

= Toothcomb =

A toothcomb ( also tooth comb or dental comb ) is a dental structure found in some mammals , comprising a group of front teeth arranged in a manner that facilitates grooming , similar to a hair comb . The toothcomb occurs in lemuriform primates ( which includes lemurs and lorisooids ) , treeshrews , colugos , hyraxes , and some African antelopes . The structures evolved independently in different types of mammals through convergent evolution and vary both in dental composition and structure . In most mammals the comb is formed by a group of teeth with fine spaces between them . The toothcombs in most mammals include incisors only , while in lemuriform primates they include incisors and canine teeth that tilt forward at the front of the lower jaw , followed by a canine @-@ shaped first premolar . The toothcombs of colugos and hyraxes take a different form with the individual incisors being serrated , providing multiple tines per tooth .

The toothcomb is usually used for grooming . While licking the fur clean , the animal will run the toothcomb through the fur to comb it . Fine grooves or striations are usually cut into the teeth during grooming by the hair and may be seen on the sides of the teeth when viewed through a scanning electron microscope . The toothcomb is kept clean by either the tongue or , in the case of lemuriforms , the sublingua , a specialized " under @-@ tongue " . The toothcomb can have other functions , such as food procurement and bark gouging . Within lemuriforms , fork @-@ marked lemurs and indriids have more robust toothcombs to support these secondary functions . In some lemurs , such as the aye @-@ aye , the toothcomb has been lost completely and replaced with other specialized dentition .

In lemuriform primates , the toothcomb has been used by scientists in the interpretation of the evolution of lemurs and their kin . They are thought to have evolved from early adapiform primates around the Eocene or earlier . One popular hypothesis is that they evolved from European adapids , but the fossil record suggests that they evolved from an older lineage that migrated to Africa during the Paleocene ( 66 to 55 mya ) and might have evolved from early cercamoniines from Asia . Fossil primates such as Djebelémur , ' Anchemomys ' milleri , and Plesiopithecus may have been their closest relatives . The lack of a distinct toothcomb in the fossil record prior to 40 mya has created a conflict with molecular clock studies that suggest an older divergence between lemurs and lorisooids , and the existence of a ghost lineage of lemuriform primates in Africa .

= = Homologous and analogous structures = =

The toothcomb , a special morphological arrangement of teeth in the anterior lower jaw , is best known in extant strepsirrhine primates , which include lemurs and lorisooid primates ( collectively known as lemuriforms ) . This homologous structure is a diagnostic character that helps define this clade ( related group ) of primates . An analogous trait is found in the bald uakari ( *Cacajao calvus* ) , a type of New World monkey .

Toothcombs can also be found in colugos and treeshrews , both close relatives of primates ; however , the structures are different and these are considered to examples of convergent evolution . Likewise , small- or medium @-@ sized African antelopes , such as the impala ( *Aepyceros melampus* ) , have a similar structure sometimes referred to as the " lateral dental grooming apparatus " . Living and extinct hyraxes ( hyracoids ) also exhibit a toothcomb , although the number of tines in the comb vary throughout the fossil record .

Dating to the Eocene epoch over 50 mya , Chriacus and Thryptacodon ? two types of arctocyonids ( primitive placental mammals ) ? also possessed an independently evolved toothcomb .

= = Anatomical structure = =

The toothcomb of most lemuriforms includes six finely spaced teeth , four incisors and two canine teeth that are procumbent ( tilt forward ) in the front of the mouth . The procumbent lower canine teeth are the same shape as the incisors located between them , but they are more robust and curve upward and inward , more so than the incisors . In the permanent dentition , the canines erupt

after the incisors . The crowns of the incisors are also angled in the direction of the forward tilt , and the crowns of both the incisors and canines are elongated and compressed side @-@ to @-@ side . The apical ridge , following along the front edges of the toothcomb teeth , is V @-@ shaped in most lemuriforms , tapering off from the midline . As a result of this dental reconfiguration , the upper and lower incisors do not contact one another , and often the upper incisors are reduced or lost completely .

The French anatomist Henri Marie Ducrotay de Blainville first identified the two lateral teeth of the lemuriform toothcomb as canines in 1840 . Canine teeth are normally used to pierce or grasp objects . With modified lower canine teeth , the first lower premolars following the toothcomb are usually shaped like typical canine teeth ( caniniform ) and assume their function . These premolars are commonly confused with canines . Normally the true canines in the lower jaw sit in front of the upper canines , and in toothcombed primates , the caniniform premolars rest behind it .

The lemuriform toothcomb is kept clean by the sublingua or " under @-@ tongue " , a specialized muscular structure that acts like a toothbrush to remove hair and other debris . The sublingua can extend below the end of the tongue and is tipped with keratinized , serrated points that rake between the front teeth .

Among lemurs , the toothcomb is variable in structure . Among indriids ( Indridae ) , the toothcomb is less procumbent and consists of four teeth instead of six . The indriid toothcomb is more robust and wider , with shorter incisors , wider spaces between the teeth ( interdental spaces ) , and a broader apical ridge . It is unclear whether this four @-@ toothed toothcomb consists of two pairs of incisors or one pair of incisors and one pair of canines . In fork @-@ marked lemurs ( Phaner ) the toothcomb is more compressed , with significantly reduced interdental spaces . All six teeth are longer , straighter , and form a more continuous apical ridge . In the recently extinct monkey lemurs ( Archaeolemuridae ) and sloth lemurs ( Palaeopropithecidae ) , the toothcomb was lost and the incisors and canines resumed a typical configuration in the front of the mouth . The aye @-@ aye also lost its toothcomb , replacing it with continually growing ( hypselodont ) front teeth , similar to the incisors of rodents .

In colugos , the toothcomb has a completely different structure . Instead of individual incisors and canine teeth being finely spaced to act like the teeth of a comb , the biting edge of the four incisors have become serrated with as many as 15 tines each , while the canine acts more like a molar . These serrated incisors are kept clean using the front of the tongue , which is serrated to match the serrations of the incisors . Similarly , the hyracoid toothcomb consists of incisors with multiple tines , called " pectinations " . In contrast to the colugos , the size and shape of the tines are more uniform .

The toothcomb of treeshrews is like the lemuriform toothcomb in that it uses interdental spaces to form the comb tines , but only two of its three pairs of lower incisors are included in the toothcomb and the canines are also excluded . The lateral two incisors in the toothcomb are generally larger . In the extinct arctocyonids , all six lower incisors were part of the toothcomb . In African antelopes , the toothcomb is strikingly similar to that of lemuriforms in that it consists of two pairs of incisors and a pair of canines .

= = Functions = =

As a homologous structure in lemuriforms , the toothcomb serves variable biological roles , despite its superficially stereotypic shape and appearance . It is primarily used as a toiletry device or grooming comb . Additionally , some species use their toothcomb for food procurement or to gouge tree bark .

= = = Grooming = = =

The primary function of the toothcomb , grooming , was first noted by the French naturalist Georges Cuvier in 1829 , who pointed out that the ring @-@ tailed lemur ( *Lemur catta* ) had lower incisors that " sont de véritables peignes " ( " are real combs " ) . More than 100 years later , the grooming

function was questioned since it was difficult to observe and the interdental spaces were thought to be too small for fur . Observations later showed the teeth were used for that purpose and that immediately after grooming , hair may be found trapped in the teeth , but is removed by the sublingua later .

In 1981 , scanning electron microscopy revealed fine grooves or striations on the teeth in lemuriform toothcombs . These grooves were only found on the sides of the teeth on the concave surfaces between the sides , as well on the back ridge of the teeth . Between 10 and 20  $\mu\text{m}$  wide , these grooves indicate that hair moved repeatedly across the teeth . Inside these grooves were even finer grooves , less than 1  $\mu\text{m}$  , created by abrasion with the cuticular layer of the hair .

Among non @-@ primates , the extinct Chriacus exhibits microscopic grooves on its toothcomb , but the Philippine colugo ( *Cynocephalus volans* ) does not . The toothcomb of the colugos is generally considered to function as a toothcomb , but due to the lack of striations on the teeth and no documented observations of toothcomb use during oral grooming , its use seems to be limited to food procurement .

In African antelopes , the lateral dental grooming apparatus does not appear to be used during grazing or browsing . Instead , it is used during grooming when the head sweeps upward in a distinctive motion . It is thought to comb the fur and remove ectoparasites .

= = = Olfaction in lemuriforms = = =

In lemuriform primates , the toothcomb may also play a secondary role in olfaction , which may account for the size reduction of the poorly studied upper incisors . The toothcomb may provide pressure to stimulate glandular secretions which are then spread through the fur . Furthermore , the size reduction of the upper incisors may create a gap between the teeth ( interincisal diastema ) that connects the philtrum ( a cleft in the middle of the wet nose , or rhinarium ) to the vomeronasal organ in the roof of the mouth . This would allow pheromones to be more easily transferred to the vomeronasal organ .

= = = Food procurement and other uses = = =

Mouse lemurs ( *Microcebus* ) , sifakas ( *Propithecus* ) , and the indri ( *Indri* ) use their toothcombs to scoop up fruit pulp . Other small lemuriforms , such as fork @-@ marked lemurs ( *Phaner* ) , the hairy @-@ eared dwarf lemur ( *Allocebus* ) , and galagos ( particularly the genera *Galago* and *Euticus* ) use their toothcombs to tooth @-@ scrape plant exudates , such as gum and sap . In fork @-@ marked lemurs , the toothcomb is specially adapted to minimize food trapment since the interdental spaces are greatly reduced . The herbivorous colugos in the genus *Cynocephalus* may also use their toothcomb for food procurement .

Indriids such as the sifakas use their toothcombs to gouge bark or dead wood ( bark @-@ prising ) , which is done prior to scent @-@ marking with the gland on their chest . The more robust structure of their toothcomb is thought to help it withstand the compressive forces experienced during regular bark @-@ prising .

= = Evolution in lemuriforms = =

The origins of the lemuriform toothcomb and the clade it characterizes have been the center of considerable debate for more than a century . In 1920 , British palaeoanthropologist Wilfrid Le Gros Clark proposed that the toothcomb found in treeshrews ( which he believed were primates ) was an early version of the dental structure found in lemuriforms . Because he viewed the fossil lorisoids from the Miocene as not having fully developed the modern lemuriform toothcomb , he implied that lemurs and lorisoids had evolved the trait independently . This view was later overturned , and the monophyletic relationship between lemurs and lorisoids is now accepted .

The ancestral condition of the anterior dentition on the lower jaw , based on Eocene primate fossils , suggests that earliest primates had lacked a differentiated toothcomb . Most fossil strepsirrhines

lacked the stereotypic lemuriform toothcomb . Collectively , early strepsirrhine primates are known as adapiforms . Adapiforms are considered to be a paraphyletic group ( containing many but not all of the descendants of the last common ancestor of the group 's members ) because the lemuriforms are assumed to have evolved from one of several groups of adapiforms . In terms of ecology , the evolution of the toothcomb is assumed to have required a folivorous ( leaf @-@ eating ) diet among the ancestral adapiform population , since that would select for reduced incisors , which would serve as an exaptation ( a trait with adaptive value for something other than what it was originally selected for ) , which could then be used for personal or social grooming . However , the inclusion of the canines into the toothcomb must have required exceptional conditions , since large lemuriforms have secondarily modified caniniform premolars to substitute for the loss .

A popular hypothesis about the origins of the lemuriform clade is that they evolved from European adapiforms known as adapids . In some adapids , the crests of the lower incisors and canines align to form functional cropping unit , and the American paleontologist Philip D. Gingerich has suggested this foreshadowed the development of the lemuriform toothcomb . However , no lemuriform toothcomb has been found in the fossil record of the Eocene , and the European adapid lower jaws from that time did not resemble the derived state seen in lemuriforms .

Lemuriforms are currently thought to have evolved in Africa , and the earliest known strepsirrhine primates from Africa are azibiids from the early Eocene , which likely descended from a very early colonization of the Afro @-@ Arabian land mass in the Paleocene ( 66 to 55 mya ) . Stem lemuriforms , including *Djebelemur* and '*Anchomomys* ' *milleri* , have been found in Africa and date from 50 to 48 mya and were very distinct from European adapiforms . However , they lack a toothcomb . These stem lemuriforms suggest an early common ancestry with cercamoniines from outside of Europe . Based on large , procumbent lower teeth , *Plesiopithecus* , a fossil primate found in late Eocene deposits at the Fayum Depression in Egypt , is thought to be most closely related to lemuriforms . Together , *Djebelemur* , ? *Anchomomys* ? *milleri* , and *Plesiopithecus* are considered to be sister taxa ( the closest relatives ) of lemuriform primates .

= = = Dating inconsistencies = = =

Although stem lemuriforms like *Djebelemur* may have been contemporaneous with related toothcombed primates around 50 to 48 mya , the sparse African fossil record suggests toothcomb differentiation occurred around 52 to 40 mya according to the French paleoanthropologist Marc Godinot . This would conflict with the molecular clock estimates by evolutionary anthropologist Anne Yoder and others , which predict lemur ? lorisoid divergence dating between 61 and 90 @.@ 8 mya .

In 2001 , the discovery of *Bugtilemur* , a fossil primate from Pakistan dating to the Oligocene and initially thought to be a cheirogaleid lemur , further challenged the theory of lemur origins ; however , it was later shown to be a type of adapiform primate and not a lemur .

The minimum paleontological estimate for the divergence of lemurs and lorisoids nearly doubled when additional discoveries were made in northern Egypt during the 2000s of a stem galagid ( *Saharagalago* ) and a stem or crown lorisoid ( *Karanisia* ) dating to 37 and 40 mya respectively . *Karanisia* is the oldest fossil primate to exhibit a distinct lemuriform toothcomb . This , as well as studies of other African adapiforms like ? *Anchomomys* ? *milleri* , suggests a more ancient ghost lineage for lemuriforms in Africa .

= = = Original function of the lemuriform toothcomb = = =

The selective pressure that shaped the original lemuriform toothcomb has been a topic of considerable debate since the 1970s . Evidence can be seen as supporting a grooming function , food procurement function , or both . In the early 1900s , there was less debate . Grooming was seen as the primary function since primates lack the claws needed to adequately comb the fur , although prosimian primates ( strepsirrhines and tarsiers ) possess at least one grooming claw on each foot to compensate . Grooming ? in the form of fur @-@ combing ? is generally considered the

primary function and original role of the lemuriform toothcomb , and subsequent changes in morphology across multiple lineages have altered its function and obscured its original function .

The hypothesis that the toothcomb evolved for food procurement was based on observations of recent lemuriform taxa , such as cheirogaleid lemurs ( particularly fork @-@ marked lemurs and the hairy @-@ eared dwarf lemur ) and galagos , which demonstrate tooth @-@ scraping of plant exudates , as well as sifakas , which practice bark @-@ prising . Each of these were considered " primitive " forms among the living strepsirrhines , suggesting the first lemuriforms exhibited similar behaviors . Also , strong selective pressure from feeding ecology placed on the anterior dentition was emphasized , based on the specialized upper anterior dentition seen in the recently extinct koala lemurs ( *Megaladapis* ) . If feeding ecology could have such profound effects on the shape of the anterior dentition , then convergent evolution might explain the similarities seen between the compressed lower incisors of the lemuriform toothcomb and the exudate feeding adaptations in the genus *Callithrix* ( a type of marmoset ) .

In contrast , the grooming hypothesis emphasized that all lemuriforms use their toothcombs for grooming , and long , thin teeth are poorly suited for the mechanical stress of gouging and exudate feeding . Also the interdental spaces seen in most lemuriforms favor fur combing and would also promote bacterial growth and tooth decay if used for exudate feeding . Supporting this , reduced interdental spacing is found in exudate feeding lemuriforms . Furthermore , the canine included in the toothcomb provides additional interdental spacing for fur combing . Even the behavior of young lemuriforms suggests that grooming plays a more important role in the use of the toothcomb than food procurement .