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# A Sort of Revolution: Systematics and Physical Anthropology in the 20th Century

Matt Cartmill

Boston University  
and Duke University

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## **ABSTRACT**

During the first four decades of the 20th century, a system of ideas about the evolution and systematics of humans and other primates coalesced around the work of George Gaylord Simpson and W. E. Le Gros Clark. Buttressed by the "new physical anthropology" of the 1950s, that system provided an authoritative model — a disciplinary matrix or paradigm — for the practice of that aspect of biological anthropology. The Simpson-Le Gros Clark synthesis began to unravel in the 1960s and collapsed in the 1970s under the onslaught of cladistic systematics. The cladistic "revolution" resembles a paradigm shift of the sort proposed by Thomas Kuhn because it was driven, not by new biological discoveries or theories, but by a change in aesthetics.

People have been writing about revolutions in science at least since the 1700s, and talking about *the* Scientific Revolution (of the 1600s) for over a hundred years. When most people talk about a revolution in some science, the associated picture is one of a leap forward, leading to progress in human knowledge and a better understanding of the world. But what that phrase chiefly conjures up in the minds of historians of science is the work of their fellow historian Thomas Kuhn, who pictured scientific revolutions in a different light.

In his 1962 book *The Structure of Scientific Revolutions*, Kuhn proposed that a mature science cycles back and forth through two phases. In the ground state, which he called "normal science," the science's practitioners are agreed on what counts as a problem and how one should go about solving it. Their agreement — the system of shared assumptions that unites a group of researchers into a community — constitutes what Kuhn variously called a "disciplinary matrix" or a "paradigm." The latter term has stuck and become a vague synonym for "norm" in common parlance, so that journalists now write stories about paradigm shifts in home financing or ice cream.

In Kuhn's model, scientists working during the normal-science phase try to "articulate" a paradigm by making and testing predictions based on its assumptions, and trying to cover any failed predictions by tweaking the paradigm or the observations a bit. When the anomalies become sufficiently large, numerous, intractable, and annoying, somebody rethinks the subject from its foundations upward and comes up with a new paradigm with different concepts and assumptions, in which the former anomalies become predictable and understandable. The science then enters an excited "revolutionary" state, in which the proponents of the old and new paradigm argue past each other from different premises. Once all the defenders of the old paradigm are converted or dead, the community regroups around the new paradigm and a new period of normal science commences its reign.

Kuhn's picture is far more subtle and fine-grained than the preceding sketch, and it has a lot to recommend it. It has played a big role in subsequent discussions of the history of science. There are problems with it — for one thing, the distinction between normal and revolutionary science, between paradigm tweaking and paradigm replacement, is vaguer and more gradated than Kuhn made out — but everyone would agree that there have been "revolutionary" periods in the histories of some sciences that resemble Kuhn's paradigm-shift model. What made Kuhn's account intriguing and controversial was his insistence that a decision to drop an old paradigm and adopt a new one represents a leap of subjective faith, akin to the new light that dawns in the mind of a religious convert — "a conversion experience that cannot be forced" by objective evidence or rational arguments (Kuhn, 1970, p. 151). Because a paradigm shift transforms the standards by which theories are judged, "paradigm change cannot be justified by proof" and is driven to a large extent by "subjective and aesthetic considerations" (*ibid.*, p. 156). Kuhn concluded that in future it might be necessary to give up altogether on the Whiggish notion that scientific revolutions "carry scientists and those who learn from them closer and closer to the truth" (*ibid.*, p. 170).

Most practicing scientists would, I think, brush this last claim aside. Although we all grudgingly acknowledge that parts of our current pet theories are probably going to turn out to be wrong in the long run, we feel that we can say with something like perfect confidence that a lot of previous theories and theoretical entities (phlogiston, caloric, four-element chemistry, Lemuria, etc.) are now permanently off the table. Most of us also expect that when we do decide to chuck some current theory, it will be because evidence and arguments have compelled us, however reluctantly, to give it up — provided, that is, that some better alternative is available to take the place of the rejected "paradigm." (The politicians' maxim that "You can't beat something with nothing" applies equally in science.) Scientists of my age, born before 1950, had an opportunity to witness this process in action on a grand scale during the 1960s in the plate-tectonics revolution in geology, which was unarguably driven by new, unexpected empirical findings. Many of us have experienced the process more painfully on a smaller scale by seeing our own ideas refuted by such findings. Running that risk is part of being a scientist. The notion that such evidence can never compel the rejection of a theory seems contrary to both experience and common sense; and giving up on the idea that the practice of science brings us closer to the truth would for most of us render the whole scientific enterprise pointless.

But biological anthropologists of my age have also witnessed at least one scientific "revolution" that seems to conform to Kuhn's model — namely, the triumph of cladistic systematics in biology during the 1970s. In the late 1960s, when I first began working in the mammal collections of the world's great natural history museums, most of them were organized according to the classification of George Gaylord Simpson (1945), which included a mix of polyphyletic, paraphyletic, and monophyletic taxa. Today, fifty years later, most of those collections have been regrouped into strictly cladistic categories, following the classification of McKenna and Bell (1997) or one of its alternatives or modifications. This change represents a significant shift in specimens in museum cabinets, and arguably in Kuhnian paradigms. And just as Kuhn's account would have predicted, it was not forced on scientists by any new empirical findings during the 1960s and '70s; it was brought about by something much more like a religious conversion experience.

In what follows, I will tell the story of this Kuhnian revolution as it looked from the standpoint of one physical anthropologist of the 20th century. I am going to argue that its conformity to Kuhn's model was imperfect, and that the reason it conformed to that model to some extent was that it was not a scientific event.

## THE OLD PARADIGM AND ITS ORIGINS

When I entered graduate school in 1964, evolutionary anthropology was dominated by the systematics of G. G. Simpson, the evolutionary narrative of W. E. Le Gros Clark, and the bias towards taxonomic lumping that was part of the "new physical anthropology." These three items were all grounded in taxonomic theory. They complemented and reinforced each other, combining to wield an authoritative clout that dictated the standards and procedures of "normal science" in the study of primate and human evolution. But although these three things added up to what Kuhn might have recognized as a paradigm, they had achieved their predominance

not through a Kuhnian revolution, but through a gradual accretion of small changes in mammalian systematics and evolutionary theory.

The accretion of the Simpson-Le Gros Clark "paradigm" goes back to the early 20th century, around the time of the founding of the *American Journal of Physical Anthropology*. The process began with a cascade of changes in the taxonomic status of the tree shrews (Tupaiaidae). Most nineteenth-century systematists had assigned the tupaiaids to the order Insectivora, a paraphyletic grab-bag of mainly small, nocturnal, unspecialized, insectivorous eutherian mammals: shrews, moles, chrysochlorids, hedgehogs, solenodontids, tenrecs, elephant shrews, and tree shrews (and sometimes colugos), plus a flock of similar and related fossil forms. Elephant shrews and tree shrews differed from typical Insectivora in having bigger eyes, a bony auditory bulla, an intestinal cecum, and generally diurnal habits. Some systematists followed Ernst Haeckel in grouping them into an order of their own, the Menotyphla.

Noting certain lemur-like features in tupaiaid skulls, hands, and feet, the American paleontologist W. K. Gregory proposed in 1910 that primates might have evolved from "large-brained arboreal Insectivores resembling in many ways" the tree shrews *Tupaia* and *Ptilocercus*. In 1922, the Swedish anatomist Albertina Carlsson went a step further. Tallying up a host of resemblances between tree shrews and the lemurs of Madagascar — including the "intrabullar" tympanic ring, the postorbital bar, the comb-like lower front teeth (and the correlated presence of a brush-like sublingua), and certain features of the hands and feet — Carlsson concluded that "the Tupaiaidae should not be counted among the Insectivora, but ought to constitute a special suborder of the Prosimiae."

Carlsson's publication was read with interest by the English anatomist W. E. Le Gros Clark, who had just returned to England from a posting as a medical officer in Borneo, where he had studied tree shrews. His initial reports on *Tupaia* and *Ptilocercus* (Le Gros Clark, 1924a, b, 1926) went little beyond Gregory's conclusion that *Tupaia* represents a "morphologically annectant form between the true insectivores and the lemuroids." Le Gros Clark suggested that "*Ptilocercus* and *Tupaia* represent two successive phases in the evolutionary development of a lemurid from a primitive, insectivorous, eutherian mammal" (Le Gros Clark, 1926). But in the context of the grade-based systematic practice of the time, this did not necessitate assigning them to the Primates; and Le Gros Clark at first stopped short of doing so.

Two publications by the young American paleontologist G. G. Simpson appear to have transformed Le Gros Clark's thinking about primates. The first was Simpson's landmark 1928 study of Mesozoic mammals, in which he concluded that the crucial anatomical markers of mammalian status (temporomandibular joint, three middle-ear ossicles, etc.) had evolved separately in four different lineages of Mesozoic synapsids. However, Simpson declined to split Mammalia into four different orders on that basis, because the ancestral stocks of the four line-crossing lineages were closely related, and the parallel changes had presumably been driven by identical selection pressures in all four. He accordingly accepted Mammalia as a coherent but polyphyletic grouping, adopting the principle that a taxon can be defined by parallel trends in closely related lineages (Cartmill, 2012). As Simpson put it thirty years later,

"In practice it is a sufficient principle for evolutionary taxonomy that each taxon arose wholly from one of lower categorical level, as Class Mammalia from Order Therapsida" (Simpson, 1959).

The second work of Simpson's that had a big impact on Le Gros Clark was Simpson's 1931 study of the skeleton of the Oligocene mammal *Anagale*. This creature's skull, with its big orbits, long snout, and inflated bulla (Fig. 1), looks something like that of *Tupaia*, although *Anagale* shares no significant apomorphies with tree shrews and is now generally thought to be a distant relative of rodents and rabbits (McKenna, 1963; Van Valen, 1964). Simpson, however, convinced himself that *Anagale* probably had an "intrabullar" tympanic ring, like lemurs and tree shrews, and resembled lemurs more closely than living tupaiids in its cheek teeth and in having flattened nails rather than claws on its hind feet. He assigned it to a superfamily Tupaioidea within the Menotyphla, but argued that "the existence in *Anagale* of all of the lemur-like characters of the tupaioids" (apart from a few "rather trivial" features like the postorbital bar) strengthened the case for the tree shrews' primate affinities.

In his 1934 book *The Early Forerunners of Man*, Le Gros Clark cited Simpson's work in arguing the following propositions:

- (a) Tree shrews are lemuroid primates, more closely related to the lemurs of Madagascar than to the lorises.
- (b) *Anagale* is a primitive tree shrew, and therefore is also a lemuroid primate, more closely related to lemurs than to lorises.
- (c) Therefore, the distinctive modern-primate traits that are absent in living tree shrews (e.g., flattened nails), or in *Anagale* (the postorbital bar), or in both (e.g., grasping hind feet) must have evolved separately in lemurs and lorises.
- (d) Therefore, those traits must also have evolved separately in anthropoids, and probably also in tarsiers.

From all this, it follows that the primates are united, not by the shared inheritance of any particular anatomical features, but by a shared tendency to evolve in a monkey-like direction. The distinctive apomorphies shared by living lemurs, lorises, tarsiers, and anthropoids — flattened nails, grasping feet, enlarged brains, keen, forward-facing eyes mounted in bony rings, and so on — have evolved repeatedly in multiple parallel lines of descent from an ancestral primate that lacked these features. Shared trends, not shared traits, thus defined the order Primates for Le Gros Clark, just as they defined the class Mammalia in Simpson's view. Accepting Le Gros Clark's analysis, Simpson transferred the Tupaioidea (including *Anagale*) to the lemur infraorder Lemuriformes (excluding the lorises and galagos) in a 1935 paper written in consultation with Le Gros Clark, and he retained that arrangement in his canonical 1945 classification of the mammals (Simpson, 1945, pp. 61-62).

In his 1934 book, Le Gros Clark had attributed the primate evolutionary trends to hereditary tendencies inherent in the primate genome, with a nod toward the orthogenetic evolutionary theories preached by Henry Fairfield Osborn. Evolution, he wrote,

...is the manifestation of an inherent tendency in the germ-plasm to vary along definite and limited lines; the modification of an organism is not due to the natural selection of apparently fortuitous variations which may occur in any direction, but rather to a process of continuous change which is taking place in the germ-plasm itself. (1934, p. 287)

But as the "new evolutionary synthesis" solidified during the 1930s and '40s, Simpson and its other architects thrust orthogenesis and other non-Darwinian forces and processes out of the theoretical picture. Swimming with the intellectual current, Le Gros Clark dropped Osborn and orthogenesis from *The Antecedents of Man*, the 1959 expansion of his 1934 book, and from his shorter introductory text *History of the Primates* (Le Gros Clark, 1956). In those books, he deferred to the new consensus and attributed the primate evolutionary trends to natural selection, as "a natural consequence of an arboreal habitat" that had favored the evolution of grasping feet, flattened nails, vertical postures, big eyes, big brains, and reduced noses (Le Gros Clark, 1959, pp. 43, 126, 174, 228). This narrative account, and the Simpsonian model of systematics that went with it, were accepted as textbook verities during my years in college and graduate school, and Le Gros Clark's books were universally regarded as authoritative.

The third major component of the old taxonomic paradigm was a distinct preference for lumping over splitting. This too had its roots in the neo-Darwinian synthesis, which placed powerful theoretical stress on the importance of variation within populations. Both Occam's Razor and neo-Darwinian theory therefore promoted seeing differences between specimens as examples of that variation whenever possible. The old habit of using taxonomic labels to flag almost any sort of morphological differences between two fossil hominins or other primates, which had led to a riotous multiplication of species and genera of ancient humans, was condemned as "typological" thinking, and it was regarded as scientific and virtuous to make one genus or species grow where two, three, or a dozen had previously flourished.

Neo-Darwinism famously burst upon biological anthropology in 1950 at the fifteenth Cold Spring Harbor Symposium, convened around the topic "Origin and Evolution of Man." This meeting brought young and old physical anthropologists together with population geneticists and such important contributors to the new synthesis as Simpson, Theodosius Dobzhansky, and Ernst Mayr. This symposium and its sequelae represent as close an approach to a confrontation between defenders of competing paradigms as can be found in the history of biological anthropology, and the confrontation is sometimes described in Kuhnian terms (Tuttle, in press). The 39-year-old leader of the new-paradigm party, Earnest Hooton's student Sherwood Washburn, laid down a manifesto, subsequently articulated in several influential publications (Washburn, 1951a, b, 1953), proclaiming that classification considered in the abstract, without regard to the adaptive meaning of the traits involved, is vacuous, typological, and unbiological. "If one is interested in the mechanics of evolution, in the understanding of process," wrote Washburn (1951a), "a cumbersome and constantly changing classification is a



great liability and the tendency will be to lump, to leave fragmentary bits unnamed, and to create new groups only when absolutely necessary."

At the 1950 symposium, perhaps the most radical expression of this preference for lumping was Mayr's reclassification of the fossil hominids (as hominins were then called). Asserting that the total range of morphological variation within the entire order Primates was no greater than that seen within the fruit-fly genus *Drosophila*, Mayr proposed to reduce the clutter of named hominid genera — *Homo*, *Australopithecus*, *Plesianthropus*, *Paranthropus*, *Eoanthropus*, *Meganthropus*, *Pithecanthropus*, *Sinanthropus*, and so on — to a single genus, with three species: *Homo transvaalensis* (all the australopithecines), *H. sapiens* (including Neandertals), and *H. erectus* for all the creatures in between. *Homo transvaalensis* never caught on, but Mayr's concept of *H. erectus* has proved more durable. Following Mayr's example, the paleontologists Elwyn Simons and David Pilbeam (1965) carried out a similar massacre of Miocene ape taxa, collapsing a bewildering array of 53 named species attributed to two dozen genera into just three genera — *Ramapithecus*, *Gigantopithecus*, and *Dryopithecus* — containing only 9 species. For me and other students who were struggling to learn our fossil primates in the late 1960s, this new "scientific" classification came as a huge relief.

The rhetoric surrounding these taxonomic moves was one of uncompromising, hard-nosed scientism. A favorite rhetorical device, which has tended to recur throughout the history of our discipline, was to berate physical anthropologists for not keeping up with the truly scientific ideas and norms prevailing in other areas of biology. "Those interested in human evolution," declared Washburn (1951), "must borrow their general theories and principles from others who have access to wider data and more manageable subjects. The task of the anthropologist is to fit knowledge of the primates into the framework of modern evolutionary theory, as described by numerous authors in *Genetics, Paleontology, and Evolution* (Jepsen, Simpson, Mayr, 1949) and as developed in *The Meaning of Evolution* (Simpson, 1949)." "Vertebrate taxonomists are, of course, well accustomed to taking account of groups of characters in their assessment of the zoological status of an animal," wrote Le Gros Clark (1955, p. 181), "and they are quite conversant with the phrase 'character complex'. But anthropologists and human anatomists (perhaps from lack of experience in the practice and principles of taxonomy) often tend to focus their attention rather on single characters in their discussion of relationships." These condescending sentences were quoted approvingly by Simons and Pilbeam (1965). With equal condescension, Mayr (1951) chided Franz Weidenreich for his "inability to understand" mosaic evolution — a defect manifested in Weidenreich's stubborn contention that the jaw and braincase of Piltown Man belonged to different species. "It is obvious," wrote Mayr, "that one type does not change into another type evenly and harmoniously, but that some features run way ahead of the others. The inability to understand this has been the reason for Weidenreich's insistence that *Eoanthropus* was an artifact."

## PRELUDE TO A SORT OF REVOLUTION

If the advent of the "New Physical Anthropology" was a Kuhnian paradigm shift, the period of "normal science" that followed was remarkably short. Le Gros Clark's books of the 1950s (1955, 1956, 1959) had barely ascended to the seat of canonical authority before the

taxonomic foundations of the whole "classical primatological synthesis" (Cartmill, 1982a) began to shift and disintegrate.

The upheaval began, innocuously enough, with some new terminology. The innovator was Julian Huxley, a contributor to the neo-Darwinian synthesis and a fertile coiner of new ideas and terms, who had invented the concept of a "cline" to discourage the naming of subspecific taxa (Huxley, 1938) and made the New Evolutionary Synthesis a thing by giving it that label (Huxley, 1942). In a brief note published in *Nature* in 1957, Huxley borrowed the then-novel term and concept of "cladogenesis" from the German biologist Bernhard Rensch (1954) and contrasted it with a term of his own devising, "anagenesis," to contrast two different ways in which new species can come into being. Huxley then introduced the terms "clade" and "grade," to distinguish the species and higher taxa produced in these two ways.

Although "clade" was a new word, the underlying concept was not novel. What we would now call clades were sometimes distinguished from other sorts of taxa by various labels (e.g., as "strictly monophyletic" or "natural" groups), and debates over the relative merits and practicality of "morphological" (horizontal or gradistic) versus "phylogenetic" (vertical or cladistic) classification were of long standing (Weller, 1949; Wright, 1950; Simpson, 1951, 1959). But as is often the case, giving the clade concept a special label all its own made it easier and more convenient to think about it.

As systematists digested that concept and thought about it, the idea that all taxa should be clades soon raised its head. A 1959 paper by Simpson reaffirming his polyphyletic conception of the class Mammalia was attacked straightaway by the American anthropologist Charles A. Reed (1960), who cited Julian Huxley in asserting that "a taxon should be a clade (whenever determinable) and not a grade." Simpson's ex-student Leigh Van Valen (1960) seconded Reed in arguing that the mammal-like therapsid "reptiles" should be included in the mammals in order to make the class Mammalia monophyletic.

Attacks on the primate status of the tree shrews, a cornerstone of the Simpson-Le Gros Clark synthesis, followed shortly. The paleontologist Malcolm McKenna (1963) reexamined the known fossils of *Anagale* and demolished Simpson's (1935) arguments for calling it a tupaoid. In 1965, Van Valen invoked cladistic principles in arguing that all the supposed resemblances between modern tupaiids and lemurs were either false homologies (e.g., the auditory bulla), primitive retentions (e.g., the palatine-lacrimal contact), or convergences. "Retention of primitive characters and independent acquisition of the remainder seem to me adequately to account for the total pattern of resemblance," wrote Van Valen. "It should be axiomatic that retention of the same primitive characters is of no use whatever in establishing vertical relationships. Only characters modified from the primitive condition in the same or different directions (preferably unusual directions) provide valid evidence one way or the other." Similar cladistic arguments and conclusions were advanced by R. D. Martin (1968), who introduced Remane's (1961) terms "synapomorphy" and "symplesiomorphy" for the first time into the literature of anthropological classification and used them systematically in analyzing previous claims about tupaiids.

Although Van Valen and Martin both relied on cladistic reasoning in reconstructing phylogeny, their systematic practices were not cladistic. They represented a sort of "purified Simpsonism" (Cartmill, 2012) that paved the way for the ascendancy of Hennigian phylogenetic systematics in the following decade. The axioms of this intermediate approach were that all taxa should be monophyletic in the broad sense (meaning that the last common ancestor of all members of a taxon should also be included in that taxon) and that "The origin of the large majority of groups of organisms which can reasonably be called higher taxa is accompanied by an important change in their way of life" (Van Valen, 1971). It was in the context of this still basically Simpsonian systematics that F. S. Szalay and I proposed conflicting definitions of the Primates, grounded in conflicting concepts of the adaptive shift that had generated the modern primates' synapomorphies (Szalay, 1968; Cartmill, 1972, 1974). None of us debating the boundaries of the order — Van Valen, Martin, Szalay, myself, or Robert Sussman and his colleagues later on (2013) — ever did so in the context of a consistently "phylogenetic" (vertical) systematics. If we had, there would have been little to argue about beyond the furcation sequence of plesiadapiforms, euprimates, and Dermoptera (Kay et al., 1992; Bloch et al., 2007; Ni et al., 2013). But arguments about taxon boundaries marked by adaptive shifts were swept away by the ascendancy of cladistics in the 1970s.

## THE REVOLUTION BEGINS

The Newton or Einstein of the new cladistic paradigm was the German entomologist Willi Hennig, who began in the 1950s to articulate a system of exclusively vertical classification (Hennig, 1950, 1968). In Hennig's system, the delimitation of taxa was based exclusively on the sequence of phyletic divergence, so that what we now call the cladogram — the graph of sequential branchings — was read out directly as a Linnaean classification into nested sets (Fig. 2).

Hennig's method and principles stood in diametrical opposition to another would-be revolutionary systematics of the time, the "numerical taxonomy" or phenetic systematics developed and promoted by the microbiologist P. H. A. Sneath and the entomologist R. R. Sokal. In their system, the species being classified are analyzed into a series of characters, each of which has two or more states in the total sample. These character-state data are converted into numbers (e.g., 1's and zeroes for a two-state character), and computer-generated similarity coefficients are used to group the species data into nested sets — Linnaean taxa — that maximize the number of shared character states in each set. Sneath and Sokal (1962) insisted that taxonomic relationships should be evaluated purely on the basis of the patterns of phenetic resemblance existing in the material at hand. Speculation about phylogenetic relationships ought to play no role in classification. If clustering on the basis of similarity yields polyphyletic groupings, this is a matter of indifference to the numerical taxonomist (Sneath and Sokal, 1962). "A natural classification," wrote Sokal (1963), "is one whose constituent classes have many attributes in common and which is most useful for a wide range of purposes ... The recognition of natural groups as entities sharing the largest number of properties ... frees us from the other interpretation of natural groups as representing lines of common descent."

None of this had much immediate impact on anthropological systematics, nor did the work of Hennig and his earliest followers. Biological anthropologists might still be operating on the Van Valen model today (as indeed a few of them are), had it not been for the dedicated efforts of two scientists: the anthropologist Morris Goodman and the ichthyologist Gareth Nelson.

Outside of biological anthropology, Nelson's contributions to the cladistic revolution are better known and understood than Goodman's, and his influence may have ultimately been decisive. The philosopher-historian David Hull (1978) contends that "Not until Gareth Nelson took up the cause did Hennig's views begin to catch on among American systematists." But Nelson's arguments for cladistics, which began to appear in *Systematic Zoology* in the early 1970s (Nelson, 1971, 1972, 1973), were preceded by almost a decade by Goodman's.

Goodman's ideas about taxonomy emerged from his immunological studies on antisera to primate proteins, in which *Pan*, *Gorilla*, and *Homo* consistently clustered together to the exclusion of all other primates. Asserting that "A major objective of post-Darwinian systematics is to create a truly evolutionary taxonomy in which organisms are grouped according to their propinquity of descent and their degree of genotypic similarity" (Goodman, 1963a), Goodman cited Reed and Van Valen in dismissing Simpson's polyphyletic class Mammalia:

It is generally recognized that grouping the Synapsida which contain the Therapsida with the Reptilia rather than Mammalia is an arbitrary convention ... used to express grade relationships. The acceptance of this convention by most systematists suggests that the pre-Darwinian concept of the *scala naturae* in which an animal series progresses from simple to morphologically complex organisms still operates in post-Darwinian systematics.

Rejecting all criteria other than propinquity of descent, Goodman proposed to move chimpanzees and gorillas from the Pongidae over into the Hominidae:

All these serological findings argue for a revision of the taxonomy of the Hominoidea since in the classifications now in use *Gorilla* and *Pan* are invariably placed with *Pongo* rather than *Homo*. A broadening of the Hominidae to include *Gorilla* and *Pan* would reflect more closely the cladistic and genealogical relationships suggested by the serological data. (Goodman, 1963b)

This was a startling heresy in the context of the Simpson-Le Gros Clark "paradigm." Nevertheless, it was taken seriously as a debatable issue by the leading authorities. Responding to Goodman's ideas in their 1965 revision of the dryopithecines, Simons and Pilbeam deferred to Simpson as the authority in these matters:

*Pan*, *Gorilla*, and *Homo* seem to be related more closely phylogenetically to each other than is *Pongo*. Whether the African apes

are placed in the Hominidae or whether 3 groups of coordinate status should be retained would depend on whether greater emphasis is placed on the fact that the Hominidae have shifted to a new and distinct adaptive plateau, or on the close phyletic consanguinity between *Homo* and the African apes. This problem is clearly summarized by Simpson [1963, Fig. 5], and we agree with his conclusion that 2 families, Pongidae and Hominidae, are justified.

In the cited 1963 article — which was also written in response to Goodman — Simpson had concluded that "Both arrangements are equally consistent with our present understanding of hominid phylogeny, but the proposed new arrangement is less consistent with other evolutionary considerations, notably that of adaptive divergence." But this was not a decisive rejoinder to Goodman, since the point at issue was precisely whether adaptive divergence should count for anything in classifications.

By the mid-1960s, then, biological anthropologists were familiar with both cladistic and Simpsonian "evolutionary" classifications of Hominidae and other primate taxa, and could choose between the two approaches. As Simons and Pilbeam intimated, this was regarded essentially as a matter of taste, depending on whether one chose to place greater emphasis on adaptive modes or phyletic consanguinity. None of this had much of a revolutionary flavor. Some additional rhetorical moves were required to elevate the discussion from aesthetics to the level of a Kuhnian confrontation between an old, unscientific paradigm and a new, scientific one.

The additional boost was provided by Nelson and his colleagues and converts at the American Museum of Natural History in New York, who began working assiduously in the early 1970s to present Hennigian cladism as the one true bearer of the standard of science in biological systematics. One initial move was to rechristen cladism as "Darwin-Hennig classification" (Nelson, 1972), with reference to Darwin's suggestion in the *Origin* that "Propinquity of descent, the only known cause of the similarity of organic beings, is the bond ... which is partially revealed to us by our classifications" (Darwin, 1859, p. 414). Another was to contrast the supposedly rigorous and objective cladistic system with the fuzzy and subjective "artistry" generally conceded to be involved in drawing grade boundaries between ancestor and descendant groups in Simpsonian systematics. A third point urged in favor of cladism was that since it employs only a single criterion in classifying, it allows information about phylogeny to be recovered immediately from the classification, whereas no such recovery was possible with the mixed system of Simpson (Nelson, 1972).

Perhaps the most effective move was that made by Nelson's colleague E. O. Wiley (1975). Wiley argued that a cladogram can be falsified (by showing that some other cladogram better fits the facts), whereas a Simpsonian "evolutionary" classification cannot. Because it can be falsified, a cladogram (or its isomorphic Linnaean readout) qualifies as a scientific hypothesis by the demarcation criterion of the philosopher Karl Popper. An "evolutionary" classification does not. It follows that phylogenetic systematics alone deserves to be called scientific.

Other American Museum cladists, beginning with the arachnologist Norman Platnick (1978), soon followed Wiley in hailing cladograms as falsifiable hypotheses and in laying claim to the laurels of true Popperian science. A complex and subtle debate ensued over a host of related philosophical questions. Are non-universal (singular) statements falsifiable in Popper's sense? Are they even testable? Are taxa sets, or logical individuals? If they are individuals, can they function as terms in falsifiable hypotheses? If we assign varying probabilities to different cladograms, does that count as a test of any of them? Does Popper's philosophy withstand the numerous criticisms advanced by other philosophers? These questions have largely subsided from the journals of biological systematics, but they continue to crop up in the writings of philosophers and historians of biology. Interested readers can refer to the useful summaries and analyses of this literature by Hull (1978) and Vogt (2014).

Another move that added to the scientific luster of cladistics was its appropriation of the numerical taxonomists' methodology, which proved just as well adapted to evaluating taxa by counting shared synapomorphies as it had been to evaluating them by counting shared resemblances of all sorts. Quantitative methods, and the debates that followed over the relative merits of different computer algorithms and criteria for assessing and comparing probabilities, enhanced the aura of methodological rigor and theoretical depth that surrounded the cladistic enterprise. It should also be admitted that our ability to generate a classification by key-punching a mass of character-state ones and zeroes and pressing a button lends the product an air of impersonal objectivity and authority, and alleviates the need for thinking about its details or assuming personal responsibility for its defects.

The final outcome of this confrontation between competing "paradigms" has been the almost complete triumph of phylogenetic systematics on the Hennigian model, with the addition of some further technical terms and a great expansion and refinement of the model's quantitative implementation. The triumph was reflected in Sneath and Sokal's increasing insistence, from 1973 on, on the value of numerical methods for phylogenetic inference (Sneath and Sokal, 1973; Sokal, 1985; Sneath, 1995). In biological anthropology today, vertical classification is the norm, and Goodman's classification is almost universally accepted (Fig. 2, C). The specifically human clade (i.e., excluding *Pan*) within the hominoids is now almost always labeled as "hominin," and the word "hominid" tends to be avoided because there is little agreement on whether it includes gorillas or not.

One important side effect of the victory of cladistics has been the abandonment of the preference for taxonomic lumping that characterized the "new physical anthropology" of the 1950s and '60s. Because every furcation in a cladogram generates two sister taxa at some rank, the number of taxonomic ranks required for a complete Linnaean readout of a dichotomously-branching cladogram for say, a genus containing 16 species will be between 5 and 16, depending on the topology of the cladogram (Fig. 3). This awkward requirement can be addressed in four ways: (1) splitting the genus up into multiple genera, (2) naming taxa at all the available intermediate ranks (subgenus, infragenus, superspecies) plus inventing some new ones, (3) printing the cladogram but not completing the associated classification, and (4) giving up on the Linnaean hierarchy. Option (4) has not caught on, and the solutions adopted in practice tend to be some combination of the other three. This produces continual pressure for increased splitting of taxa above the species level.

## A SCIENTIFIC REVOLUTION?

In many ways, the shift from the systematics of Simpson and Van Valen to that of Hennig and his successors fits Kuhn's description of a scientific revolution or paradigm shift. The shift from one systematic paradigm to the other happened rather quickly in the decade between 1970 and 1980. In the debates of the 1970s, advocates of the two schools did a great deal of talking past one another and hurling words like "absurd," "unbiological," and "arbitrary" at each other's heads, just as Kuhn's account would lead us to expect. Adherents of the old systematics found it preposterous that anyone would group chimpanzees but not orangutans with humans, given that *Pan* and *Homo* are radically different in adaptation and share no anatomical synapomorphies. And proponents of the new system found it incomprehensible that anyone would group turtles and *Velociraptor* together as "reptiles" to the exclusion of birds, given the close phyletic and anatomical affinities between birds and dinosaurs. (I have at least twice heard young biologists say that prior to the 1970s, scientists did not realize that birds are closely related to dinosaurs.) There really was a shift in people's ways of seeing the world, or at least the narrow aspect of it involved in issues of biological classification.

It also seems fair to say that the change met Kuhn's description in being "a conversion experience" that was not forced by new facts or objective evidence. The facts are compatible with either system of classificatory practice. Given a particular evolutionary tree (phylogram), one can with equal fidelity to the facts convert the phylogram into a cladogram and read that out directly as a phylogenetic classification (Fig. 2, C), or produce an evolutionary classification by drawing taxonomic boundaries on the phylogram as closed curves, positioned so that the branches of the tree cross those curves at points corresponding to major adaptive shifts (Fig. 2, B). The two systems are different ways of using the same phylogeny in classification. An evolutionary classification utilizes both phyletic and adaptive information, and there is an arbitrary or artistic element in deciding how to weigh and combine them; but neither system is more "scientific" than the other. It is true that once one has arrived at a preferred cladogram, there is no artistry involved in converting it into a phylogenetic classification. But arriving at that cladogram involves making artful and arbitrary decisions — e.g., concerning what is to go to count as a character, or concerning how characters are to be weighted. (Automatic equal weighting of all characters is still arbitrary, and is in fact known in advance to be wrong.) As Zachos and Hossfeld (2010) write:

Any phylogenetic analysis has to be based on characters or, more exactly, on character states, and in order to be able to define character states one must have an idea of what a character is, or, in other words, one must have made a choice of which structures are considered to be comparable and which are not. No systematist would ever interpret the reduction of teeth and the reduction of limbs as two states of one character. Thus, *a priori* hypotheses (those about the definition of characters) are indispensable for the deductive concept of homology.

*A priori* assumptions, embodying the traditions of our discipline concerning what is to count as a character or as parsimony, are also involved in evaluating cladograms. And once we have decided what we are going to count as characters, we are compelled to make other artistic judgments in deciding how to analyze those characters into character states. It is possible to describe anatomical structures in different ways that are equally faithful to morphology but which result in different evaluations of cladograms (Cartmill, 1982b). "The application of the parsimony principle," writes the philosopher R. A. Richards (2002), "is ultimately indeterminate because the choice and individuation of characters that figure in parsimony computations are indeterminate. The cladistic approach is Kuhnian because the application of parsimony depends on persuasion, background, training and tradition."

The claim that a phylogenetic classification is a scientific hypothesis in Popper's sense seems wrong. A phylogenetic classification is directly inferred from a cladogram. The cladogram is in turn deduced from a matrix of character states. It is obvious that a character-state matrix is not a hypothesis about anything. Neither is its filtered form, the optimized cladogram. A cladogram forbids nothing to happen, because biological theory gives us no grounds for expecting that the next character we look at will fit the pattern inferred from its predecessors, or that synapomorphies will ultimately outnumber or outweigh other sorts of resemblances in our data set. As the German systematist Lars Vogt (2014) writes, "a given tree, in combination with descent with modification as background knowledge, does not *prohibit* any specific character-state distribution ... As a consequence ... cladograms are not falsifiable in principle and thus not testable in a Popperian sense."

The "scientific revolution" in biological (or at any rate zoological) systematics in the late 20th century thus does not appear to have been "scientific" in any sense that most scientists would acknowledge. Was it a revolution in Thomas Kuhn's sense?

I think that it was. To be sure, the fundamental assumptions underlying cladistic methods in reconstructing phylogeny were not novel in 1970, or even in 1950 when Hennig published his first book. Throughout the 20th century, most biologists interested in systematics and classification vaguely understood and accepted the principle that only synapomorphies count in assessing phylogeny. A hundred years ago, Chalmers Mitchell (1919) wrote that "Primitive characters may be useful for the definition or description of a group—they have no value for assigning degrees of affinity." Throughout his 1928 monograph on Mesozoic mammals, G. G. Simpson evaluated various traits invoked in earlier reconstructions of synapsid phylogeny and rejected many of them as irrelevant because they were either symplesiomorphies — "primitive characters which give no evidence of special affinity" (Simpson, 1928, p. 167) — or convergences. In urging the hominin status of the australopithecines, Le Gros Clark (1967, p. 23) insisted that the things that *Australopithecus* has in common with apes are only "characters of common inheritance" — what we call symplesiomorphies — and therefore of no use in determining relationships. But the humanlike traits of the australopithecines were "characters of independent acquisition" — that is, synapomorphies — and they show that the australopithecines are stem-group hominids. None of these principles were alien to the old, pre-cladistic paradigm in systematics.



But although the proponents of that older paradigm understood and used cladistic concepts and reasoning, they lacked words like "clade," "paraphyletic," and "synapomorphy." And words make a difference. The vocabulary of cladistics, and the more precise ways of posing and thinking about questions of phylogeny that came in with it, sharpened the focus of discourse about phylogenetic reconstruction. Earlier biologists understood and occasionally articulated the principles involved, but their thinking was muddled by nebulous talk of "affinities" and "annectant" forms — the verbal equivalent of the dotted lines and question marks that populate the evolutionary tree diagrams of pre-cladistic systematists. The algorithmic methods of the numerical taxonomists, which cladistic systematists adapted and improved on for the construction and evaluation of alternative phylogenies, also represented a big methodological improvement over their precursors. The science of systematics has benefitted significantly from all these innovations in the study of phylogenetic relationships.

However, phylogenetic relationships are not the same thing as taxonomy or classification. (The proposition that they ought to be is of course the distinctive assumption of cladistic systematics.) Most of the key concepts in the new vocabulary — clade, grade, anagenesis, cladogenesis, synapomorphy, symplesiomorphy — were invented by evolutionary systematists between 1954 and 1961, before the advent of cladistics. The foundations of the new quantitative methods were laid down during the same period by the numerical taxonomists. I suspect that if Willi Hennig had never lived, and the version of evolutionary classification adopted in the 1960s by Van Valen and others had become the norm of 21st-century systematic practice, our terminology and techniques of phylogenetic inference would look much the same as they look today. We would generate and evaluate phylogenies in the same way, but our classifications would be different.

What, then, was the nature of the paradigm shift that led to the triumph of vertical classification in the closing decades of the last century? To me, it seems clear that it did not involve any changes in biological theory. Rather, it was a change in prevailing art styles, propelled by the sort of "subjective and aesthetic considerations" that Kuhn believed were the drivers behind all major changes in scientific thought. Cladistics won out because systematists began to perceive it as *ugly* to, say, draw a horizontal boundary separating birds from other dinosaurs, overlooking their numerous synapomorphies and genetic affinities. Conversely, their opponents thought it ugly to lump human beings and chimpanzees together in one subfamily to the exclusion of gorillas, ignoring their huge adaptive differences and poverty of synapomorphies. Today's surviving representatives of that older school find it ugly to lump killer whales and sheep together in the same taxon to the exclusion of (say) horses or seals, because killer whales and sheep are not distinguished from horses and seals by any shared properties beyond the genetic synapomorphies that reveal their unique common ancestry. But there is no disagreement between the two schools about the phylogenetic facts, or about the evolutionary theory that accounts for those facts. The disagreement goes no deeper than a wrinkling of the nose. It is a matter of taste.

Insofar as the Kuhnian "scientific revolution" in 20th-century systematics was scientific, then, it was not a revolution; and insofar as it was a revolution — a paradigm shift in Kuhn's sense — it was not scientific. Admitting this does not amount to a criticism or a rejection of the new paradigm. Both systems have their virtues and defects, and neither

represents an improvement over the other in any scientific sense, any more than (say) Cubism represents a scientific advance over Impressionism. But great Impressionist paintings can be beautiful in ways that Cubist paintings are not, and vice versa. It may be possible in the century ahead to arrive at new styles in classification that will combine some of the beauties, and avoid some of the uglinesses, of both taxonomic approaches. That outcome will depend on the creativity and artistry of future systematic theorists. It will come about only when and if young scientists come to perceive current systematic practice as less than ideal, and set to work to do something about it.

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## REFERENCES

- Bloch, J. I., Silcox, M. T., Boyer, D. M., Sargisa, E. J. (2007) New Paleocene skeletons and the relationship of plesiadapiforms to crown-clade primates. *Proc. U. S. Natl. Acad. Sci.*, 104: 1159-1164.
- Cartmill, M. (1972) Arboreal adaptations and the origin of the order Primates. In R. H. Tuttle (Ed.), *The Functional and Evolutionary Biology of Primates* (pp. 97-122). Chicago: Aldine-Atherton.
- Cartmill, M. (1974) Rethinking primate origins. *Science*, 184: 436-443.
- Cartmill, M. (1982a) Basic primatology and prosimian evolution. In F. Spencer (Ed.), *A History of American Physical Anthropology, 1930-1980* (pp. 147-186). New York: Academic Press.
- Cartmill, M. (1982b) Assessing tarsier affinities: is anatomical description phylogenetically neutral? *Geobios*, mémoire special 6: 279-287.
- Cartmill, M. (2012) Primate origins, human origins, and the end of higher taxa. *Evol. Anthropol.*, 21: 208-220.
- Cartmill, M. (in press) Taxonomy and classification: conceptual history. In W. Trevathan (Ed.), *The International Encyclopedia of Biological Anthropology*. Hoboken, NJ: John Wiley and Sons.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*. London: J. Murray.
- Goodman, M. (1963a) Serological analysis of the systematics of Recent hominoids. *Human Biol.*, 35: 377-436.
- Goodman, M. (1963b) Man's place in the phylogeny of the Primates as reflected in serum proteins. In S. L. Washburn (ed.), *Classification and Human Evolution* (pp. 204-234). Chicago: Aldine.
- Gregory, W. K. (1910) The orders of mammals. *Bull. Amer. Mus. Nat. Hist.*, 27: 1-524.
- Hull, D. L. (1978) The principles of biological classification: the use and abuse of philosophy. *Proc. Philos. Science Assoc.*, 1978 (2): 130-153.
- Huxley, J. (1938) Clines: an auxiliary taxonomic principle. *Nature*, 142: 219.
- Huxley, J. (1942) *Evolution: The Modern Synthesis*. London: Allen & Unwin.
- Huxley, J. (1957) The three types of evolutionary process. *Nature*, 180: 454-455.

Jepsen, G. L., Mayr, E., Simpson, G. G. (Eds.) (1949) *Genetics, Paleontology, and Evolution*. Princeton, N. J.: Princeton University Press.

Kay, R.F., Thewissen, J.G.M. Yoder, A.D. (1992) Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *Amer. J. Phys. Anthropol.*, 89: 477-498.

Kuhn, T. S. (1970) *The Structure of Scientific Revolutions*, 2nd edition. Chicago: University of Chicago Press.

Le Gros Clark, W.E. (1924a) The myology of the tree-shrew (*Tupaia minor*). *Proc. Zool. Soc. London*, 1924, 461-497.

Le Gros Clark, W. E. (1924b) On the brain of the tree-shrew (*Tupaia minor*). *Proc. Zool. Soc. London*, 1924, 1053-1074.

Le Gros Clark, W. E. (1926) On the anatomy of the pen-tailed treeshrew (*Ptilocercus lowii*). *Proc. Zool. Soc. London*, 1926, 1179-1309.

Le Gros Clark, W. E. (1933) The brain of the Insectivora. *Proc. Zool. Soc. London*, 1933, 975-1013.

Le Gros Clark, W. E. (1934) *Early Forerunners of Man: A Morphological Study of the Evolutionary Origin of the Primates*. Baltimore: William Wood and Co.

Le Gros Clark, W. E. (1955) *The Fossil Evidence for Human Evolution*. Chicago: University of Chicago Press.

Le Gros Clark, W. E. (1956) *History of the Primates: An Introduction to the Study of Fossil Man*. London: British Museum.

Le Gros Clark, W. E. (1959) *The Antecedents of Man: An Introduction to the Evolution of the Primates*. Edinburgh: Edinburgh University Press.

Le Gros Clark, W. E. (1967) *Man-apes or Ape-men? The Story of Discoveries in Africa*. New York: Holt, Rinehart & Winston.

Martin, R. D. (1968) Towards a new definition of primates. *Man*, 3: 377-401.

Mayr, E. (1951) Taxonomic categories in fossil hominids. *Cold Spring Harbor Symp. Quant. Biol.*, 15: 109-118.

McKenna, M. C. (1963) New evidence against tupaoid affinities of the mammalian family Anagalidae. *Amer. Mus. Novitates*, 2158: 1-16.

- McKenna, M. C., Bell, S. K. (1997) *Classification of Mammals Above the Species Level*. New York: Columbia University Press.
- Mitchell, P. C. (1919) In MacBride, E. W. (Chair), Discussion on the zoological position and affinities of *Tarsius*. *Proc. Zool. Soc. London* 1919: 465-498.
- Nelson, G. (1971) 'Cladism' as a philosophy of classification. *Syst. Zool.*, 20: 373-376.
- Nelson, G. (1972) Comments on Hennig's 'Phylogenetic Systematics' and its influence on ichthyology. *Syst. Zool.*, 21: 364-374.
- Nelson, G. (1973) Classification as an expression of phylogenetic relationship. *Syst. Zool.*, 22: 344-359.
- Ni, X., Gebo, D. L., Dagosto, M., Meng, J., Tafforeau, P., Flynn, J. J., Beard, K. C. (2013) The oldest known primate skeleton and early haplorhine evolution. *Nature*, 498: 60-64.
- Panchen, A. L. (1991) Early tetrapods: classification and the shapes of cladograms. In H.-P. Schultze, L. Trueb (Eds.) *Origins of the Higher Groups of Tetrapods: Controversy and Consensus* (pp. 110-144). Ithaca: Cornell University Press.
- Platnick, N. I. (1977) Cladograms, phylogenetic trees, and hypothesis testing. *Syst. Zool.*, 26: 438-442.
- Reed, C. A. (1960) Polyphyletic or monophyletic ancestry of mammals, or: what is a class? *Evolution*, 14: 314-322.
- Remane, A. (1961) Probleme der Systematik der Primaten. *Z. wiss. Zool.* 165: 1-34.
- Rensch, B. (1954) *Neuere Probleme der Abstammungslehre*, 2nd edition. Stuttgart: F. Enke.
- Richards, R. A. (2002) Kuhnian values and cladistic parsimony. *Perspectives on Science* 10: 1-27.
- Simons, E. L., Pilbeam, D. R. (1965). Preliminary revision of the Dryopithecinae (Pongidae, Anthropeoidea). *Folia Primatol.* 3: 81-152.
- Simpson, G. G. (1928) *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. London: British Museum (Nat. Hist.)
- Simpson, G. G. (1931). A new insectivore from the Oligocene, Ulan Gochu horizon, of Mongolia. *Amer. Mus. Novitates*, 505: 1-21.
- Simpson, G. G. (1935) The Tiffany fauna, Upper Paleocene. 2, Structure and relationships of *Plesiadapis*. *Amer. Mus. Novitates*, 816: 1-30.

- Simpson, G. G. (1945) The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.*, 85, 1-350.
- Simpson, G. G. (1949) *The Meaning of Evolution*. Calcutta: Oxford and IBH Publishing Co.
- Simpson, G. G. (1951) The species concept. *Evolution*, 5: 285-298.
- Simpson, G. G. (1959) Mesozoic mammals and the polyphyletic origin of mammals. *Evolution*, 13, 405-414.
- Sneath, P. H. A., Sokal, R. R. (1962) Numerical taxonomy. *Nature*, 193: 855-860.
- Sneath, P. H. A., Sokal, R. R. (1973) *Numerical Taxonomy*. San Francisco: Freeman.
- Sneath, P. H. A. (1995) Thirty years of numerical taxonomy. *Syst. Biol.*, 44, 281-298.
- Sokal, R. R. (1985) The principles of numerical taxonomy: twenty-five years later. In M. Goodfellow, D. Jones, F. G. Priest (Eds.), *Computer-Assisted Bacterial Systematics* (pp. 1-20). Orlando, FL: Academic Press.
- Sokal, R. R., Sneath, P. H. A. (1962) Numerical taxonomy. *Nature*, 193, 855-860.
- Sokal, R. R. (1963) The principles and practice of numerical taxonomy. *Taxon*, 12: 190-199.
- Sussman, R. W., D. T. Rasmussen, and P. H. Raven (2013) Rethinking primate origins again. *Amer. J. Primatol.*, 75: 95-106.
- Szalay, F. S. (1968) The beginnings of Primates. *Evolution*, 22: 19-36.
- Tuttle, R. H. (in press) New physical anthropology. In W. Trevathan (Ed.), *The International Encyclopedia of Biological Anthropology*. Hoboken, NJ: John Wiley and Sons.
- Van Valen, L. (1960) Therapsids as mammals. *Evolution*, 14: 304-313.
- Van Valen, L. (1965) Treeshrews, primates, and fossils. *Evolution*, 19: 137-151.
- Van Valen, L. (1964). A possible origin for rabbits. *Evolution*, 18, 484-491.
- Van Valen, L. (1971) Adaptive zones and the orders of mammals. *Evolution*, 25, 420-428.
- Vogt, L. (2014) Popper and phylogenetics, a misguided rendezvous. *Austral. System. Botany*, 27: 85-94.
- Washburn, S. L. (1951a) The analysis of primate evolution with particular reference to the origin of man. *Cold Spring Harbor Symp. Quant. Biol.*, 15: 67-78.

Washburn, S. L. (1951b) The new physical anthropology. *Trans. N. Y. Acad. Sci., Ser. II*, 13: 298-304.

Washburn, S. L. (1953) The strategy of physical anthropology. In A. L. Kroeber (Ed.), *Anthropology Today: An Encyclopedic Inventory* (pp. 714-727). Chicago: University of Chicago Press.

Weller, J. M. (1949) Paleontologic classification. *Jour. Paleont.*, 23: 680-690.

Wiley, E. O. (1975) Karl R. Popper, systematics, and classification: a reply to Walter Bock and other evolutionary taxonomists. *Syst. Zool.*, 24: 233-243.

Wright, C. W. (1950) Paleontologic classification. *Jour. Paleont.*, 24: 746-748.

Zachos, F. E., Hossfeld, U. (2010) Adolf Remane (1898-1976) and his views on systematics, homology and the Modern Synthesis. *Studies Hist. Biol.*, 2: 51-64.



## FIGURE CAPTIONS

Fig. 1. Lateral view of the skull of the Oligocene eutherian *Anagale*. (From Cartmill, 2012, after Simpson, 1931. Used by permission of John Wiley & Sons.)

Fig. 2. Evolutionary vs. phylogenetic classification. A: a simplified evolutionary tree diagram (phylogram) with a time axis (not to scale), showing how the human species *Homo sapiens* is genealogically and temporally related to some of its ancestors and collateral relatives. B: an evolutionary classification draws taxonomic boundaries directly on the phylogram, producing grade boundaries between ancestral (primitive) and descendant (derived or specialized) groups. The grade boundaries are positioned to coincide with major changes in adaptation — here, between arboreal apes (pongids) and terrestrial bipeds (hominids), and between *Australopithecus* and *Homo*. The ancestral groupings below each grade boundary (Pongidae, *Australopithecus*) constitute paraphyletic or *wastebasket* taxa. Such groupings may include relatively primitive forms surviving later in time (e.g., *Pan*, *Gorilla*, and *Pongo*). C: a phylogenetic (cladistic) classification has no time dimension. All forms being classified are placed on the same line (gray band) and connected by a branching tree showing their phylogenetic relationships, with suspected ancestor-descendant pairs (e.g., *Homo erectus* and *H. sapiens*) represented either as conspecific (a single species) or as nearest relatives (sister groups). The resulting atemporal tree diagram (the *cladogram*) is then read out as a Linnaean classification by translating the successive branchings into nested sets (brackets at top). All taxa are clades, and there are no grade boundaries. As a result, many taxa (e.g., Hominidae) have no distinctive adaptations or morphologies. A complete phylogenetic classification of this part of the tree of life would include more species and more levels of branching, and would therefore use additional levels of the Linnaean hierarchy (super- and sub-genera and tribes, superspecies, etc.); see Fig. 3. (From Cartmill, in press. Used by permission of John Wiley & Sons.)

Fig. 3. The number of taxonomic ranks ( $r$ ) needed for a complete transcription of a cladogram into a Linnaean classification depends on the number of terminal branches involved ( $n$ ) and the topology of the cladogram. In the diagrams above,  $n = 16$  (black dots). When the cladogram is perfectly symmetrical at all levels and  $n$  is an integral power of 2,  $r$  is minimal ( $r = 1 + \log_2 n$ : top diagram). When the cladogram is "pectinate" — that is, uniformly right- or left-branching —  $r$  is maximized ( $r = n$ : bottom diagram).