# Function of the mandibular tooth comb in living and extinct mammals

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**Among the most interesting mammalian dental specializations is the mandibular 'tooth comb' or 'tooth scraper' that evolved independently in certain primates and other mammals. Its occurrence is most widely known in lemurs and lorises, where it is comprised of the long, slender, procumbent incisors (one or two pairs) and incisiform canines (Fig. 1). In non-primates the canines are not incorporated into the comb. Some tree shrews (Tupaiidae) possess a tooth comb consisting of the four central incisors, and some early Tertiary arctocyonid condylarths had a similar structure composed of all six lower incisors[1]. The extant flying lemurs (Dermoptera: *Cynocephalus*) also have a dental 'comb' but it is very different from the ones already mentioned, consisting of two pairs of pectinate incisors, each tooth modified into a comb with as many as 15 tines. This condition, although sometimes said to be similar to that in lemurs, is unique to *Cynocephalus*. One of the principal functions of the tooth comb in primates is to comb the fur, and we present here indirect evidence that condylarths used this structure in the same way, millions of years before tooth combs evolved in prosimians. We also show that the comb-like incisors of *Cynocephalus*, contrary to popular belief, probably do not function to comb the fur.**

The function of the mammalian tooth comb has been controversial. Its comb-like appearance in prosimian primates led very early to the suggestion that it is used in grooming the fur[2], a hypothesis that persisted unchallenged for more than a century[3–6]. Some authors have doubted[7] or even denied[8] such a function for the tooth comb, but behavioural studies have confirmed its use during grooming[9–12]. Tupaiids have been reported to use their tooth combs for grooming in the same manner as do lemurs[6]. It is now recognized that grooming is not the sole function of the prosimian tooth comb. Several smaller lemurs and lorises (for example, *Phaner furcifer, Euoticus elegantulus* and *Galago senegalensis*) use this structure in procuring gum[13–15], and the sifaka, *Propithecus verrauxi*, uses its comb to gouge bark and dead wood, particularly in the dry season[16,17]. Some lemurs (such as *Microcebus murinus, Propithecus verrauxi* and *Indri indri*) scoop fruit pulp with their dental combs[12,18].

There has been disagreement as to whether prosimians, when grooming, use their tooth combs to comb the fur or merely to scrape it. Buettner-Janusch and Andrew[12] found fine hairs caught between the incisors of *Galago* after grooming—compelling indirect evidence of combing. One of us (A.W.) has observed hair-combing with the tooth comb in several captive lemurs and lorises. Martin[18], citing observations of R. Every, reported that teeth in the comb of lemurs bear " 'whip marks' produced by hairs pulled between the teeth".

Using scanning electron microscopy (SEM) to examine teeth from prosimian combs, we have confirmed the presence of fine vertical grooves (~10–20 μm wide, also visible with the light microscope), presumably made by hairs, on the lateral and medial sides of the teeth and on their median dorsal (lingual) ridges (Figs 1, 2). The grooves are discontinuous, being absent from the intervening concave surfaces between the sides of each tooth and the median ridge. Within these grooves are long, finer microstriations (<1 μm wide), which may have resulted from scratching by the cuticular layer of the hair. Similar grooves are visible on the incisors of some tupaiids (for example, *Tupaia glis, Tupaia tana*).

When did the prosimian tooth comb evolve, and for how long has it been involved in grooming? There is no tooth comb in early Tertiary Adapidae (considered the oldest lemuriform primates by many authors), although one species, *Adapis parisiensis*, shows modifications of the lower anterior teeth that may foreshadow a tooth comb[19]. Aside from adapids, the oldest known lemuriforms are early Miocene lorisoids from East Africa[20,21] and late Miocene lorisoids from Asia[22]. Crowns of the anterior teeth are not yet known for early Miocene lorisoids, but the configuration of canine and incisor roots in some specimens indicates that the tooth comb was fully developed by that time[23]. The most ancient lorisoid in which the crowns of the comb teeth are known (and also the only fossil one in which they are known) is *Nycticeboides simpsoni* (holotype, YGSP 8091) from the Siwalik Group, Pakistan, probably between 7 and 8 million years old[22,24]. These comb teeth, including the crowns of

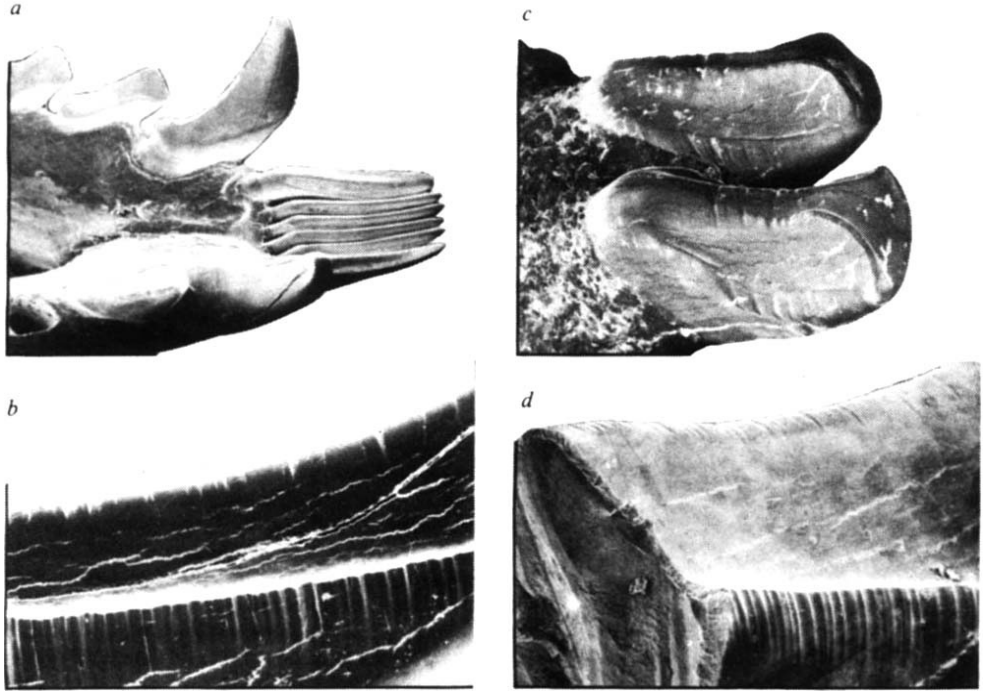


**Fig. 1** *a*, Mandibular comb of *Euoticus elegantulus*. *b*, Left central incisor of *Galago crassicaudatus*, showing hair grooves on the median ridge (above) and on the interstitial facet (below). *c*, Left incisors of a middle Palaeocene arctocyonid from Montana (Carter County Museum no. 79-5) showing hair grooves on interstitial facet and extending across extensive dentine exposure on median ridge. *d*, Left incisor of an early Eocene arctocyonid (cf. *Thryptacodon antiquus*, Princeton University no. 20853) from Wyoming, showing hair grooves almost identical to those in the modern *Galago*.

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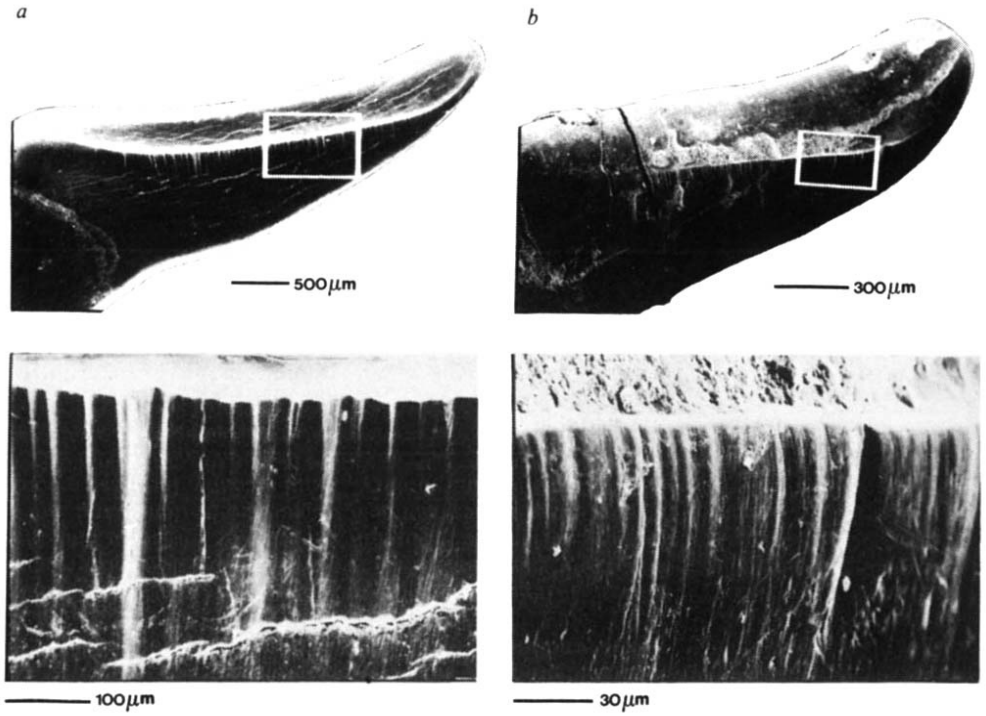


**Fig. 2** *a*, Left incisor of *Galago crassicaudatus* showing hair grooves on the interstitial facet. *b*, Comparative scanning electron micrographs of the left incisor of the type of *Nycticeboides simpsoni*, showing similar grooves.

one canine and two incisors, are morphologically very similar to corresponding teeth in modern lorises and galagos. Scanning electron micrographs of these comb teeth reveal grooves (10–15 μm wide) and finer scratches (<1 μm) remarkably similar to those formed on the comb teeth of modern lorisoids that use the tooth comb for grooming (Fig. 2). Thus it seems that grooming behaviour like that performed by extant lorisoids had evolved by the late Miocene. The type specimen of *N. simpsoni* documents, therefore, the earliest record of tooth comb grooming behaviour in prosimian primates.

Gingerich and Rose[1] reported the occurrence of a lemur-like tooth comb in an earliest Eocene (Clarkforkian) arctocyonid condylarth (cf. *Thryptacodon* from Wyoming) and postulated that it functioned in grooming. SEM examination of this specimen reveals the presence of closely spaced fine grooves (~25 μm wide), virtually identical in size and form to those on prosimian comb teeth (Fig. 1). These grooves indicate that *Thryptacodon*, like lemurs, combed its fur with its tooth comb.

A recently discovered specimen of a middle Palaeocene (Torrejonian) arctocyonid from Montana possesses a tooth comb like that in the Eocene specimen, but with larger incisors that are more heavily worn. SEM examination of this specimen also reveals grooves on the sides and median dorsal ridge of the incisors (Fig. 1). That these grooves formed during life is demonstrated by their continuation across the enamel edges and dentine exposure of the median dorsal ridge of each incisor. The

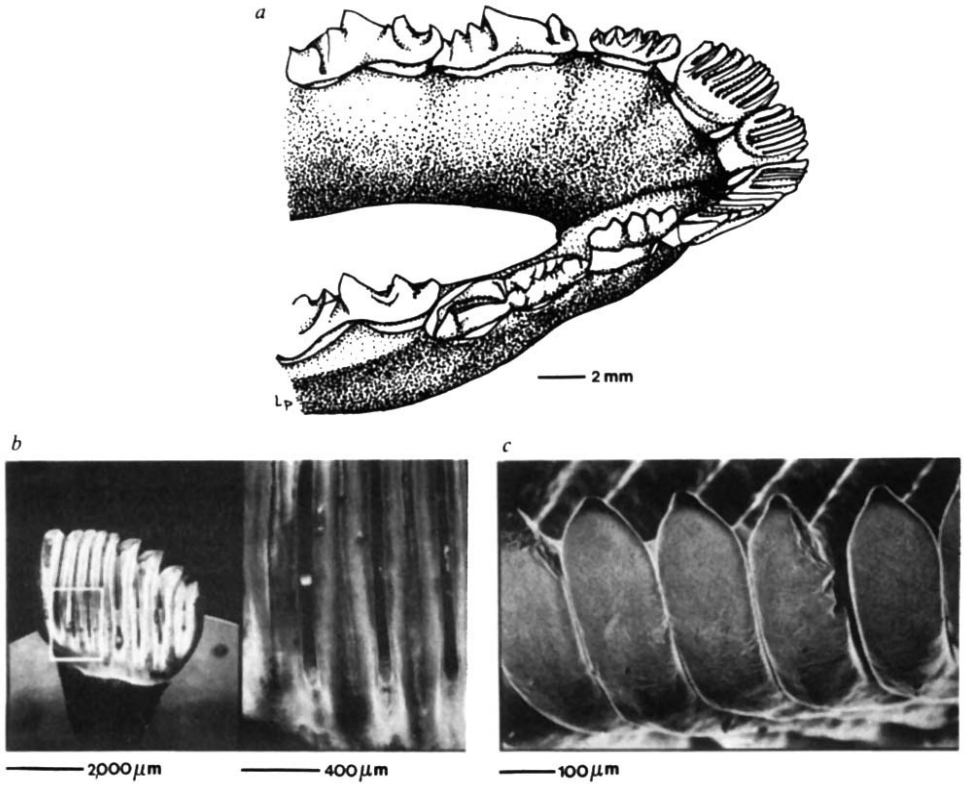


**Fig. 3** *a*, Drawing of the anterior dentition of *Cynocephalus variegatus*, showing comb-like incisors. *b*, Scanning electron micrographs of a central incisor of *Cynocephalus* (left). Note that no grooves are evident between the tines of the tooth. *c*, Scanning electron micrograph of labial apical facet on incisor of *Cynocephalus*, showing exposure of dentine tubules.

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grooves on these teeth are considerably broader (~100 μm wide) than those on the incisors of cf. *Thryptacodon*, and probably represent the coalescence of several smaller grooves—a consequence of much heavier wear in this specimen.

Early Eocene (Wasatchian) specimens of the arctocyonid *Chriacus* from Wyoming also possess an incisor comb very similar to that in cf. *Thryptacodon* and, similarly, minute grooves can be detected on the sides of the incisors[25].

These arctocyonid specimens document the earliest known occurrence in the mammalian fossil record of grooming with a dental comb, predating the oldest evidence of a tooth comb in fossil primates by at least 40 Myr. They may represent three different genera of smaller arctocyonids, suggesting that fur-combing with the incisors was an important behavioural trait in several early Tertiary condylarths.

Recently primatologists have concentrated on the question of the original function of the tooth comb. Martin[18,26] proposed that the tooth comb initially functioned in procuring gum, especially in smaller species, and that grooming was a secondary function. Other authors have contended that the comb must have evolved primarily as a grooming apparatus[12,27]. The arctocyonid tooth combs described above are relevant to this problem. Grooming was clearly performed by even the oldest mammal (middle Palaeocene) known to possess a tooth comb, but this form also shows heavy wear of the incisors, especially at the apices. The tips of the incisors seem to have formed a single cutting edge, similar to the condition in bark-gouging primates such as *Propithecus*. Thus the oldest available evidence indicates that the tooth comb functioned for both grooming and food procurement. The specimen of cf. *Thryptacodon* is less worn than the Palaeocene specimen, and its incisors are relatively longer and more slender. Moreover, they are pointed at the tips, as in *Lemur*, and do not form a single cutting edge. Eocene *Chriacus* resembles cf. *Thryptacodon* in these features. Thus, in cf. *Thryptacodon* and Eocene *Chriacus*, food procurement may have become subordinate to grooming, or may no longer have been a significant function of the tooth comb. The question of whether gum-eating or grooming was the earliest function of the combs of the ancestors of lemurs and lorises is still unanswered, as even those species that eat gum today seem to have no distinctive wear resulting from that activity.

The function of the comb-like incisors of *Cynocephalus* (Fig. 3) is unclear, but it has been widely stated that they, too, are used to comb the fur[28–30]. A few authors disagree with this view[8] or consider that grooming is not the principal function[31,32], and we know of no documented observations of flying lemurs using their incisors for combing. Indeed, Wharton[33] reported that *Cynocephalus* grooms by licking its fur; he did not mention use of the incisors—the incisors probably serve in food procurement. *Cynocephalus* is strictly herbivorous, feeding largely on leaves, blossoms and fruits[30,33,34], and it has even been suggested that the incisors are used for 'scraping the green colouring matter out of leaves'[35]. Though this is difficult to substantiate, stomach contents we examined were dominated by small bits of leafy matter, confirming Wharton's[33] observations. The lower incisors may function to crop leaves against the edentulous part of the premaxilla (as in many artiodactyls)[36], or to scrape leaves[29].

Our SEM examination of incisors of both extant species of *Cynocephalus* (*C. volans* and *C. variegatus*) revealed no evidence of the fine grooves seen on incisors of lemurs, lorises, tupaiids and arctocyonids, and inferred to be caused by hair-combing. A wear facet is present on most specimens on the labial (ventral) side of the tooth, at the apices of the tines. It probably results from contact with the edentulous part of the premaxilla and is consistent with a cropping function for the dermopteran tooth comb. The precise function of the elaborate tooth comb of *Cynocephalus* remains uncertain, but it seems very unlikely that this apparatus, the most comb-like of such structures, is actually used to comb the fur.

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# Miocene lorisid primates from the Pakistan Siwaliks

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**In 1975–79, joint expeditions from Yale University and the Geological Survey of Pakistan (YGSP) recovered fossil lorisids in the Siwalik Group of Pakistan from four localities, spanning a period before 10 Myr ago to about 7 Myr ago[1,2]. In three of the localities, only isolated teeth or fragments were found, whereas the fourth and youngest locality yielded dental, cranial and some postcranial remains of a single individual described here as a new genus and species. These specimens are the first fossil lorisids known from outside East Africa, and include the only recovered postcranial remains from slow-moving arboreal lorisines. The findings indicate that significant tracts of forests in the Siwalik environmental mosaic may have been utilized by hominoid primates, notably *Ramapithecus*.**

Modern lorisids (the galagos, bushbabies, pottos and lorises) occur today in Asia, from forested India eastwards, and in Africa. Two genera of slow-moving lorises occur in Asia, and about four genera in Africa, two of which are slow movers and two others leapers. The slow movers (or lorisines) and the leapers (or galagines) can be distinguished by dental and especially postcranial morphology[3]. Until recently, the fossil record

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