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Old World monkeys: three decades of development and change in the study of the Cercopithecoidea

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Introduction

In 1969, John and Prue Napier brought together researchers from a variety of fields with the intention of examining the systematics of a relatively neglected primate taxon – the Old World monkeys. After a week of intensive discussion, the revised presentations were collated and published in 1970 as *Old World Monkeys: Evolution, Systematics, and Behavior* (henceforth “OWM I”). The conference was noteworthy in that it marked a new phase in the study of the cercopithecoid monkeys, as a taxon meriting detailed attention in its own right.

The present volume was conceived as a tribute to the initiators and editors of OWM I, now, sadly, both deceased. We have aimed to bring together a collection of papers to exemplify important, currently active areas of research on cercopithecoid monkeys. Every scientific work is a product of a unique time and context. This is as true of this volume as it was of OWM I 1970. We therefore use this introductory chapter as a comparison between the two books to illustrate some of the paradigm shifts and (if we dare use the word) progress that has marked evolutionary primatology over the past three decades.

At the beginning of the 1970s, the cercopithecoid monkeys were, for many anthropologists, important as the “poor relations” of the hominoid primates in general, and the human species in particular. This teleological approach, derived from non-darwinian progessionism and ultimately from the pre-evolutionary *Scala Naturae*, had the effect of reducing the rich and internally varied cercopithecid radiation to a single rung on a ladder leading towards *Homo sapiens*. To some extent, it was exemplified by Adoph Schultz’s contribution to OWM I, in which he stated that “under the skin” cercopithecoids were remarkably similar – a generalization which has been repeated many times since its original formulation.

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As Cliff Jolly recalls, the inadequacy of the prevailing, one-dimensional view of the cercopithecids was brought home to John Napier during in his investigation of the early Miocene catarrhines, especially *Proconsul africanus* (now *P. hesloni*). At the time, discussions of the evolutionary position of *P. africanus* tended to focus upon whether it fell “above” or “below” the divide between cercopithecoid monkeys and their supposed ape descendants. To the extent that it was unlike the one, it was assumed that it should have resembled the other. In his investigation of its functional anatomy, however, Napier showed that (in many respects) *Proconsul* resembled neither group and was often closer to the larger platyrrhine monkeys. Contrary to expectation, the cercopithecoid monkeys were unsuitable models for early catarrhines because they showed a number of specialized (we would now say “derived”) postcranial features that were neither primitive retentions, nor foreshadowed the developments seen in apes. Napier interpreted these features as a heritage from a common ancestor that was – unlike early apes – semi-terrestrial in its habits. This interpretation has stood the test of time remarkably well. The bilophodont molars of cercopithecids, though less unambiguously interpreted (see contribution by Brenda Benefit, Chapter 6), also pointed to ancestral cercopithecoid adaptations that were neither primitive nor ape-like.

Comparative studies of the cercopithecid postcranial skeleton and dento-facial complex also revealed a considerable internal diversity. The cercopithecids were not only the most widespread and successful of the extant catarrhine superfamilies, they showed a wide range of variation, much of it clearly related to function. The fossil record demonstrated that much of this diversity was the result of a late Neogene radiation that replaced that of *Proconsul* and similar catarrhines.

In both respects, therefore, cercopithecid monkeys appeared to be the successors of the hominoids, rather than their antecedents, and it was in the light of this conceptual change, and the interest that it generated about cercopithecid diversity, that the original Old World monkey conference and volume were conceived. As a logical organizing principle, the papers considering cercopithecoid diversity were focused upon the aim of producing a consensual classification of the group. The new approach seen in the 1970 volume – the study of cercopithecoids as interesting animals in their own right – was much more than simple taxonomic justice. In hindsight, we can see it as an early manifestation of an approach that was to become dominant later in the decade – a clade-based, “bushy” concept of organic diversity, in which major groups, including divisions of the order Primates, are organized according to their derivation *from* a series of common ancestors, rather than by their approach *towards* an implied endpoint.

Although there are many continuities between OWM I and the present volume, there are also major differences resulting from the growth and development of primatology and related fields in the late twentieth century. It is no longer possible to invite a sizeable proportion of scientists working on cercopithecids to assemble around a single table. Nor can we insist that the full diversity of the taxon be included, though there is still a danger of bias because some genera are far better known than others.

We have designed the current volume to incorporate fields that did not exist 30 years ago (such as socioendocrinology) plus the approaches that reflect John and Prue Napier's own interests and are still valuable today. The volume is divided into two broad divisions. The first consists of chapters that deal with evolution, functional morphology, and systematics. The second focuses on social behavior, socioendocrinology, and ecology.

Evolution, morphology, and systematics of the Cercopithecoidea

A decade ago, Patterson (1987:1) wrote that,"To retrieve the history of life, to reconstruct the evolutionary tree is still the central aim of evolutionary biology." The authors of OWM I sought to achieve this goal by searching for a taxonomic scheme based upon multiple lines of evidence. At the time, both evolutionary taxonomists and pheneticists (the latter were not represented in the 1970 book) tended to emphasize that maximum accuracy and repeatability came from including as many uncorrelated traits (morphological, molecular, behavioral) as possible in a classification. In addition, the late 1960s and 1970s were the heady days of the multidisciplinary approach to evolutionary and ecological questions; a different scenario from the increasingly specialized biology of the past decade. A glance at OWM I also reveals that two major approaches of modern systematics – cladism and molecular techniques – had just begun to penetrate into the study of cercopithecoid history.

Molecular approaches

Patterson (1987:1) identifies the "oldest" and "newest" approaches toward the study of phylogeny, comparative morphology and molecular biology, and asks "Do molecules and morphology give the same picture, or two more or less distorted views of the same picture, or two quite different pictures?" In primatology, these questions date at least as far back as the

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controversies surrounding Miocene hominoids – which were contemporaneous with OWM I.

Although Jukes (1966) had laid the basis for the field, molecular systematics was still in its infancy in 1970. It is a sign of the Napiers' farsightedness that they included two contributions from this field. One of these, by Barnicot and Wade (1970) presented a very preliminary analysis of hemoglobin polymorphisms and erythrocyte enzyme variation. While it was limited in its conclusions, it represented an approach that was used extensively in the study of primate population biology during the next 15 years.

Sarich (1970a) presented a general paper that focused on the value of molecular studies and embraced the neutral mutation explanation for the "regularity of protein evolution" (Sarich, 1970a: 23). This view was further expanded in his second contribution (Sarich, 1970b) and applied to a variety of primates. Indeed, Cliff Jolly recalls that the most animated discussion was of hominoid rather than Old World monkey data. Of Sarich's (1970b) specific conclusions, by far the least palatable to paleontologists was his insistence that the only reasonable interpretation of the evidence placed the human species nesting phylogenetically within the African great ape clade, probably next to the chimpanzee, and that immunological data made a great antiquity for the ape–human split improbable. Since 1970, this "troglodytian" conclusion has been so fully accepted that we often forget that this interpretation of the evidence (also espoused by the Huxley–Gregory–Washburn morphologically-based intellectual lineage) was only one of several competing scenarios. Sarich's (1968, 1971) positioning of the last common ancestor of humans and African apes at no more than four to five million years (Myr) competed strongly with the morphologically-based paradigm (Simons, 1972), which identified specific ancestors for hominids, the gorilla and the chimpanzee in the Miocene.

Sarich's (1970a,b) papers carried a more general, and more revolutionary, implication that had direct relevance to cercopithecoid systematics: that the power of molecular evidence so far outweighs that of morphology and behavior, that the most parsimonious strategy is to reconstruct phylogeny entirely from the biomolecules. This was explicitly stated when Sarich (1971:76) wrote that "the body of molecular evidence on the *Homo–Pan* relationship is sufficiently extensive so that one no longer has the option of considering a fossil specimen older than about eight million years as a hominid *no matter what it looks like.*" If this conclusion attacked the foundations of morphological study of hominoid evolution, which had received considerable attention, it could easily be extended to morphological study of the phylogeny of other primate families. Indeed, if both Sarich (1970a,b) and Schultz (1970) were correct, then the morphological study of cercopithecoid evolution would be unproductive.

Sarich's (1970b) second contribution dealt more directly with issues of cercopithecoid phylogeny. After presenting an exposition of the immunological method as applied to albumin, and of the validity of the molecular clock, Sarich presented a number of conclusions: catarrhines and platyrrhines had diverged at no more than 35–40 Myr from a common "monkey-grade" ancestor; the cercopithecoid–hominoid divergence occurred about 22 million years ago (Ma); the colobine-cercopithecine split occurred at about 16 Ma; the divergence of *Nasalis and Pygathrix* took place at approximately 5 Ma; there was a "recent" common ancestor for all macaques; patas monkeys and vervets "share a common ancestral lineage subsequent to the divergence of the other species tested" (an affiliation that has received support from both Disotell, Chapter 2, and Groves, Chapter 4); and the drill and mandrill cluster together in contrast to *Papio* baboons and the gelada. Napier (1970) pointed out that some of these conclusions were contrary to prevailing paleontologically-based ideas, for example, the separation of colobines and cercopithecines in the late Oligocene or early Miocene.

Since 1970, molecular data relevant to phylogenetic resonstruction have increased enormously in diversity and information content, and interpretations have become more sophisticated. Immunologically-based analyses of phenetic distance have been replaced by cladistic analyses based upon molecular sequences. Early enthusiasm for the molecular clock has been tempered by the realization that the evolution of particular proteins, and the DNA sequences that code for them, often varies from time to time, from taxon to taxon, and among loci (Avise, 1994; Strauss, 1999). This necessitates careful choice of the "timepiece" according to the problem at hand. Nevertheless, conclusions drawn from well-established molecular data are so widely accepted that they serve as a check on the wilder speculations of evolutionary biologists, and as an impetus to further molecular and morphological research.

Todd Disotell, in Chapter 2 exemplifies these new data and ideas, which he combines with a discussion and reanalysis of previously published information. His analysis produces reassuringly few inconsistencies, major surprises or deviations from the accepted, morphologically-based cercopithecoid phylogeny. A few contentious points, such as the phyletic position of *Nasalis* and the holophyly of groups such as the genus *Macaca*, the Asian colobines, and the African papionins, are resolved in favor of the traditional interpretation. The evidence of a special relationship between patas and vervet monkeys, suggesting the removal of the latter from the genus *Cercopithecus*, is non-traditional and supports Groves's analysis of morphological data (1989; see also Chapter 4).

This consistency, however, throws the few apparent conflicts between morphology and molecules into sharper relief. Most notable of these is the paraphyly of both of the subgroups traditionally recognized among the African papionins; neither the *Papio*–gelada–mandrill cluster nor the mangabey genus *Cercocebus* is holophyletic. Baboons, geladas, and black mangabeys (separated as *Lophocebus*) form a clade that does not include the other genera, which may themselves form another, much older, clade. This unorthodox phylogeny is now supported by additional molecular data (Harris and Disotell, 1998), and by re-analysis of morphological features (Fleagle and McGraw, 1999).

Disotell emphasizes the need for a broader molecular database, and cautions against uncritical acceptance of single-locus phylogenies. Yet one cannot fail to be impressed, in hindsight, by how often such phylogenies have been supported as more robust sequence data become available. The analyses of electrophoretic patterns of hemoglobin and isozymes (Barnicot and Wade, 1970) and immunological similarity of albumins (Sarich, 1970b) are cases in point.

Population genetics

Today, virtually all "hands-on" field studies – and many that do not involve capture at all – can collect materials (blood, hair, faeces) from which genetic information can be derived. Ever since Darwin's (1859) formulation of natural selection as a primary evolutionary mechanism, and with the development of theoretical and quantitative population genetics, the notion of intra-populational diversity has been crucial to conceptualizations of evolutionary process at all levels. In the earlier decades of this century, theory was ahead of the technical means needed to measure genetic diversity in natural populations empirically. For cercopithecids, skeletal and dental biometrics provided virtually the only means of estimating natural diversity. Such data were linked to population genetic theory by the bridge provided by contemporary quantitative genetics. For population genetic models to be tested against nature, it was necessary to find appropriate Mendelian (and therefore countable) genetic markers and to survey them in real populations. By 1970, such work was being carried out (some of it by Nigel Barnicot and Cliff Jolly, participants in the conference) but none of it was included in OWM I.

Since the 1970s, several generations of genetic markers (simple, discrete, one-locus variants inherited in a Mendelian manner) have replaced each other as favorites of empirical population geneticists and have been used to analyze wild cercopithecid populations. This succession has been driven by three major considerations. One is ease of application (for example, isozyme electrophoresis is technically simpler and more easily interpreted than is immunological determination of erythrocyte antigens). A second is the power of the method as a population genetic tool, which is proportional to the amount of variation revealed (variable microsatellite loci, unlike polymorphic isozymes, are virtually unlimited in number and may have far more alleles per locus and higher heterozygosity than do isozyme loci).

A third, theoretically-driven, consideration is the selective neutrality of the variation. Models used to derive the effect size of breeding populations and subpopulations from the distribution of genetic diversity make the simplifying assumption that subpopulation differentiation is driven by a combination of mutation, genetic drift, and gene flow. Variation, neutral or not, is potentially subject to drift in any finite population, and drift is a particularly important evolutionary force in small populations. The context-specific action of natural selection on non-neutral variation is an unwelcome complication in applying real-world data to such models, and workers tend to make the simplifying assumption that the variation is neutral in regard to selection. The idea that most genetic variants are selectively neutral has a background in theoretical population genetics of the first half of the century (Wright, 1931) and received support (Harris, 1966; Lewontin and Hubby, 1966; Kimura, 1968; King and Jukes, 1969; Kimura and Ohta, 1971; Lewontin, 1974) at the time of OWM I. It was also a strong plank in the platform of advocates of a protein-based molecular clock driven by stochastic processes. However, because mutations recognizable by isozyme electrophoresis change the physico-chemical properties of an active protein, it is difficult to sustain the assumption of universal selective neutrality for such variation (Hudson, 1996; Fogleman *et al.*, 1998). For this reason, as well as ease of application, population geneticists have eagerly adopted techniques that carry the search for genetic variation to the level of the genetic material itself.

The contribution by Jeff Rogers (Chapter 3) illustrates the developments that have occurred since 1970, and discusses the use of the rich genetic data that can now be generated for natural populations. His study of genetic variation in yellow baboons of Mikumi, Tanzania, was the first on DNA-level variation in a natural cercopithecid population. He used restriction

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fragment length polymorphism (RFLP) techniques to uncover variation in nuclear DNA sequences that are non-coding, and therefore assumed less likely to be directly influenced by natural selection. It is, however, quite possible for such loci to be influenced by selection upon coding sequences to which they are linked. Since the Mikumi study was completed, further technical developments – in which Jeff Rogers himself is a major participant – have led to the replacement of RFLP technology by a more prolific source of genetic markers, microsatellite analysis. Neither RFLP nor microsatellite variation can be shown to be universally neutral because proving the absence of selection is even more difficult than the converse. Such loci, however, are so numerous and widespread in the genome that it is in principle possible to distinguish those whose distribution is so far from the overall, stochastically driven pattern of variation as to suggest powerful selection on a linked locus, or on the microsatellite itself.

The most striking finding of Rogers' Mikumi study is that baboon populations carry high levels of intra-populational diversity, presumably because of universal male dispersal before breeding. This has important implications for modes of speciation in cercopithecines. Highly outbred populations are able to sustain a high frequency of normally unexpressed genes for recessive traits, often, but not universally, deleterious. Cliff Jolly argues that, if such a population is subdivided by habitat fragmentation, its subpopulations would be forced to inbreed and would have the potential for rapid (and not necessarily habitat-driven or "adaptive") evolutionary change and diversification as these genes are phenotypically expressed. Genetic tools that enable us to compare the population structure of species with wide and restricted distributions open the way to test alternative, theoretical models of speciation that are of particular relevance to the cercopithecoids, a speciose and comparatively young evolutionary radiation.

Morphology

In these days of emphasis on molecular approaches to the study of evolution, we often forget that early in the twentieth century Driesch (1908) could confidently assert that the study of morphology was at the "center" of biology. Nyhart (1995: 1–2) eloquently articulates the current attitude when she writes "Morphologists might be expected to sit among dusty museum cabinets, puzzling over mange-ridden specimens . . . while more progressive scientists uncovered the real secrets of nature in their laboratories." Yet, the study of morphology is more than a purely descriptive enterprise, since it is a field that continues to generate new paradigms and approaches to the study of evolution. Morphology not only remains a viable approach to the study of phylogeny (as evidenced by Groves, Chapter 4, and Maier, Chapter 5), and the most direct method of studying the history of the primates (see Benefit, Chapter 6, and Gundling and Hill, Chapter 7), it also provides information on rates (Gingerich, 1993) and pattern of evolution (Anderson, 1993; Leakey, 1993), ontogeny and size-shape relationships (Ravosa and Profant, Chapter 9), and function (Whitehead and Larson, 1994; Hiiemae, Chapter 8). The role and methodology of modern comparative anatomy has been discussed by Duncker (1985), Dullemeijer (1989), Gans (1989), and Riedl (1989).

The fields of comparative morphology, paleontology, and paleobiogeography were of professional interest to John Napier, and he wrote on each of these areas during his career. OWM I included a number of contributions in these "traditional" fields of primatology by Adolph Schultz, Elwyn Simons, Cliff Jolly, and John Napier.

The study of morphology in primatology has been revolutionized since the publication of OWM I by the introduction of cladistic methodology and philosophy, the application of experimental techniques to the study of function, and an increased emphasis on the study of size in functional and phylogenetic interpretations. Gans (1989) identifies phylogeny, ontogeny, size-shape, and function as the four basic "dimensions" of comparative morphology; all four areas are represented in this volume.

Cladistic systematics

At the time of publication of Napier and Napier (1970), few primatologists were aware of the basic principles and methodology of cladistics. The dominant paradigm was the less formalized "evolutionary systematics" that had grown out of the New Synthesis. Publications such as Simpson's (1961, 1963) and Mayr's (1969) were considered the standard texts on the philosophy and procedure of classification, and the major challenge to evolutionary systematics in the United States was phenetics (Sokal and Sneath, 1963).

Thorington's (1970) contribution to the original volume reflected the general view, when he characterized phenetic and cladistic classification as "useful." Mayr (1974) tended to be somewhat more critical. In fairness to the practitioners of primate classification at that time, it must be remembered that the population-based perspective of the New Synthesis was an important advance. Previously, some primatologists had erected new taxa on the basis of relatively minor morphological variation (e.g. Elliot, 1913),

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and so there was an effort to bring the systematics of modern and fossil primates into the context of population variability. The contributions in Washburn's (1963) *Classification and Human Evolution* reiterate this point, and Simons and Pilbeam (1965) is an outstanding example of application of population thinking to the fossil record.

Hennig's system of classification was first articulated about 15 years before it was available in English (Hennig, 1950, 1965, 1966), and was not widely applied to primates until after the publication of OWM I. A paper that was specifically directed at cercopithecoid phylogeny was among the first to explicitly use cladistics; Delson (1975) is a classic because it details cladistic approaches, presents cladograms of the colobinae and papionini, and identifies ancestral morphotypes that have dominated the literature (see Benefit, Chapter 6).

The widespread use of cladistics changed not only the procedures used in erecting classifications, but also shifted the kinds of questions asked by primatologists and their paradigms of evolutionary change. For example, rather than focusing on the traditional question of ancestor–descendant relationships, often couched in an anagenetic paradigm, cladists now concentrated on the identification of sister-groups among taxa through the analysis of character states (Forey, 1992; Panchen, 1992). Simons (1970, 1974) exemplifies the older mind-set, when he attempts to draw a relationship between *Parapithecus* and cercopithecoids on the basis of similarity between a Fayum mandible and *Miopithecus talapoin*. This interpretation was later disputed (Delson and Andrews, 1975), and a cladistic perspective led to the suggestion that derived features in *Parapithecus* indicate ecological-functional convergence to cercopithecoids (Szalay and Delson, 1979).

Cladism not only signaled a formalization of systematic methodology, but also an emphasis on speciation (cladogenesis) rather than anagenetic change. Krishtalka (1993) discusses anagenetic versus punctuated models of Eocene primate evolution. This shift is logical, because the widespread application of cladistics has paralleled the rise of punctuated equilibrium as a dominant model of the tempo and pattern of evolution. Punctuated equilibrium was in the process of formulation (Eldredge, 1972; Eldredge and Gould, 1972) at the time of publication of OWM I. Paul Whitehead points out that a relation between cladism and punctuated equilibrium should be expected, since a close reading of Hennig (1966) reveals that many of the assumptions of punctuated equilibrium were already built into cladism. He would also argue, however, that it is unfortunate that there has been adherence to Mayr's (1942, 1963) model of peripatric speciation