doi 10.4436/jass.89005

JASs *H*istorical *C*orner
Journal of Anthropological Sciences
Vol. 89 (2011), pp. 93-107

Evolutionary trees and the rise of modern primatology: the forgotten contribution of St. George Mivart

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Summary - *The modern concept of the tree of life originated as a popular, iconic synthesis of the Darwinian evolutionary theory of descent by modification even if Darwin's own trees were hypothetical and abstract. It is generally thought that Ernst Haeckel in 1866 was the first to publish a true evolutionary tree which showed actual taxa. It is apparently forgotten that St. George Mivart beginning in 1865 made significant contributions to the development of evolutionary based trees of life which dealt with primate evolution, including human phylogeny. His trees were built on the most extensive sets of original data published up to that time, and were clearly articulated as working hypotheses. Mivart's trees were surprisingly modern for appearance and for content. Not only are most taxonomic names still in use today, but also many of the issues he raised are still under discussion in current scientific literature. The history of biology and especially that of primatology in the 19th century can benefit from a more thorough knowledge of how the image of the tree was used in scientific writings, especially after Darwin in the context of the theory of evolution by descent from common ancestors. A reappraisal of Mivart's scientific achievements is necessary to better establish the origins and the development not only of evolutionary trees but of modern primatology. The history of primatology, a discipline that is fundamental for investigating the place of humans in nature, would also benefit from a reappraisal of Mivart's role in Victorian biology.*

Keywords - *Comparative anatomy*, *Homoplasy*, *Phylogeny, Anthropology.*

Historical Background

A tree is an image that holds symbolic meaning in many human cultures in different times and contexts. The modern concept of the tree of life originated as a popular, iconic synthesis of the Darwinian evolutionary theory of descent by modification. Barsanti (1992) explored the idea of the tree metaphor in western culture and in natural science until the time of Darwin. Tassy (1991) investigated the rise of the phylogenetic trees from Darwin on and focused his attention on its developments in recent scientific debates.

The image of the tree has ancient roots. One of the first usages was in the "trees of life", *lignum vitae* or tree of the Holy Cross. This tree had an exegetic-mystical function, to select biblical messages and, through their proper distribution, to indicate ways of meditation. The image of the tree was later reinterpreted for gnoseological-epistemological use (as in Lullo's trees) to illustrate how principles governing research articulate and how knowledge could be organized. The image of a tree was also utilized in the field of nosology to visualize dicotomical keys (as in the "trees of fevers"). Finally the image of a tree also supported methodological- practical aims, as, for example, in the alchemic trees, indicating phases and procedures of the *magnum opus*.

In the context of Natural Sciences the metaphor of the tree was diffused in the second half of 1700s with the publication of Buffon's *Discours*

de la Dégénération des animaux (1766). Buffon organized various "families" of mammals along a main trunk from which secondary stems, branches and twigs diverged, to affirm the "transformation" of species and to illustrate the order of their derivation. At this point explicit discussions of genealogical trees began (Duchesne, 1766) and even Bonnet (1781) had to abandon the traditional image of the linear *scala naturae.*

However, it was only in 1801 when this genealogical metaphor of the tree was actually visualized by the botanist Augier. He drew a tree with three stems (along which five tribes of plants find their position) and 20 branches (classes), ramifying into fifty four twigs (orders) that bear two hundred and sixty five leaves (families). The purpose of the image consisted not only in showing the morphological affinities of plants, but also in reconstructing the journey that nature apparently had traveled in their successive production. A few years later Lamarck presented trees within an evolutionary perspective even if the theoretical basis was still unclear. In his *Philosophie zoologique* (1809) Lamarck used the tree image to show "the origin of various animals" and in the *Histoire naturelle des animaux sans vertèbres* (1815) to suggest "their order of formation", hypotheses that could finally be tested experimentally (cf. Barsanti, 1992 for further details, iconography and bibliography).

When Lamarck's instructive paradigm, postulating an evolutionary process inducted only by environmental causes, was not supported by the evidence, it was substituted by the principle of selection, founded on individual variability scrutinized by natural selection. At this stage Wallace (1856) and Darwin (1859) provided a foundation for a second generation of trees. An early sketch of a tree appears in Darwin's Notebook B (1837-1838) with the suggestive note "I think". Finally Darwin proposed the famous diagram in the *Origin of Species* (1859) with the momentous innovation of integrating a fourth dimension, time (linked to thousands of generations). Darwin's tree represents a hypothetical phylogeny without any direct correlation to specific taxa or morphological data. It is an abstract scheme with only numbers and letters; it is without words, or names of taxa.

The merit of the first clear and detailed phylogenetic drawings is commonly attributed to Haeckel (1866) as confirmed in a recent article in the Journal of the History of Biology by J.D. Archibald (2009), which explored the development of scientific illustrations using trees. The author writes the following lines about the use of trees after *Origin of Species*:

> *"The German biologist and evolutionist Ernst Haeckel (1834-1919) was the first to exploit fully the tree analogy beginning in 1866 with numerous branching trees as well as branching stick diagrams, both showing actual taxa….Haeckel was a consummate artist and unlike tree representations before and after, some of his have a quite gothically gnarled, mysterious, and even grotesque appearance"* (Archibald, 2009).

From this passage, it appears as if Archibald, as many other scholars, is unaware of the work of St. George Mivart (1827-1900). Indeed, the year before the publication of Haeckel's celebrated tree, Mivart (1865) had published an article in which copious, original data on primate anatomy were summarized in a final evolutionary tree where different taxa of primates including humans were identified by their scientific names and allocated to specific, phylogenetic positions.

Mivart's Role in the Debate on Darwinism

Unfortunately, in the history of evolutionism little space is dedicated to St. George Mivart and his contribution to building evolutionary trees especially of primates and humans is apparently forgotten. Mivart is usually only remembered for his objections to Darwin's theory of natural selection. It is well known that he contrasted gradualism with a saltationist vision of evolution and sustained the inability of natural selection to account for the incipient stages of useful structures.

Indeed, Darwin added a new chapter to the sixth edition of the *Origin of Species* to answer

Mivart's objections. Charles Darwin's reactions to Mivart's objections are well documented by his correspondence with friends and colleagues.

Charles Darwin appears rather confident in his letter to J.D. Hooker referring to Mivart's *Genesis of Species* (1871):

Down, September 16th [1871].
"….I am preparing a new and cheap edition of the 'Origin', and shall introduce a new chapter on gradation, and on the uses of initial commencements of useful structures; for this, I observe, has produced the greatest effect on most persons. Every one of his [Mivart's] cases, as it seems to me, can be answered in a fairly satisfactory manner. He is very unfair, and never says what he must have known could be said on my side…."

But Wallace reports in *My life* (1905, Vol II pp.10-11) a more complex reaction from Darwin:

"….On July 9, 1871, he wrote me a long letter, chiefly about Mr. Mivart's criticisms and accusations in his book on 'The Genesis of Species', and again in a severe article in the Quarterly review. These he proposed replying to in a new edition of the 'Origin', but the incident worried him a good deal. In a postscript he says: 'I quite agree with what you say, that Mivart fully intends to be honourable, but he seems to me to have the mind of a most able lawyer retained to plead against us, and especially against me. God knows whether my strength and spirit will last out to write a chapter versus Mivart and others; I do so hate controversy, and feel I shall do it so badly….' Again, on July 12, he writes: 'I feel very doubtful how far I shall succeed in answering Mivart. It is so difficult to answer objections to doubtful points and make the discussion readable. The worst of it is, that I cannot possibly hunt through all my references for isolated points-it would take me three weeks of intolerably hard work'…."

Darwin, badly hurt from Mivart's attacks to his theory, attributed the cause of this betrayal to his religious bigotry (see discussion section).

Mivart was a very complex individual that went through conflicts and changes on many levels. He strove to harmonize evolutionary thinking with religion. During the estrangement from Huxley and Darwin he started widely to write about philosophy and theology. His relationships with influential Catholic personalities intensified. His book "*Lessons from nature*" (1876), consisted in a collection of papers thought as a continuum on the relations between science, evolution and catholicism. It opens with a long dedication to Cardinal Newman. The volume became object of sharp criticisms in a review of the same year on the journal "Popular Science Monthly" where it was defined "… a book full of rancorous controversy and bitter polemics" and again Mivart's bigotry was underlined : " Mr. Mivart has achieved some reputation as an anatomist and biologist, and is by no means destitute of expository power, but the discussions in this volume show that he is more a theologian than a scientist, more a bigot than a philosopher…" (Vol. 9 pag, 373)

His contributions gave him temporary fame and acknowledgement by less conservative Catholic circles and finally he even received the degree of Doctor of Philosophy from Pope Pius IX in 1876.

Mivart never interrupted completely his scientific career even after being excluded from the inner circle of Darwin and Huxley. He kept on publishing papers in first rate scientific journals and widely diffused monographies. He was even invested of important responsibilities in scientific societies of the Victorian world. It is perhaps informative to note that one reflection of the esteem Mivart's contemporaries held for him was that he was elected vice president of the Linnean Society and twice vice president of the Zoological Society of London. He also was president of the Biological Section of the British Association. In addition to being a Fellow of the Royal Society, he became also a member of the Metaphysical Society whose membership included the intellectual elite of London, including Huxley (Gruber, 1960).

However, his efforts to harmonize evolution and Catholicism were, in the long run, apparently

in vain. His religious life also took a dangerous turn, which brought him into open conflict with the Roman Catholic Church on many issues (Cantor & Brookes, 2000; Artigas *et al.*, 2006; Hess & Allen, 2008). Certainly he strongly defended his personal opinions against Catholic authorities on many matters, including the request to leave complete freedom to scientific research. This position contrasts sharply with the label of bigotry that he had gained in previous years. Mivart died in 1900 after being excluded from sacraments (Artigas *et al.,* 2006). A few months before his death he had very clearly and publicly stated his disillusion:

> *"Thus it is now evident that a vast and impassable abyss yawns between Catholic Dogma and science, and no man with ordinary knowledge can henceforth join the communion of the Roman Catholic Church if he correctly understands what its principles and its teaching really are, unless they are radically changed"* (Mivart, 1900, p. 22).

His family and friends attributed the cause of his conflict with Catholic authorities to diabetes and consequent mental insanity, asking for a proper burial. After a long and painful series of requests by his family, Mivart was at the end allowed to be buried in Holy Ground only in 1904. He has never been rehabilitated, neither as a scientist, nor as a catholic.

Mivart's Trees

Even if Mivart was a strong critic of Darwin he nevertheless made significant contributions to the development of an evolutionary based tree of life. Mivart's trees are true phylogenetic trees and the issues he raised are still under discussion in current scientific literature. The history of biology and especially primatology and therefore anthropology in the 19th century can benefit from a more thorough knowledge of how the image of a tree was used in scientific writings, especially after Darwin in the context of the theory of evolution by descent from common ancestors. Although Mivart held reservations about the effectiveness of natural selection, he was nevertheless a strong supporter of evolutionary descent. Mivart's detailed anatomical works were based on evolutionary comparisons between species and over his scientific career, Mivart published a number of detailed evolutionary trees including two which included species from all the major taxonomic divisions of primates.

Given the recent attribution to Haeckel for the first evolutionary tree listing actual taxa (Archibald, 2009) in the Journal of the History of Biology, it is important to note that Mivart's first evolutionary tree of primates was published before that of Haeckel. This first primate tree was a wide ranging, comprehensive tree of primate phylogeny, which in addition to *Homo sapiens* included species from 29 primate genera. Below we will explore this and other evolutionary trees produced by Mivart over a 16 years period beginning in 1865, six years after the publication of Darwin's *Origins of Species* and seven years before Darwin specifically treated the subject of human evolution in the *The Descent of Man* (1871).

Mivart's Tree of primate and human evolution from 1865

Mivart's first published tree from 1865 (Fig. 1) was contained in an article of 47 pages published on the Proceedings of the Zoological Society of London entitled, "*Contributions towards a more complete knowledge of the axial skeleton in the Primates*". This article employed taxonomic names easily recognized today and was based on a detailed osteological analysis of the vertebral columns of a wide range of 29 primate genera. In Mivart's words:

> *"…it has appeared to me probable that the results of an extension of similar minute observations carried through every family of the order, comparing the various forms with each other and with Man, may not be without a certain interest as exhibiting the manner in which the human vertebral column becomes modified*

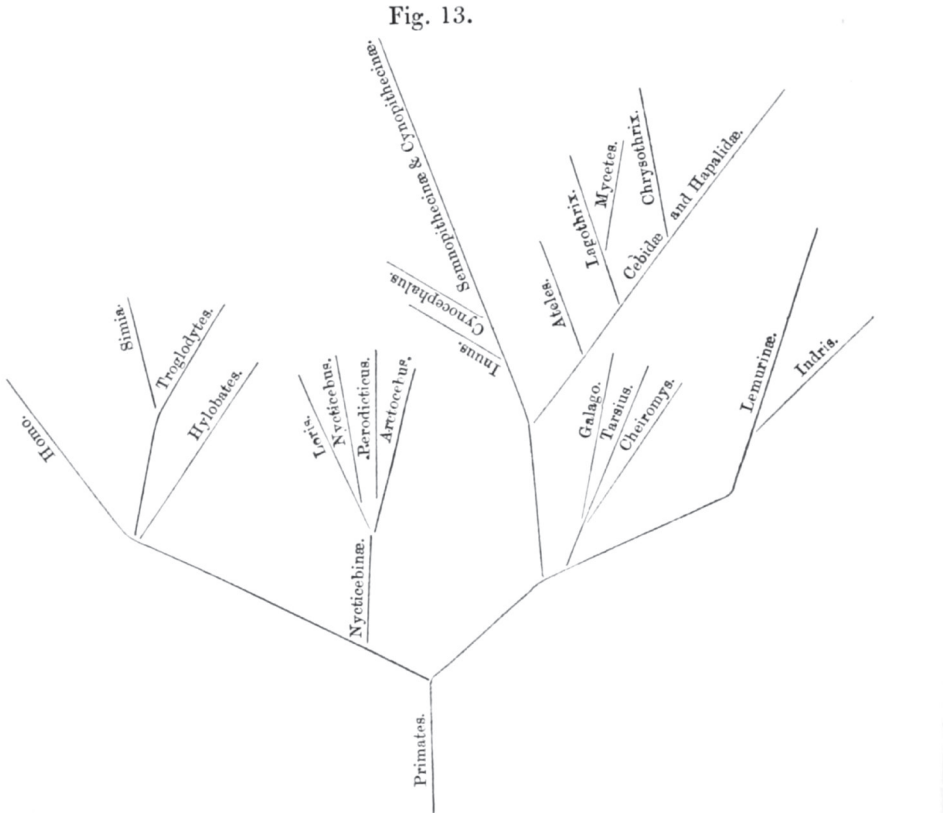

Fig. 1 - Tree of primates published by Mivart in 1865 and based on his comparative study of the axial skeleton. This may well be the first evolutionary tree published after* Darwin's Origins of Species *(1859) in which taxa names are reported. It has special significance because Homo is included well within primates as a lateral branch on the left hand side of the tree.

(so to speak) into that of the ordinary mammal, as adding a further clue to the affinities of the different groups composing the order, and finally as another contribution (however small a one) to a more correct appreciation of the anatomical and zoological value of the structural differences between Man and the highest of the Apes." (Mivart, 1865, p. 546)

The detailed comparisons carried on the vertebral column can be presented in a significant and coherent picture, the 'symbol of a tree':

"To sum up the results of these observations, the Primates present us (as regards their vertebral column only) with four principal types of structure, well represented, respectively, by (1) Simia*, (2)* Cercopithecus*, (3)* Nycticebus*, and (4)* Lemur*,- the first having, however, many points in common with the third, and the second with the fourth; so that the affinities between the various groups of the order (as regards their spinal characters) may be represented under the symbol of a tree"* (Mivart, 1865, p. 591).

Mivart clearly states the anatomical characters examined and the scientific principles on which the tree is built, something for which Haeckel was less precise. Not only does he use taxonomic names still largely in use today, but, surprisingly,

Homo is not the apex or culmination of evolution (as it is in Haeckel's trees), in fact it is placed on a lateral diverging branch. This position of humans provides his tree with a particularly modern appearance and is perfectly consistent with the trees or bushes that Darwin drew. Mivart gives a detailed description of his '*Tree of Primates*':

"The trunk of such a tree (fig. 13) divides into two main branches-one of them representing the forms possessing few caudal vertebrae, an elongated tapering sacrum, inconspicuous metapophyses of anapophyses, neural spines of trunk nearly always vertical of backwardly inclined, and that of the axis more or less bifid or trifid, cervical vertebrae short, and cervical spines sometimes very produced-that is to say, the forms included in the family Hominidae *and in the subfamilies* Simiinae *and* Nycticebinae*; the other main branch representing all the rest of the order, and possessing the characters attributed above to the* Simiidae *(other than the* Simiinae*), the* Cebidae*, the* Hapalidae*, and the* Lemuridea *in common.*
The first main branch gives off a secondary one to represent the Nycticebinae *and then divides into three others for (1)* Homo*, (2) for* Troglodytes *and* Simia*, and (3) for* Hylobates*.*
The second main branch bifurcates,-its first division representing the Simiidae *other than the Simiinae, together with the* Cebidae *and* Hapalidae*; its second denoting the* Lemuroidea *other than the* Nycticebinae*. From both the* Semnopithecinae *and* Cynopithecinae Inuus *and* Cynocephalus *distinguish themselves as separate twings; and* Ateles *diverges from the* Cebidae *generally, and very interestingly parallels* Hylobates *in its long cervical neural laminae, backwards inclined neural spines of trunk-vertebrae, large transverse diameter of thorax, and slightly marked metapophyses and anapophyses.* Mycetes *and* Lagothrix *also, with their marked hyperapophyses, and* Chrysothrix*, with its undivided caudal transverse processes, are also special forms. The genera* Galago*,* Tarsius*, and* Cheiromys*, with their rudimental cervical spines, diverge so much from the typical Lemurs that they might almost be represented as a distinct primary division of the second main branch, instead of a subdivision of that bifurcation which culminates in* Lemur*, and which gives off a twig to represent* Indris*-a form, as we have seen, almost, if not quite, as distinct amongst the* Lemuroidea *as* Homo *is amongst the* Anthropoidea*."* (Mivart, 1865, pp.591-592).

Additionally, the conclusions of Mivart's article communicate an important, surprisingly modern, scientific interpretation: the choice of a set of characters influences the shape of the tree and the proposed phylogeny, a vexing argument that is still currently being discussed (Wilson, 1998; Whelan, 2008).

"Thus the vertebral column in Primates, though it does not give us such marked and distinct characters as are presented by the cranium and dentition, yet exhibits peculiarities which are far from being destitute of significance. These peculiarities if considered alone would lead to an arrangement of groups and an interpretation of affinities somewhat differing from, yet in part agreeing with, the classification founded on cranial and dental characters; so that the study of that part of the axial skeleton in the Primates which is posterior to the skull may fairly be regarded as well adapted to assist us in the determination of the natural affinities of the groups composing the order while at the same time it conduces to a correct appreciation of the relations existing between the human vertebral column and that of the ordinary four-footed mammals." (Mivart, 1865, p. 592)

This is a problem repeatedly raised by Mivart and underscored in many articles. For example in an article of 1888 "*On the possibly dual origin of the Mammalia*" (published in the Proceedings of the Royal Society of London, Vol. 43, pp. 372-379) Mivart again very clearly expresses this quandary. He adds an additional item that is still subject to contemporary discussions: structures shaped by adaptation are less reliable indicators of evolutionary relationships.

"The most valuable evidences of affinity are commonly afforded by structures less distinctly related to habits of life. Thus, for example, the course taken by the internal carotid artery has often a more profound significance than has either the structure of the teeth or shape of the limbs, while the possession by any two animals of a prehensile tail- in spite of the niceties of structure which concur to produce it- cannot alone be accepted as a test that they belong even to the same order.
The shape of the teeth, having a manifest direct relation to conditions of life, requires, then a very careful criticism before any evidence it may seem to afford can be relied on as a test of affinity." (Mivart, 1888, p.372)

Character weighing is a problem still discussed in current research on evolutionary relationships and continues to be a difficult problem.

Mivart's second evolutionary tree of primate and human evolution, 1867

A second tree of Primates (Fig. 2) was contained in an article, "*On the appendicular Skeleton of the Primates*", published by Mivart in 1867 to support the request for admission to the Royal Society, which was signed by Charles Darwin (for personal knowledge) in the same year. The article was presented to the Royal Society in a reading on the 10th of January 1867 by T.H. Huxley and was then published in the Philosophical Transactions. The circumstances were described by Mivart (1897) in "*Some Reminiscences of Thomas Henry Huxley*":

"For the next two years much of our work harmonised, and ultimately a paper, describing in great detail the limb-bones of all the Primates*, gained me, with his kind support, the Fellowship of the Royal society. One day, when I was at work at the College of Surgeons, he came to me from the Royal Society Council, and told me gaily: 'It is to be published;* totus, teres, atque rotundus!*'- another proof of his considerate kindness"* (Mivart, 1867, p. 993).

The article concerns "the interesting question regarding the number and value of the anatomical resemblances and differences existing between Man and the rest of the Primates" and examines the material supplied by the rich collections of the British Museum and of the Royal College of Surgeons. Mivart wanted to investigate more about the relations among the Primate order:

"After considering the skeleton of each entire limb, and of every segment of each, and describing the several bones in some detail, after also giving the dimensions and proportions of these parts, I propose to consider the number and value of the peculiarities presented by the more aberrant forms, and especially by Man and finally to enumerate some of the more obvious characters of the several groups (as deducible from their appendicular skeleton), and the relations thence derivable of such groups to each other" (Mivart, 1867, p. 300).

Mivart reported in18 tables detailed data of measures and proportions of all appendicular bones relative to 29 primate genera including "Man". Importantly, he openly discussed the limitations of generally using measures and proportions of a single specimen for most genera, instead of an average value drawn from the comparison of a considerable number of specimens. This point is particularly important because Mivart has sometimes been characterized as an essentialist who lacked the populational perspective of evolutionists (Mayr, 1982). Instead, it is clear that he appreciated the importance of intraspecific variability and often remembers the necessity to take into consideration this factor:

"An average, drawn from the comparison of a considerable number of specimens in each case, would have been more satisfactory […]. I venture to think, therefore, that it may be left to such succeeding observers as may confine themselves to special groups, to rectify the results here given." (Mivart, 1867, p. 371).

On these data Mivart builds a new tree of Primates that takes in account different sets of

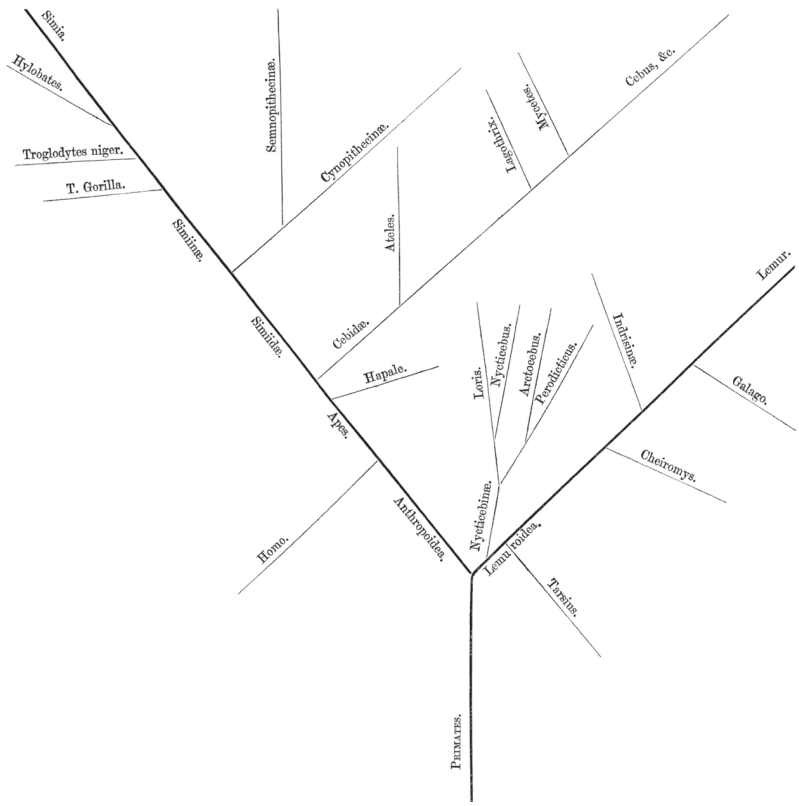

***Fig. 2 - Tree of primates published by Mivart in 1867 and based on his comparative study of the apendicular skeleton. Note the position of Homo as an internal twig on the left hand side of the tree. Mivart's work on the primates was essential for defining what primates are. It included the prosimians (lemurs and lorids) as well as* Homo**.

characters. In contrast with the Haeckel's trees where Man is placed at the very top of the tree as apex of the evolution, Mivart placed Man (*Homo*) on a secondary lateral branch as one of the most derived forms. It is interesting to note that even today anthropologists make a central point of the fact that the transformation of the appendicular skeleton is one of the most distinctive characteristics of the human line (Wood, 2005). Mivart notes:

"Having now enumerated the principal modifications in the form, size, and proportions of the several segments and bones entering into the composition of the appendicular skeleton, it is desirable to consider the more remarkable points of structure presented by some of the most specially modified and peculiar forms of the order, such as Man, the Orang, Hapale, Indris, Loris, Tarsius, and Cheiromys." (Mivart, 1867, p. 390).

Again Mivart clearly states the meaning and the limitations of his tree.

"…and perhaps the affinities between the various groups of the order (as regards the characters offered by their appendicular skeleton exclusively) may be fairly represented under the symbol of a tree." (Mivart, 1867, p. 424).
"It should be borne in mind that this is only an attempt to express the degrees of resemblance existing amongst the appendicular skeletons of

primates, not the affinities indicated by their osteology generally, still less that evidenced by the totality of their organization. It is, in great part, the ossa innominata which cause Man to diverge so from the other Anthropoidea." (Mivart, 1867, p.424, footnote).

At the end of the 1860s and early of the 1870s Mivart entered in a critical period that took him on a divergent path, both at professional and personal level, from Darwin and Huxley (Desmond & Moore, 1991; Cantor & Brooke, 2000). This scientific crisis was reflected in Mivart's discussion of the symbol of a tree to represent relations among taxa. This point can be illustrated by examining the 1873 article published in the Proceedings of the Zoological Society of London entitled, "On Lepilemur and Cheirogaleus and on the Zoological rank of the Lemuroidea". In this article Mivart clarified the problems that frustrated his efforts to delineate the "tree of natural groups". Mivart questioned if it was legitimate to formulate hypotheses on "natural groups". He knew well that the topology of the tree and the position of different taxa on it depend on the set of characters studied. Is the similarity due to real affinity or only the result of independent adaptation? We find already well delineated the problems created by homoplasy (convergence), a well known phenomenon that has been widely debated ever since and no more so than today. The conclusions of this article are important to understand Mivart's scientific development and how this influenced his use of the tree to represent evolution:

"A judicious scepticism seems to me to be somewhat needed at the present moment. The considerations here advanced are by no means intended to support the assertion that views as to genetic affinity are mere dreams. Far from so believing, I conceive the theory of evolution to be probably true; and if so, real genetic affinity must exist, and when it can be securely detected must be most important. But the response of organization to need being such as it is (structure and function manifesting themselves so simultaneously), the discrimination between genetic and adaptive families must long, if not ever, continue a work of extreme delicacy and difficulty. The hasty way in which a few detected (often superficial) resemblances have of late, from time to time, been made to do duty as sufficient evidence of affinity and descent, seems to me to be unscientific as well as unphilosophical." (Mivart, 1873, p. 510)

We need to underline again that Mivart's trees, were always built on the most extensive sets of data published up to his time. Even so they were always presented with caution as working hypotheses certainly subject to future revisions. This situation contrast sharply with the pictorial images, popular still today, of the all-comprehensive evolutionary trees such as those portrayed by Haeckel. It is instructive to read in Mivart's own words his view on this type of representation, which lacked in his assessment the needed scientific and theoretical support. Apparently there was no way out: evolution is too complicated to be fairly represented with the 'symbol of the tree'.

"If, as I believe, so many similar forms have arisen in mutual independence, then the affinities of the animal kingdom, or even of the Mammalian class, can never be represented by the symbol of a tree. Rather, I believe, we should conceive the existence of a grove of trees, closely represented, greatly differing in age and size, with their branches interlaced in a most complex entanglement." (Mivart, 1873, p. 510)

However motivated, the description of this "grove of trees" seems strangely close to some recent proposals (Doolittle, 1999; Woese, 2002) even if these modern authors are talking about horizontal gene transfer and the very reticulated pattern found in microbes. Certainly this is a iconograph convergence and a full discussion would necessitate further research.

In 1874 Mivart published his book *Man and Apes* that had no evolutionary trees. The conclusions stressed the importance that differences of degree and kind bear in the comparison of humans towards other monkeys.

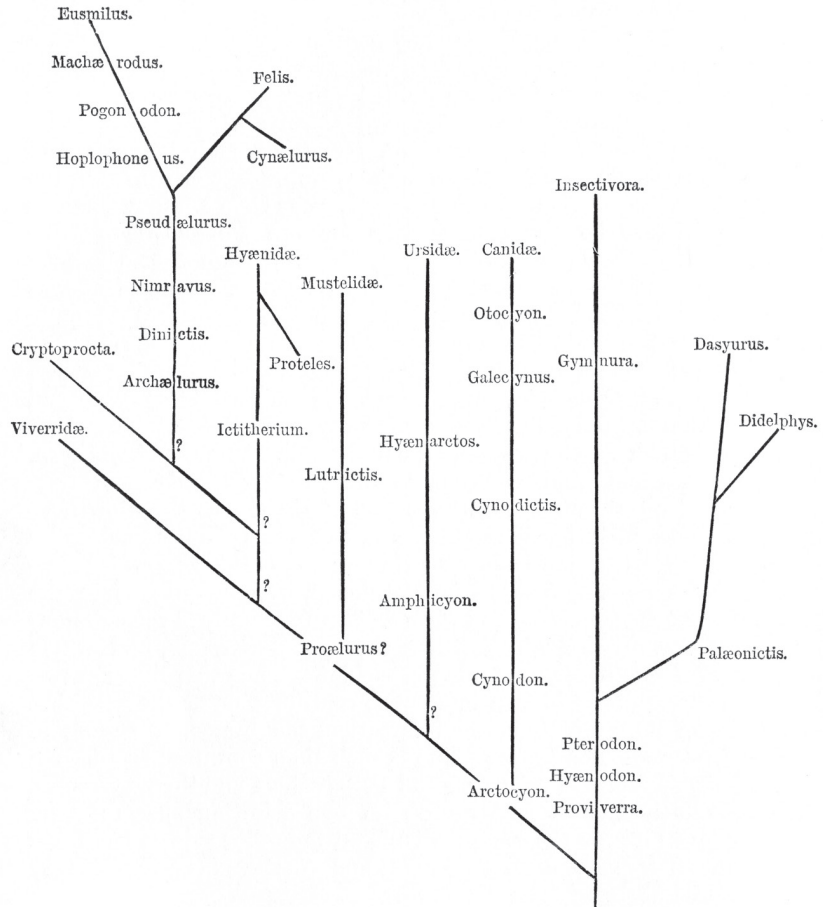

Fig. 3 - Tree published by Mivart in 1881 in his book* "The cat". *It presents a reconstruction of the evolutionary path of* Felidae *starting from Insectivora and including related groups. Fossil taxa are included and question marks indicate the most difficult to define points of divergence. It was mainly based on a comparative study of teeth.

*"But however near to apes may be the body of man, whatever the kind or number of resemblances between them, it should be always borne in mind that it is to no one kind of ape that man has any special or exclusive affinities- that the resemblances between him and lower forms are shared in not very unequal proportions by different species; and be the preponderance of resemblance in which species it may, whether in the Chimpanzee, the Siamang, or the Orang, there can be no question that at least such preponderance of resemblance is not presented by the much vaunted Gorilla, which is essentially no less a brute and no more a man than is the humblest member of the family to which it belongs." (*Mivart, 1874, p. 193).

In his book, *Man and Apes,* Mivart, the foremost Victorian expert on monkeys, renounced the most profound meaning and the innovating spirit of his first articles on primates that had raised so much enthusiasm in Huxley and Darwin: Mivart himself denied their importance and implications.

In spite of reservations expressed in this phase of his professional life, Mivart in 1881 produced one of his most complete evolutionary trees in a book of 557 pages entitled, *The cat, an introduction to the study of backboned animals especially Mammals* (Fig. 3). The doubts expressed in the 1870's were evidently somehow overcome, but not forgotten. Mivart used question marks in this carnivore tree to underline the difficulties of reconstructing phylogenies. A tree was more then ever presented as a cautious proposal, an instrument of work with limited and temporary value, a series of hypotheses to be continuously tested.

> *"This hypothetical genealogy is only offered as a speculation, especially that part of it which represents conditions anterior to the evolution of the viverrine branch. It reposes mainly upon dental characters, and teeth are organs which not only might be expected to vary with varying conditions of life, but which we know to be sometimes very differently formed in different members of one and the same family. Yet we must accept their evidence or none. It is the only evidence which is largely available, nor will there be much danger of serious error in making use of it, if the caution here offered as to its defective nature be duly borne in mind."* (Mivart, 1881, pp.517-518).

The task was daring: to reconstruct the evolutionary steps "from unknown insectivora-like mammals" to Felidae, including related natural groups, still living and also extinct. In his somehow ambiguous scientific path, Mivart resurrected the use of the tree with many scrupulous observations and reaffirmed his faith in evolution, but in a context safely far away from any involvement of human species.

His reconstruction...

> *"…ends in the typical genus* Felis *on one side-an aberrant twig being given off for* Cynælurus-*while on the other side it continues on though* Hoplophoneus, Pogonodon *and* Machærodus *to the very specialized aberrant form* Eusmilus*."* (Mivart, 1881, p. 517).

Discussion

To understand the historical importance of Mivart's evolutionary trees, especially those relevant to the development of primatology, it is important to refer to the scientific debate of the time. In this regard, Mivart himself gives us important information in his 'Reminiscences of T. H. Huxley', published in 1897.

> *"Cuvier, in his world-renowned Règne Animal, had placed man in an order by himself, which he distinguished as two-handed and named 'Bimanes'. Apes and lemurs, as having four 'hands', he classed in his order Quadrumanes, corresponding with the Vier-händer of the German naturalists.*
> *In this he was widely followed, and the orders* Bimana *and* Quadrumana *were adopted by English writers, and by Owen amongst them.*
> *Professor Huxley taught, with perfect reason, that the organisation of man and apes is so much alike that they cannot reasonably be classed in different orders, since zoological classification depends on form and structure exclusively. He therefore proposed to revert to the older system of Linnæus, who had classed man, apes, and lemurs in a single order (*Primates*), excluding from it the bats, which had been included in it by the great Swedish naturalist."* (Mivart, 1897, p. 992).

Mivart's meticulous works on primates were a solid support to Huxley's claim and therefore the enthusiasm he manifested for the 1867 article was well motivated and not due only to friendly feelings. During his life and scientific career, Mivart never questioned the principle supported by his first works, that *Homo* must be included in the same order as the other primates.

Mivart disappointed Darwin in more then one way and in a few years he was excluded by his inner circle of friends (Gruber, 1960; Desmond & Moore, 1991; Browne, 2002). The causes of what is sometimes considered his scientific heresy are generally attributed to his bigotry as a catholic convert, as stated by Darwin himself in more then one letter. For example in 1871 (July 9) Darwin wrote from Down: *"My*

dear Wallace…I conclude with sorrow that though he [Mivart] *means to be honourable he is so bigoted that he cannot act fairly...".* In the same year, on September 16th he wrote to J.D. Hooker: *"I cannot understand him; I suppose that accursed religious bigotry is at the root of it".*

However, even Darwin, in spite of his difficulties with Mivart, in a letter to the Marquis de Saporta April 8, 1872 had to admit that Mivart was the one scientist in England who knew most about the order Primates.

"I will reflect on what you have said, but I cannot at present give up my belief in the close relationship of Man to the higher Simiae…. The man who in England knows most about the structure of the Simiae, namely, Mr. Mivart, and who is bitterly opposed to my doctrines about the derivation of the mental powers, yet has publicly admitted that I have not put man too close to the higher Simiae, as far as bodily structure is concerned.

It is interesting to take notice of how Mivart is remembered by the co-discoverer of evolution by natural selection. The last of the great Victorians, Alfred Russel Wallace, collecting his memories at the dawn of the new century, when Darwin, Huxley and Mivart were all deceased, described Mivart's competence and humanity with these words:

"Considering the period of life at which Mivart first turned his attention either to science or literature, the amount of knowledge of comparative anatomy acquired, largely from dissections and study carried on at home, was very great, and placed him in the first rank among the many great anatomists of his time. This is the opinion of the very competent writer of his obituary notice in Nature (vol. lxi, p.569). His writings on biological subjects were almost as extensive as those of Darwin himself, and his total literary work, largerly metaphysical and generally of high merit, was very much larger. In the excellent obituary notice already referred to full justice is done both to the wide knowledge, the intellectual ability, and the charming personality of one whose friendship I continue to look back upon with pleasure and satisfaction." (Wallace, 1905, p. 45).

The importance of Mivart in the development of evolutionary trees and primatology has not been well appreciated by modern authors even if his definition of primates is still found in textbooks and forms the basis of all modern definitions of the order. Gruber (1960) wrote the only biography of this Victorian scientist and minimizes Mivart's contribution.

"Mivart's emphasis upon the skeleton reflects a limitation which he was never able to overcome and which, as the post-Darwinian years brought biology to its maturity, became an increasingly greater liability to him. Despite his acknowledged competence in osteology, he virtually ignored in his personal research the myological problems of the class in which he was so much interested- the mammals…." (Gruber 1960, p.30).

Gruber's statement is hard to explain, especially since a complete bibliography of Mivart's publications is found in an appendix to Gruber's biography. Apparently he did not take a careful look at the actual scientific publications. Here we do not consider Mivart's more ample production on philosophical and more theoretical issues or on his numerous books published both in England and in the United States. Instead we focused on Mivart's anatomical publications in scientific journals. From 1864 to 1898 Mivart published more than 120 papers dealing with biological and zoological subjects in the most influential British journals of his time: 34 publications in Proceedings of the Zoological Society of London, 16 in Nature, 6 in Transactions of the Zoological Society of London, 3 in Transactions of the Linnean Society of London, 3 in Proceedings of the Royal Society of London, 2 in Journal of Anatomy and Physiology, 2 in Journal of the Linnean Society of London, 1 in Philosophical Transactions of the Royal Society of London. A page count shows that 692 pages were dedicated to osteology, but 528 pages deal

with muscle, soft tissue, and organs, behaviour, physiology and development. Therefore it is clear that the anatomical competence and interests of Mivart were wide ranging included surely the skeleton, but also myology, organs, physiology, and development and even on what he called "Hexicology" a forerunner of ecology (Ascot *et al.*, 1998; Wall, 1994).

In the Preface of the already cited book "*The Cat"* for example we find this series of statements:

> *"The present volume is expressly intended to be an introduction to the natural history of the whole group of the back-boned animals […]; but the subject has been so treated to serve as an introduction to Zoology generally, and even to Biology itself: the main relations borne by cats, not only to the leading groups of animals, but also to plants, being here pointed out.[…]*
> *It has been thought better not to separate the study of physiology from that of anatomy, and, accordingly, an explanation of the functions performed by each different system of parts of which the body is made up, will be found to follow the account of their structure."* (Mivart, 1881, p.ix)

Chapters are therefore dedicated to the cat's skeleton, skin, organs and systems, development, psychology, place in nature, hexicology, and genetic relations (phylogeny).

A few voices of the last century tried to note Mivart's competence (Jones, 1948) and to remember his role as a primate taxonomist (Cartmill, 1974).

> *"The Linnean concept of the order primates, which included the bats and colugos, was still current as late as 1870. In 1873, Darwin's antagonist Mivart proposed ordinal boundaries which excluded these animals, but which (unlike the taxonomies then advocated by Milne-Edwards, Grandidier and Gervais) included the prosimians as a suborder of Primates. Mivart also proposed a list of traits that distinguished prosimians and anthropoids from other placental mammals. These traits included a complete bony ring around the eye, a well developed occipital lobe of the cerebral cortex, and a grasping hind foot with an opposable, clawless first toes."* (Cartmill, 1974, p. 436)

But scientists who expressed appreciation of Mivart's role are a minority. In Groves's influential '*Primate Taxonomy*' (2001) Mivart is not even cited in the Index. A brief paragraph in the historical introduction remembers him for his definition of primates, and make an allusion to his "sloppy thinking" (p. 3), a very stark appraisal indeed. Groves later (2008) dealt more at length with Mivart, but essentially maintained the same view (Groves, personal communication).

Why Mivart's trees were forgotten and Haeckel's images are still today so widely cited? The first reason is that Haeckel's trees were scientifically weaker, but very much easier to understand. They appealed the esthetic taste of the time and were well connected to a long tradition of popular collective imagination. They did not require comprehension of complicated terminology and methodological subtleties and they simply became well accepted icons of the "Great Tree of Life".

The second reason was the strategy that Darwin and Huxley adopted. After the years of open conflict with Mivart they simply ignored him. It was a comprehensible reaction to a brilliant student and collaborator that had betrayed their friendship, trust and great expectations.

Finally Mivart was the worst enemy of himself. While the first articles with primates' trees clearly stated the necessity to establish phylogenetic trees including humans, he became more and more ambiguous about different aspects of a theory of evolution and especially about the position of Man in the overall picture. Mivart himself did nothing to promote his first scientific efforts, but, on the contrary, he tried to conceal them.

We believe that a careful look at the scientific contribution of Mivart and the role of evolutionary trees in that contribution is essential for our understanding of the origins and foundations of modern primatology, a discipline that is fundamental for investigating the place of the human species in nature.

Acknowledgements

The authors would like to thank Colin Groves and two other anonymous reviewers for their useful comments.

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Editor, Giovanni Destro-Bisol