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Source: Primate Conservation, 22(1) : 146-150

Published By: Conservation International

URL: <https://doi.org/10.1896/052.022.0117>

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Primate Genetics – Is Taxonomy a Trivial Pursuit?

Review of *Primate Cytogenetics*, edited by Stefan Müller, Ludwig Maximilian University, Munich, Germany. S. Karger, Basel, Switzerland. 268pp. ISSN: 1424–8581. 111 Figures, 56 Tables. Hardcover: 122.00 Swiss francs, Eur87.00, US\$111.00. 2005. A reprint of *Cytogenetic and Genome Research*, Volume 108(1–3).

In appearance this book is like an oversize (285 mm × 215 mm), hardbound *Folia Primatologica*, but with a red spine and lettering. There are 30 articles, divided into three sections: Comparative Genomics and Molecular Evolution (13); Comparative Molecular Cytogenetics and Chromosome Evolution (14); and Primate Meiosis and Nuclear Architecture (3). Sixteen of the articles are dedicated to the human genome and the comparative genetics of humans and apes (and in one case Old World monkeys in general).

The first article (Ryder) is a most interesting essay on “conservation genomics,” the relevance of studies of complete genomes for conservation measures for threatened species. A further three articles examine aspects of primate phylogeny in terms of their place in the evolution of mammals (Froenicke), the phylogenetic relationships of the major primate groups (Hominoidea, Cercopithecoidea, Platyrrhini, Tarsioidea, and Strepsirrhini) (Schmitz *et al.*), and a definition of the ancestral karyotype (chromosome morphology, and banding patterns) for primates (Ruiz-Herrera *et al.* [the copy editor should surely have spotted the adjective being used as an adverb in the title of this paper]). Schmitz *et al.* examine primate origins and their affiliations with such as the Dermoptera and Scandentia, and provide a very interesting discussion of the place of the Tarsioidea—the dichotomy of the haplorhines, including tarsiers, and the strepsirrhine lemurs.

For their investigation of the ancestral primate karyotype, Ruiz-Herrera *et al.* used data on 36 primates, 24 of them platyrrhines, from 20 published sources, besides information from their own work on *Lagothrix* (their Table 1, p.163). What is striking looking at the table is that there is one article from 1982, another from 1992 and all the remainder are from 1996 or later. The studies are quite contemporary, but a number of the scientific names are outdated. This is curious in showing that either the authors are very conservative, or disagree with recent taxonomic arrangements or are just straight inattentive, or have been victims of a copy editor with an ancient taxonomy. This is not a problem in most cases. The species name should always identify the animal involved—whether it changes genus or is placed as a subspecies should not matter. Ruiz-Herrera *et al.*, for example, listed *Ateles paniscus chamek* (of Kellogg and Goldman [1944]), citing a study of G-banding by Medeiros *et al.* (1997). Seuánez *et al.* (2001) also refer to *Ateles paniscus chamek*. Medeiros (1994) and Medeiros *et al.* (1997) in fact regarded the form *chamek* to be a subspecies of *belzebuth* not *paniscus* (as was also argued by Froehlich *et al.* [1991] and more recently by Collins and Dubach [2000]). Four of the six authors of Ruiz-Herrera *et*

al. are also authors of Medeiros *et al.* (1997). Either there has been an unexplained about turn or there was an intrusive copy edit not seen by Ruiz-Herrera *et al.* Although De Boer and Bruijn (1990), Froehlich *et al.* (1991), Medeiros (1994) and Medeiros *et al.* (1997) argued that *A. paniscus* is a distinct form with no subspecies, it is listed in the table of Ruiz Herrera *et al.* as *A. paniscus paniscus*. Most odd. However, this has no particular importance besides misleading and creating confusion, because the form *chamek* has not been redefined. *Ateles paniscus chamek* is perfectly identifiable as what is considered today to be either *A. belzebuth chamek* or *Ateles chamek* (of De Boer and Bruijn [1990], Groves [1989, 1993, 2001, 2005] and Rylands *et al.* ([1983, 2000])).

The major problem arises when the definition of a given name is changed. For example, Table 1 of Ruiz-Herrera *et al.* lists studies of *Callicebus molloc* [sic] and *Saimiri sciureus* by Stanyon *et al.* (2000) as part of their data set. *Callicebus moloch* was one of just three species of titi monkeys recognized by Hershkovitz (1963). It was divided into seven subspecies. In Hershkovitz's 1988 and 1990 re-evaluation, *Callicebus moloch* was divided into eight species and 14 species and subspecies, as part of the “*Callicebus moloch* Group.” Kobayashi (1995) split the “*Callicebus moloch* Group” into two, placing four species (five species and subspecies) into the “*moloch* Group” and the form *Callicebus cupreus* into its own group (three subspecies). Groves (2001) has eight species (13 species and subspecies) in his “*Callicebus moloch* Group,” and Van Roosmalen *et al.* (2002) recognizing also a separate “*Callicebus cupreus* Group” decided on six species. Could the real *Callicebus molloc* stand up? With time passing, probably not—complicating at best and invalidating at worst any future use of the data provided by Ruiz-Herrera *et al.*

Saimiri sciureus, likewise, has, still, a highly disputed taxonomy. Silva *et al.* (1993) recognized just one species throughout the Amazon and Central America, while Costello *et al.* (1993) recognized two species, and Hershkovitz's widely accepted taxonomy (1984, 1987) listed four species and 12 species and subspecies. Thorington (1985) proposed a taxonomy slightly divergent from Hershkovitz (1984). He recognized *S. madeirae*, considered by Hershkovitz (1984) to be a synonym of *S. ustus*. It is necessary to refer to Stanyon *et al.* (2000) to know what exactly is the “*Saimiri sciureus*” listed in Table 1 of Ruiz Herrera *et al.* The identity (current name) of both the *Callicebus* and *Saimiri* according to any of the above authors can be ascertained as long as Stanyon *et al.* give the exact provenance of all the specimens they used for their ZOO-FISH analysis.

For geneticists, having the correct name and definition of the animal whose DNA they are analyzing is paramount, and they surely recognize that. So why does one perceive a certain pocurante attitude to the whole issue of taxonomy? Geneticists are after all responsible now for much reshuffling in primate taxonomy—some lumping, much splitting, discoveries of new populations which are awarded the status of “new species”, and in many cases the discovery that what we thought was X (they look very alike) is in fact something different

with a “Y”. These are not just new primates with new names, they are redefining species. Research on the marmoset *Callithrix jacchus* as defined by Hershkovitz in the 1970s, may well today be research on *Callithrix penicillata*.

Examining particularly Old World primates, Stanyon *et al.* show that fissions (non-Robertsonian and Robertsonian) are the main mechanism driving the evolution of progressively higher diploid numbers in the Cercopitheciini, and their findings suggest an early bifurcation of lineages represented by *Cercopithecus neglectus*/*C. wolfi* on the one hand and *Erythrocebus patas*/*Chlorocebus aethiops* on the other, already suggested by a number of earlier authors. Warter *et al.* provide a review of the application of molecular cytogenetics to the phylogeny of Lemuriformes. They examined 21 species and reconstructed the presumed ancestral karyotype for all the lemurs except for the aye-aye. Their results largely confirm the ancestral karyotype proposed by Rumpler and Dutrillaux (1990), and indicate an early divergence of the Daubentonidae, with the subsequent radiation into four families: Cheirogaleidae, Indriidae, Lepilemuridae and Lemuridae.

New World primates are well represented in this book. Seuánez *et al.* provide a most useful review of the contributions that genetics have made to our understanding of the phylogeny of the platyrrhines. They summarize classifications and phylogenies at the family level (they argue for three clades—Cebidae [including Cebinae, Callitrichinae and Aotinae], Pitheciidae [including Pitheciinae and Callicebinae] and Atelidae [including Alouattinae and Atelinae])—and then discuss each in terms of the key findings and phylogenetic issues. Nascimento *et al.* examined the cytochrome b gene in two howler monkeys, *Alouatta caraya* and *Alouatta belzebul*. They showed that *A. belzebul* was paraphyletic for individuals from Paraíba in Northeast Brazil and from the left bank of the Rio Tocantins at Tucuruí, and also confirmed their common ancestry with the brown howler, *A. guariba*. Their results (Figure 4) also indicate an early split (5.3 MYA) of clades leading to *A. caraya*, the red howlers, and *A. nigerrima* on the one hand, and *A. guariba* and *A. belzebul* on the other. This may suggest that the Atlantic forest and the Amazon forests were separated at this time, to be reunited later when *A. belzebul* invaded Maranhão and the basins of the Rios Tocantins and Xingu. Most interesting in their Figure 4 is the inference that all these South American howlers shared a common ancestry with the Mesoamerican species, *A. palliata* and *A. pigra*, splitting off some 6.46 MYA.

In the last paper of the book, Solari and Rahn describe the fine structure and meiotic behavior of the male multiple sex chromosomes in *Alouatta caraya* and *A. palliata*, and summarize the studies carried out to date on this phenomenon, especially those of the Argentinean research group of which they are a part. They conclude that although a trivalent sex chromosome is found in *A. palliata*, that a quadrivalent system arose early in the evolution of howler monkeys.

Ferguson-Smith *et al.* review the contributions of chromosome sorting and painting techniques to the study of primate karyotype evolution. They summarized the different

applications of this method to the New World monkeys, and concluded that they have resulted in new insights into the ancestral karyotype and their phylogenetic relationships. Wienberg also reviews the application of modern cytogenetic analysis techniques, and provides a brief and useful summary of the main results to date for Callitrichidae, Cebidae and Atelidae. Wienberg includes *Callicebus* in the Cebidae, but it seems that no work had been done or published by that time on the remaining Pitheciidae. The author concludes that “chromosome painting demonstrates that karyotypes of New World monkeys have been considerably reshuffled when compared to the ancestral karyotype of all primates,” and that the evidence argues for a monophyletic origin for all of them (p.147).

Chromosomes of three atelid species, the miquiri, *Brachyteles arachnoides* (or was it *hypoxanthus*?), and two spider monkeys, identified as *Ateles belzebuth marginatus*, and *Ateles paniscus paniscus*, were subjected to multi-directional painting by Oliveira *et al.* Including data from *Ateles geoffroyi*, *A. belzebuth hybridus*, *Lagothrix lagothricha*, *Alouatta caraya* and *Cebus apella* (outgroup), their attempt to clarify the phylogeny at the generic level was frustrated because *B. arachnoides* and *L. lagothricha* conserved what is considered to be the ancestral karyotype for the atelins. They did find evidence of a synapomorphism linking *Brachyteles*, *Lagothrix* and *Ateles* to the exclusion of *Alouatta*. Among the spider monkeys, they concluded that *A. b. hybridus* was sister to *A. geoffroyi*, and *belzebuth* was paraphyletic, with *marginatus* branching off first from a lineage which gave rise to *A. p. paniscus* and *A. b. hybridus*. Collins and Dubach (2000), analyzing mitochondrial DNA, argued that *hybridus* is a species, which would resolve that problem. Oliveira *et al.* concluded also that *A. b. hybridus* should be re-classified, since its karyotype shares no synapomorphies exclusively with *A. b. marginatus*, but does share a derived inversion of chromosome 6 with *A. geoffroyi*.

Also included in this collection of papers is a report by Neusser *et al.* on the cytogenetics of the hybrid twins born in 1998 to a male pygmy marmoset, *Cebuella pygmaea*, and a female common marmoset, *Callithrix jacchus*. The findings are what the authors refer to as a “balanced karyotype” and a healthy morphology, although fertility had yet to be ascertained. They argue that this hybridization reinforces other genetic evidence for the two marmosets to be placed in the same genus, a step sufficiently disagreeable to those who know these monkeys that, as pointed out by the authors, Rylands *et al.* (2000) resurrected the genus *Mico* for the Amazonian marmosets to avoid a paraphyly hinted at by DNA sequence comparisons (*Cebuella* phylogenetically closer to the Amazonian marmosets than the Amazonian marmosets are to the Atlantic forest marmosets) (see Groves, 2004).

I have concentrated on the articles dealing with New World monkeys but, as mentioned above, this is not the main emphasis of the book. Although I am no expert in the matter there is no doubt that it details major contributions—descriptions of research investigations and reviews, to primate molecular and chromosomal phylogeny, evolutionary dynamics of

the primate genome, karyotype evolution and chromosome breakpoint analyses, meiotic studies, comparative functional genomics and nuclear architecture, as emphasized in the editor's preface. Strange to me, however, is what would appear to be a cavalier disregard for the niceties of taxonomy when numerous authors espouse the importance of genetics for our understanding of the systematics and phylogenetic relationships of the morphological, geographic and genetic entities which comprise the Order.

While citing Froehlich *et al.* (1991) who argued cogently that the spider monkey described as *marginatus* was not a subspecies of *belzebuth*, that *chamek* was not a subspecies of *paniscus*, and that *paniscus* has no subspecific forms, and knowing that nobody has disputed this since—neither morphologists, nor zoogeographers, nor geneticists—it is quirky, to say the least, that Oliveira *et al.* should continue to use these names in the title of their paper. They make no mention of the fact that Collins and Dubach (2000) (whom they cite for other reasons) had argued that *Ateles hybridus* should be a species separate from *belzebuth*, even though this concurs with and explains their findings (they mention that *A. belzebuth hybridus* needs reclassifying, as if this had not been suggested—done—before). *Ateles hybridus* is now considered to have a subspecies. Subspecies of *L. lagothricha* are now considered species, so one is left wondering whether the study of Oliveira *et al.* was on *L. peoppigii* or *L. cana* (which has a subspecies) or *L. lugens* or the nominate form. *Cebus apella* as defined by Groves (2001) is restricted to the Guiana shield. Was the tufted capuchin of Oliveira *et al.* in fact *Cebus nigrinus*? Humans give names to animals that have been named previously, and their definitions of their essential differences when compared with others are, as we well know, often disputed—both within and between the disciplines. For a species to exist it must have not only a name and description but it must occur somewhere. Knowing that Oliveira *et al.*'s *Cebus apella* came from the Iguazú National Park, for example, would complete the tripod needed to sustain its Linnean identity—its taxonomic definition. 1) the given name, 2) the person who gave it (where its name was published and by whom) and 3) its type locality (where it lives). If there is no information about where the animal came from, it is necessary to depend on the often subjective description and, often ephemeral, definition of the “species”. The “occurring somewhere” is a vital parameter, and is helpful to the extent of the precision concerning where it occurs. Whereas in the past primates were labeled as having come from the “Brazils”, today GPS allows for no excuses when describing a new species. The type locality of a specimen should be indisputably precise.

Rylands and Brandon-Jones (1998) explained at length that *Simia straminea* Humboldt, 1812 is a synonym of *Alouatta caraya* and therefore unavailable for the red howlers, *Alouatta seniculus*. The name *Alouatta macconnelli* Elliot, 1910 may be the next available for the red howlers of the Guianas, but this requires that other candidates, such as *Mycetes laniger* and *Mycetes auratus*, both of Gray (1845), be discounted first. Bonvicino *et al.* (1995) resurrected *A. macconnelli*, first

described from Georgetown, Guyana, arguing that it is distinct from *S. straminea*, based evidently on a cursory reading of Hill (1962), and/or an uncritical interpretation of his provisional subspecific distribution map. The name was taken out of its coffin and applied to animals on the left bank of the lower Rio Trombetas in Brazil, at least 1000 km from Georgetown. The name *macconnelli* may well be the correct one but a careful revision of the red howler monkeys is required first. Bonvicino *et al.* (2001), Nascimento *et al.*, Oliveira *et al.* (2002), Ruiz Herrera *et al.*, Seuánez *et al.*, Solari and Rahn, and Wienberg continue to use the name *stramineus* for those west of the Rio Trombetas. The name *stramineus* is not available for red howlers—the holotype is a female *Alouatta caraya*. Besides this particular example, there are numerous mentions of *Cebus nigrivittatus*, which has long been recognized as a junior synonym of *C. olivaceus* (see Rylands, 1999). The name *Callithrix emiliae* was wrongly applied to the marmosets described by Vivo (1985) from Rondônia (see Rylands *et al.*, 1993, 1995), but continues to be used by Seuánez *et al.* and numerous other geneticists. Wienberg includes *Callicebus* in the Cebidae. *Callicebus moloch* continues to be used *sensu* Hershkovitz (1963). Seuánez *et al.* manage to review the classification and taxonomy of Neotropical primates with no reference to Groves (1993, 2001).

This book illustrates well the developments in, and the importance of, the use of cytogenetic (and molecular genetic) analyses in improving and refining our understanding of primate diversity, evolution and phylogeny, but also illustrates the pitfalls of paying little heed to the niceties of names and their histories. Taxonomy is not trivial—it identifies the owner of the chromosomes, hopefully for eternity; it underpins the comparative method; it labels and defines what is being compared. The short shrift it receives from many geneticists is illogical and potentially ruinous.

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