

# Well-groomed predecessors

from R. D. Martin

RECONSTRUCTIONS of mammalian phylogeny have depended heavily on dental evidence, since teeth are preferentially preserved in the fossil record. As a rule anterior teeth (especially incisors) are easily lost in fossilization and most weight has been placed on the characteristics of cheek teeth (premolars and molars). However, there are some striking modifications of the lower anterior teeth among living mammals and these provide not only useful diagnostic features but also valuable functional clues. A good example is the 'tooth-comb' formed by the procumbent lower front teeth in mammal groups such as the tree-shrews, strepsirhine primates (lemurs and lorises) and 'flying lemurs' (which actually are not lemurs and do not fly — they are unusual gliding mammals relegated to their own order, Dermoptera). The tooth-comb of lemurs and lorises is particularly unusual in that the lower canines are incorporated along with the incisors, and it is now widely accepted that a unique six-tooth comb (two canines and four incisors) was probably an ancestral feature of lemurs and lorises.<sup>1,2</sup> In tree-shrews, by contrast, the tooth-comb is formed by some or all of the six lower incisors without involvement of the canine teeth, and in flying lemurs the four lower incisors all have crenulated tips and act as individual combs. These are doubtless convergent developments.

The tooth-comb has often been seen as an adaptation for grooming of the fur. Indeed, virtually all tree-shrew, lemur and loris species have been seen using the tooth-comb in a characteristic rake-and-lift action to groom the fur, though no such use of the lower incisors has been recorded for the flying lemur. Despite some past claims to the contrary<sup>3,4</sup> there is now no doubt that the tooth-comb serves a valuable grooming function in tree-shrews and in strepsirhine primates. Nevertheless, in recent years evidence has accumulated that all of these species also use their anterior lower teeth for feeding. For instance, soft fruit pulp may be scooped out with the tooth-comb and detailed field observations of nocturnal lemurs and lorises<sup>5</sup> have revealed that many species feed upon gums (natural polysaccharide exudates from trees). For one species — the lesser bushbaby (*Galago senegalensis*) — clear evidence of the use of the tooth-comb in gum-feeding has been collected<sup>6</sup>. Further, the greatest development of the tooth-comb (once body size has been taken into account) is found in two species which feed predominantly on gums, the needle-clawed bushbaby (*Galago elegantulus*) and the fork-crowned lemur (*Phaner furcifer*).

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It has been claimed<sup>7</sup> that the tooth-comb in small-bodied lemurs and lorises is too fragile to allow for its use in feeding, but fruit pulp provides no great resistance and gums are usually collected in a semi-liquid state. It is therefore a moot point whether grooming or feeding was the primary function of the tooth comb in lemurs and lorises, but it is certain that both functions are served in extant species.

Our understanding of the origin of tooth-comb grooming has now been considerably advanced by the report by Rose, Walker and Jacobs (see this issue of *Nature* p583) that wear patterns produced by repeated passage of hairs between the lower anterior teeth can be clearly recognised with the scanning electron microscope (SEM). SEM photographs of the lower anterior dentitions of extant strepsirhine primates, such as *Galago crassicaudatus*, reveal fine vertical grooves on the sides of the teeth. Similar grooves are found on the lower incisors of certain tree-shrew species, but no such wear patterns are found on the comb-like lower incisors of the flying lemur, suggesting that their function is restricted to feeding. This new evidence is particularly valuable because the findings can be extended back through the fossil record. A tooth-comb consisting of six lower incisors has been reported<sup>8</sup> for early Tertiary (Palaeocene/Eocene) arctocyonid condylarths and Rose *et al.* have demonstrated that the lower incisors of these early placental mammals bear grooves closely resembling those found on the comb-teeth of modern lemurs, lorises and tree-shrews. This neatly confirms the proposal made by Gingerich and Rose that the lower incisors of these condylarths were used for grooming. This would seem to be the earliest direct fossil evidence of a mammalian behaviour pattern, and it would certainly appear to be the most reliable demonstration that mammalian hair was definitely in existence over 55 million years ago! Significantly, the earliest (mid-Palaeocene) condylarth species examined by Rose *et al.* also exhibited wear on the tips of the comb-teeth, indicating a combined grooming and feeding function.

Reconstruction of the evolutionary history of the tooth-comb in lemurs is hampered by the poor fossil record. Until recently, the only reliable early fossil forms were early Miocene lorises from East Africa (approx. 18-20 million years old). On the basis of indirect evidence, all three recognised East African lorisid genera from the Miocene (*Komba*; *Progalago*; *Mioeuoticus*) are thought to have possessed tooth-combs like their modern relatives, but no anterior tooth crowns are known<sup>9</sup>. Now Jacobs (see this issue of *Nature* p585) has reported new fossil finds

from the late Miocene Siwalik deposits of Pakistan (some 7-10 million years old) assigned to the lorisid species *Nycticeboides simpsoni*. This newly-discovered species definitely had a tooth-comb, and Rose *et al.* have applied their SEM procedure to the crowns of one canine and two incisors. These teeth closely resemble their counterparts in modern lorises and SEM examination revealed the fine vertical grooves characteristic of use in grooming. Thus, the use of the lorisid tooth-comb in grooming can be definitely traced back at least 7 million years. Unfortunately, though, feeding on gum or soft fruit pulp is not known to leave characteristic wear patterns on the tooth-comb, so possible dietary function remains untested.

Jacobs regards *Nycticeboides simpsoni* as belonging to the subfamily Lorinae (including the slow-moving pottos and their relatives), rather than to the Galaginae (the agile, saltatory bushbabies). It is true that *Nycticeboides* shares with modern lorises specific characters such as simple rear premolars, relatively weak development of the fourth cusp (hypocone) on the upper molars, and poor development of the ectepicondylar flange on the humerus. However, such characters only indicate a phylogenetic link between *Nycticeboides* and lorises if they emerged *after* the divergence between galagines and lorises (that is, if they are not primitive features of the lorises), and this remains to be demonstrated. But if Jacobs is right, the presence of *Nycticeboides* in the Siwalik deposits could have a wider significance, since *Ramapithecus* (regarded by many palaeontologists as an early relative of man) also occurs in the Siwaliks. All modern lorisid species, unlike some bushbabies, are confined to relatively dense forests with virtually continuous arboreal pathways. Modern tree-shrews are similarly confined to forested regions and fossil tree-shrews have already been reported from these same Siwalik deposits<sup>10,11</sup>. The combined evidence of forest conditions provided by fossil lorises and tree-shrews in the Siwaliks raises the possibility that *Ramapithecus* was also at least partly a forest-living primate. If *Ramapithecus* does lie close to the origin of the hominid line, as many authorities believe, confirmation of a forest background for this Miocene genus would be of great value, if only in ruling out some of the speculative suggestions which have been made in the past. □

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