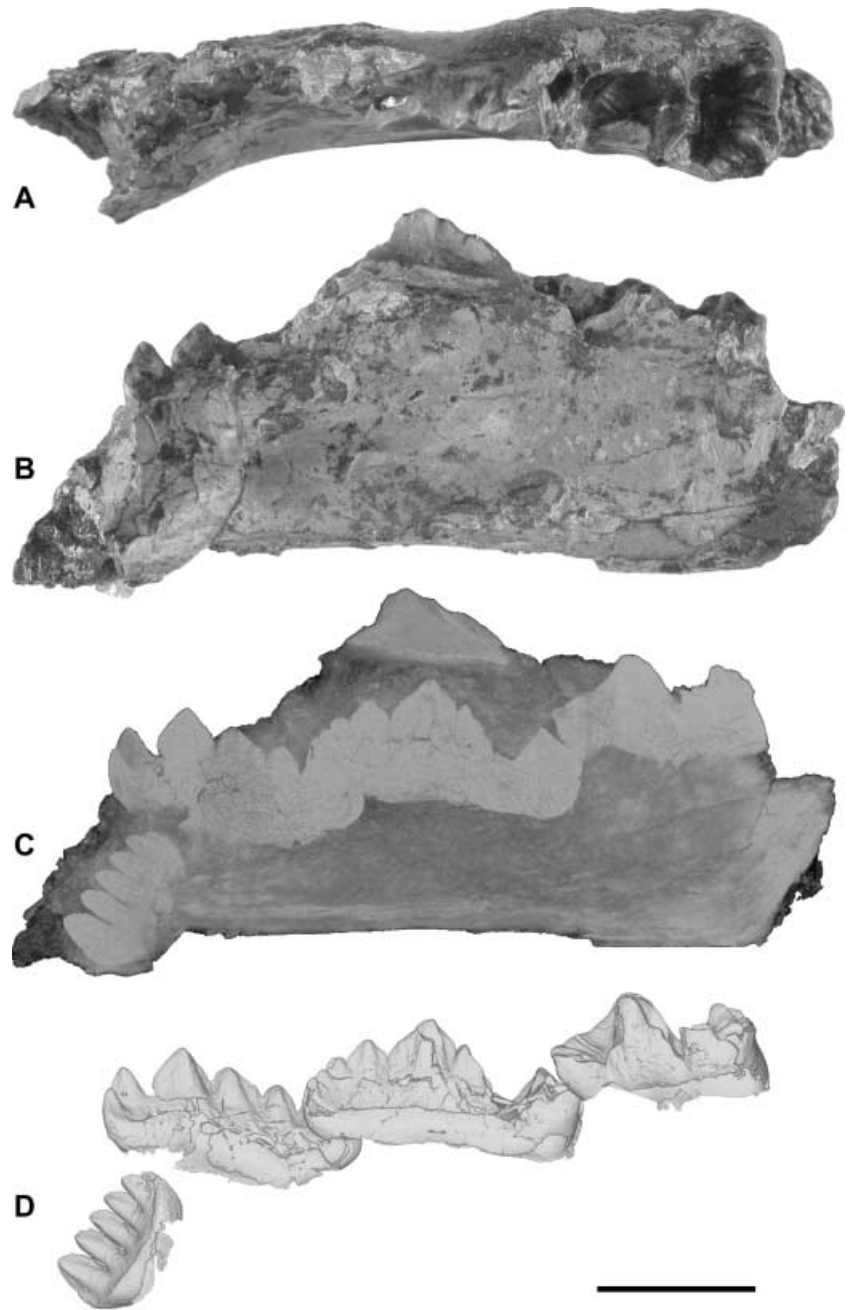


Fig. 3 A–D. SHM-CP 363, fragment of right mandible of a juvenile individual of *Dermotherium chimaera* new species, from the late Oligocene Nong Ya Plong coal mine (Cha Prong pit) in Thailand. —A. Occlusal view; —B. lingual view; —C. pseudo-microradiograph of the mandible revealing the presence of definitive i3, c, p3, and p4 inside the dentary (on the top, note the remaining fragment of a deciduous p3). —D. Lingual view of teeth virtually extracted from the jaw by 3D segmentation of their enamel cap. The pictures C and D have been generated from 3D data obtained by X-ray synchrotron microtomography (SR- μ CT). Scale bar, 5 mm.

strong and taller metaconids from p4 to m3, in having upper molars with protocones less mesially displaced, stronger buccal cingula, the presence of two additional cusps (protoconules α and β) on the buccal extremities of the protocone cristae, and in showing better development of preparaconule cristae and postmetaconule cristae. Differs from *Cynocephalus* in having i3, c and the trigonid of p3 serrated, lower molars with U-shaped talonid lingual notches, and in showing the

hypoconulids and entoconids close but well distinct. Differs from *Galeopterus* in showing lower teeth decreasing in size from p4 to m3, lower molars having their trigonids less mesiodistally constricted, talonids with stronger distocuspids, cristid obliquae distolingually connected to protoconids, a postcristid–distocuspids connection, and in having upper molars with V-shaped centrocrisae and the presence of accessory enamel wrinkles.

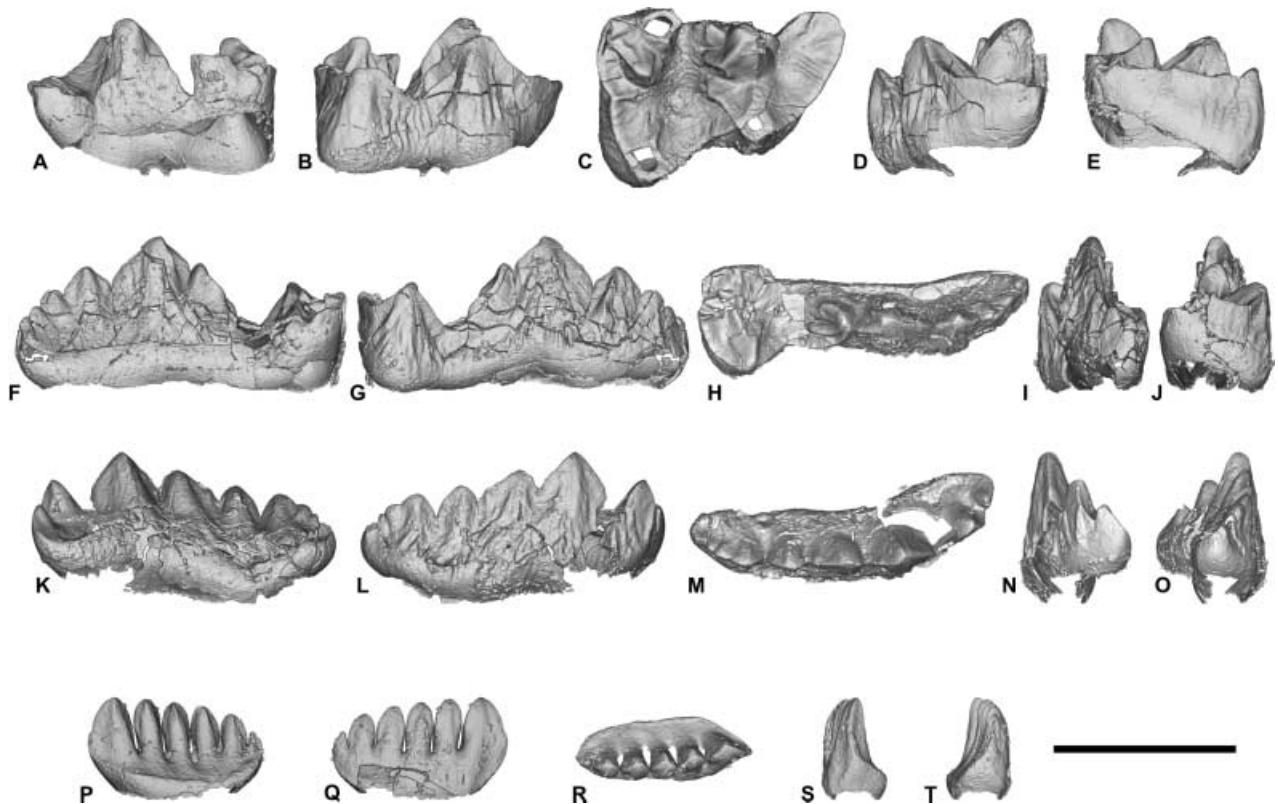


Fig. 4 A–T. Three-dimensional (3D) rendering of the tooth germs of SHM-CP 363. —A–E. p4 in lingual (A), buccal (B), occlusal (C), mesial (D), and distal (E) views. —F–J. p3 in lingual (F), buccal (G), occlusal (H), mesial (I), and distal (J) views. —K–O. Canine in lingual (K), buccal (L), occlusal (M), mesial (N), and distal (O) views. —P–T. i3 in lingual (P), buccal (Q), occlusal (R), mesial (S), and distal (T) views. The pictures have been generated from 3D data obtained by SR- μ CT. Scale bar, 5 mm.

***Dermotherium chimaera* sp. n.**

Holotype. SHM-CP 363, fragment of right mandible bearing permanent i3, c, p3, and p4 inside the dentary (Figs 3A–D and 4A–T). The specimen is stored in the palaeontological collections of the Department of Mineral Resources (DMR) in Bangkok, Thailand.

Hypodigm. SHM-CP 374, fragment of right mandible bearing m2 and m3 (Figs 5A–C and 9B); SHM-CP 368, fragment of right m1 and m2 (Fig. 9C); TF 6183, left M1 (Fig. 6F–J); TF 6184, left M2 (Fig. 6A–E).

Type locality. Cha Prong pit, Nong Ya Plong coal mine, Phetchaburi Province, northern part of the Peninsular Thailand (Fig. 1).

Age. Late Oligocene (Marivaux *et al.* 2004).

Etymology. Latin ‘*chimaera*’, chimera. The name derives from the peculiar nature of the dental morphology of this new fossil, which exhibits a mosaic of characters found in both extant dermopterian taxa (*Cynocephalus volans* and

Galeopterus variegatus, the Philippine and Sundaic flying lemurs, respectively).

Diagnosis. Differs from *Dermotherium major* in having lower molars with trigonids less buccolingually constricted, talonids with hypoconulids much more mesially displaced, the development of strong and long post-hypoconulid cristids, and in bearing small but well-distinct distocuspids on the distolingual corners of teeth.

Description

Lower dentition (virtually revealed by SR- μ CT). The i3 of SHM-CP 363 bears six tines, which are pectinately arranged in showing a mesiodistal decrease in the tine height (Fig. 4P–T; Table 1). Tines nos 2, 3, 4, and 5 are similar in width, while tine no. 1 (mesial) is twice as wide, and tine no. 6 (distal) is very thin and squat.

The canine of SHM-CP 363 is buccolingually narrow, mesiodistally elongated, slightly curved mesially, and entirely serrated (Fig. 4K–O; Table 1). Structurally, it consists of a series of cuspsules (six) along the crest of the tooth (buccal

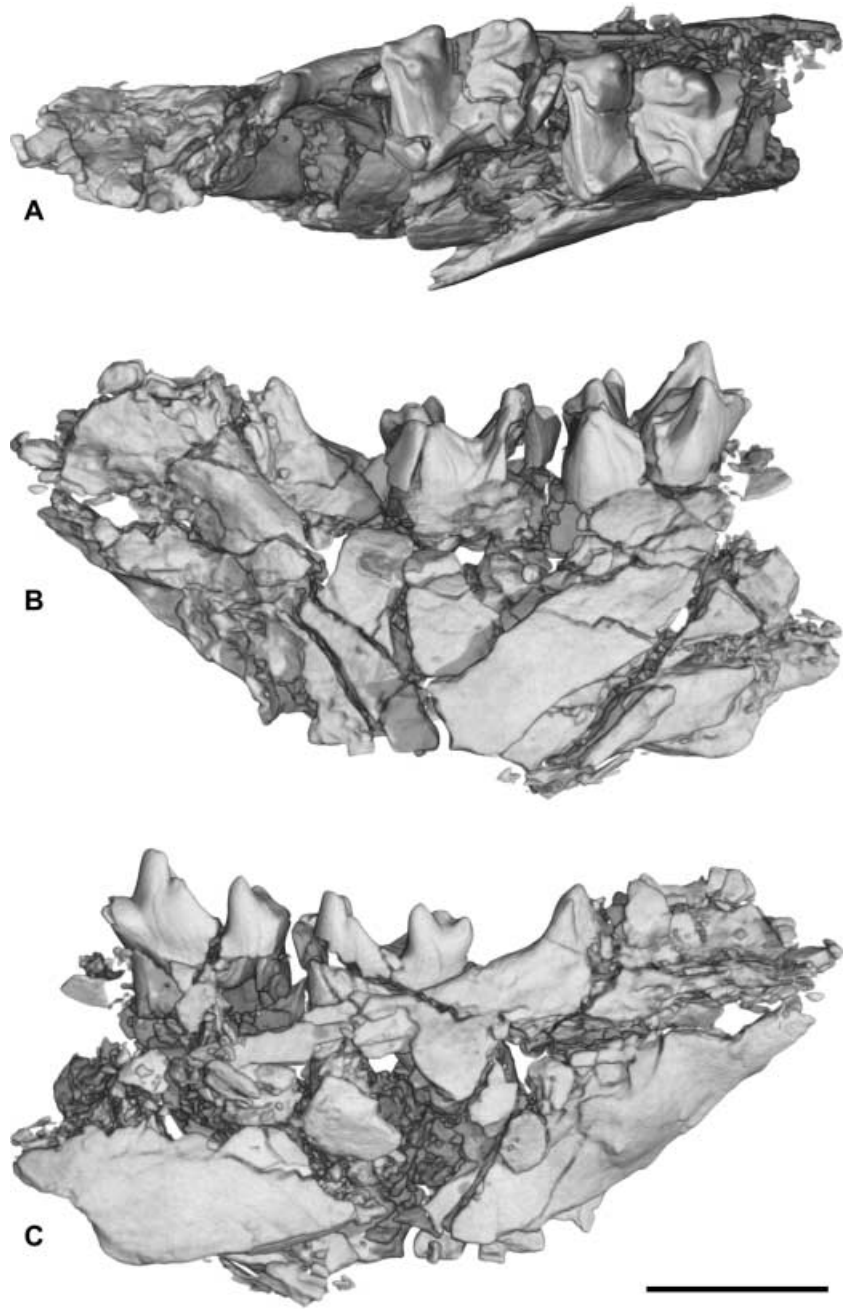


Fig. 5 A–C. Three-dimensional (3D) rendering after removal of the lignite matrix by thresholding of SHM-CP 374, fragment of right mandible bearing m2 and m3 of *Dermotherium chimaera* new species, from the late Oligocene Nong Ya Plong coal mine (Cha Prong pit) in Thailand. —A. Occlusal view; —B. buccal view; —C. lingual view. The pictures have been generated from 3D data obtained by SR- μ CT. Scale bar, 5 mm.

margin). One of these cuspules (the third from the front) is slightly larger and higher with respect to the others, and might correspond to the protoconid. There are two cuspules mesial to this main cuspid and three distal to it, which decrease in size mesiodistally. The distal cuspule is low and shows a secondary serration on its distal edge.

As the canine, the p3 of SHM-CP 363 is mesiodistally elongated and slightly curved mesially (Fig. 4F–J; Table 1). On this tooth, only the mesial part is buccolingually narrow

(blade-like trigonid) and serrated. The distal part is, in contrast, wider and forms a talonid. The mesial serration consists of a series of cuspules situated on both sides of the very high and buccolingually compressed protoconid (four on the mesial side and one on the distal side). The first cuspules distal and mesial to the protoconid could correspond to a metaconid and a paraconid, respectively. Distobuccally, the talonid shows a strong and elevated hypoconid that is connected to a short and lingually orientated cristid obliqua. A smaller but well-defined

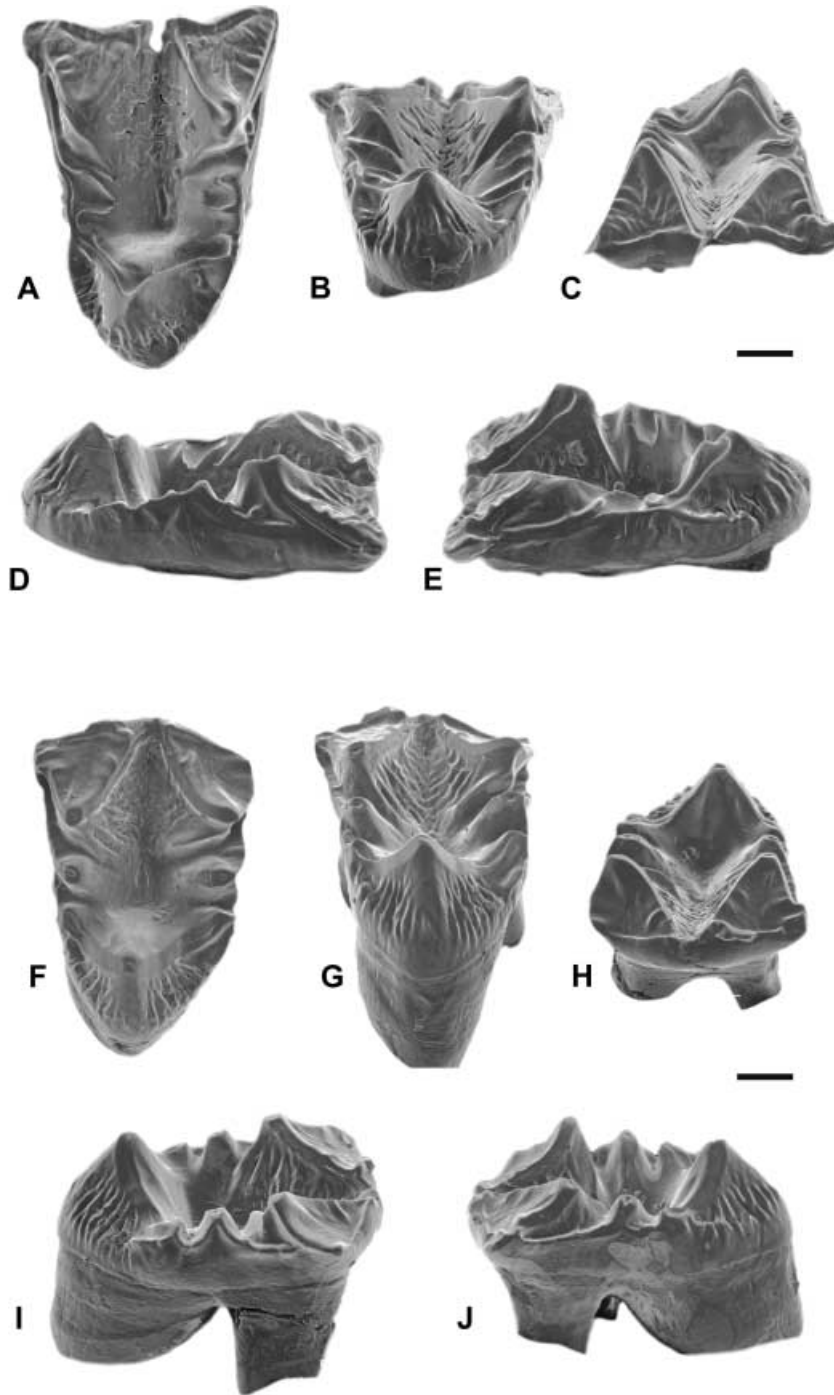


Fig. 6 A–J. Isolated upper teeth (SEM micrographs) of *Dermotherium cbimaera* new species, from the late Oligocene Nong Ya Plong coal mine (Cha Prong pit) in Thailand. —A–E. TF 6183, left M1 in occlusal (A), lingual (B), buccal (C), distal (D), and mesial (E) views. —F–J. TF 6184, left M2 in occlusal (F), lingual (G), buccal (H), distal (I), and mesial (J) views. Scale bar, 1 mm.

hypoconulid occurs lingual to the hypoconid on the lingual margin of the tooth. There is seemingly no distinct entocoid. These two talonid cusps are well separated but linked distally by a sharp posteristid. The cristid obliqua and the posteristid delimit a rudimentary and shallow talonid basin.

The p4 of SHM-CP 363 is molariform and shows broad trigonid and talonid basins (Fig. 4A–E; Table 1). A low and

sweeping paracristid expands mesiolingually to form a broad mesial lobe. There is no cuspidate paraconid. The metaconid appears as the tallest cuspid of the tooth. However, the surface of wear (post-mortem since p4 was unerupted) on the apex of the protoconid suggests that this cuspid was certainly of similar height to the metaconid. A short protocristid extends distolingually and ends in the mesial part of the

Table 1 Dental measurements of dermopterans from the Palaeogene of South Asia. Length (L) and width (W) in mm (measurements made with a measurescope Nikon 10, coupled with a digital counter CM-6S). Measurements on the virtual teeth of SHN-CP 363 were performed on the 3D pictures using Photoshop 5.5 after a calibration of the pixel size.

Taxon	Locality	Age	Specimen	Tooth	L	W
<i>Dermotherium chimaera</i>	Nong Ya Plong (Thailand)	Late Oligocene	SHM-CP 363	right i3	5.3	1.9
				right c	8.1	2.3
				right p3	9.2	3
				right p4	6.6	4.8
<i>Dermotherium chimaera</i>	Nong Ya Plong (Thailand)	Late Oligocene	SHM-CP 368	right m1	5.2	4.2
				right m2	5	4.3
<i>Dermotherium chimaera</i>	Nong Ya Plong (Thailand)	Late Oligocene	SHM-CP 374	right m2	5.4	4.8
				right m3	5.1	4.2
<i>Dermotherium chimaera</i>	Nong Ya Plong (Thailand)	Late Oligocene	TF 6183	left M1	5.4	7.1
<i>Dermotherium chimaera</i>	Nong Ya Plong (Thailand)	Late Oligocene	TF 6184	left M2	4.7	6.6
<i>Dermotherium cf. chimaera</i>	Bugti Hills (Pakistan)	Early Oligocene	UMC-DBC 2190	left M2	4.3	6
<i>Dermotherium major</i>	Krabi (Thailand)	Late Eocene	TF 2580	left m2	5.4	4.9
				left m3	5.4	4.6
<i>Dermoptera indet.</i>	Pondaung (Myanmar)	Latest middle Eocene	Pkg 240	left c	6.4	2
<i>Dermoptera indet.</i>	Pondaung (Myanmar)	Latest middle Eocene	Pkg 355	right m2	6.2	4.2

talonid basin. A short hypometacristid develops also from the metaconid and extends distobuccally towards the distal extremity of the protocristid. A short postmetacristid slightly lengthens the lingual wall of the metaconid distally. The talonid is twice as wide as the trigonid due to the buccal displacement of the hypoconid with respect to the protoconid. The cristid obliqua joins the base of the protoconid and ascends its distolingual face. Lingually, the entoconid and postmetacristid are separated by a narrow and deep notch. The hypoconulid is lingually and mesially displaced, and occurs slightly distolingually to the entoconid. Both cuspids are equivalent in size and are twinned. A thin post-hypoconulid cristid extends distolingually from the hypoconulid, and ends at the distolingual corner of the tooth. The distal extremity of this crest shows a minute enamel swelling that corresponds to the distocuspids. The postcristid occupies the whole breadth of the tooth, passes distal to the hypoconulid, and connects the post-hypoconulid cristid at the level of the distocuspids.

The lower molars (m1, m2, and m3) have a dental pattern similar to that of the p4. The description of these three molars derives from the observation of two fragments of mandible, one bearing m1 and m2 (SHM-CP 368; Fig. 9C; Table 1), the other bearing m2 and m3 (SHM-CP 374; Figs 5A–C and 9B; Table 1). Despite the composite molar association making up the toothrow (SHM-CP 363–368–374), it clearly appears that the size of teeth slightly decreases from p4 to m3. Molars differ from p4 in showing a trigonid much more constricted mesio-distally. On the better-preserved specimen (SHM-CP 368), the trigonid is characterized by the presence of a strong and cuspidate paraconid, which is mesiolingual to the metaconid. There is a low and thin paracristid linking the paraconid to the protoconid. The protocristid is short and distolingually directed,

and it ends in the mesial part of the talonid basin. On the three molars, the metaconid is the tallest cuspid, and it is more buccal with respect to the paraconid and the entoconid. The postmetacristid is short and buccolingually directed, and bears a small enamel swelling in its mesial part (metastyloid). The postmetacristid and the entoconid are separated by a deep and narrow U-shaped lingual notch. The talonid of the molars is broad with a hypoconid more buccal than the protoconid. The cristid obliqua reaches the base of the trigonid wall and ascends the distolingual face of the protoconid. The entoconid is mesially displaced and occurs slightly more mesial with respect to the hypoconid (along the buccolingual axis). As on p4, the hypoconulid is lingually and mesially displaced, and appears distolingual to the entoconid (hypoconid–entoconid twinning). Both cuspids are equivalent in size and form a structure that raises above the talonid basin. The post-hypoconulid cristid extends distolingually and bears a distinct distocuspids on its distal extremity, which occupies the distolingual corner of the teeth. From the hypoconid, the postcristid extends lingually, passes distal to the hypoconulid, and connects to the distocuspids. The distocuspids abuts against the paraconid of the following tooth, involving a strong intermolar contact lingually.

Upper dentition. The upper molars (Fig. 6) are characterized by strong developments of both paracone cristae (pre- and post-) and metacone cristae (pre- and post-). These buccal crests constitute the dominant and highly dilambodont (W-shaped) eocrista. On both teeth, the buccal flanks of the paracone and metacone are strongly canted and buccally limited by a continuous gutter-like cingulum. The centrocrista (postparacrista + premetacrista) appears as a V-shaped buccal notch. M2 (TF 6184; Fig. 6A–E; Table 1) differs from M1

(TF 6183; Fig. 6F–J; Table 1) in having well-developed and distinct conules, and in showing shorter preparacrista and postmetacrista buccally. On M2, the paraconule and metaconule are lingual and isolated from the paracone and metacone, respectively. Mesially, the paraconule develops a thin and low preparaconule crista, which reaches the preparacrista buccally. Similarly but distally, the metaconule develops a thin and low postmetaconule crista, which reaches the postmetacrista buccally. On M1, the paraconule is lacking and the metaconule is reduced and rather crestiform (pinched mesiodistally). Lingually, the protocone is slightly displaced mesially and develops both strong and long preprotocrista and postprotocrista, which are mesio buccally and distobuccally orientated, respectively, and not connected to the conules. The postprotocrista is nearly as long as the preprotocrista. These two protocone cristae exhibit small enamel swellings on their buccal extremities, which are identified here as protoconule α and protoconule β (see Fig. 2). Mesially, the paracone, paraconule and protoconule α are buccolingually aligned. Similarly, the metacone, metaconule and protoconule β are buccolingually aligned. The protocone is bordered mesially and distally by low and short cingula that connect the two protoconules (α and β) buccally. There is neither lingual cingulum nor hypocone. Upper molars are also characterized

by the presence of accessory enamel wrinkles that occur on the lingual flank of the protocone, and in the trigon basin, especially on the flanks of the paracone and metacone.

Comparison

Teeth of *Dermotherium chimaera* sp. n. from Nong Ya Plong are nearly as large as those of the modern ‘megadont’, *Cynocephalus volans*, from the Philippines, and approximately three times as large as teeth of the most dwarfed subspecies forms of *Galeopterus variegatus* from the Sundaic Province. The fragment of left mandible, SHM-CP 363, although worn and badly broken, is particularly interesting since it bears a part of the permanent front dentition (i3 and C) and two premolars (p3 and p4) still included in the dentary (revealed by SR- μ CT; Fig. 3). The computed 3D virtual reconstruction of the dentition of this juvenile individual (Fig. 4) provides an important set of characters that are essential for understanding the affinities of this new species. One of the most significant feature is the unusual pectination of the front dentition (i3 and c), which extends farther back to influence the mesial part of the p3. Such a condition matches that observed in *Galeopterus*, and differs from that in *Cynocephalus*, in which the pectination stops at the level of i3 (Fig. 10). In *Cynocephalus*, i3 has three to five tines (Table 2), while i3 in *Galeopterus* is

Table 2 Comparisons of dental features in fossil and extant dermopteran taxa from South Asia.

Lower teeth	<i>Cynocephalus volans</i>	<i>Galeopterus variegatus</i>	<i>Dermotherium chimaera</i> sp. n.
i3, number of tines	3–5	4–7	6
Canine	Tall, not serrated	Squat, serrated	Squat, serrated
Trigonid of p3	Blade-like	Blade-like, serrated	Blade-like, serrated
Tooth size on the toothrow	Decreases from p4 to m3	Increases from p4 to m3	Decreases from p4 to m3
Metaconid/protoconid from p4 to m3	> on p4 and m1 < on m2 and m3	> on p4 and m1 < on m2 and m3	> from p4 to m3
Molar trigonid shape	V-shaped	V-shaped but mesiodistally constricted	V-shaped
Molar paraconid	Small	Minute	Strong
Molar metaconid position	Mesial to entoconid	Mesial to entoconid	Mesio buccal to entoconid
Metastylid	Absent	Absent	Present
Talonid lingual notch	V-shaped	U-shaped	U-shaped
Cristid obliqua direction and termination	Point distolingual to protoconid	Point distobuccal to protoconid	Point distolingual to protoconid
Hypoconulid-entoconid twinning	Cuspids merged	Cuspids close but separated	Cuspids close but separated
Distocuspid	Strong	Small	Strong
Post-hypoconulid cristid	Short	Short	Long
Postcristid connection	Distocuspid	Hypoconulid (distally)	Distocuspid
Intermolar contacts	Strong	Absent (interstitial spaces)	Strong
Upper teeth			
Protocone position	Mesially displaced	Mesially displaced	Slightly mesially displaced
Protoconules (α and β)	Absent	Absent	Present
Centrocrista	V-shaped	U-shaped	V-shaped
Metaconule	Hypertrophied and distolingually displaced	Strong and slightly distally displaced	Strong but not distally displaced
Paraconule	Small	Strong	Strong
Preparaconule crista	Weak and short	Weak and short	Well-developed and long
Postmetaconule crista	Weak and short	Absent	Well-developed and long
Buccal cingulum	Weak but well-distinct	Weak, indistinct	Strong (gutter-like)
Enamel wrinkles	Trigon basin	Absent	Trigon basin and lingual flank of protocone

lower and exhibits four to seven tines (Stafford & Szalay 2000). The i3 in *D. chimaera* is rather *Galeopterus*-like in showing six tines. As in *Galeopterus*, the canine in *D. chimaera* is low and serrated (mesially and distally to the main cuspid), while it is monocuspidate, taller, and without serration in *Cynocephalus* (Fig. 10). The same is true for the mesial part of the p3, which is characterized by a blade-like trigonid in both living taxa and in *D. chimaera*, but only in *Galeopterus* and *D. chimaera* is the trigonid serrated. In *Cynocephalus*, the protoconid is taller and the paracristid and protocristid are elevated and sharp, while in *Galeopterus* and *D. chimaera*, the protoconid is much more squat and the mesial and distal crests are very short, strongly attenuated, and disrupted by cuspules. As in *Galeopterus* and *Cynocephalus*, the trigonid of p3 in *D. chimaera* lacks the entoconid, and the hypoconulid is mesially displaced and far lingual to the hypoconid. As we have already mentioned in the description, despite the composite molar association making up the lower toothrow of *D. chimaera* (SHM-CP 363–368–374), it clearly appears that the size of teeth slightly decreases from p4 to m3. Such a condition matches that observed in *Cynocephalus* and *D. major*, and differs from that in *Galeopterus*, in which there is generally a slight increase from p4 to m3 (Fig. 10). The molars of *D. chimaera* have a tricuspidate trigonid with a strong and elevated paraconid (observable in SHM-CP 368; Fig. 9C). A paraconid is present in lower molars of *Cynocephalus* and *Galeopterus* but significantly lower and even absent on the m3 of *Galeopterus*. The configuration of the trigonid in *D. chimaera* is close to that in *Cynocephalus* (i.e. lingually open and V-shaped), while it is mesiodistally and buccolingually constricted, somewhat shrunken in *Galeopterus* (Fig. 10). This trigonid reduction on molars of *Galeopterus* involves small intermolar interstitial spaces, while there are strong intermolar contacts on lower toothrows of *Cynocephalus* and *D. chimaera*. In *Cynocephalus* and *Galeopterus*, the protoconid is the tallest cuspid on p4 and m1, while the metaconid is the tallest on m2 and m3. *Dermotherium chimaera* differs from both living genera in showing a strong metaconid on each tooth, which remains the tallest cuspid from p4 to m3. In *D. chimaera*, the position of the metaconid differs also from both living genera in being buccally displaced with respect to the entoconid (Fig. 9B–C). As in *D. major*, lower molars of *D. chimaera* develop a stronger and buccolingually directed postmetacristid, which bears a distinct metastylid in its mesial part. Such a dental feature does not occur in *Galeopterus* and *Cynocephalus*. As in *Cynocephalus* and *D. major*, the cristid obliqua in *D. chimaera* reaches the base of the trigonid wall and ascends the distolingual face of the protoconid, while it joins the base of the protoconid slightly more buccally in *Galeopterus*. In the three genera, the hypoconulid is lingually and mesially displaced (mesial displacement much less marked in *D. major*; Fig. 9A), and it is twinned with the entoconid in forming a structure that

raises above the talonid basin. However, in *Galeopterus* and *Dermotherium*, the hypoconulid and entoconid remain distinct and well separated, while both cuspids are merged in *Cynocephalus*. In *Galeopterus*, the postcristid reaches the hypoconulid distally (mesial extremity of the post-hypoconulid cristid), while in *Cynocephalus* and *D. chimaera*, this crest is longer, passes distal to the hypoconulid, and reaches the distocuspids, which is stronger than in *Galeopterus*. In *D. major*, the post-hypoconulid cristid and the distocuspids are lacking, the postcristid ends distolingually to the hypoconulid. Finally, the talonid lingual notch between the metaconid and the entoconid is widely open mesiodistally (U-shaped) in *D. chimaera* as it is in *D. major* and *Galeopterus*, while it forms a slightly more acute angle (V-shaped) in *Cynocephalus*.

As for the lower teeth, upper molars of *D. chimaera* differ substantially from those of *Cynocephalus* and *Galeopterus*, and also exhibit some specific affinities with each of both genera (Table 2). In overall morphology, upper molars of *D. chimaera* have a better bilateral symmetry in showing their protocone less mesially displaced than it is in *Cynocephalus* and *Galeopterus*. Both upper molars of *D. chimaera* differ significantly in having two additional cusps that we identify as protoconules (α and β), which are situated at the buccal extremities of the preprotocrista and the postprotocrista, respectively. The conules are also smaller and slightly more buccal in position and close to the paracone and metacone than they are in *Cynocephalus* and *Galeopterus*. As in *Cynocephalus*, the centrocrista in *D. chimaera* is V-shaped (acute angle between the postparacrista and the premetacrista), while it is U-shaped in *Galeopterus* (Fig. 10). Finally, upper molars of *D. chimaera* show accessory enamel wrinkles, a feature that can be also observed (but not generally) in *Cynocephalus*.

Dermotherium cf. *chimaera*

Material referred. UMC-DBC 2190, left M2 (Fig. 7A–E). The specimen is housed in the collection of the Palaeontology Department, University of Montpellier II, France.

Locality. Paali Nala level C₂ (DBC₂), Gandoi syncline, south side of the Zin anticline, Bugti Hills, eastern Balochistan, Pakistan (Fig. 1).

Age and formation. Bugti Member, Lower Chitarwata Formation, early Oligocene (Welcomme *et al.* 2001).

Description

UMC-DBC 2190 (Fig. 7A–E; Table 1) exhibits a well-marked dilambdodont eocrista with a V-shaped centrocrista. The paracone, metacone, and protocone are strong and similar in size. The buccal flanks of the paracone and metacone are strongly canted, and the buccal cingulum is faintly visible. The conules are particularly well developed (nearly as

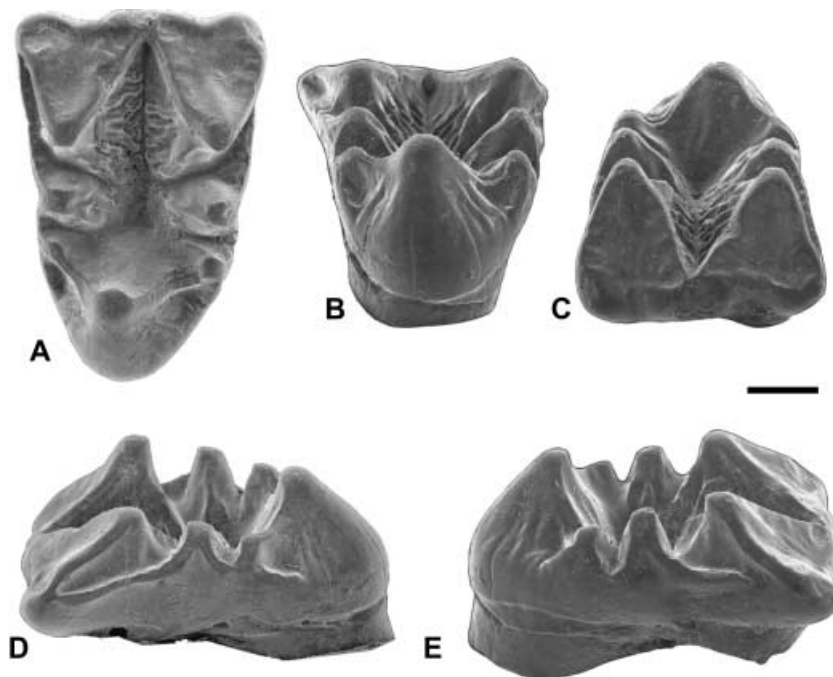


Fig. 7 A–E. Isolated upper tooth of *Dermotherium* cf. *chimaera* from the early Oligocene Chitarwata Formation (Bugti Member) of the Bugti Hills (Paali Nala, DBC₂) in Pakistan: UMC-DBC 2190, left M2 in occlusal (A), lingual (B), buccal (C), distal (D), and mesial (E) views. Scale bar, 1 mm.

large as the main cusps), isolated, and lingual to the buccal cusps. The paraconule and metaconule develop thin and low preparaconule crista and postmetaconule crista, respectively, which both reach the eocrista buccally (preparacrista and postmetacrista, respectively). The protocone is slightly displaced mesially. The protoconule β is relatively large (slightly smaller than the metaconule), while the protoconule α is minute. The two protoconules are separated from the conules and linked to the protocone by strong preprotocrista and postprotocrista. The paracone-paraconule-protoconule α as well as the metacone-metaconule-protoconule β are each buccolingually aligned. Lingually, there is neither cingulum surrounding the protocone nor hypocone. Accessory enamel wrinkles occur in the trigon basin, especially on the flanks of both the paracone and metacone, but not on the lingual flank of the protocone.

Comparison

This single isolated tooth (UMC-DBC 2190) from early Oligocene deposits of the Bugti Hills (Pakistan) is morphologically similar to those found from the late Oligocene coal mine in Nong Ya Plong (Thailand). The specimen from Pakistan differs, however, in being slightly smaller, in showing stronger development of conules and protoconules (α and β), less marked buccal cingulum, and in lacking enamel wrinkle on the lingual flank of the protocone. This tooth differs from the upper molars of *Galeopterus* and *Cynocephalus* by the same aforementioned character association that allows to distinguish the Thai form of Nong Ya Plong (*Dermotherium chimaera* sp. n.) from the two living dermopteran genera.

Dermoptera indet.

Material referred. Pkg 355, right m2 (Fig. 8A–E); Pkg 240, left lower canine (Fig. 8F,G). These specimens are stored in the National Museum of the Union of Myanmar, Yangon.

Locality. Paukkaung Kyitchaung locus no. 2 (PK2), north of the village of Paukkaung, Pondaung area, central Myanmar.

Age and formation. Lower part of the Upper Member of the Pondaung Formation, latest middle Eocene (Benammi *et al.* 2002; Tsubamoto *et al.* 2002).

Description

We identify as lower canine of dermopteran affinities a serrated tooth (Pkg 240; Fig. 8F,G; Table 1), which is double-rooted, buccolingually narrow, mesiodistally elongated, and slightly curved mesially. The structure of this tooth consists of a series of enamel cuspsules (five to six) that are in line along the crest of the buccal margin of the tooth. The third front cuspsule is slightly larger and higher with respect to the others, and might correspond to a protoconid. The homology of the remaining cuspsules is uncertain. There are two cuspsules mesial to this main cuspid and three distal to it, which decrease in size mesiodistally. The lingual margin of the tooth displays a low and rounded cingulid that extends mesiobuccally from the first to the last cuspsule.

The lower molar, Pkg 355 (Fig. 8A–E; Table 1) is characterized by a very broad talonid basin, which is nearly three times as broad as the trigonid basin. The trigonid is mesiodistally

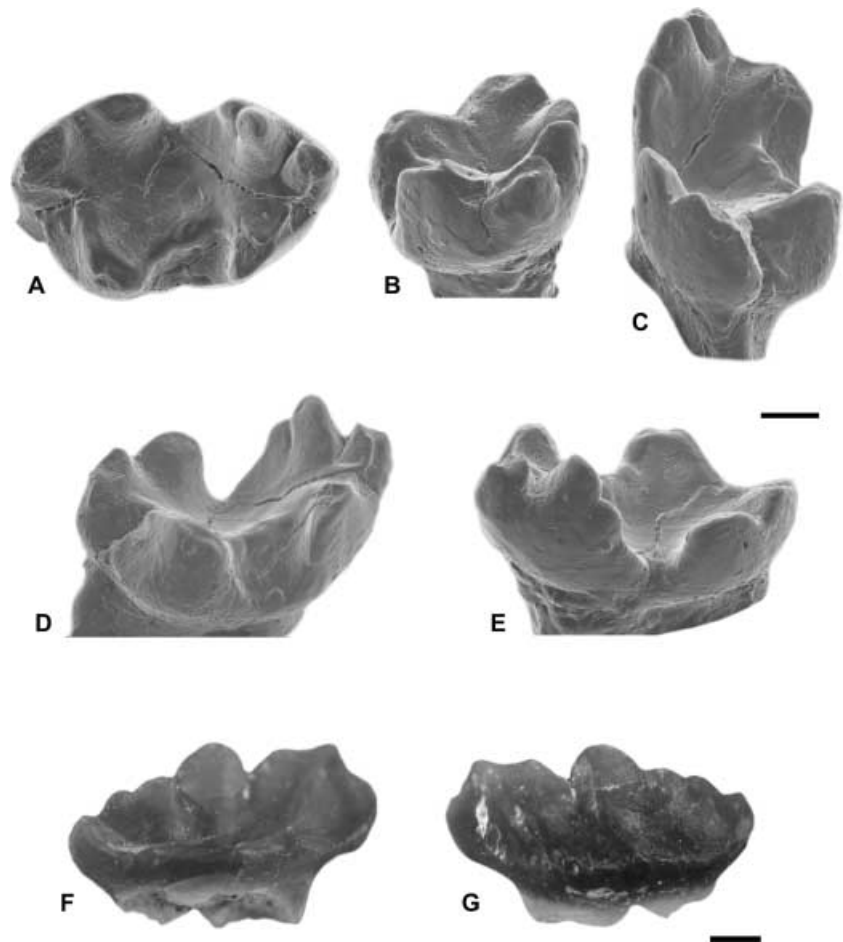


Fig. 8 A–G. Isolated lower teeth of a Dermoptera indet. from the late middle Eocene Pondaung Formation of the Paukkaung area (PK2) in Myanmar. —A–E. Pkg 355, right m2 in occlusal (A), mesial (B), distal (C), buccal (D), and lingual (E) views. —F–G. Pkg 240, left lower canine in lingual (F) and buccal (G) views. Scale bars, 1 mm.

constricted and significantly higher than the talonid. The main cuspids of the trigonid are very acute. The paraconid is strong and nearly as large as the metaconid. The protoconid is broken, but the surface of break suggests that this cuspid was certainly similar in proportion to the metaconid and paraconid. The metaconid appears as the tallest cuspid of the tooth. There is a short postmetacristid that is slightly inflated in its mesial part, thereby forming a small metastylid. A short and nearly indistinct protocristid extends distolingually, and does not reach the metaconid. The talonid cuspids are much larger than the trigonid cuspids, and are situated far distally from the distal trigonid wall. The entoconid is lingually opposed to the hypoconid. The hypoconulid is lingually displaced but far distally positioned from the entoconid. The hypoconulid and the entoconid are equal in size and marginally positioned. The hypoconid is slightly more buccal than the protoconid. A strong posteristid links the hypoconid to the hypoconulid. This posteristid is lingually orientated and does not follow the distal margin of the tooth, thereby creating a small distal fovea. From the hypoconid, a low and

rounded cristid obliqua reaches the base of the trigonid wall at a point distolingual to the protoconid. Lingually, there is a wide, deep and U-shaped notch that separates the entoconid from the postmetacristid (metastylid).

Comparison

The scalloped tooth that we identify as a left lower canine (Pkg 240) is undoubtedly of dermopteran affinities, inasmuch as the arrangement of the cuspules along the crest of the tooth is otherwise found only in dermopteran taxa such as *Dermotherium chimaera* (Fig. 4K–O) and the living *Galeopterus variegatus* (Fig. 10B). In contrast, the lower m2 (Pkg 355) shows a set of unusual characters that cast doubt on the dermopteran status of this specimen. The structure of the trigonid of this tooth is similar to that of the lower teeth (m2–3) of *D. chimaera* in being mesiodistally constricted and in showing a strong and elevated paraconid, a metaconid buccally displaced, the presence of a metastylid, and in having a protocristid distolingually orientated. The paraconid is, however, much more developed than in

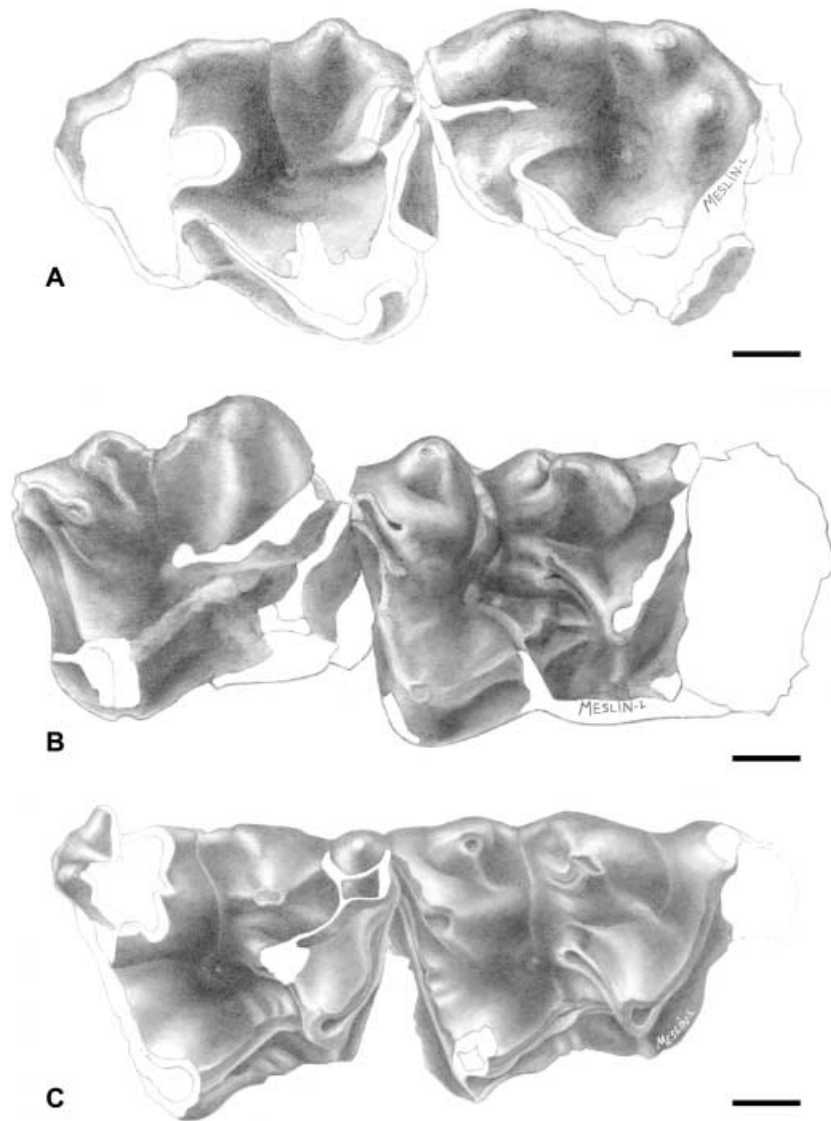


Fig. 9 A–C. Comparison between *Dermotherium major* from the late Eocene Krabi coal mine (Wai Lek pit; Ducrocq *et al.* 1992), and *Dermotherium chimaera* new species from the late Oligocene Nong Ya Plong coal mine (Cha Prong pit). —A. *D. major*, TF 2580, fragment of left mandible bearing m2 and m3. —B. *D. chimaera* sp. n., SHM-CP 374, fragment of right mandible bearing m2 and m3. —C. *D. chimaera* sp. n., SHM-CP 368, fragment of right m1 and m2. Scale bar, 5 mm. Original art by Laurence Meslin, copyright CNRS-Meslin.

D. chimaera, and much more elevated than in *Galeopterus* and *Cynocephalus*. Pkg 355 differs substantially from *D. chimaera*, *Galeopterus* and *Cynocephalus* in lacking the typical dermopteran talonid structure that raises above the talonid basin. In Pkg 355, although the hypoconulid is lingual in position, it is not mesially displaced as in more recent dermopteran taxa, and furthermore, this tooth lacks both the post-hypoconulid cristid and the distocuspoid. This condition is reminiscent to that found in *D. major* (Fig. 9A), in which the hypoconulid is noticeably less mesially displaced than in *Cynocephalus*, *Galeopterus* and *D. chimaera*, and both the post-hypoconulid cristid and distocuspoid are lacking. In Pkg 355, the hypoconulid forms a small distolingual talonid heel.

Discussion

Palaeoecological and evolutionary implications

Dermotherium was originally described by Ducrocq *et al.* (1992) from a fragment of mandible (TF 2580) bearing two extremely worn teeth (m2–3; Fig. 9A). Because of its poor preservation and the limited dental evidence, the dermopteran affinities of this fossil from the late Eocene of Krabi (Thailand) have been questioned (e.g. Stafford & Szalay 2000). The new fossils that we describe here, notably those from the late Oligocene of Nong Ya Plong, allow us to emend the diagnosis of the genus and to provide compelling morphological evidence attesting to the dermopteran status of *Dermotherium*. However, this new material is not referred to the type species of *Dermotherium* (*D. major*), but to a new

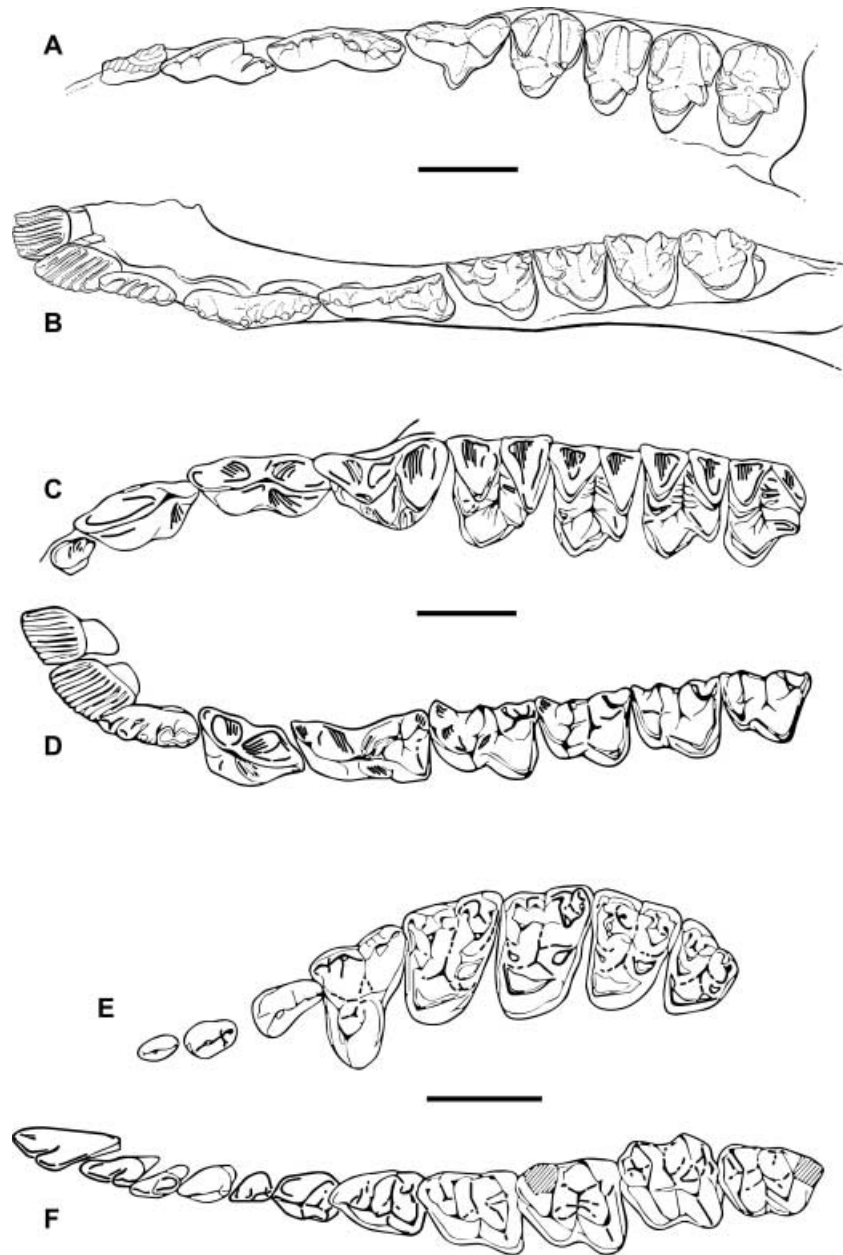


Fig. 10 A–F. Simplified drawings of upper and lower dentitions of modern dermopteran cynocephalids and fossil plagiomenids. —A. Upper dentition of *Galeopterus variegatus* (UMC-002V); —B. lower dentition of *Galeopterus variegatus* (UMC-002V); —C. upper dentition of *Cynocephalus volans* (USNM 239191; modified after MacPhee *et al.* 1989; Fig. 9B); —D. lower dentition of *Cynocephalus volans* (USNM 239191; after MacPhee *et al.* 1989; Fig. 9F); —E. upper dentition of *Plagiomene multicuspis* (AMNH-VP 15208; after MacPhee *et al.* 1989; Fig. 9A0); —F. lower dentition of *Plagiomene multicuspis* (YPM-PU 14552; after MacPhee *et al.* 1989; Fig. 9E). Scale bars, 5 mm. A and B: original art by Laurence Meslin, copyright CNRS-Meslin.

species of the genus: *D. chimaera*. Indeed, although the comparison of the new material with the holotype of *D. major* (TF 2580) is limited to only two teeth (m2 and m3), the lower molars of SHM-CP 368 and SHM-CP 374 exhibit a set of distinctive features (trigonids less buccolingually constricted, talonids with hypoconulids much more mesially displaced, development of strong and long post-hypoconulid cristids, small but distinct distocuspids) that allows us to identify a new species. The material referred to *D. chimaera* sp. n. consists of two isolated upper teeth and three fragments of mandibles that form a virtually complete but composite lower

toothrow (i3, c, p3–4, m1–3). Especially intriguing is the dental pattern of this new species, which is in fact a mosaic of characters found in both extant cynocephalid taxa (Table 2). In some aspects, upper and lower molars of *D. chimaera* resemble those of *Cynocephalus* (shape, talonid/trigonid proportion, development and topography of cuspids and crests; Table 2), while its lower front teeth (i3 and c) and its lower premolars (p3–4) rather exhibit a *Galeopterus*-like morphology (pectinate i3 with a similar number of tines, squat and serrated canine, serration extending farther distally to influence the mesial part of the p3; Table 2). As mentioned by Stafford

& Szalay (2000), in terms of morphology, wear facets and occlusal relationships, the anterior dentition (upper and lower) in *Cynocephalus* appears more suited for shearing food than in *Galeopterus*. In that latter, the interdigitating serration of the canines (C and c) and third premolars (P3 and p3) seems, by contrast, better suited for shredding and puncturing food. The molariform dentition also differs between *Cynocephalus* and *Galeopterus*. In several morphological aspects, the molars of *Cynocephalus* appear more heavily reliant on shearing than crushing. Indeed, these teeth display an important set of efficient shearing crests (e.g. hypertrophied eocrista, strong post- and preprotocone cristae, paracristid, prominent cristid obliqua, long and strong postcristid and post-hypoconulid cristid) that are clearly not so well developed on molars of *Galeopterus* (for details see Stafford & Szalay 2000). The molariform dentition in *Galeopterus* seems, in contrast, to be more reliant on crushing. Indeed, the relatively broader and more open talonid basin of its lower molars seems to emphasize a stronger protocone-talonid crushing than it does in *Cynocephalus* (Stafford & Szalay 2000). However, other morphological details of the molariform dentition in *Cynocephalus* (such as hypertrophied and distally displaced metaconule, strong distocuspids, intermolar contacts) demonstrate that molars of this taxa have also an important crushing action (lingual phase), somewhat different than that in *Galeopterus* (Stafford & Szalay 2000). In light of these detailed morphological and functional observations made on the dentition of living flying lemurs, and considering the aforementioned mosaic of dental features characterizing teeth of *Dermotherium chimaera* sp. n. (Table 2), it may be expected that this fossil dermopteran was adapted to a diet that required a great degree of shredding by the anterior dentition (as in *Galeopterus*), and both shearing and crushing by the molariform dentition (as in *Cynocephalus*). However, compared with molars of *Cynocephalus*, the presence of a stronger and elevated paraconid and the development of additional small cusps mesiobuccally and distobuccally to the protocone (protoconules α and β) on molars of *D. chimaera*, probably provided a more extensive crushing and puncturing surfaces than it does in *Cynocephalus*.

In having a mosaic of dental characters shared with both extant genera, *D. chimaera* is therefore particularly interesting to formalize the ancestral cynocephalid morphotype. In the absence of a comprehensive cynocephalid fossil record, Stafford & Szalay (2000) have attempted to draw the ancestral cynocephalid condition in analysing morphological differences observable between *Cynocephalus* and *Galeopterus*. In fact, the morphological patterns of deciduous vs. replacement dentition of canines and premolars proved to be particularly useful for interpreting the polarity of the dental differentiation. In that respect, Stafford & Szalay (2000) concluded that the absence of serration on both canines and premolars (Table 2) in the adult of *Cynocephalus* represents a derived condition

inasmuch as the morphology of its deciduous canines and premolars (which are serrated) closely resemble that of deciduous and permanent teeth of *Galeopterus*. Indeed, both deciduous canines and premolars of *Galeopterus* are morphologically similar to their successors, thereby indicating that the dental pattern in *Galeopterus* represents the ancestral condition, and that the simplified pattern in *Cynocephalus* is derived (loss of serration). The four erupting permanent teeth (i3, c, p3–4) revealed by SR- μ CT on the fossil SHM-CP 363 (Fig. 3) are morphologically similar to their homologues in *Galeopterus* (i.e. squat and serrated). The presence in this fragment of a mandible from the Oligocene of permanent canine and permanent premolars that are both serrated, demonstrates that the morphological pattern of the anterior dentition of *D. chimaera* matches well the primitive condition expected from extant species. Even if the canines and premolars of *Cynocephalus* appears as evolutionarily advanced over those of *Galeopterus*, Stafford & Szalay (2000) have suggested that the molariform dentition of *Galeopterus* was, in contrast, probably highly derived compared with that of *Cynocephalus*, or more generally with the ancestral condition. The molariform dentition of *Galeopterus* is characterized by a reduction in the tooth size, more specifically an important reduction of their trigonids, involving a limited or even an absence of intermolar contact (interstitial spaces; Table 2). The molar trigonids of *Galeopterus* are mesiodistally constricted, the paraconids are minute to indistinct, and the protoconids and metaconids are both strongly reduced with respect to the hypoconids. The lower molars of *Cynocephalus* do not show such a reduction of their trigonid, maintain intermolar contacts (lingual contacts: paracristids–distocuspids), and have their protoconids and metaconids as strong and elevated as their hypoconids — an overall morphological condition that is reminiscent to that found in *Dermotherium* (Table 2). The molar paraconids of *Cynocephalus* are also better differentiated than on molars of *Galeopterus*, but much less prominent than on molars of *Dermotherium*. Therefore, if *Galeopterus* exhibits a molariform dentition highly derived and, in some extent, secondarily simplified (lower teeth with a trigonid reduction, upper teeth with conules and centrocrista reduced), it may be expected that the molariform dentition of *Cynocephalus* characterized by the presence of a wide V-shaped trigonid with well-distinct paraconid, strong protoconid and metaconid, and with strong cristid obliqua on lower molars, strong conules and hypertrophied centrocrista on upper molars, represent a plesiomorphic molar condition in cynocephalids. This assumption is substantiated by the molar morphology of *Dermotherium*, which exhibits all these aforementioned characters. All things considered, it is interesting to note that the set of dental features assumed as primitive in both extant cynocephalid genera, characterizes, in fact, the dentition of *Dermotherium*. The dental pattern of this

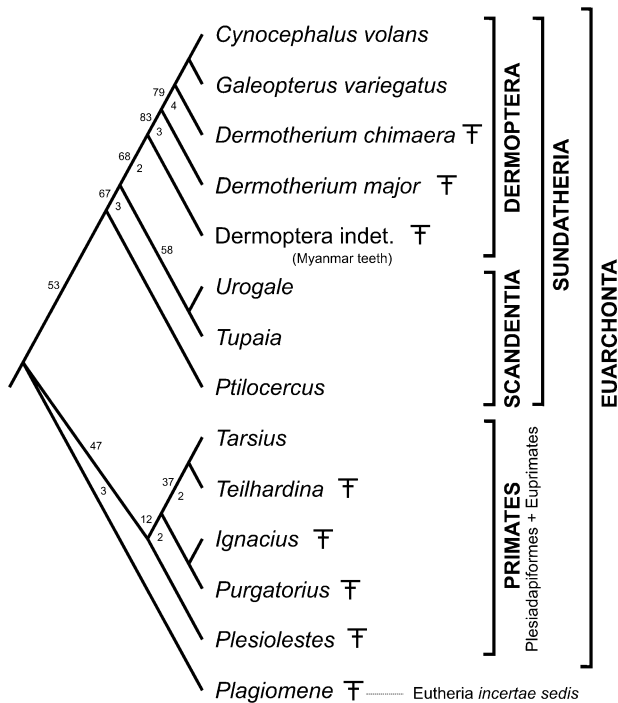


Fig. 11 Result of the cladistic assessment of the dental evidence. The Branch and Bound searches yielded one single tree of 164 steps (CI = 0.54; RI = 0.59). Decay (DI) and bootstrap (BP) values are indicated by the numbers labelled under and above internal branches, respectively (DI > 1; BP > 5). Note that the monophyly of Scandentia is here not identified from the dental evidence alone. However, several works have demonstrated the monophyly of Scandentia based on larger morphological dataset (e.g. Wible & Zeller 1994; Szalay & Lucas 1996; Sargis 2002b,c) and molecular evidence (e.g. Olson *et al.* 2005).

fossil cynocephalid is therefore a mosaic of plesiomorphic characters, and as such, it probably documents a form close to the ancestral morphotype from which the two extant taxa are derived (as formalized by a cladistic assessment presented in Fig. 11). This fossil dental evidence demonstrates, in turn, that *Cynocephalus* and *Galeopterus* each have distinct parts of the dentition highly morphologically conservative. While it appears certain that the interdigitating serration of the canines and premolars is a primitive condition among cynocephalids, and furthermore already achieved at the end of the Palaeogene, it may be wondered how and when was setting up such a complex dental structure. Interesting in this regard are the dental remains found from the late middle Eocene of the Pondaung Formation in Myanmar. The specimen Pkg 240 that we identify as a left lower canine (Fig. 8F,G), shows an unusual scalloped crown (mesiodistal main crest) that could correspond to an incipient serration. If our interpretation of Pkg 240 is correct, this tooth probably

documents an early evolutionary stage of the front dental specialization in dermopterans (Fig. 11). Pkg 355 (Fig. 8A–E), the second isolated tooth from Pondaung, is also interesting for interpreting some morphological adaptive transformations of the molariform dentition in early dermopterans. Pkg 355 is a lower right m2 having a trigonid with a configuration similar to that in lower molars of *Dermotherium* (V-shaped with strong protoconid, metaconid and paraconid). This tooth differs substantially, however, in lacking the unusual talonid structure (entoconid–hypoconulid twinned associated with post-hypoconulid cristid and distocuspid) raising above the talonid basin that characterizes lower molars of *D. chimaera*, *Cynocephalus* and *Galeopterus*. As we have mentioned in the description of the specimen, the hypoconulid is not mesially displaced but forms a small distolingual talonid heel. This condition is reminiscent to that found in *D. major* (Fig. 9A) from the late Eocene of Thailand (Krabi basin), in which the hypoconulid is noticeably less mesially displaced than in *Cynocephalus*, *Galeopterus* and *D. chimaera*. The hypoconulid position in Pkg 355 is characteristic of many other eutherian taxa, and thus, could correspond to the ancestral condition characterizing early Dermoptera (Fig. 11). The mesial migration of the hypoconulid and the formation of the dermopteran talonid structure occurred subsequently, illustrating a shift towards a better molar shearing (with the post-hypoconulid cristid) and crushing (with the distocuspid) tied to a specific diet.

Phylogenetic implications

At first glance, one might expect that extant flying lemurs are phylogenetically isolated from other eutherian mammals because of their exceptional attributes, such as the very extensive gliding membrane, a comb-like structure of the lower front dentition, and several other morphological features. However, although represented by only two extant genera (*Cynocephalus* and *Galeopterus*), dermopterans play a critical role in the higher-level eutherian phylogeny. Regardless of the ongoing controversy over their affinities (Archonta vs. Euarchonta; for a summary see Silcox 2002; Springer *et al.* 2004), dermopterans represent together with tree shrews (Tupaiaidae, Scandentia) the closest outgroups of primates. Given the great antiquity of the Primates clade (Plesiadapiformes + Euprimates), for which the fossil record extends back to the early Palaeogene on all Holarctic continents and in Africa, it is then surprising that the evolutionary history of the order Dermoptera *sensu stricto* (Cynocephalidae) has so far remained undocumented, with the exception of *Dermotherium major* (Ducrocq *et al.* 1992). The same is true for the order Scandentia, for which the fossil record is extremely restricted and limited to sparse tupaiaid fossils from South Asia (e.g. Chopra & Vasishat 1979; Chopra *et al.* 1979; Jacobs 1980; Qiu 1986; Tong 1988). The discovery of Palaeogene

cynocephalid dental remains from different regions of South Asia is therefore particularly significant since it provides an unequivocal spatio-temporal glimpse into the evolutionary history of dermopterans in Asia.

Several studies have defended (e.g. Matthew 1918; Rose 1973; Rose & Simons 1977) and still defend (Silcox 2001) the view that the early Palaeogene North American Plagiomenidae belong in or near the order Dermoptera. These conclusions are founded primarily on some morphological and functional features of the teeth that resemble those observed in living cynocephalids (although the two groups differ in details of cusp morphology and in the form of the front dentition; see Fig. 10). For some authors (e.g. MacPhee *et al.* 1989), these resemblances [such as molarization of P3–4 and p3–4, crenulated enamel, large conules, absence of a hypocone, a deep transverse valley separating the paracone and paraconule from metacone and metaconule, a broad styler shelf with lingually situated paracone and metacone, a low paraconid, a low cristid obliqua that joins the trigonid buccally, lower incisors with divided crowns, and similar mode and pattern of molar wear (list after MacPhee *et al.* 1989, p. 345)] are admittedly suggestive of plagiomenid-dermopteran affinities but far from compelling because of the large timespan separating plagiomenids from living cynocephalids. In addition, MacPhee and colleagues (1989) have pointed out a set of dental characters, which are ‘unequivocally derived traits found in *Plagiomene* but not in *Cynocephalus*’ (markedly molariform third premolar, accessory styler cusps, reduction in molar size distally, strong mesiolingual cant of the cheek teeth, development of an entoconulid lingual of the entoconid, complete and mesiodistal buccal cingulid). In fact, considering the cranial morphological evidence (notably the basicranial characters) of plagiomenids, all these aforementioned apparent dental affinities between cynocephalids and plagiomenids appear to be convergent resemblances (MacPhee *et al.* 1989). Indeed, extant cynocephalids lack all the basicranial apomorphies characterizing plagiomenids, thereby suggesting that there is no close phylogenetic relationship between these two groups. However, there is little reason to exclude plagiomenids from Dermoptera on the basis of autapomorphic features of their basicranial morphology. In fact, Plagiomenids could be basal stem members of the dermopteran radiation that are radically different from cynocephalids in their cranial morphology. This latter point of view would imply that plagiomenids diverged from cynocephalids well back in the early Tertiary or even in the Cretaceous. Recent molecular data suggest that dermopterans diverged from scandentians in the Cretaceous (e.g. Springer *et al.* 2003), which thus argue in favour of a great antiquity of dermopterans. However, up to now, there is no fossil attesting for such a deep time occurrence of that group or even its closest outgroups (i.e. Scandentia, Primates, Lagomorpha and Rodentia: Euarchontoglires, e.g.

Springer *et al.* 2004). In the absence of a comprehensive fossil record, the question of the potential phylogenetic relationships between plagiomenids and cynocephalids is far from being answered, and so it is perhaps premature to dismiss all of the aforementioned dental affinities as functional convergences (homoplasies). From the current palaeontological evidence, it appears that the evolutionary history of cynocephalids is exclusively restricted to Asia. The fossil record is still incomplete for claiming the origin of Dermoptera in Asia. Nonetheless, the apparent long history of endemism of cynocephalids in South Asia, and their close and well-supported phylogenetic relationships with the Asian tupaiids (Sundatheria, Olson *et al.* 2005; Springer *et al.* 2004; our results, Fig. 11), strongly suggest a deep evolutionary root in Asia for the order Dermoptera. However, such a hypothesis requires more palaeontological evidence than is currently available. Up to now, the two isolated specimens from the late middle Eocene of Myanmar (Pkg 355 and Pkg 240) represent the oldest fossil cynocephalids (or dermopterans if plagiomenids are not included in the order) to be discovered.

Palaeobiogeographic and palaeoenvironmental implications

Extant flying lemurs inhabit rainforests of the south-eastern Asian mainland (southern Cambodia and Vietnam, Peninsular Thailand and Malaya; Fig. 12; but see Rugeri & Etterson 1998) and the offshore islands of the Sunda Shelf (Sumatra, Borneo, Java, southern Philippines; Fig. 12). This modern geographic range of dermopterans is comparable to that displayed by living tupaiid scandentians (e.g. *Tupaia*, *Dendrogale*, *Urogale*, *Ptilocercus*) and lorisid primates (e.g. *Nycticebus*) in south-eastern Asia, except that both lorises and tupaiids extend about 10° farther north in latitude than colugos (i.e. ~25°N; including North Vietnam and Laos, Cambodia, southern China, Myanmar). Furthermore, unlike dermopterans, lorises and tupaiids are not exclusively restricted to South-East Asia, but have a more widespread distribution extending into the Indian subcontinent [e.g. *Loris* (lorisids); *Anathana* (tupaiids)]. However, owing to the new palaeontological evidence we present here, it is now obvious that the modern geographic restriction of dermopterans in south-eastern Asia is clearly a relictual distribution. The new fossils from the Palaeogene of Thailand, Myanmar and Pakistan provide substantial changes to our understanding of the historical biogeography of dermopterans in South Asia. The unique upper molar of *Dermotherium* recovered from the Oligocene of the Bugti Hills (Paali Nala, DBC₂) in Pakistan demonstrates that dermopterans actually had a more widespread distribution during the Palaeogene, which extended from South-East Asia into the Indian subcontinent (the Greater India; Fig. 13). The subtropical and equatorial regions that extant dermopterans inhabit are characterized by warm and humid multi-stratal rainforest ecosystems. Because of their anatomical and

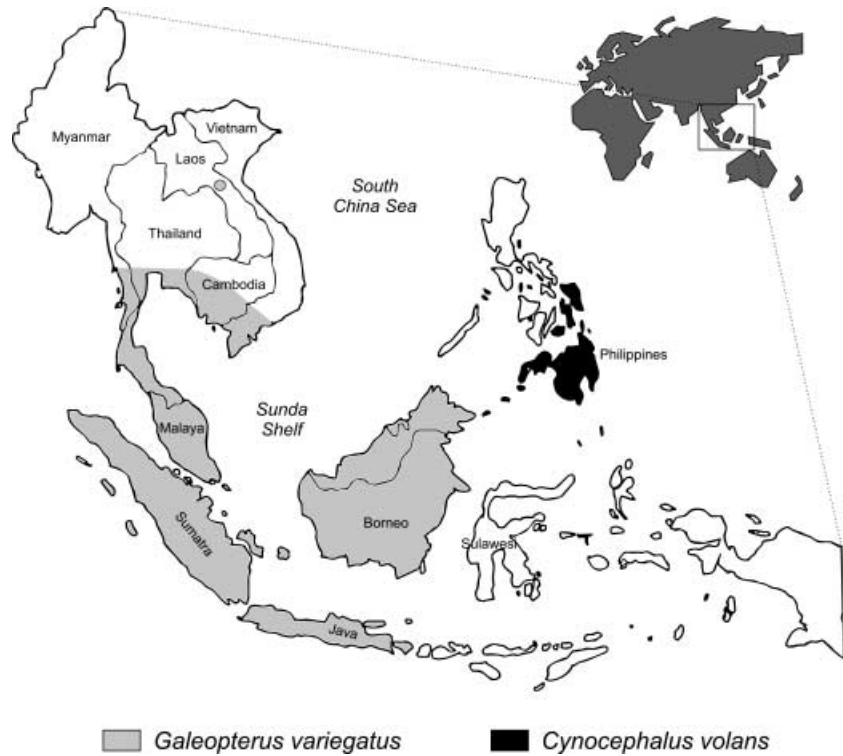


Fig. 12 Distribution of extant dermopterans (*Galeopterus variegatus* and *Cynocephalus volans*) in south-eastern Asia (modified after Stafford & Szalay 2000). The grey point in central Laos indicates the location of the unique Ban Lak dermopteran specimen reported by Rugeri & Etterson (1998).

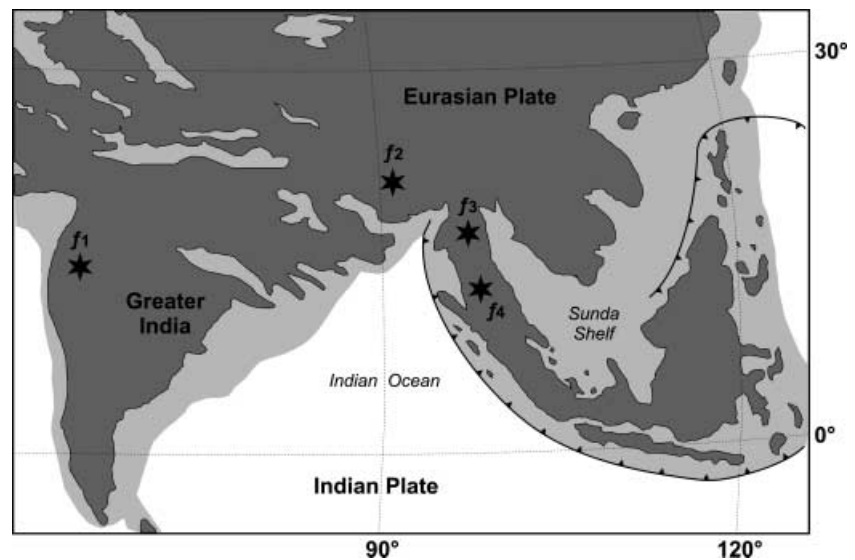


Fig. 13 Palaeogeographic reconstruction of South and South-East Asia at the Oligocene showing the fossiliferous localities having yielded dental remains of dermopterans. Note that the palaeolatitude of the Bugti Hills *c.* 31 million years ago was $\sim 14^\circ$ farther south than in recent times (29°N) due to the northward drift of the Indian Plate (Greater India; Mattauer *et al.* 1999). The map is modified after R. Blakey (available at <http://jan.ucc.nau.edu/~rcb7/RCB.html>) and after Hall (2002).

ecological specializations, flying lemurs are entirely dependent on forest habitats, and as such, are highly sensitive to environmental changes. In that respect, their ancient widespread distribution implies that the Indian subcontinent, at least the region of the modern-day Bugti Hills, displayed palaeoclimatic conditions favourable to rainforest ecosystems during

the Palaeogene (see Collinson & Hooker 2003 for the Eocene conditions in India). In fact, such palaeoenvironmental conditions are conceivable on the basis of palaeogeographic reconstructions (Fig. 13). Indeed, the palaeolatitude of the Bugti Hills *c.* 31 million years ago was $\sim 14^\circ$ farther south (i.e. $\sim 15^\circ\text{N}$, equivalent to the present-day latitude of Bangkok in

Thailand) than in recent times (29°N) due to the northward drift of the Indian Plate (e.g. Mattauer *et al.* 1999). The composition of the associated mammal fauna from the Paali Nala locality (DBC₂), from which the single upper molar of *Dermotherium* is reported, is also particularly informative in terms of palaeoenvironment, because it suggests warm and humid environmental conditions at this period. This locality contains small-bodied strepsirrhine and anthropoid primates (Marivaux *et al.* 2001, 2002a, 2005), lophiomerycid and tragulid artiodactyls (Métais *et al.* in press), petauristine sciurid and anomaluroid rodents (Marivaux 2000; unpublished data), for which their closest living relatives are mostly related to dense forested habitats, notably tropical and subtropical forests. These apparent favourable palaeoenvironmental conditions on the drifting Indian Plate and in South-east Asia during the Oligocene contrast markedly with those recorded on the rest of the Eurasian continent and also in North America. The late Eocene–early Oligocene interval was indeed one of the most significant episodes of Tertiary climatic changes, which is characterized by a global cooling (e.g. Berggren & Prothero 1992). This climatic deterioration has involved drastic environmental changes that seem to have been lethal for several mammalian communities across the Holarctic continents (e.g. Hooker 1992; Hutchison 1992; Stucky 1992; Janis 1993; Meng & McKenna 1998; Hartenberger 1998; Jablonski 2005). The persistence of primates (tarsiids, amphipithecids, eosimiids, sivaladapids), rodents, tree shrews, some artiodactyls (tragulids) and dermopterans in South Asia (Indian subcontinent + South-East Asia) throughout the Oligocene indicates that this region, which extended in lower latitudes, provided a continuous access to tropical refugia during the mid-Cenozoic climatic deterioration (e.g. Beard 1998; Qi & Beard 1998; Jaeger *et al.* 1998; Marivaux *et al.* 2002a,b, 2004, 2005; Antoine *et al.* 2003; Jablonski 2003, 2005; Dawson *et al.* 2006). Given the present-day restriction of dermopterans to southern Asia, a critical question then arises about their subsequent evolution on the Indian subcontinent. The fossil record of Neogene dermopterans is non-existent, and it is thus difficult to determine both the timing and causes of their apparent demise on the Indian subcontinent. However, the major palaeogeographic and geomorphologic events that have affected South Asia at the end of the Oligocene might have been at the origin of the extinction of dermopterans on the Indian subcontinent. Indeed, the progressive retreat of the epicontinental Paratethys Sea and the formation of orogenic highlands, both in relation with the India–Eurasia collision, have reformed the atmospheric circulation in drastically modifying the climate over the Central and South Asia (e.g. Ramstein *et al.* 1997; Fluteau *et al.* 1999). These climatic changes on the Indian subcontinent have certainly contributed to a degradation of the optimal environmental conditions for dermopterans (i.e.

warm and humid rainforests). This hypothesis is substantiated by the mammal compositions reported from the late Oligocene deposits of the Bugti Hills in Pakistan (mainly represented by macromammals thus far), which are locally indicative of drier and more open environments at this period (Welcomme *et al.* 2001; Antoine *et al.* 2003; Métais *et al.* 2003). In contrast, fossil mammals from the coeval deposits in Nong Ya Plong (Thailand), including dermopterans, megachiropterans (unpublished data), carnivorans (Peigné *et al.* in press), and a browser rhinocerotid (Antoine, pers. comm. 2003), are for the most part indicative of a forest ecosystem, thereby demonstrating that palaeoenvironmental conditions remained stable in South-East Asia during the end of the Palaeogene. In fact, the survival of dermopterans in South-East Asia to the recent time (as for the tarsiers and tree shrews) was certainly mediated by the geographic configuration of this region, which allowed a continuous access to low latitudes (subtropical and equatorial) characterized by stable, warm and humid rainforest ecosystems from the earliest Tertiary to the present day (Gursky 1999; Morley 2000). Their current distributional patterns on the offshore islands of the Sunda Shelf, the southern Philippines, and in south-eastern Asian mainland (Fig. 12), are primarily the result of more recent dispersal or vicariance events in relation to changes in sea level associated with periodic glaciations (e.g. Flenley 1985; Groves 1985; Heaney 1985, 1986, 1991; Michaux 1994; Ollier 1985; Ruedi 1996; Tougaard 2001). It would be, however, interesting to determine more precisely when and how *Galeopterus* and *Cynocephalus* diverged. As we have shown, the common ancestor of these two extant species was probably morphologically close to *Dermotherium*. This raises the possibility that cynocephalids achieved their current geographic range, notably their isolation on the Philippine islands, during the Neogene and not recently (Quaternary, Pleistocene), as generally suggested for interpreting the mammal colonization of the Philippines (e.g. Heaney 1985). In the absence of more recent dermopteran fossil record in this region of South-East Asia, molecular investigations might be actually very useful for estimating the antiquity of the divergence between *Cynocephalus* and *Galeopterus*. This estimation, compared with the eustatic sea level movements, would provide a temporal window during which the common ancestor of both extant species reached (via dispersal) the Philippines or was isolated (via vicariance) on this archipelago.

The fossil record of dermopterans is still widely incomplete, but this new palaeontological evidence from the Palaeogene of Pakistan, Myanmar and Thailand testifies to a long history of endemism in South Asia for these mammals. When and how did dermopterans achieve their gliding adaptation? These interesting questions remain open. Additional palaeontological evidence, in particular cranial and postcranial elements, is necessary for better understanding of the anatomical and

ecological specializations through time of this enigmatic and fascinating mammal group.

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Appendix 1 Selected dental characters for the cladistic analyses

The multistate characters were considered as ordered (labeled by an asterisk) if changes from one state to another required passing through intermediate states. With such an *ad hoc* assumption, character state assignments do not convey *a priori* judgements about character polarity (unconstrained parsimony), except for the characters 5 and 8 for which we consider a polarity deriving from the morphological patterns of deciduous versus replacement dentition. The scores of ‘?’ and ‘–’ are used if information is unavailable due to a lack of material and if the character does not apply to a particular taxon, respectively.

Lower teeth

- 1 *Number of tines on i1: (0) reduced 1–2; (1) 5–8; (2) 9–10.
- 2 *Number of tines on i2: (0) reduced 1–2; (1) 7–10; (2) 11–13.
- 3 *Number of tines on i3: (0) reduced 1–2; (1) 3–5; (2) 5–7.
- 4 Tine height on i3: (0) mesiodistal decrease; (1) same height.
- 5 *Canine serration: (0) absent; (1) present; (2) secondarily lost (following the morphological patterns of deciduous vs. replacement dentition).
- 6 First premolar: (0) present; (1) absent.
- 7 Second premolar: (0) present; (1) absent.
- 8 *p3 trigonid serration: (0) absent; (1) present; (2) secondarily lost (following the morphological patterns of deciduous vs. replacement dentition).

- 9 p3 paraconid: (0) absent; (1) present.
- 10 p3 metaconid: (0) absent; (1) present.
- 11 *p3, lingual cingulum: (0) complete; (1) incomplete; (2) absent.
- 12 *p4 metaconid: (0) absent; (1) weak; (2) strong.
- 13 p4 paracristid shelf: (0) absent; (1) present.
- 14 *m1 paraconid: (0) strong; (1) weak; (2) minute, (3) absent.
- 15 *m2 paraconid: (0) strong; (1) weak; (2) minute, (3) absent.
- 16 *m3 paraconid: (0) strong; (1) weak; (2) minute, (3) absent.
- 17 *Molar paraconid position: (0) lingual to metaconid; (1) mesial to metaconid; (2) buccal to metaconid.
- 18 Molar protocristid: (0) thin; (1) strong, trenchant.
- 19 Molar protocristid direction: (0) lingually, toward the metaconid; (1) linguodistally.
- 20 Molar metaconid position: (0) mesial to entoconid; (1) slightly buccally displaced.
- 21 *Molar metastylid (postmetacristid): (0) absent; (1) weak; (2) strong.
- 22 Molar trigonid shape: (0) wide, V-shaped; (1) V-shaped but narrow and mesiodistally constricted.
- 23 *Molar (m2) width trigonid/talonid: (0) same width; (1) trigonid slightly buccolingually pinched; (2) trigonid frankly buccolingually pinched.
- 24 Metaconid/protoconid (p4 → m3): (0) equal in size (or protoconid > metaconid); (1) > on p4 and m1 and < on m2 and m3; (2) > from p4 to m3.
- 25 Molar talonid lingual notch: (0) V-shaped; (1) U-shaped.
- 26 *Molar buccal cingulid: (0) absent; (1) limited; (2) long, mesiodistally developed.
- 27 *Molar pre-entocristid: (0) absent; (1) weak and short; (2) strong and long or with an entostylid.
- 28 *Molar (m1) cristid obliqua direction and termination: (0) point distobuccal to metaconid; (1) point distolingual to protoconid; (2) point distobuccal to protoconid.
- 29 *Molar hypoconulid-entoconid twinning: (0) absent; (1) present but cuspids not very close; (2) present with cuspids very close.
- 30 *Molar hypoconulid position (buccolingual axis): (0) distal to entoconid; (1) slightly mesially displaced with respect to state (0); (2) buccal to entoconid.
- 31 *Molar post-hypoconulid cristid: (0) absent; (1) short; (2) long.
- 32 *Molar distocuspids: (0) absent; (1) minute; (2) strong.
- 33 Molar postcristid connection: (0) hypoconulid; (1) distocuspids.
- 34 Tooth size (m1 and m2): (0) m1 > m2; (1) m1 = m2; (2) m1 < m2.
- 35 Intermolar contacts: (0) present, strong; (1) absent, interstitial spaces.

Upper teeth

- 36 *Molar protocone position: (0) lingual and central; (1) slightly mesially displaced; (2) frankly mesially displaced.

- 37 Molar metacone size: (0) as the paracone; (1) larger than the paracone.
- 38 Molar protoconules: (0) absent; (1) present.
- 39 *Molar paraconule: (0) minute to absent; (1) weak; (2) strong.
- 40 *Molar preparaconule crista: (0) absent; (1) weak and short; (2) strong and short; (3) strong and long.
- 41 *Molar postparaconule crista: (0) absent; (1) weak and short; (2) strong and long.
- 42 *Molar metaconule: (0) minute to absent; (1) weak; (2) strong (hypertrophied).
- 43 *Molar metaconule position: (0) standard position; (1) slightly distally displaced; (2) frankly distally and lingually displaced.
- 44 *Molar premetaconule crista: (0) absent; (1) weak and short; (2) strong and long.
- 45 *Molar postmetaconule crista: (0) absent; (1) weak and short; (2) strong and short.
- 46 *Molar hypocone: (0) absent; (1) weak; (2) strong.
- 47 Molar parastyle: (0) absent; (1) present.
- 48 *Molar preparacrista: (0) weak and short; (1) strong but moderate in length; (2) strong and long.
- 49 *Molar postparacrista: (0) weak and short; (1) strong but moderate in length; (2) strong and long.
- 50 *Molar premetacrista: (0) weak and short; (1) strong but moderate in length; (2) strong and long.
- 51 *Molar postmetacrista: (0) weak and short; (1) strong but moderate in length; (2) strong and long.
- 52 Molar centrocrista configuration: (0) U-shaped; (1) V-shaped.
- 53 *Molar buccal cingulum: (0) absent; (1) weak; (2) strong (gutter-like).
- 54 *Molar enamel wrinkles: (0) absent; (1) few; (2) numerous.

Appendix 2 Data matrix of the phylogenetic analyses

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Cynocephalus volans</i>	2	2	1	0	2	1	1	2	0	0	0	2	1	1	1	2	1	1	1	0
<i>Galeopterus variegatus</i>	1	1	2	0	1	1	1	1	1	1	1	2	1	2	2	3	0	0	1	0
<i>Dermotherium chimaera</i>	?	?	2	0	1	1	1	1	1	1	2	2	1	1	0	?	0	1	1	1
<i>Dermotherium major</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	1	1	0
<i>Dermoptera indet. (Myanmar)</i>	?	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	2	1	1	1
<i>Ptilocercus</i>	0	0	0	—	0	1	0	0	0	0	1	1	0	1	1	1	1	1	0	0
<i>Urogale</i>	0	0	0	—	0	1	0	0	0	0	2	2	1	0	0	0	1	1	0	0
<i>Tupaia</i>	0	0	0	—	0	1	0	0	0	0	1	2	1	1	1	1	1	1	0	0
<i>Tarsius</i>	0	—	—	—	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
<i>Teilhardina</i>	0	0	—	—	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1
<i>Ignacius</i>	0	—	—	—	—	1	1	0	0	0	2	0	0	0	0	1	1	1	0	0
<i>Plesiolestes</i>	0	0	—	—	0	1	0	0	0	0	2	2	0	0	1	1	1	1	0	0
<i>Purgatorius</i>	?	?	—	—	0	0	0	0	0	0	2	0	0	0	0	0	1	1	0	0
<i>Plagiomene</i>	0	0	0	1	0	0	0	0	1	0	2	2	0	0	1	1	1	2	0	0
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Cynocephalus volans</i>	0	0	1	1	0	0	0	1	1	2	1	2	1	0	0	2	1	0	1	1
<i>Galeopterus variegatus</i>	0	1	2	1	1	0	0	2	2	2	2	1	0	2	1	2	1	0	1	2
<i>Dermotherium chimaera</i>	2	0	1	2	1	0	0	1	1	2	2	2	1	0	0	1	0	1	1	3
<i>Dermotherium major</i>	1	0	2	2	1	0	0	1	1	1	0	0	1	1	0	?	?	?	?	?
<i>Dermoptera indet.</i>	2	0	0	0	1	1	0	1	1	0	0	0	0	?	?	?	?	?	?	?
<i>Ptilocercus</i>	0	0	1	0	1	2	1	1	1	0	0	0	0	2	0	0	0	0	1	2
<i>Urogale</i>	0	0	0	0	1	1	2	0	1	0	0	0	0	1	1	0	0	0	0	0
<i>Tupaia</i>	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	2
<i>Tarsius</i>	1	0	0	0	1	2	1	1	0	0	0	0	0	2	0	0	0	0	1	3
<i>Teilhardina</i>	0	0	0	0	1	2	1	1	0	0	0	0	0	2	0	0	0	0	1	3
<i>Ignacius</i>	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	3
<i>Plesiolestes</i>	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	3
<i>Purgatorius</i>	0	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	1	3
<i>Plagiomene</i>	0	0	1	0	1	2	2	1	0	2	0	0	0	2	0	1	0	0	0	1
	41	42	43	44	45	46	47	48	49	50	51	52	53	54						
<i>Cynocephalus volans</i>	1	2	2	1	1	0	0	2	2	2	2	1	2	1						
<i>Galeopterus variegatus</i>	0	2	1	0	0	0	0	1	2	2	2	0	1	0						
<i>Dermotherium chimaera</i>	0	1	0	0	2	0	0	2	2	2	2	1	2	2						
<i>Dermotherium major</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?						
<i>Dermoptera indet.</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?						
<i>Ptilocercus</i>	0	1	0	0	0	1	1	0	1	1	2	1	2	?						
<i>Urogale</i>	0	0	—	—	0	1	1	2	2	2	2	0	2	0						
<i>Tupaia</i>	0	0	—	—	0	0	1	2	2	2	2	1	2	?						
<i>Tarsius</i>	1	1	0	1	1	1	1	0	1	1	0	—	1	0						
<i>Teilhardina</i>	1	1	0	1	2	0	1	0	0	0	0	—	2	0						
<i>Ignacius</i>	1	1	0	1	0	0	1	0	0	0	1	—	1	?						
<i>Plesiolestes</i>	1	1	0	0	2	0	1	0	0	0	1	—	2	0						
<i>Purgatorius</i>	1	0	0	1	2	0	1	0	1	0	2	—	2	0						
<i>Plagiomene</i>	0	1	1	0	1	0	1	0	0	0	—	1	0							