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Book Review

Anthropoid Origins: New Visions. Edited by Callum F. Ross and Richard F. Kay.
New York: Kluwer Academic/Plenum Publishers. 2004. 530 pp. \$175.00 (cloth).
ISBN 0-306-48120-0.

Clarity is not one of the “new visions” editors Callum Ross and Richard Kay easily inspire in compiling this large complex volume on the origins of higher primates, not for this anthropoid anyway. The topics that matter most in such a book are phylogeny, adaptation and cool fossils. Too much of the systematics here is fuzzy and deeply overanalyzed. It is steeped in the mirage that PAUP will illuminate this problem of deep phylogeny, which means it stretches well beyond the last common ancestor of living anthropoids and into dimly lit reaches where scientific resolution is a serious issue. Maybe the most ardent practitioners writing in this volume (Ross, Kay, Williams and their followers) are beginning to see this, for their use of PAUP often seems more like nosing and probing around altered states as opposed to the lit up hyper-rigorous objective application that was once meant to supplant less formulaic styles of character analysis. *Let's see what happens if you order states, or maybe just some states. Let's try scaling (i.e., weighting) the characters. Let's only use the postcranials or the dentition. What about adding temporal and geographic information as characters? Now, let's explain why we prefer the tree we prefer because we prefer it.*

Of course, this is but a caricature and I am not accusing my colleagues of being so cavalier. Rather, I applaud them. For, overall, their default solutions are tempered by scholarly sensibilities and excellent morphology. Much of the solid macro-cladistic background to anthropoid origins (e.g., monophyly of anthropoids, haplorhines, strepsirhines, euprimates, a tarsiiform rather than adapid origin for Anthropoidea) worked out over the past 30 years is accepted in spite of the unruly behavior of some PAUPograms. At another level, they are not blinded by the numbing abundance of input (hundreds of characters) and the inevitably conflicting output (numerous consensus trees) these data produce, remaining true to many of the star characters we knew and loved before PAUP churned them. Thus they escape from a small wilderness of trees that would conceal the sister-group relationship of tarsiers and Anthropoidea because both have homologously shared and derived postorbital septa. (A debatable point, but reasonable.) In other words, our colleagues' introspection about homology comes toward the end of the analysis, with hindsight, rather than at the beginning. Most importantly, it comes before deciding which cladogram to choose. Circular? Subjective? Let us call it reciprocal illumination. For we are also cautioned about PAUP's many pitfalls (faulty identifications of fossils, vacant data cells, poor taxonomic sampling) and its ultimate source of uncertainty—the To Be or Not To Be question: Shall we use total

evidence or partitioned data? That somewhat “new vision” gives me hope that the phenetic distance between PAUPers and non-PAUPers is narrowing. Its unintended consequence may intone the slow beginning of the end of PAUP as we now know it.

As we see, even using sensible machinations to try and make PAUP work does not exorcise the devil from the details. Thus, as important taxa are driven to settle at alternative nodes on trees with radically different branching sequences, the normal state of deep-phylogeny fogginess approaches zero visibility. For example, the analysis of Kay *et al.* reveals at several stages that one group of possible early anthropoids, the Eocene amphipithecids of Myanmar and Thailand, are either strepsirhines or haplorhines, depending on how you code the data. Yes we know; my eyes begin to glaze over. In another example, one of the finest and most important Oligocene primate specimens, the undistorted and nearly complete omomyid skull that is *Rooneyia*, appears in about five different positions, some wildly contradictory. *Rooneyia* (which radiates evidence of Haplorhini right between the eyes) is important to anthropoid origins because it is the only tarsiiform skull that lacks a suite of autapomorphic features shared by the group’s more tarsier-like members. It has a relatively smaller orbit, capacious snout, moderately inflated bulla and flat temporomandibular joint articulation. I wonder: If we cannot get this one right—according to Kay *et al.* even as to Semioorder or Suborder—why should we think PAUPing can get right today’s leading candidate for earliest anthropoid, *Eosimias*, in spite of its beautifully complete dentition, and more? At least five different cladistic options for *Rooneyia* are offered. Four place it outside the haplorhines and within variously permuted strepsirhine clusters, sometimes with amphipithecids included among them. Sometimes it sits closer to adapiforms than to lemuriforms, unless it is the other way around. The one solid nesting amidst haplorhines, based on cranial data, fixes *Rooneyia* among a stash of the Fayum anthropoids (and amphipithecids), along with catarrhines, platyrrhines and eosimiids—but within a monophyletic group that embraces strepsirhines and stands opposite another one that is exclusively tarsiiform, living and extinct.

Well, I guess a few poisoned traits sickened those trees. But *Rooneyia* is long dead, one of a kind, with outlier teeth and barren of DNA. What about the lively *Tarsius*, that hyper-bug-eyed primate at the hot center of the anthropoid origins debate? Three brief chapters in *New Visions*, on molecular and cytogenetic phylogeny, are meant to zero in on this question. There is one vote for tarsiers as strepsirhines (Eizirik *et al.*), one for tarsiers as haplorhines (Schmitz and Zischler) and one abstention tendered in the absence of data (Stanyon *et al.*). The morphologists (Kay *et al.*) also seem to have a problem. At least seven different options are given, with tarsiers falling mostly among tarsiiforms, and less often as a link to anthropoids.

The problem I have with all this is very basic. The results from each of these experiments are not being replicated. Each run seems to falsify previous findings. While the experiments themselves are perhaps described well enough to make them repeatable, with taxa like *Tarsius*, *Rooneyia* and Amphipithecidae bouncing all over the branches—many polyphyletic—I have little confidence that the form-and-function of this analysis will land us closer to the root-truth of the anthropoid’s phylogenetic origins. See the light here. Cladistic ambiguity is what sustains some of the core adaptive hypotheses in *New Visions*, like Heesy and Ross’s inference that haplorhines were primitively nocturnal and anthropoids stemmed from a visual predator. These big ideas would pop in a winking photon if *Rooneyia* was viewed as a haplorhine or *Tarsius* was seen as a tarsiiform.

But *New Visions* is not all about phylogeny. There is adaptation and the sheer wonder of fossils, too. The papers on functional morphology and adaptation are quite satisfying. Contributors are wide-eyed to the possibilities (though rarely to the limitations imposed by deep phylogeny) of extrapolating the biology of long extinct species using correlational methods, biomechanics and phylogenetic inference. Canine dimorphism is examined as an indicator of sociality (Plavcan) and various features of craniodental biomechanics are also well reviewed (Ravosa). In a twin feat, Elwyn Simons, the doyen of paleo-anthropoidology, shows us that his unusually acute haplorhine fovea is still able to spy the prized fossil. His extended description of a relatively complete and undistorted skull of *Parapithecus grangeri* from Fayum, Egypt, shows us it is starkly primitive and replete with adaptive information. Very cool. His work is complimented by Bush *et al.*, who use X-ray vision to extract more, i.e., computerized tomography.

New Visions is the product of a working conference held in 2001. It consists of 25 well-organized chapters written by 36 authors. The composition of authors is significant. About a dozen—almost all of the American morphologists—are now or have been faculty, students and/or postdocs at Duke University, the *de facto* nerve center of paleo-anthropoidology. At least five contributors wrote or co-wrote three or more articles. Editors Ross and Kay are listed on five and four papers, respectively. So, while these chapters reveal some differences of opinion, I cannot recall seeing an ensemble of paleoprimateologists that argues so little. The reality is that this esteemed gathering reflects who is currently doing what in the field. This is the braintrust that rallies to Matt Cartmill's Visual Predation Hypothesis of Primate Origins—while decamping the plesiadapiforms to the archontan dustbin and modeling the earliest primates on lorises. Here it offers up the Visual Predation Hypothesis of Anthropoid Origins—while exiling omomyids from anthropoid ancestry and arguing that the foveate retina of the tarsier-like eo-anthropoid required a postorbital masticatory shield so that its bearer could make a living by hunting and chewing insects at the same time. Right or wrong—and I do not wish to belittle these perfectly valid, exciting and serious proposals—I cannot help but think that a little more intellectual polyphyly would be good for the cause.

In general terms, the book is divided into sections on paleontology and systematics, molecular systematics, and functional morphology and adaptation. There is an interesting collection of seven papers in the section “Evolution of Anthropoid Adaptations” that are devoted to sight and the visual system. It includes articles on the retinal ganglion cells (Tetreault *et al.*), photopigments and color vision (Jacobs), the biological role of chromatic vision in feeding (Dominy), the eyeball of tarsiers (Ross), PAUPed reconstructions of activity patterns, color vision and diet in haplorhines (Heesy and Ross), and a CT tomography study of *Parapithecus* (Bush *et al.*), focusing on its brain size and optic nerves. Kirk and Kay assess the visual competence of many early fossil primates, with complicated albeit interesting results.

More than a dozen papers are basically concerned with fossils and cladistic analysis. Kudos to Ross and Kay for inviting papers by scientists from Myanmar and Thailand (Aye Ko Aung, Tin Thein and Yaowalak Chaimanee) who have worked directly on the geology and paleontology of primates from their countries, as well as our better known Japanese colleagues (Masanaru Takai and Nobuo Shigehara) who wrote detailed morphological analyses of middle Eocene Pondaung primates. This body of work becomes one-half of Exhibit A in the case for early Tertiary anthropoids outside of Africa. Unfortunately, the other half makes only a cameo appearance. No major paper is devoted to *Eosimias* and its

allies. These Eocene primates from China have received a great deal of attention in the ten years since their discovery. Chris Beard (who did attend the conference) and his colleagues have touted eosimiids and allies as early anthropoids, largely on craniodental grounds. Some of the foot bones from *Eosimias* sites are regarded as haplorhine protoanthropoids (Gebo and Dagosto). Nearly all the volume's morphologists treat eosimiids as anthropoids, although the Simons cadre is less sure. I think *Eosimias* is phyletically a tarsiod (or tarsiid?), as Fred Szalay has argued elsewhere in detail (Szalay, 2000; Rosenberger, 2000). I also believe that the phylogenetic relationship between living tarsiers and anthropoids has been oversold in the absence of knowledge about tarsiid differentiation. It has been evident for a while (Rosenberger, 1985; Beard *et al.*, 1991) that there was an adaptive radiation of forms within a clade whose only living member is *Tarsius*, which makes the tarsier-anthropoid hypothesis an artifact of sampling (paleontological and neontological) and narrow (cladistic) phylogenetic definition. Even so, emphasizing the strength of this linkage has had profound consequences that are evident in *New Visions*, an *Eosimias* bandwagon which fulfills the quest for a tarsier-like, as opposed to an omomyid-like, First Anthropoid.

With this book, the editors and publisher have established something of a tradition. Plenum (now part of Kluwer) first printed an anthology on anthropoid origins in 1980 under a title and context that was right for the time—*Evolutionary Biology of New World Monkeys and Continental Drift*, edited by Ciochon and Chiarelli. It was followed in 1994 by *Anthropoid Origins*, edited by Fleagle and Kay. Now, 10 years later, it is *New Visions*. The arc of these volumes, and the efforts of the only two authors who traveled this odyssey by writing papers in all three, Rich Kay and Russ Ciochon, reveals how research on anthropoid origins and early primates has evolved over the course of 25 years. As implied above, one illustrates a radical shift in the fashion of phylogeny reconstruction. The other reveals where the touchstones to the story lay—fossils, fossils, fossils. Some of this is nicely set up in Ross and Kay's opening chapter—a must read for graduate students—where they deftly introduce the literature, present different points of view fairly, and show appreciation for taxonomic context and depth of analysis. It would be great fun to use *all three books together* as the core of a graduate seminar on anthropoid origins.

Since the first book, perhaps the most profound change in thinking and evidence involves *The Asian Question: Couldn't anthropoids have appeared first in Asia?* Ciochon saw the problem in these stark geographic terms. His work helped internationalize the search for early primate fossils in Asia and succeeded in finding new specimens of *Amphipithecus* and *Pondaungia* in Myanmar. Unfortunately, it seemed, the more we learned of them from 1980 to 1994 to 2003, the more they looked like adapids, as Szalay inferred years ago (Szalay, 1970) from scrappy material. No problem for Ciochon, though. One school of thought strongly advocated in 1980 and afterwards held that anthropoids evolved from adapids or their allies and not from a haplorhine. Now, with indisputably strepsirhine postcranials having arrived in association with dental remains of these fossils (Ciochon and Gunnell), their heads not showing a postorbital septum (Takai and Shigehara), and the evidence that anthropoids are haplorhines rising beyond the point of serious challenge, Ciochon has thrown in the towel on two accounts: neither the adapids nor the Pondaung fossils have anything to do with anthropoids. Several of the others in *New Visions* have trodden the same path, and so they euphemistically label amphipithecids as the “large-bodied” primates or the “possible anthropoids” in chapter titles. This retreat may be one of the factors that

explains a precipitous decline in continental-drift/biogeographic emphasis in *New Visions*. Only one paper (Seiffert *et al.*) stabs at it. Too bad. Since the hunt for protoanthropoids in Asia will continue for good reason, and current thinking has primatologists projecting an early, pre-Cenozoic differentiation of the order, paleobiogeography is even more important today.

One last grumpy comment on what these books show as a trilogy ought to be an object lesson for all of us. They demonstrate a frustrating decline in production values—paper stock, image quality and copy editing . . . the works. An opportunity was missed by not packing *New Visions*' accompanying CD with a set of high quality images of the fossils, many of which show too poorly on paper to count for much. Happily, there are seven color photos of *Siamopithecus*, but the rest of the CD is loaded with deadly character matrices that could have been easily distributed in other ways to anyone who is interested in seeing them, which should be all of us with serious interest in the subject. About the overall editing, I wish Kluwer/Plenum would realize that none of us are going to do the job the way it should be done. This book is part of their *Developments in Primatology* series. I would like to see them take more pride in the product and invest the necessary resources to make it right.

The *New Visions* book is timely in gathering research from several relevant fields of study whose practitioners rarely interact or publish in the same places, and complimenting that with a collection of papers by a group that has been working on the problems of ancient anthropoids intensively in recent years. That is the book's strength. But for matters JME readers have an eye for, how much this advances our understanding about the *origins and differentiation* of higher primates, I am not so sure. Hindsight tells me that the shelf-life of this volume will not equal the more wide ranging paleontology, systematics and comparative morphology of Fleagle and Kay's 1994 volume, or Ciochon and Chiarelli's 1980 effort, which is actually a gem of a primatology book. During the next five years, though, my copy of *New Visions* is going to become sorely worn, for Ross and Kay have served up a generous helping of things to bite and chew on, over and over.

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