

ARE TARSIERS REALLY A TAXONOMIC ENIGMA?

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Why are tarsiers indeed such a taxonomic enigma? Over the past century there has been no real agreement among physical anthropologists and primatologists alike towards tarsier phylogeny. Based on numerous shared ancestral traits, some experts say they are more related to prosimians. Others say they are more related to anthropoids. And then there are some that say they are not linked to either of the aforementioned sub-orders and that they should belong exclusively to their own sub-order. Thus, I will attempt my own phylogenetic analysis towards solving this huge taxonomic nightmare. I will compare a series of genetic, behavioral, and morphological traits among the genus *Tarsius* along with two prosimian genera: *Galago* and *Microcebus*; and one nocturnal anthropoid genus: *Aotus*. Each specimen evaluated will serve as a comparable representation of the sub-orders: Prosimii and Anthropoidea. Upon these comparisons, I aim to find out a closer phylogenetic tie towards one of these particular sub-orders or perhaps even neither.

According to Sharon Gursky (1999) in her essay titled "The Tarsiidae: Taxonomy, Behavior, and Conservation Status" within the anthology *The Nonhuman Primates*, there are two major opponents on the issue of tarsier phylogeny. The first one, which is essentially centered on the pioneering research of W.K. Gregory (1915), aligns tarsiers with numerous prosimian species based upon the presence of various ancestral traits. However in 1918, R. Pocock debated the issue on the already mentioned course towards tarsier phylogeny and argued that tarsiers are indeed anthropoids based upon the fact that tarsiers exhibit numerous morphological synapomorphies or shared derived traits. Thus, with the classification under anthropoids, Pocock is essentially establishing a classification scheme based upon allocating tarsiers into the sub-order Haplorrhini versus Strepsirrhini (Gursky, 1999: 140; Yoder, 2003: 161-162). I therefore have constructed a table that simplifies the two arguments based upon the morphological traits that are present and shared among the sub-orders. Please note that the sub-orders of Anthropoidea and Prosimii can be substituted for the orders Haplorrhini and Strepsirrhini to accommodate Pocock's argument. My results are as follows:

Tarsius: Dry Rhinarium

Haemochorial Placentation
 Fovea Centralis
 Reduced Olfactory Bulbs
 Promontory Artery
 Flexible Upper Lip
 Small Body Size
 Unfused Mandibular Symphysis
 Grooming Claws
 Multiple Mammae
 Biocornuate Uterus

Anthropoidea: Dry Rhinarium

Haemochorial Placentation
 Fovea Centralis
 Reduced Olfactory Bulbs
 Promontory Artery
 Flexible Upper Lip

Prosimii: Small Body Size

Unfused Mandibular Symphysis
 Grooming Claws
 Multiple Mammae
 Biocornuate Uterus

*Data from Gursky, "The Tarsiidae: Taxonomy, Behavior, and Conservation Status," in Dolbinow and Fuentes', *The Nonhuman Primates*, Mayfield, 1999; 140-141.

Upon drawing conclusions from this table, it may be more evident that there is a strong anthropoid link. In other words, I would have to agree with Pollock when considering this table as being quite obvious that tarsiers do contain more traits that are in common with anthropoids. For example, the fact that tarsiers have noticeable haplorrhine traits such as a dry rhinarium, reduced olfactory bulbs, fovea centralis, and a flexible upper lip would almost guarantee a slam-dunk case in a strong correlation with anthropoids. However, some experts agree that some of these traits, as well as the other aforementioned traits, are highly debatable as being purely anthropoidean.

Jeffrey H. Schwartz utilizes other individuals' previous research and comparative analysis in his own article within the anthology *Tarsiers: Past, Present, and Future* to test these so-called unquestionable similarities between both sub-orders. For one, there is no real agreement on whether the development of a fovea centralis in *Tarsius* is shared completely with anthropoids. He adds that galagids have even been noticed to have a minute presence of a fovea. In addition, he goes onto to state that the nocturnal New World anthropoid genus, *Aotus*, is also very unique in its development of a fovea centralis in that it is the only primate species

to have a fovea with an extremely high rod to cone ratio. This characteristic makes it more than well adapted for night vision (Schwartz, 2003: 55). Yet Colin Groves asserts in his chapter on primates in the *Encyclopedia of Mammals*, that both *Tarsius* and *Aotus* are quite different from all primate species in that they are the only ones that have an exceedingly large fovea with retinas completely saturated with rods (133). Regardless, this particular trait is not something that is seen to be widespread throughout the realm of primates.

As for the dry rhinarium and the unattached upper lip, there is no question that these characteristics are indeed shared in common with anthropoids. However, the overall structure of the nasal section may be more similar morphologically to prosimians. Hofer, in his 1980's research upon this particular matter, noted that the laterally wrinkled nasal structure observed in tarsiers matched more closely to several pro simian species (Hofer 1980). Yet, because tarsiers do indeed have a dry rhinarium along with a flexible upper lip, it cannot be denied that this is more of an anthropoid trait.

Elwyn Simons adds further to the anthropoid/prosimian debate by employing a quote from Starck's 1955 research also in the anthology *Tarsiers: Past, Present, and Future* on tarsier haemochorial placental development. According to Starck's this anthropoidean characteristic is something that is only noticed once tarsiers fully mature. Prior to this point, the development of the placenta resembles more closely to that of pro simians (Simons, 2003: 11). Therefore tarsiers could be displaying a stage between both anthropoid and prosimian placental development by showing the retention of a primitive trait and then later on developing the more derived form.

Furthermore, according to J.R. and R.H. Napier in their book, *The Natural History of Primates* (1985), tarsiers are seen to exhibit a grooming claw on the second phalange of the foot, which is similar to prosimians who have a grooming claw on either the second or third phalange (32; Dolhinow and Fuentes, 1999: 121). However, what is interesting is that tarsiers also exhibit a grooming claw on the third phalange as well. This unique display of having two grooming claws is not shared in common with prosimians, or any other primate for that matter (Napier & Napier, 1985: 17). However, grooming claws are indeed predominantly a pro simian trait.

In terms of confirming body and weight similarities to prosimians, I aimed at conducting a table of various body sizes and weight measurements of *Tarsius*, *Microcebus murinus*, *Galago senegalensis*, and *Aotus* obtained from the book *Walker's Primates of the World* written by Ronald M. Nowak (1999). (Table 1):

Table 1: Body Size and Weight

	Head/Body Length	Tail Length:	Adult Weight:
Tarsius:	85-160mm	135-275mm	80-165gm
Galagosenegalensis:	88-210mm	180-303mm	95-300gm
Microcebus murinus:	125-150mm	125-150mm	39-98gm
Aotus:	240-370mm	316-400mm	.6-1kg

Based on the measurements obtained, tarsiers do indeed share more similarities in length and weight with the above-mentioned prosimian specimens, particularly *Galago senegalensis*. On the other hand, *Aotus* shows a clear deviation from these particular pro simian small-bodied species. However to be somewhat fair, I decided to further compare the body, tail, and weight measurements of *Cebuella pygmaea* to see if *Tarsius* was still comparable to this small bodied New World anthropoid (Table 2):

Table 2: Tarsier and Cebuella Data

	Head/Body Length:	Tail Length:	Adult Weight:
Cebuella pygmaea:	117-152mm	172-229mm	85-140mm

Based on these particular results, the body length and weight of the pygmy marmoset is comparable. In fact, both *Cebuella pygmaea* and *Microcebus murinus* are the only ones that fit within the measurable ranges of *Tarsius*. However, anthropoids for the most part are large-bodied. And prosimians on the other hand, are commonly represented by a large number of small-bodied species. Consequently, a larger weight of evidence obtained from body, tail, and weight measurements does support a strong pro simian relation. Yet, this small body size may not be due to the retention of traits from a primitive ancestor, but rather could be homoplasy.

But those aforementioned traits alone gathered to support Gregory's and Pocock's classification schemes are not at all satisfying. As a matter of fact, there are other morphological traits that exist beyond these highly generalized comparisons between tarsiers and other primates. For instance in relation to body size, I also constructed a table (Table 3) consisting of data from E. Christopher Kirk's (2004) research on comparing average measurements of the diameter of the eye and cornea among 147 primate specimens to see if there was a match in data among the species compared: *Tarsius syrichta*, *Microcebus murinus*, *Galago senegalensis*, and *Aotus*. Furthermore, ratios are shown in order to get a relative measurement of cornea to eye diameter. In addition to this table, I created another table displaying the average body size along with the average

cornea and eye diameter obtained from the first table in order to see which primate considered, shared similar eye and cornea proportions in relation to body size that may or may not point to a more anthropoid or prosimian connection. Table 3 and 4 are as followed:

Table 3

Mean Transverse Diameter:	Cornea:	Eye:	CD/ED Ratio:
Tarsius syrichta:	14.1mm	17.9mm	.79
Microcebus murinus:	8mm	9.4mm	.85
Galago senegalensis:	8.8mm	9.6mm	.92
Aotus:	13.4mm	19.2mm	.70

Table 4

Mean Transverse Diameter:	Cornea:	Eye:	Body Length:	Cornea/ Body/Eye/ Body:
Tarsius syrichta:	14.1mm	17.9mm	122.5mm	.16/.15mm
Microcebus murinus:	8mm	9.4mm	137.5mm	.06/.07mm
Galago senegalensis:	8.8mm	9.6mm	149mm	.06/.06mm
Aotus:	13.4mm	19.2mm	305mm	.04/.06mm

To sum up these two tables, it is quite clear that *Aotus* shares similar diametrical averages in eye and cornea length to *Tarsius syrichta*. However, when considering the relative proportion of cornea to eye diameters, it is quite evident that *Microcebus murinus* comes the closest. Moreover, *Microcebus murinus* also closely resembles *Tarsius syrichta* in overall eye diameter in relation to average body length. Nevertheless, *Tarsius syrichta* evidently stands out the most among all four specimens. Therefore, *Tarsius syrichta* may be displaying a unique adaptation and requirement for extremely large eyes that are useful for nocturnal habitation and possibly ambush hunting behaviors. However, *Microcebus* may be exhibiting an evolutionary trend towards developing the same traits due to its partial dietary reliance on insect prey (Nowak, 1999: 66).

Aotus has the smallest relative size of cornea to eye diameter, and relative cornea/eye diameter to body size. This could possibly be attributed to the com-

plete saturation of rods within the fovea centralis that aids *Aotus* in seeing nocturnally without a requirement for extremely large eyes or tapetum lucidum. Not only that, but very little of this particular primate's diet consists of insects or small bodied fauna. Therefore, there is little need for excessively large eyes to aid them in the visual detection of moving prey (Nowak, 1999: 112). But again, tarsiers and night monkeys are both unique in that they fail to exhibit any cones within the retinas of their massive eyes. In addition, they both have been noticed to display a macula region commonly seen in diurnal anthropoids. This highly suggests that they both share a relationship with a diurnal ancestor (Groves, 2003: 133). However in regards to the tables stated above, there may be more of a closer link between tarsiers and small-bodied prosimians.

To further compare morphological similarities, the hind limb morphology of tarsiers does indeed draw attention. When comparing particular galagids, mouse lemurs, and night monkeys, it does become evident that tarsiers may be exhibiting an ancestral form of hind limb morphology. For instance, A.B. Howell (1944) in his research noticed that all galago and mouse lemur species are seen to have a lengthened calcaneus with a minute cuboid. Furthermore, tarsiers, galagos, and mouse lemurs are unique in that they not only display lengthened tarsal bones, but also display a longer foot length in comparison to the femora or tarsal bones. As a matter of fact, galagos and tarsiers share very similar intermembral indexes that are both extremely low. Also, galagos, mouse lemurs, and tarsiers exhibit noticeable bone fusion among the tarsal and femoral bones (Schwartz, 2003: 67~68). This elongation and fusion of the hind limbs among these three specimens could possibly be due to displayed similarities in their forms of arboreal locomotion, known as vertical leaping (Nowak, 1999: 61, 66, 95). *Aotus*, however, is more of an arboreal quadruped that shows very little leaping (Nowak, 1999: 112).

Table 5: Comparison of Teeth

	Dental Formula:	Total Number of Teeth:
Tarsius:	2/1-1/1-3/3-3/3	34
Microcebus:	2/2-1/1-3/3-3/3	36
Galago:	2/2-1/1-3/3-3/3	36
Aotus:	2/2-1/1-3/3-3/3	36

Other morphological aspects that could be further analyzed are the dental formula and morphology of tarsiers to see if they show an ancestral or derived state. Table five compares the dental formula and number of teeth among *Tarsius*, *Galago*, *Microcebus*, and *Aotus* (Napier and Napier, 1985: 40 and 106).

It is evident that tarsiers stand out the most from these particular specimens in that they generally lack a second lower incisor. Yet, the ways in which the teeth of tarsiers are arranged along with the independent morphology of the teeth are noticeably primitive. In fact, due to Musser and Dagosto's research (1987) on anterior tooth morphology in *Tarsius pumilus*, it can be concluded that the anterior teeth of this particular specimen resembles very closely to the dental comb arrangement in lorises and lemurs. Furthermore, the bottom set of molars, canines, and premolars among *Tarsius* show a derived morphology from the ancestral condition seen in galagos and not in anthropoids. These include such traits as premolariform canines and sharp, tall cusps on the molars (Schwartz, 2003: 66.67).

More morphological similarities that can be mentioned are what Patricia Wright (2003) noted in the introduction to the journal anthology *Tarsiers* with information from her 1986 written journal article titled "Reproductive cycles in *Tarsius bancanus*" that Horsfield tarsier females show swollen genitalia during estrous, which indeed is an anthropoid trait (1). Elwyn Simons (2003) in her article "The Fossil Record of Tarsier Evolution" in the same anthology further claims that tarsiers have been seen to exhibit other anthropoid traits such as a thin mandibular ramus with a poorly developed mandibular process and an anterior positioning of the foramen magnum. However, these characteristics are again highly questionable as being homoplasy rather than shared derived traits among anthropoids (10). Also, there is a tubular ear bone extension that is noticed in tarsiers that very much resembles the lengthened ear canal seen in Old World anthropoids, including humans (Napier and Napier, 1985: 106).

In terms of behaviors, it has been stated that tarsiers do indeed show a number of primitive behaviors that have been debated among primatologists over the past several years (Gursky, 1999: 140). For one, the nocturnal habitation exhibited by tarsiers is commonly associated with almost all pro simians. In contrast, nocturnality in anthropoids is something that is only seen among owl monkeys (Napier and Napier, 1985: 17,18, 115). Even Simon Bearder (1987) in his essay "Lorises, Bushbabies,- and Tarsiers: Diverse Societies in Solitary Foragers" in the anthology *Primate Societies* clearly asserts that anthropoids have been primarily diurnal throughout their entire phylogenetic history (11). However, the fact that tarsiers show the morphology that also coincides with diurnal anthropoids should not be overlooked as purely a primitive trait. In fact, Bearder further argues that it is quite possible that tarsiers may be exhibiting a new phase in nocturnal adaptation (11).

Another ancestral behavior noticed is the way in which mothers among most species of tarsiers often practice "parking" their infants when hunting and carrying their infants orally when moving (Gursky, 1999: 140). Similarly, dwarf

galagos engage in these same mother-infant behaviors as well (Norwak, 1999: 65). Yet to say this behavior is something that is purely shared with pro simians may be misleading in that this may be a distinctive, successful adaptation in occupying a tropical niche with a small number of potential predators rather than an ancestral phenotypic expression.

I constructed a table delineating the particular diets as being exhibited among tarsiers, dwarf galagos, and mouse lemurs (Bearder, 1987; Napier and Napier, 1985; and Harste and Wright, 1997).

Table 6: Diet Percentage

Diet %:	Insects:	Fauna:	Fruit:	Other:	Source:
Tarsier:	90	10	0	0	Bearder, 1987
Dwarf Galago:	70	0	20	10	Napier & Napier, 1985
Mouse Lemur:	70	0	30	0	Harste & Wright, 1997

Based upon this table, it is clear that tarsiers exhibit a closer relationship to pro simians due to the overwhelming amount of invertebrate and vertebrate prey that is consumed. On the other hand other galagids, such as *Galago senegalensis*, display a greater preference for fruits (Napier & Napier, 1985: 99). Yet for the most part, the diets among both pro simians and tarsiers are very different from the primary frugivorous dietary compositions that are seen in anthropoids, including *Ao/us* (Napier & Napier, 1985: 115). However, complete sustenance on a diet of insects and fauna in itself is very exclusive to tarsiers in respect to all other primates that fail to show full subsistence on living prey.

In addition to the diets of these particular specimens, the hunting behaviors can also be compared among them. Galagos and tarsiers are the only ones that exhibit an ambush style of obtaining prey. Also, they are the only ones that show distinct similarities in the ways in which they grasp and consume insects, which is usually head first (Bearder, 1987; Napier & Napier, 1985: 99).

Furthermore, the social behaviors exhibited by tarsiers can be further analyzed to draw a potential phylogenetic connection. Tarsiers tend to not live in large collective groups, but are rather independent in their social behaviors. They are often documented as either living solitary or within monogamous pairs with

offspring. Unfortunately however, the social composition of tarsiers is something that is still highly debated as being universally monogamous or solitary (Wright, Pochron, Haring, Simons, 2003: 260).

In fact, both *Tarsius bancanus* and *Tarsius spectrum* show a considerable amount of variation in their social organization and behaviors. Both species have been observed ranging in mix-sexed groups. They also rely mainly on olfactory communication via scent markings and urine washing in addition to the audio forms used to correspond between members. This is also commonly seen among pro simians (Barrett & Dunbar, 2000:63). In *T. bancanus*, very little audio communication and physical contact exists among males and females. Whereas *T. spectrum*, shows a considerable amount of auditory communication and close affiliative behaviors such as grooming, tail twinning, and other forms of close physical contact among members. In general, the social organization exhibited by tarsiers is not found to be similar in *Microcebus* or among most galagids. In reality the ranging pattern as seen by *Microcebus* is divided according to sex. But, the social forms displayed by tarsiers do show a greater correlation with *Aotus trivirgatus* where individual males, females, and offspring cooperate together as a group for resources and territorial defense within their habitat (Bearder, 1987:11,21-22; Napier & Napier, 1985: 84, 116).

Lastly, molecular phylogenetic evidence can further be applied in an attempt to put this debate to rest. A table consisting of the various tests done in genetics and immunological comparative analysis among tarsiers to prosimians and anthropoids are listed along with their outcome (Morales, Disotell and Melnick, 1999: 19-20 and Yoder, 2003: 167-168).

Table 7: Tests Done in Genetics and Immunological Comparative Analysis

Test:	Relation of Tarsiers: Anthropoid, Prosimian, or Neither
Immunological:	Neither
Protein Sequencing:	Anthropoid
Chromosomal Analyses:	Neither
DNA Hybridization:	Anthropoids
Nuclear Gene Sequencing:	Neither (Yet 3/5 supports anthropoid link)
IRBP Nucleotide Sequencing:	Prosimians
aA-Crystallin Locus:	Prosimians
Mitochondrial Genome Sequencing:	Neither (Yet shows a close Prosimian link)
*Alu Repeat Sequencing:	Anthropoid
*Alu RNA Sequencing:	Anthropoid

In consideration of the evidence stated in the table above it is quite obvious that most of the tests conducted support a closer affiliation with anthropoids. Protein sequencing, DNA hybridization, Alu repeat, and Alu RNA sequencing all support a close tie with anthropoids. Even the nuclear gene-sequencing test confirms a greater haplorhine relationship. However, the table mainly supports the notion that tarsiers are separate sister-taxa to the aforementioned sub-orders (Morales, Disotell, & Melnick, 1999: 19-20).

Moreover, disputes very much center on these various tests due to discrepancies and flaws in methodologies. For example, previous immunological tests showed a clear link to anthropoids. However, until recently, new immunological data has supported a sub-order of their own that differentiates them from both pro simians and anthropoids.

In regards to methodologies, missing data from original tests in protein sequencing have been considered to be a major flaw. Therefore this data cannot be considered valid until it has been re-conducted properly (Morales, Disotell, and Melnick, 1999: 19-20). Furthermore, Yoder (2003) in her essay accuses researchers in the nuclear gene comparative analysis of overlooking other genetic characteristics in lieu of this potentially strong trend towards supporting a more proximate tarsier relationship to anthropoids. She adds that the ignorance of relevant data and sampling bias is also prevalent in the mitochondrial genome sequencing in attempt to draw a chain towards prosimians. She also points out that only 3 Alu markers among a group of 118 within the Alu RNA sequencing shows a closer affinity towards anthropoids (167-168). Thus, these cannot realistically, nor reliably, be used to draw any conclusive link to anthropoids or pro simians due to these mistakes.

Conclusion

In conclusion, tarsiers may not be such a taxonomic enigma after all if considering an individual sub-order for tarsiers in general. As exemplified by the presented data on morphology, behavior, and molecular studies, there is, undeniably no clear agreement as to placing tarsiers within each of the aforementioned sub-orders: Anthropoidea and Prosimii. And much of the reason as to why they remain such a taxonomic enigma lies in the presence of numerous ancestral and derived traits, as well as the subsequent attempts to accommodate all of these characteristics into one of those all inclusive sub-orders. Robin Dunbar and Louise Barrett (2000) argue in their book, *Cousins*, that the reason as to why tarsiers exhibit such a mix of traits is not purely because of the phylogenetic retention of these traits, but rather due to homoplasy as a result of occupying a nocturnal, tropical niche over long periods of time (57). Therefore by placing

tarsiers into their own sub-order, this unique accumulation of traits can appropriately be accommodated and the argument can finally be put to rest.

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