

FIRST FOSSIL FLYING LEMUR: A DERMOPTERAN FROM THE LATE EOCENE OF THAILAND

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ABSTRACT. The first unequivocal fossil dermopteran (flying lemur) is reported here. It comes from the Tertiary Basin (Upper Eocene) of Krabi, Thailand, and appears to be close to the ancestor of the extant forms. Other supposed dermopterans reported previously from North America cannot be referred to this Order.

THE Order Dermoptera Illiger, 1811 is characterized among the mammals by a number of peculiar morphological characters associated with gliding adaptations and by the comb-like lower incisors. The phylogenetic position of the Dermoptera is still obscure, although this order is often classified close to the Primates (Sarich and Cronin 1980). Extant dermopterans have a very restricted geographical range, living only in the forests of south-east Asia where they are represented by two species of the genus *Cynocephalus* Boddaert, 1768: *C. volans* and *C. variegatus* (Walker 1985). The fossil record that until now was attributed to the Order Dermoptera is limited, geographically restricted, and attributed to families distinct from that of the extant genus. Nine species, distributed among seven genera, characterize one extinct family, the Plagiomenidae from the early Palaeocene to the late Oligocene of North America, which has been referred to the Dermoptera (Matthew and Granger 1918; Simpson 1927, 1928, 1937; Rose 1973, 1975; Krishtalka and Setoguchi 1977; Bown and Rose 1979; McKenna 1990), together with one monogeneric family, the Placentidentidae, from the early Eocene of Western Europe (Russell *et al.* 1973, 1982). In other respects, it has been recently suggested that the Paromomyidae (plesiadapiforms) show cranial and postcranial synapomorphies with the extant South-East Asian genus (Beard 1990; Kay *et al.* 1990) but plesiadapiforms have teeth that are very different from extant dermopterans. We report here the discovery of the first fossil dermopteran from the Eocene of South-East Asia. This record represents the only absolutely unambiguous fossil record for the entire Order Dermoptera and for the extant Family Galeopithecidae; it also reinforces the hypothesis according to which plagiomenids and placentidentids can no longer be thought of as dermopterans.

SYSTEMATIC PALAEOONTOLOGY

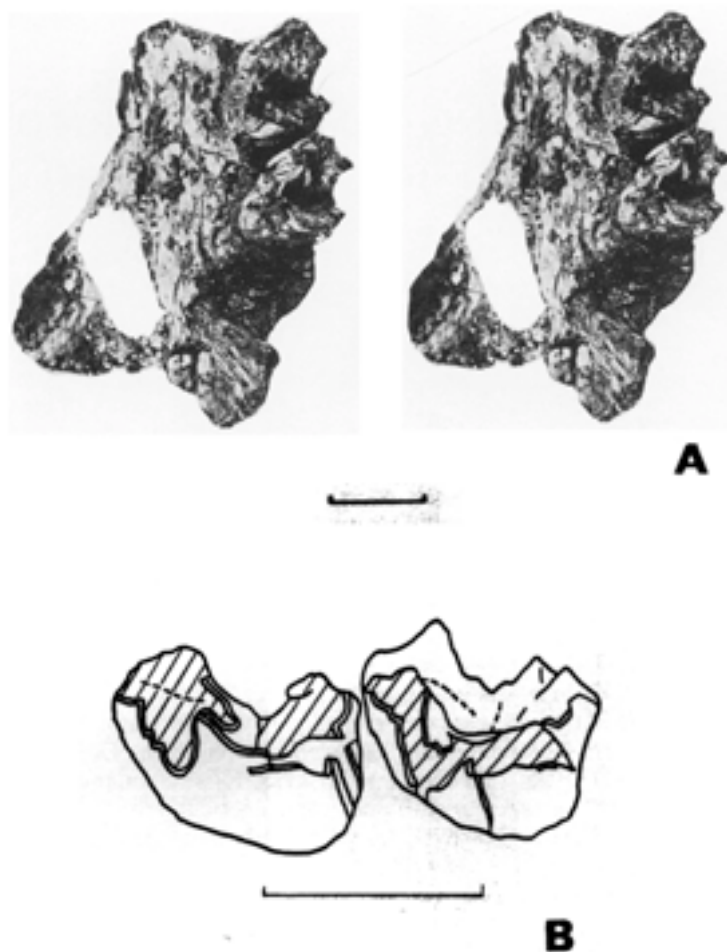
Order DERMOPTERA Illiger, 1811
Family GALEOPITHECIDAE Gray, 1821
Dermotherium major gen. et sp. nov.

Holotype. A left lower jaw with M₂ and M₃, No. TF 2580, Collections of the Palaeontological Section, DMR, Bangkok.

Type locality. Wai Lek lignite pit, Changwat Krabi, southern Thailand (latitude, about 8° N; longitude, about 99° E).

Horizon. Main lignite seam of the Krabi Tertiary Basin. Upper Eocene (see Ducrocq *et al.* in press for discussion about the age).

Diagnosis. Resembles the extant genus *Cynocephalus* by its triangular lower molars with the trigonid

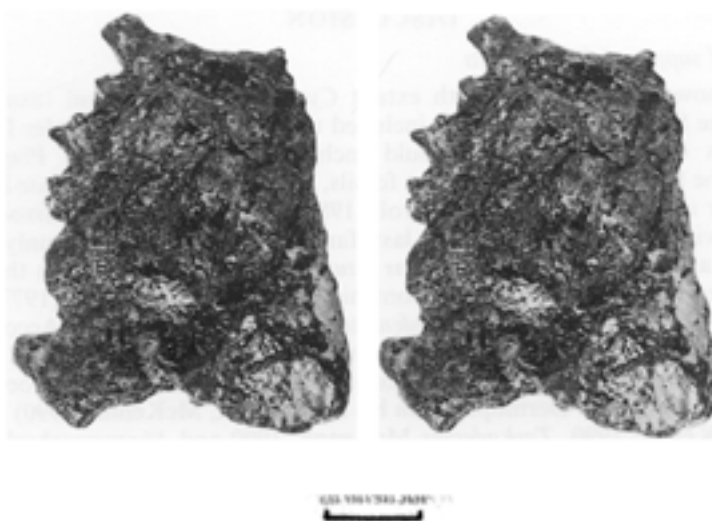


TEXT-FIG. 1. *Dermosterium major* gen. et sp. nov. TF 2580; Upper Eocene of Wai Lek, Thailand; left lower jaw with M_2 - M_3 . A, occlusal view, stereo pair. B, labial view, interpretative drawing. Scale bar, 5 mm.

much narrower than the talonid and compressed antero-posteriorly, its unreduced M_3 with respect to M_2 , its V-shaped and labially salient hypoconid, the presence of a paraconid lingually situated and rather high on the crown, its hypoconulid lingually displaced and close to the entoconid, its rather deep talonid basin, its retro-molar space behind M_3 , its angular area of the jaw strong and ventrally inflated and by its coronoid crest anteriorly directed. It differs from *Cynocephalus* by its larger size, the divergent apices of the anterior trigonid cusps, the presence of the anterior part of the postprotocristid, the shallow talonid basin, the entoconid of the same size of the hypoconulid and by its wrinkled enamel. It is closer to *C. variegatus* by its angular hypoconid with the anterior arm joining the middle of the posterior wall of the protoconid, and by its rather strong paraconid. It differs from *C. volans* by the shape of the hypoconid, the less canted distal wall of its metaconid, and by its entoconid mesial to the hypoconid.

Measurements (in mm): M_2 : Length = 5.45; width = 4.90. M_3 : Length = 5.45; width = 4.65.

Description. The material consists of a partial left lower jaw including parts of the horizontal and vertical rami



TEXT-FIG. 2. *Dermotherium major* gen. et sp. nov. TF 2580; lingual view, stereo pair. Scale bar, 5 mm.

with M_1 - M_2 (Text-figs 1-2). As in *Cynocephalus*, the horizontal ramus enlarges strongly just behind M_2 . In lateral view, the horizontal ramus describes a convex curve below M_2 and M_3 . The anterior border of the ascending ramus is almost vertical.

The third lower molar shows the general structure seen in the extant genus: it is slightly smaller than the second, and in both M_2 and M_3 the trigonid is reduced and the talonid strongly expanded such that the hypoconid occupies a very labial position. The hypoconid is V-shaped with two widely open arms whose anterior one, as in *C. variegatus*, joins the middle of the posterior wall of the protoconid. A paraconid is present, being low and rather lingually situated on the anterior edge of the trigonid: it is weaker in M_2 than M_3 contrary to the condition seen in *Cynocephalus* (Text-fig. 3). There is a lingual notch between the trigonid and the talonid which is deeper on M_2 than on M_3 .

M_3 is the best preserved tooth. Its crenulated enamel shows strong vertical ridges. The trigonid is narrow and the paraconid is reduced and lingually situated. The metaconid is higher than the protoconid and the apices of both cusps are divergent when they are not in both species of *Cynocephalus*. The distal wall of the metaconid is also a little more canted, as in *C. volans*. A protocristid is well differentiated, although short, and is directed towards the disto-lingual part of the tooth. The metaconid and the entoconid are laterally compressed. The talonid is greatly enlarged, with a very labially situated and V-shaped hypoconid. The talonid basin is moderately deep, less than in the two extant species, and the talonid shows three well-differentiated cusps. A small enamel ridge is situated in the valley separating the metaconid from the entoconid; this structure is absent in the extant genus. The entoconid is the highest of the talonid cusps and occupies a more mesial position than the hypoconid, when it is more distal in *C. variegatus* and it is aligned with the hypoconid in *C. volans*. The hypoconulid occupies a lingual position very close to the entoconid on the postero-lingual part of the tooth, and is more robust than the entoconid. In both species of *Cynocephalus*, the entoconid is weaker than the hypoconulid. The entoconid and hypoconulid form a somewhat isolated unit towards the postero-lingual corner of the tooth, and are united by a rather high crest while these cusps are integrated in the crown and more distinct in *Dermotherium*. The hypoconulid also constitutes a small ridge on the postero-lingual wall of the molar although it is not expanded to form a salient posterior lobe as commonly seen among mammals.

The structure of M_2 is rather similar to that of the M_3 although slightly enlarged. Unfortunately, because of the bad preservation, only the entoconid can be clearly discerned on M_2 .

Several characters indicate that this jaw belongs to a dermopteran: the inflated angular region, the relative size of the lower molars, and the configuration of the molar cusps.

DISCUSSION

Previous reports of supposed Dermoptera

The Thai fossil shows affinities with both extant *Cynocephalus* and fossil taxa. There is some confusion about the fossil families and taxa included until now within the Order Dermoptera. For Rose and Simons (1977), this order should include only the families Plagiomenidae and Galeopithecidae, the former, known only from fossils, being the most appropriate known ancestors of the latter. Other authors, for example Carroll (1988), also included the ?Mixodectidae and the Placentidentidae within Dermoptera. This last family is represented by only one subfamily (Placentidentinae) and one species, *Placentidens lotus* Russell *et al.*, 1973, from the Lower Eocene of France. However, it is referred to the Plagiomenidae by Rose and Simons (1977) while Dawson *et al.* (1986) reject the assignment of *Placentidens* to the Order Dermoptera. According to Carroll (1988), the Mixodectidae should include the genera *Eudaemonema* Simpson, 1937 and *Mixodectes* Cope, 1883 from the Middle Palaeocene of North America. Gunnell (1989) does not accept the Mixodectidae within the Order Dermoptera. In his recent work, McKenna (1990) added three new genera (*Tarka* McKenna, 1990, *Tarkadectes* McKenna, 1990 and *Ekgmowechashala* Macdonald, 1963) to the family Plagiomenidae and proposed a new subfamily, Ekgmowechashalinae, for these forms. According to the same author, *Thylacaelurus* Russell, 1954 is not a dermopteran but a lipotyphlan insectivore.

On the basis of basicranial anatomy, MacPhee *et al.* (1989) concluded that plagiomenids were not related to dermopterans and relegated Plagiomenidae and Mixodectidae to Eutheria, *incertae sedis*.

Finally, Beard (1990) and Kay *et al.* (1990) argued for linking plesiadapiforms and Paramomyidae with dermopterans on the basis of postcranial and basicranial anatomy. All fossils previously described as dermopterans should not be placed in that Order (Beard, personal communication), since similarities in dental morphology have been convergently attained.

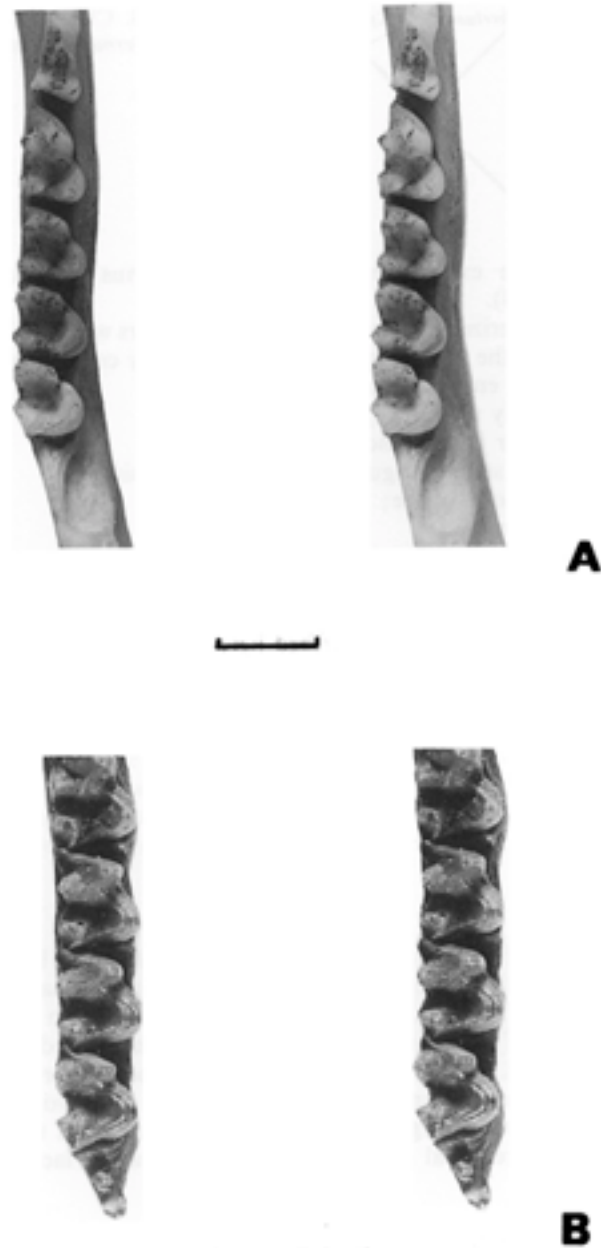
The status of the Asian dermopteran

All the North American fossils previously attributed to the Order Dermoptera, as well as the genus *Microsyops* from early to late Eocene of North America (Gunnell 1989) show a general structure rather different from that of *Dermotherium*. Indeed, they are distinguishable from the Thai fossil in several features: slightly reduced trigonid relative to the talonid, the presence of a hypoconulid which forms a third lobe on the M_3 , possession of a cingulid, and of a paraconid which is generally lost in the Subfamily Ekgmowechashalinae. A system of accessory cuspids also occurs in this latter group, the lingual cusps are distally located with respect to the labial cusps in *Placentidens*, and in this latter genus the trigonid is nearly as wide as the talonid on M_3 .

The M_3 morphology and structure of the Thai fossil is, in general, very different from that of the other fossil genera previously attributed to the dermopterans. *Dermotherium* exhibits the following autapomorphic characters: great size relative to that of the American and European fossil genera, the presence of a labial portion of the protocristid which issues from the protoconid at mid-height and runs disto-lingually towards the talonid basin, lingual cusps laterally compressed, divergent apices of the anterior cusps, and marked antero-posterior compression of the trigonid relative to the talonid.

The Thai fossil shares with extant *Cynocephalus* a triangular outline of the lower molars (M_2 and M_3) which contrasts with the quadrangular lower molars of all other fossils (due to the enlargement of the talonid and the bucco-lingual narrowing of the trigonid). Additional similarities include the presence of a retro-molar behind M_3 , the inflated lower part of the jaw, an anteriorly directed coronoid ridge, absence of a hypoconulid lobe, cingulid and of an entoconulid, a lingually displaced hypoconulid, and a transversely and antero-posteriorly compressed trigonid.

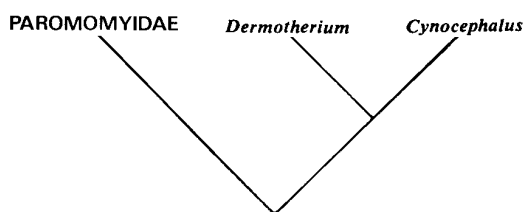
Following the hypotheses of Beard (1990) and Kay *et al.* (1990), we have compared the Thai fossil with the genera of the Family Paromomyidae from North America and Europe (Szalay and Delson 1979). In fact, all these forms are dentally very different from *Dermotherium* in possessing a trigonid as wide as the talonid, a centrally situated hypoconulid, a reduced and elongated M_3 with a



TEXT-FIG. 3. Comparison of right lower dentitions of A, *Cynocephalus volans* and B, *Cynocephalus variegatus*, stereo pairs. Scale bar, 5 mm

hypoconulid lobe, and in being much smaller in size. If the suppositions of these authors are correct, the Paromomyidae should be a lateral branch of Dermoptera that evolved independently in North America while the Galeopithecidae were evolving in Asia.

It is therefore possible to extend the cladogram published by Beard (1990) by adding the Asian



TEXT-FIG. 4. Cladogram illustrating phylogenetic position of *Dermotherium major* (modified after Beard 1990).

fossil: *D. major* plus the extant genus *Cynocephalus* thus become the sister-group of the Paromomyidae (Text-fig. 4).

Dermotherium is characterized by several peculiar characters which bring it close to *Cynocephalus*:

- trigonid narrower than the talonid and antero-posteriorly compressed;
- disto-lingually displaced entoconid and hypoconulid;
- rather strong and labially salient hypoconid;
- inflated part of the lower jaw behind M_3 ;
- the presence of a rather strong lingually situated paraconid;
- the well-marked retro-molar space;
- the absence of an ectocingulid;
- the presence of a well-marked labial notch between the trigonid and the talonid;
- and the absence of a posterior lobe on the talonid of the M_3 .

These characters, associated with the unreduced M_3 relative to M_2 , suggest that *Cynocephalus* could have had its origin in the form described here.

A comparison with both extant species reveals that *Dermotherium* shows more resemblance to *C. variegatus* (the larger species) because of its size, its angular hypoconid with the anterior arm joining the middle of the posterior wall of the protoconid, and its rather strong paraconid. However, the Thai fossil differs from *C. variegatus* in having an entoconid slightly distally located with respect to the hypoconid. *C. volans* differs from *Dermotherium* in its smaller size, more rounded hypoconid with the anterior arm joining the labial wall of the protoconid, an entoconid that is at the same level as the hypoconid, and by the more canted distal wall of the metaconid.

CONCLUSIONS

Dermotherium major was found associated with a fauna that has been dated as Upper Eocene (Ducrocq *et al.* in press); it is therefore a form that has certainly changed very little over a period of at least 34 million years. This fossil is morphologically very close to the extant genus, and perhaps related to the ancestor of *Cynocephalus*, although our current limited knowledge of *Dermotherium* prevents further precision. Since the Thai fossil is rather different from plagiomenids and placentidentids, the few resemblances that exist between the two families and *D. major* can reasonably be attributed to convergent evolution. The discovery of the Asian fossil is therefore a serious argument for the removal of both Plagiomenidae and Placentidentidae from the Order Dermoptera.

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