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The evolution of grooming and hand use in primates: an interdisciplinary perspective

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The evolution of manual grooming and its implications have received little attention in the quest to understand the origins of simian primates and their social and technical intelligence. All simians groom manually, whereas prosimians groom orally despite comparable manual dexterity between some members of the two groups. Simians also exhibit a variable propensity for the manipulation of inanimate, non-food objects, which has culminated in tool making and tool use in some species. However, lemuriform primates also seem capable of tool use with training. Furthermore, lemuriforms appear to understand the concept of a tool and use their own body parts as “tools”, despite not using inanimate objects. This suggests that prosimian primates are pre-adapted for proprioceptive object manipulation and tool use, but do not express these cognitive abilities by default. This essay explores the paleontological, anatomical, cognitive, ethological, and neurological roots of these abilities and attempts to explain this behavioural divide between simians and prosimians. Common misconceptions about early primate evolution and captive behaviours are addressed, and chronological inconsistencies with Machiavellian Intelligence are examined. A “licking to picking” hypothesis is also proposed to explain a potential link between manual grooming and object manipulation, and to reconcile the inconsistencies of Machiavellian Intelligence. Bayesian decision theory, the evolution of the parietal cortex and enhanced proprioception, and analogies with behavioural changes resulting from artificial selection may help provide new insights into the minds of both our primate kin and ourselves.

Keywords: primate hand use, primate grooming, manual grooming, object manipulation, primate evolution, oral grooming, object play, tool use, Machiavellian Intelligence, Bayesian decision theory

Primates are often defined by their hands and minds, and Napier (1993) once wrote, “a lively hand is the product of a lively mind.” Understandably, much research has gone into understanding the function, anatomy, and evolution of these beautifully complex structures. But there are still important questions we should ask. For example, do we fully grasp the behavioural differences in hand use and object manipulation between simian and prosimian primates? (See Table I for taxonomic clarification.) The switch to manual grooming appears to have occurred early in the evolution of simians, but was its impact entirely superficial? Could this change have been a pre-adaptation for other behavioural changes, including more diverse and complex forms of object manipulation and possibly social manipulation?

Initially suggested by Alison Jolly (Bishop 1962; Jolly 1964)—albeit with a stronger emphasis on “object play”—the idea that object manipulation and manual grooming played an important role in the evolution of simian intelligence took the back seat in later years as her work indirectly supported research suggesting social group size was the driving force behind increased brain size. Here, I revisit Jolly's early work, and contrast it with what is known from related fields and my own observations.

An interdisciplinary review is necessary to paint a broad picture of the poorly understood events that happened when the simian ancestors parted ways with the prosimian stock. Between highly publicised misrepresentations of early primate evolution in 2009 (Switek 2010) and the possibility of outdated introductory textbooks (Love 2006), myths about the early evolutionary history of primates have ample ground to take root outside of palaeoanthropology. The same can be said for our understanding of anatomical, neurological, behavioural, and social differences between wild and captive primates. Misconceptions are not uncommon.

The early evolution of primates is crucial to understanding the origins of human cognitive abilities and social behaviours. Yet despite an abundance of research across many fields, relatively little has been done to explain the evolution of grooming and object manipulation among early simians. Grooming is not just a physiological need, but is also crucial for psycho-social reasons (Dunbar 1991; Napier 1993; Spruijt et al. 1992); and the physical and behavioural limitations that govern hand use for object manipulation lie at the heart of tool use. Equally important, our understanding of the lemur mind and that of many other mammals may rest on our ability to fully grasp the cognitive and behavioural divide that separates the simian clade from our prosimian cousins.

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EARLY PRIMATE EVOLUTION

Much of early primate evolution remains shrouded in mystery due to gaps in the early primate fossil record, particularly in Africa and Asia—the major hotbeds of evolution for the living primates. What can be said is that the split between haplorhines and strepsirrhines likely occurred at the very base of the primate family tree, and the three major groups of living primates—lemuriforms, tarsiers, and simians—were likely distinct by sometime in the early Paleogene (see Figure I).

Among the first primates to appear in the fossil record were the strepsirrhine adapiforms and haplorhine omomyiforms, which both enjoyed initial success during the Eocene but eventually died out. The ancestors of all living strepsirrhines likely split from an Asian branch of cercamoniine adapiform by the early Paleogene, and evolved independently in Africa (Godinot 2006; Tabuce et al. 2009). On the other hand, the relationships between omomyiforms, tarsiers, and simians are unclear (Williams et al. 2010a; Williams et al. 2010b).

During the early to middle Eocene, lemuriforms diversified in Africa, although molecular clock estimates suggest an earlier divergence (Horvath et al. 2008; Poux et al. 2005; Yoder & Yang 2004). (But see Steiper and Seiffert (2012) for new calibration methods that may reconcile the discrepancy.) Stem lemuriforms from this time lacked a toothcomb, a comb-like structure of the anterior mandibular dentition (Godinot 2006). So far, this characteristic lemuriform trait first appears in the fossil record at 40 Ma in a stem lorisoid (Seiffert et al. 2005).

It can be tempting to assume that lemurs and their relatives are "primitive" primates. Indeed, they do possess several ancestral traits believed to be found in the earliest primates.

However, the same can be said of simians, and this—along with convergent evolution—is what makes the classification of fossil primates so difficult, especially when only extant primates, the current endpoints in our evolutionary lineage, are compared. Often, adapiforms are referred to as "lemur-like". Yet given the morphological and behavioural diversity of both lemurs and ancient adapiforms, this analogy can be misleading (Covert 2002), which can lead even well-respected professionals to claim that lemurs were once found outside of Madagascar and Africa (see Wilson and Hanlon (2010) for an example). Assuming a single lemuroid colonisation of Madagascar, any fossil relatives found in Africa would be either stem lemuriforms, stem lemuroids, or stem/crown lorisoids.

Simian origins are very obscure and thus hotly debated. Key African fossils once aligned with this clade have recently been shown to be strepsirrhines (Marivaux et al. 2011; Tabuce et al. 2009), while eosimiiforms—potential stem simians rooted in Asia—appear to have dispersed multiple times to Africa around the middle Eocene (Chaimanee et al. 2012). How the Asian eosimiiforms and their kin relate to the undisputed stem simians from the late middle Eocene of Africa is also debated.

What do we know about the first simians? Thanks to early Asian and African stem simian fossils, we know they were very small and that they had small brains. (Larger brains evolved independently in platyrrhines and catarrhines.) They were diurnal and showed changes in the middle ear and cranial arteries, but it is unclear when these shifts happened within early haplorhines (Kay et al. 1997). The reduction of olfaction and pheromone detection happened primarily in the catarrhine clade, not in stem simians. Enhanced visual acuity and the beginnings of a postorbital septum, or bony partition behind the eye, may have been present during the simian/tarsier split (Williams et al. 2010a), which may correspond with the shift to diurnality, which is thought to have occurred at the base of the haplorhine clade (Ross 1996, 2000; Williams et al. 2010a). Stem simians may have been slow climbers (Ryan et al. 2012) or capable of leaping, similar to lemuriforms, while specialization for above-branch arboreal quadrupedalism is thought to have first shown up in crown simians from Africa (Ross 2000). In other words—and with little surprise—it would have been very difficult to distinguish stem simians anatomically from the other early primates of their time.

Phylogenetic social trends among extant primates suggest that the first simians had transitioned from solitary foraging to forming unstable social groups, with stable social groups evolving separately and more recently in several simian lineages (Shultz et al. 2011). Furthermore, if we could travel back in time and see them in the flesh, one difference I suspect would have been obvious. Somewhere between the split with tarsiers and the evolution of crown simians, these tiny primates began to use their hands for more than locomotion, social play, and food acquisition. They began to groom manually.

GROOMING ADAPTATIONS

Simians use their hands to groom, although the manner in which they do so can vary phylogenetically. The fur is parted with the hands or fingers, usually either with flat, outstretched palms or (in the more dexterous apes) with fine manipulation of the fingers. Parasites or debris are gently picked out with the hand or by using a sort of oral grooming, although only the lips and teeth are used, not necessarily the tongue. Lemuriforms and tarsiers groom orally, like other mammals, although they occasionally grasp the fur with both hands and lick or comb between the two hand-holds. The lower anterior teeth are often raked through the fur, which is referred to as dental combing. Despite these differences in grooming technique, the frequency and function are similar in lemuriforms (Bishop 1962; Jolly 1966).

Unlike haplorhines, adapiforms, and the stem members of their clade, lemuriforms are equipped with a built-in toiletry kit in their anterior oral cavity. The toothcomb, consisting of four or six procumbent teeth (including both incisors and canines), is used to for dental combing. The toothcomb is a synapomorphy of the lemuriform clade, although it has been lost or significantly modified in some lineages, namely the aye-aye (*Daubentonia madagascariensis*) and some recently extinct subfossil lemurs (Godfrey et al. 2010; Szalay & Seligsohn 1977). Additionally, lemuriforms have a keratinised and typically serrated sublingua or "under-tongue", a lesser-known soft structure, which is used to remove hair that accumulates on the toothcomb. Following oral grooming, the sublingua is thought to flick forward, allowing its serrated, keratinised tip to fit between the tine-like anterior teeth and remove the hair (Jones 1918; Roberts 1941).

Evidence of this cleaning function of the toothcomb can be found using scanning electron microscopy, which often shows fine striations made by the passing hair on the lateral and medial sides and lingual ridges of the teeth (Rose et al. 1981). Striations indicating dental grooming have also been found in omomyiforms from the late Eocene (Schmid 1983). Tarsiers groom orally and exhibit dental combing (Crompton & Andau 1986), and according to Musser and Dagosto (1987) some tarsier species also show striations on the lower incisors and canines. However, not all species show these striations, and the differences may be due to grooming frequency, thickness and length of the pelage, and the spacing of the anterior dentition.

Although tarsiers groom orally and exhibit dental combing, they lack a toothcomb (Ankel-Simons 2007). Views that lemuriform dentition and its derived toothcomb are "primitive" for primates are dated and originally derived from the scala naturae paradigm (Rosenberger et al. 1985). However, they persist either to place fossil primates as intermediates between strepsirrhines and simians (Franzen et al. 2009) or to ally tarsiers with strepsirrhines (Schwartz 2003) contrary to molecular evidence (Schmitz et al. 2001). In the case of the latter, Schwartz went so far as to blatantly ignore that he was comparing tarsier incisors to lemuriform canines in his attempt to suggest homology. Although signs of dental microwear indicate dental combing, the lack of striations does not preclude oral grooming, nor does it imply the manual grooming seen in simians.

Lemuriforms also bear a grooming claw, a specialized "ungula" or nail on their second pedal digit. This grooming adaptation is not nearly as exclusive since it is also found in haplorhines. Tarsiers, for example, have grooming claws on both the second and third pedal digits. As with the toothcomb, grooming claws have also been given undue weight when determining the phylogeny of living and fossil primates (Franzen et al. 2009; Schwartz & Tattersall 1985). Evidence of its existence in fossil primates and in living haplorhines has been debated historically, but that has changed recently. Soligo and Müller (1999) examined the shape and histology, concluding the grooming claw was a symplesiomorphy in primates, and its disappearance in simians may have coincided with the evolution of manual grooming, improved manual dexterity, and increased social complexity. Maiolino et al. (2011) recently discovered a more reliable metric for assessing the presence or absence of grooming claws by going beyond histology and instead evaluating the apical tuft of the distal phalanges. Their results showed that grooming claws could be found to varying degrees in platyrrhines, such as owl monkeys (*Aotus*).

Consequently, the presence of a grooming claw on the second pedal digit may be a symplesiomorphic trait for primates, retained not only in lemuriforms and tarsiers, but also in some New World monkeys. Alternatively, the trait might be convergent in three lineages. Regardless, it cannot be a diagnostic feature of grooming style.

Since the absence of a toothcomb, dental microwear, or a grooming claw cannot prove the existence of manual grooming among fossil primates and the timing of its origins, its traces must be sought elsewhere. But first, why did manual grooming evolve in the first place? Surprisingly, searches of the academic literature have yielded no published conjecture. To fill the void, here are some ideas.

First, the transition away from oral grooming was probably not for health reasons since the debris and parasites removed in manual grooming are usually ingested (Spruijt et al. 1992). One possibility involves concealed grooming. To notice simians grooming, you have to watch closely if their back is turned or they are behind a tree. Very little movement can be seen to clue you in to their activities. In contrast, all one needs to see is the tip of a tail when prosimians groom. While licking, the bobbing of the head causes flexion of the spine, which shifts the whole body. Furthermore, manual grooming frees the eyes to sporadically scan for threats. This might suggest that manual grooming evolved to help conceal grooming from peers for the purpose of coalition formation. If that were the case, then “tactical deception” (in the form of rapid trial and error learning—see Byrne and Whiten (1992)) may have preceded manual grooming. However, too little information is available about the frequency coalition formation in wild simians and whether concealed grooming is actually used.

Alternatively, concealed grooming may have evolved in response to the increased predation risk associated with diurnality. By reducing sudden movements which can draw the gaze of a predator and by steadying the eyes to occasionally watch for predators, manual groomers may have had an advantage during the middle to late Eocene, especially since visual predators such as falcons, hawks, and eagles were evolving around that time (Feduccia 1999). Of course, none of this explains why simians evolved manual grooming, but social lemurs did not. Perhaps the answers to the grooming riddle will be found in genetics or neurology if it is ever found at all.

MANUAL ANATOMY AND DEXTERITY

Alison Jolly (née Bishop (1962)) once noted, “The Primate hand preceded the Primate brain.” In truth, the brain evolved with the hands. Grasping hands and feet in primates likely evolved in tandem with the visual system for visually guided predation and plant foraging (Godinot 2007; Preuss 2007a); alternatively grasping feet and hands may have evolved for a fine-branch niche (Cartmill 1992; Sargis et al. 2007). What we know is that the earliest primates had grasping hands and feet and likely used them for food acquisition and locomotion (Bloch & Boyer 2002). Given that Jolly was making reference to some of the advanced cognitive abilities seen in some simian lineages, she was, in fact, partly right—the fundamental features of the primate hand evolved early on.

The manipulative abilities and locomotor preferences found among primates are influenced not only by the elaborate neural connections affecting tactile abilities, but also by the morphology of the hand. The hands of extant primates differ according to phylogeny. Lemuriform hands have a widely divergent thumb for grasping, are typically ectaxonic (4th digit is the longest), and have long digits. In some lemuriforms, paraxony (where both 3rd and 4th digits are the longest) is seen. Simians hands have less divergent thumbs, are typically mesaxonic (3rd digit is the longest)—sometimes paraxonic, as in some cebids (Cebidae)—and have shorter digits (Ankel-Simons 2007; Jouffroy et al. 1991). The mesaxony and paraxony in simians allows for a wider range of hand positions, allowing the hand kinematics to adjust to the substrate on which the primate is moving (Lemelin & Schmitt 1998). The hands of tarsiers—which have a less divergent thumb, are mesaxonic, and have long digits—may serve as an approximation for what the first primate hands were like. If that is the case, strepsirrhines evolved a more divergent thumb to specialize in grasping, while simians mostly retained hands adapted for a generalized arboreal locomotion (Godinot 1992). Recent analysis of lemuriform and adapiform hindlimb anatomy supports the view that their common ancestor specialized in using vertical supports for clinging and leaping, whereas the common ancestor of all primates only had adaptations for leaping (Gebo 2011).

Not much is known about the manual anatomy of Eocene primates due to taphonomic bias in the fossil record. Material from the hands of a few Holarctic adapiforms has been found, which allow comparisons with living taxa. These show that adapiforms generally had widely divergent thumbs and very long digits, suggesting that their grasp lacked power (Godinot 1992). In contrast, early simians had only moderate thumb divergence and grasping ability (Godinot & Beard 1991).

The foundation for our understanding of manual dexterity and utility is largely due to Napier (1956), who studied primate hands and defined two primary types of grips: the power grip and the precision grip (Napier 1993). Among extant primates, only catarrhines are capable of true opposition of the thumb, which requires rotation of the thumb. Most prosimians and platyrrhines have pseudo-opposable thumbs (Napier 1993), while tarsiers and marmosets have non-opposable thumbs (Ankel-Simons 2007). Despite the lack of true opposition in platyrrhines, capuchins (Cebinae) have evolved especially dexterous hands capable of destructive foraging (Christel & Fragaszy 2000; MacNeilage 1990; Napier & Napier 1967; Pouydebat et al. 2009; Spinozzi et al. 2004). Otherwise, both prosimians and platyrrhines (with the exception of capuchins) have only whole-hand control and are generally incapable of a precision grip. Lemuriforms are capable of fine control of the hand, although some, such as the members of Lemuridae, have difficulty picking up small objects off a flat surface and instead favour using their teeth (Bishop 1962). Since more insectivorous prosimians use their hands when feeding—whereas herbivorous lemurs often feed directly with the mouth—hand use and dexterity seem to be greatly influenced by ecology. Also, the gripping of fur during infancy or grooming differs from that seen with food or locomotion, with the grip depending on the close contact between the phalanges (Jolly 1964). Interestingly, lemuriforms appear to possess the dexterity required for basic manual grooming (using the fur grip seen in lemur infants or flat palms to part the fur), as seen in platyrrhines, yet do not exhibit the behaviour. Torigoe (1985) noted the same discrepancy between hand use and anatomy in regards to object manipulation.

Like prosimians, platyrrhines also use the same prehensive pattern for both small and large objects, but they differ in that they tend to explore novel objects with their fingertips first rather than grab them outright, groom manually, and use a preferred hand orientation when grasping branches as part of their above-branch quadrupedalism. Some platyrrhines demonstrate more advanced hand control by using scissor grips, where objects are secured by the sides of two digits, or when they pick up an object by curling a finger around it. Extant catarrhines go beyond whole-hand control, having fully opposable thumbs, while terrestrial species exhibit finer control of the hand. Even among colobus monkeys (*Colobus*), where the thumb is reduced or nearly absent, objects are either held between the fingers and the palm or are picked up using the index finger and the stump of the thumb (Jolly 1964; Napier & Napier 1967). Hominoid hands are generally more dexterous and are capable of specialized grips (Marzke & Wullstein 1996).

Jolly proposed that increased object play or manual grooming may have been pre-adaptations for more dexterous hands (Bishop 1962). Alternatively, ecological factors such as foraging may have driven the evolution of this trait (MacNeilage 1990). As with some other “traditional simian hallmarks”, such as increased brain size, improved manual dexterity in both simian branches appears to have evolved independently and much later than object play and manual grooming, making them unlikely catalysts. This does not rule them out as pre-adaptations, although ecological factors sound like the most plausible selective force. For example, foraging by captive golden lion tamarins (*Leontopithecus rosalia*) does bear a strong resemblance to grooming, with both hands used to part the substrate through which they searched. Likewise, destructive foraging in tufted capuchins (*Sapajus apella*) mirrors the object play they exhibit in captivity (unpublished data). To understand the significance and intricacies of object manipulation among extant primates, a brief review of ethology and primate cognition is in order.

OBJECT MANIPULATION AND PLAY

Object manipulation and object play have long affected our perceptions of animal intelligence (Byrne & Whiten 1992). Intelligence tests from the 1960s and earlier focused extensively on these traits, resulting in the biased conclusions that lemurs were significantly less "intelligent" than simians—particularly capuchins (Cebinae) and some macaques (*Macaca*), which were and still are some of the most common research subjects. Since then, we have come to learn that lemurs sometimes favour using their mouth over their hands when manipulating objects, and results from newer research that factored this in have yielded results that are surprisingly contradictory to earlier conclusions (Jolly 1966). (See Fichtel and Kappeler (2009) for a thorough review.)

When Jolly began her research, she favoured object play over grooming as an explanation for the origins of simian intelligence (Jolly 1964). She later viewed social learning, which was present in prosimians, as a preadaptation for object manipulation and intelligence (Jolly 1966). This was one of the first arguments for the social hypotheses that dominate cognition studies today. But first, what are the characteristics of object manipulation, and how do they differ between primate groups?

Captive prosimians, and particularly lemurs, tend to sniff, lick, pick up, and chew novel objects. They may also pull on branches to bring food closer, as well as hold or carry objects they have picked up. Responsiveness to novel objects can range from low to high, depending on the study and the species. However, all of these responses closely resemble foraging behaviours or directly involve food. In contrast, captive simians are known to roll, twist, and bend objects (Glickman & Sroges 1966; Jolly 1964; Parker 1974; Torigoe 1985). Yet we cannot generalize these captive behaviours to all simians. Many platyrrhines and leaf-eating catarrhines appear to favour foraging responses similarly observed in lemurs (Glickman & Sroges 1966).

Jolly initially attributed very little of the object manipulations in her studies to "object play" (Bishop 1962; Jolly 1964), instead showing that prosimians use their hands in stereotyped ways, primarily for grasping food or branches. Later, she noted that food was a motivator for the rare bouts of non-stereotyped "object play". She wrote: "…there was much social play, and locomotor play in springy branches, yet the lemurs were never seen to manipulate or investigate an object other than food" (Jolly 1966). Here object play is equated with object manipulation, yet it is only a subset of such behaviour. Play behaviours are difficult to define and categorise since social play may be directed at an object, or locomotor play may include social elements (Thompson 1998). Most play behaviours are structurally similar to species-typical behaviours. However, not all object manipulation—even in adults—classifies as play. Besides being possible artefacts of captivity or domestication (Hall 1998), some behaviours, such as tool use appear to be different. Yet it seems unlikely that object manipulation arose out of play, since the purpose of play is thought to be practice for existing behavioural adaptations (Burghardt 1998), not to generate new ones.

Some object manipulation seen in primates may be adult object play. In some cases, this seems unlikely, particularly in species such as ring-tailed lemurs (*Lemur catta*), where locomotor and social play cease in adulthood, yet they are sometimes reported to "play with objects" (unpublished data). Often "play" or manipulation behaviour seen in adults reflects species-typical behaviours, such as foraging, scent-marking, and nest-building, particularly in prosimians (Ehrlich 1970; Jaenicke & Ehrlich 1982; Jolly 1964; Renner et al. 1992). Differences in object manipulation have also been noted for wild versus captive animals, with wild animals showing more interest in animate objects and recently captured animals showing less interest in objects compared to their captive-reared counterparts. The willingness to manipulate objects also merits

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consideration since this can be affected by social factors as well as unintentional conditioning or baiting (Jolly 1964, 1966).

Although baiting is often controlled for (Fornasieri et al. 1990), unintentional conditioning is frequently overlooked and nearly unavoidable in captivity. Captive animals can learn that objects placed within their enclosures are always safe and frequently contain food or other enriching properties (Glickman & Sroges 1966). Indeed, Torigoe (1985) noted that the most common object manipulation behaviours exhibited by lemurs were related to food acquisition. Although this makes distinguishing foraging manipulation from the “characteristic” simian object manipulation more challenging in a captive environment, it would still be very telling if prosimians universally failed to demonstrate unconditioned/unbaited object manipulation. However this does not necessarily suggest that advanced object manipulation evolved from foraging behaviours since many lemurs forage, and even the excessively curious aye-aye treats novel objects strictly as foraging opportunities (unpublished data).

It was Humphrey (1976) who noted that advanced object manipulation may derive from the more basic acts of exploring and manipulating our social world. Picking up where Jolly left off, his work helped spark the social hypotheses, such as Machiavellian intelligence. Yet Humphrey, nor anyone who followed in his footsteps, has explained how this manipulative ability found its way out through the hands. From what the literature seems to suggest, advanced object manipulation is a product of increased intelligence, particularly trial and error learning. Yet as we will see, even the popular social hypotheses are riddled with inconsistencies and in need of support.

SOCIAL INTELLIGENCE

The Machiavellian Intelligence hypothesis started off by focusing on the importance of social interactions for the evolution of intelligence within primates (Byrne & Whiten 1988). Over time, correlations were found between the relative size of the neocortex and the group or grooming clique size (Dunbar 1998; Kudo & Dunbar 2001).

The transition to diurnality is thought to have resulted in higher predation, necessitating the formation of semi-permanent groups, while group living increases competition for resources. The enlargement of the metabolically expensive brain offset the cost of living in groups by enabling the enhanced cognition needed for the use of manipulative tactics, which includes monitoring increasingly complex social networks (Byrne & Corp 2004). (See Figure II.) This seemed to fit primates well, since social lemurs were seen to be less cognitively developed and less socially complex (Byrne 2000). Group sizes of social lemurs are often significantly smaller than that of simians (Dunbar 1998), and grooming is used to reduce aggression between dyads, not to form coalitions (Fichtel & Kappeler 2009).

However, cracks began to appear when the social hypotheses could not explain the unusual aspects of lemur social organization and the "arrested development" of their social complexity. Indeed, the greater the social complexity in lemurs, the smaller their brain—a trend opposite to what is predicted by the social hypotheses (MacLean et al. 2009). The less supported ecological hypotheses, which contended that big brains were fuelled by high-fruit diets and that group sizes were constrained by resource availability, suggested that lemur brains and group sizes were constrained by the limitations of their extreme habitat in Madagascar (Cunningham &

Janson 2007; Kappeler 1997; Wright 1997), although the recently extinct, monkey lemurs (Archaeolemuridae) did not conform to this view. The brains of these Malagasy lemurs were quite large by strepsirrhine standards, despite being no more complex than that of indriids (Indriidae) (Godfrey et al. 2010; Tattersall 1973). Regardless, the tenets of these ecological hypotheses have since started to integrate with the social hypotheses by suggesting that large social structures seen in simians helped improve foraging tactics, favouring yet larger group sizes (Thierry 2008).

Despite the bolstering from ecological principles, problems still exist. Behaviourally, anatomically, and phylogenetically, the story does not add up. The most common theme is that we have falsely assumed that all simians are equivalent to catarrhines. We often forget how much like prosimians the platyrrhines are, especially when compared to catarrhines.

Except for the fact that prosimians are less inclined to manipulate objects without food value, both they and platyrrhines demonstrate comparable cognitive skills, differing primarily in their performance on discrimination learning tasks and numerical discrimination (Fichtel & Kappeler 2009). It should be noted that prosimians also perform slightly below cotton top tamarins on object permanence tests (Deppe et al. 2009). Socially, both groups sometimes exhibit tactical deception, which is likely the result of trial and error learning (Byrne 2000).

Social lemurs and platyrrhines are also very similar socially. Although the average troop size of lemurs is smaller than that of platyrrhines, the latter are intermediate between lemurs and catarrhines. Also, most platyrrhine species live in small lemur-sized troops (Kappeler & Heymann 1996) with only Peruvian red uakaris (*Cacajao calvus ucayalii*) living in troops with >100 individuals. Neither lemurs nor platyrrhines live in multi-level social systems (Bowler et al.

2012). Small coalitions have been observed in social lemurs, but such occurrences are rare (Fichtel & Kappeler 2009). The only other major social differences are that social lemurs exhibit an even sex ratio and troops in some species tend to be less stable (Kappeler 1997).

Shultz et al. (2011) and Shultz and Dunbar (2007) argued that the transition from loose aggregations to stable or bonded groups facilitated the evolution of the advanced social behaviours that resulted in larger brains. However, this creates a problem since according to their own data, some lemurs also live in stable or bonded groups while not all platyrrhines do. If this is correct, then big brains could not have evolved first (see Figure III).

With all of these chronological and ethological inconsistencies, along with how the social hypotheses cannot explain the emergence of non-foraging hand use—even from “socially complex” early simians—clearly a piece of the puzzle is missing. What we need is a theory of hand and mind.

MANUAL GROOMING AND OBJECT MANIPULATION: A LINK?

So how do we make sense of this? If the social and ecological models fail to explain the peculiarities of lemur sociality, and platyrrhines are more like prosimians than most people realize, then how did enhanced cognition evolve in the simian clade, and why did the hand take on a life of its own? The solution could be simple, and it may be found exactly where Jolly predicted: in a social setting—albeit the catalyst might not have acted simply as a preadaptation for a more dexterous hand. Manual grooming may have opened the door for a very primitive, calculating mind, originally evolved to respond to the physical world. This may seem unlikely, given that grooming behaviours are governed at lower levels of the brain—in orally grooming rodents (Spruijt et al. 1992). Indeed, the neural changes that followed the switch from licking to picking may have been relatively minor, and were probably not followed by a significant increase in neocortex size since neural structure can change without an increase in brain size (Preuss 2007b). However, as simians have evolved, cognitive advances have occurred as a result, based on either social or ecological selective forces, as predicted by either Machiavellian Intelligence or the integrated social and ecological hypotheses. To understand what happened at the base of the simian clade, a “licking to picking hypothesis” may prove to be the best approach.

To understand how manual grooming could spark novel hand use and an increased interest in objects, all we have to do is look at the effects of artificial selection on domestic animals. In dogs, we now know that the process of domestication has endowed our canine companions with the ability to understand pointing and gaze cues (Hare et al. 2002). Other social cognitive skills have also been documented in other domestic animals (Rosati et al. 2010). Most relevant and astounding of all is the case of Holstein cattle. According to Grandin and Johnson (2005), the process of selecting for continual eating (to increase milk production) has resulted in a breed that is notorious for manipulating objects with its mouth. Whereas other free-ranging cattle breeds might sniff and occasionally lick/chew a novel, neutral object, Holsteins will lick and chew incessantly. They are even known to open gate latches with their tongues, initially by trial and error. However, once they learn the trick, they can open the latches easily and some have mastered nearly every latch on the market.

Surprisingly, this behaviour has not been explored academically. If these observations are correct, the parallel should be obvious. Admittedly, the degree differs—most platyrrhines do not incessantly manipulate non-food objects, but all captive species have been observed to do so from time to time (unpublished data). But that could be expected given the difference in phylogeny and neural anatomy.

The next question is where this manipulative behaviour would come from. Why would compulsive eating or manual grooming trigger such radically new behaviour? The answer is that it is not radically new. In fact, practical and theoretical work on Bayesian decision theory indicates that the brain evolved for handling complex movement and interaction with the environment by handling sensory input, past experience, noise, and uncertainty to adapt to the environment. Working with each of these variables, Bayesian inference involves calculating probabilities of outcomes to enable an organism to generate the appropriate physiological response in a dynamic and changing world (Orbán & Wolpert 2011). By neurologically freeing the hands to groom manually, it could open the door for this basic proprioceptive circuitry to emerge through the hands. If this is correct, our view of cognition as an abstract, tactical planner may be anthropocentric (Barrett & Rendall 2010). At its core, the brain is about the body. The mind is an emergent property.

The basic principles of this can be seen in tool use. In the brain, tools are treated as an extension of the body plan. This proprioception occurs in the parietal cortex where somatosensory and visual inputs are merged. Our brains already perform complex calculations to manipulate the body, which suggests an embedded, neural link between self-manipulation and object manipulation (Iriki et al. 2010). To put it simply, self-manipulation evolved into object manipulation, which in turn, evolved into advance proprioception and tool use. Interestingly, the purpose of grooming may be de-arousal, in which case grooming may represent a shift from processing exteroceptive information (from the outside world) to processing proprioceptive information (Spruijt et al. 1992), further supporting the link between internal and external manipulation, with grooming acting as a potential bridge.

By viewing tool use as a proprioceptive act, we may now be able to explain some perplexing prosimian behaviours that resemble tool use. Although prosimians have not been observed using objects as tools in the wild, they can be trained to do so, yet will also select the most effective tool for the task, and not necessarily the one they were trained on. It appears they understand the functional qualities of the tool and can even manipulate and reposition tools to make them effective, which puts them on par with capuchins (Santos et al. 2005). Without training, lemurs have been observed using their tails to collect water from a pond. Some members appeared to pick this behaviour up through social learning (Hosey et al. 1997). Wild slender lorises have been observed licking their arms to make them sticky, and then placing it in the path of ants to collect them (Kumara et al. 2005). Some people consider the act of pulling a branch closer for accessing fruit or leaves as an example of tool use in primates, which is also seen in some diurnal lemurs (Iriki et al. 2010; Jolly 1964; Milliken et al. 2005). Each of these suggests that fundamental Bayesian inferencing can emerge in prosimians as basic proprioception naturally, or as an extension of the body plan with training. Simians, however, may do this automatically and more frequently.

The enlarged brain of simians includes a significantly evolved neocortex, where sensory and motor processing occurs. This includes the parietal cortex, which has undergone significant change in simians. Brodmann areas 3b, 1, 2, and 5—which are involved in object exploration, reaching, and grasping—have evolved and specialized within various simian lineages (Kass 2010; Padberg et al. 2007). Brodmann area 5 and the posterior parietal cortex in particular appear to have evolved for specialized hand use (Hinkley et al. 2007). These somatosensory and motor areas, which include the intraparietal sulcus (IPS), also assist with the understanding of intentionality in social situations (Hamilton & Grafton 2006). Sure enough object manipulation and social cognition appear to be linked in the brain (Hopkins 2010).

This makes perfect sense because social interactions follow the same basic Bayesian inference principles as object manipulation (Körding & Wolpert 2006). This falls in line with the view that tactical deception in most primates is best explained through trial and error learning (Byrne & Whiten 1992), and may clarify why lemurs sometimes demonstrated tactical deception in controlled studies and only rarely in the wild (Barrett & Rendall 2010; Fichtel & Kappeler 2009; Genty & Roeder 2006; Genty et al. 2008).

It appears that there is a relationship between object manipulation, social manipulation, and grooming within simians, but not within prosimians. This cognitive divide may seem small, yet is significant. This “Lennian divide”—named here in honour of the individual who helped me see it—sets simians apart from prosimians in their manipulation of objects, and may help explain other behavioural differences as well. Furthermore, by learning to work around the Lennian divide in our study of social lemurs and other prosimians, we may find other surprising cognitive abilities not predicted by current models. For example, might lemurs demonstrate Theory of Mind under the right circumstances? As for simians, the Lennian divide may finally explain why we think with our hands and shed light on the root of our cognitive abilities.

CONCLUDING REMARKS

What defines a crown simian as opposed to a stem simian? Is it a full postorbital septum, something special about the cusps on our molars, or the shape of the talus bones in the ankles? As a myriad of anatomical differences flesh out in the fossil record, slowly revealing the order in which they evolved, palaeontologists are left to decide which traits were most significant and best define the simian clade. Meanwhile, researchers in the behavioural sciences see distinct differences between simians and all other primates. However, behaviours do not always fossilize. Sometimes we get lucky and find an oviraptor guarding a clutch of eggs, turtles locked in coitus, or predator and prey frozen in mortal combat. But these are the exceptions.

Sociality lies at the heart of the simian clade and eventually spurred the evolution of large brains, problem solving, and social learning, but those early simian communities were no more complex than what we see in modern lemurs (Shultz et al. 2011). Here I argue that the evolution of the simian/prosimian behavioural gap, or “Lennian divide”, may stand as a defining moment in simian evolution, more so than the full convergence of a few bony plates behind the eye. As detailed above, manual grooming and advanced object manipulation may have been linked traits that emerged at the same time. It is this multi-tool of social and technical behaviours that acts as the cornerstone of the simian cognition.

Although we will probably never find manually grooming primates frozen in the fossil record, interdisciplinary scrutiny can help identify the proximate causes of this behaviour, while palaeontology can piece together the ecosystems in which our ancestors lived to slowly unveil the ultimate causes of these behavioural changes. By collaborating we can take what we know about primate behaviour, the behaviour of other animals, ecosystem evolution, palaeocommunities, neuroscience, and genetics and define crown simians by the very behaviour that unites both our clade and our social groups. The challenge is great, but evolution has honed our hands and minds for the task.

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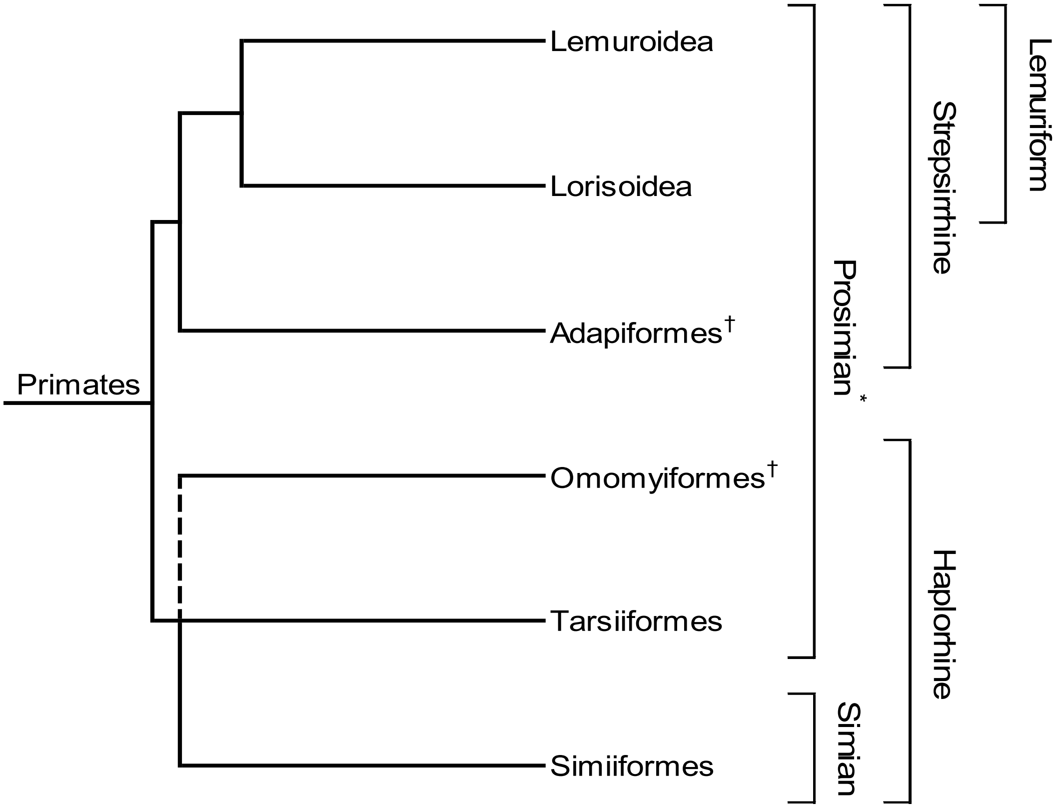
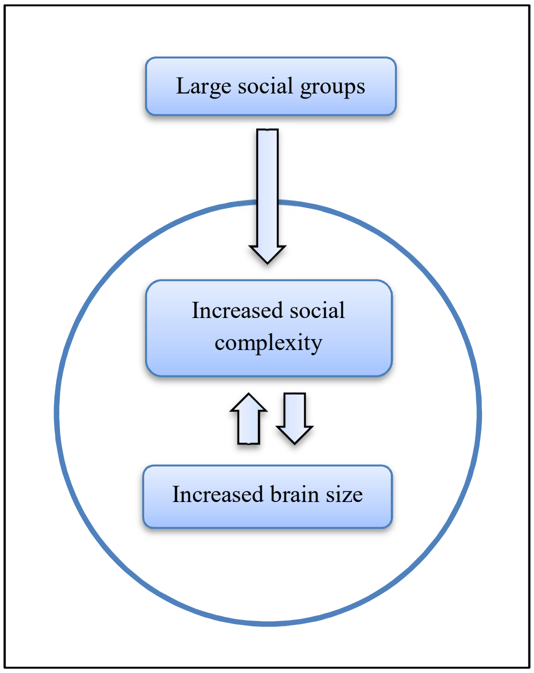
Figure I: Simplified phylogeny of primates, extant and extinct



†Extinct taxa

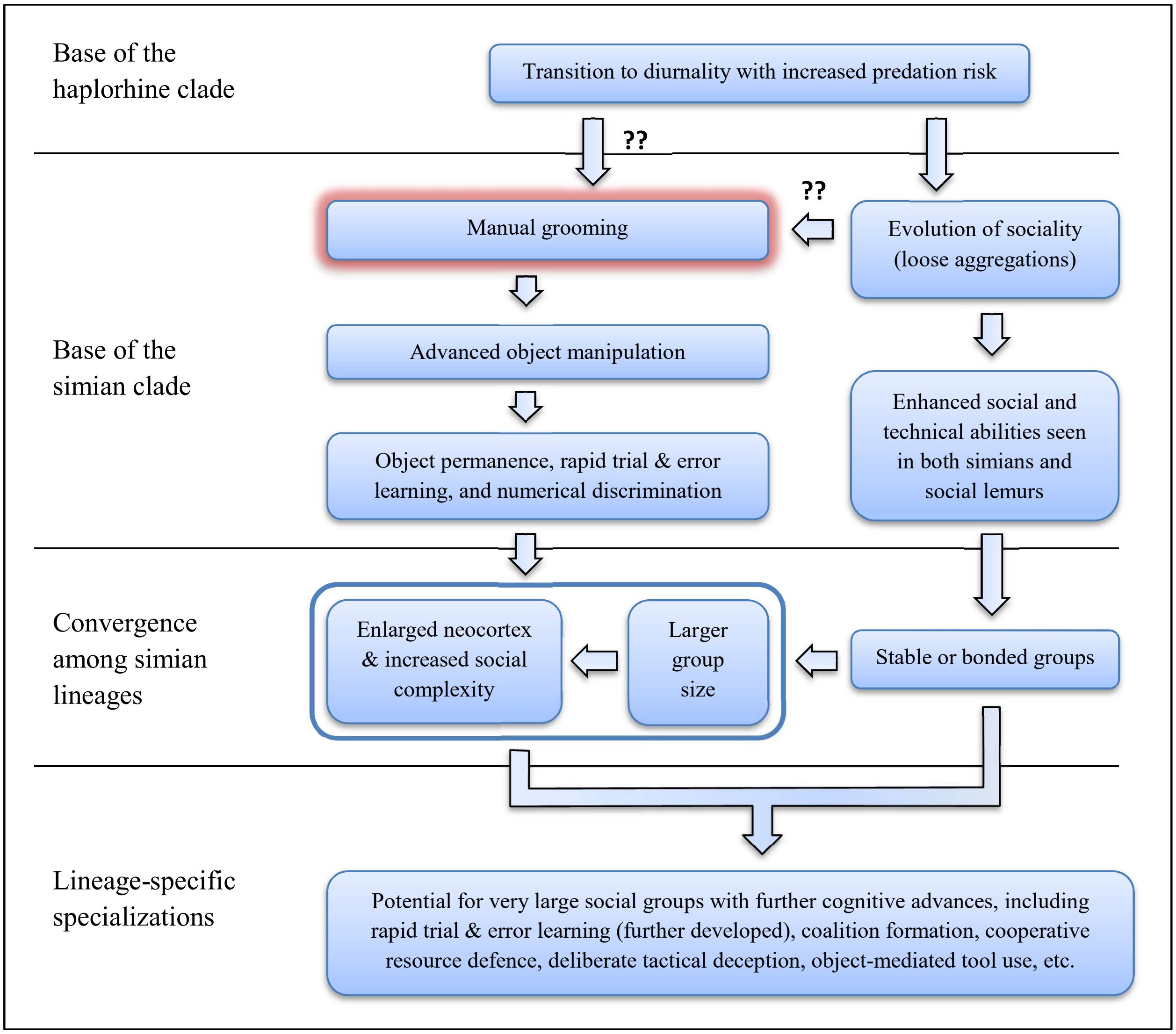
*Paraphyletic grouping

Figure II: Social hypotheses



Adapted from Byrne (1995), the social hypotheses predict that large social groups exert a selective pressure to increase both social complexity and brain size.

Figure III: Licking to Picking Hypothesis



The licking to picking hypothesis helps put the evolution of social and technical cognition into phylogenetic context. Manual grooming may have been linked to advanced object manipulation, which gave rise to the derived cognitive skills that are less developed in social lemurs. All other cognitive skills shared with social lemurs would be either convergent or ancestral (Fichtel & Kappeler 2009). This simplified illustration does not rule out the influences of social and ecological factors at various levels where not specified.

Table I: Glossary of cladistic, phylogenetic, taxonomic, and geologic terms discussed in text

Adapiform	Infraorder Adapiformes, an extinct branch of strepsirrhine primate, distantly related to lemurs
Catarrhine	Parvorder Catarrhini within Simiiformes, which includes Old World monkeys and apes (+humans).
Cercamoniine	Superfamily Cercamoniinae, a branch of adapiform primates, which may have given rise to lemuriforms very early in its radiation from Asia
Eosimiiform	Infraorder Eosimiiformes, a suspected stem group to simians originating in Asia
Haplorhine	Suborder Haplorhini, includes simians, tarsiers, and possibly the extinct omomyiforms.
Lemuriform	Infraorder Lemuriformes, includes the lemurs (lemuroids) of Madagascar and the lorises and galagos (lorisoids) of Africa and Asia.
Lemuroid	Superfamily Lemuroidea, includes only the lemurs of Madagascar; see Dunkel et al. (2011/2012) regarding the proper use of the colloquial term "lemur".
Lorisoid	Superfamily Lorisoidea, includes only the lorises and galagos of Africa and Asia.
Omomyiform	Infraorder Omomyiformes, an extinct branch of tarsier-like haplorhines
Platyrrhine	Parvorder Platyrrhini within Simiiformes, also known as New World monkeys.
Prosimian	Formerly a taxonomic rank (Prosimii), the term is still used to describe a paraphyletic group of primates (tarsiers & strepsirrhines) that exhibit low encephalisation and share behavioural characteristics.
Simian	Infraorder Simiiformes, includes monkeys and apes (+humans). Also referred to as anthropoids, but see Hoffstetter (1974).
Strepsirrhine	Suborder Strepsirrhini, includes lemuriforms and the extinct adapiforms.
Crown group	A monophyletic clade consisting of all species descended from a common ancestor, both living and extinct.
Stem group	A paraphyletic clade of extinct species descended from a common ancestor, excluding the related crown group.
Ghost lineage	Undiscovered fossil species suspected to exist due to discrepancies within the fossil record itself or between it and molecular divergence dates.
Symplesiomorphy	An ancestral trait shared by two or more taxa.
Synapomorphy	A derived trait (apomorphy) shared by two or more taxa.
Paleogene period	Paleocene–Oligocene epochs.
Paleocene epoch	~66 to ~56 Ma.
Eocene epoch	~56 and ~34 Ma, divided into the early Eocene (~56 to ~49 Ma), middle Eocene (~49 to ~37 Ma), and the late Eocene (~37 to ~34 Ma).
Oligocene epoch	~34 Ma to ~23 Ma.