The three “Cs” of behavioral reconstruction in fossil primates


As method and theory in paleoprimatology advance, researchers are increasingly questioning the reliability of interpretations of the fossil record. Reconstructing Behavior in the Primate Fossil Record, a volume edited by (and including chapters from) an impressive group of primatologists and paleoprimatologists, asks fundamental questions about reconstructing behavior in fossil species and even questions whether it is possible. This mirrors recent critiques of the reliability of fossil evidence in reconstructing primate phylogeny (Collard and Wood, 2000), and it cuts to the core of what paleoprimatologists do.

In their summary chapter Plavcan et al. emphasize a major theme of the book. Reliably reconstructing the behavior of fossil primates, or any fossil taxon for that matter, is hugely challenging. They point to many potential sources of error, including measurement error, the inappropriate association of morphology and behavior, and unhelpfully vague categories of behavior (e.g., frugivores, folivores, arboreal, etc.) in living primates, and more. They urge researchers who seek to reconstruct behavior—which after all is what makes fossil animals interesting—to proceed with caution. They conclude that multiple lines of evidence and an understanding of potential sources of error will increase the precision and accuracy of the reconstruction of the behavior of fossil taxa. Biomechanics, form-function correlations, the comparative method, paleoecology, phylogeny, and structural morphology all help to narrow the range of possible behaviors, but we will never be able to describe the behavior of fossils as if they were extant organisms. Maximizing accuracy, sometimes at the expense of precision, should be the goal of behavioral reconstruction. For example, it is probably accurate to describe Dryopithecus as an arboreal, suspensory frugivore. But so is Choloepus (the two toed sloth). While it is frustrating to be unable to describe a fossil hominid’s behavior with sufficient detail to distinguish it from an edentate, that is probably as good as it gets. Greater precision is problematic without sacrificing reproducibility. Significant differences in morphology and phylogenetic history make it likely that Dryopithecus behaved more or less like a great ape, or at least more like an ape than a sloth.

Plavcan et al. criticize behavioral reconstruction of hypothetical common ancestors (HCA). Wrangham (1987) and others (e.g., Begun, 1994; Moore, 1996; Zihlman, 1996; Richmond et al., 2001) have proposed behavioral reconstructions of the chimpanzee-human HCA based on shared behaviors. Plavcan et al. see this approach as problematic because it can predict characters that are demonstrably incorrect. Their example, from Foley (1999), supposedly predicts a chimpanzee-human LCA brain size of about 875 cc, midway...
between the chimpanzee and modern human means and much too large. The same logic would say that humans evolved from a triped, half way between a quadruped and a biped. Reconstructing attributes of the chimpanzee-human HCA relies instead on fossil evidence and shared characters of sister clades, suggesting a 300–400 cc HCA brain case (Foley’s point was in fact not about attribute reconstruction but about differences in rates of change between sister clades). Phylogeny can and should be incorporated into the tool kit of behavioral reconstruction.

Ross et al. survey recent concepts of adaptation. The thoughtful discussion will help students who are besieged with requests from their teachers to define the term. These authors wisely pass over the chance to find the “ultimate” definition of adaptation, or the “best” approach to the reconstruction of behavior, and argue instead for “consilience” (see also Padian, 1995; Wilson, 1998; Cory, 2000). The use of this term rather than the more familiar “multidisciplinary” reveals a subtle bias toward biomechanics. This is analogous to Cory and Wilson, both of whom seek a few fundamental principles to explain language, thought, and even life itself. To be fair, Ross et al. urge multiple lines of inquiry, including phylogeny and structural constraint, but they echo Lauder (1995) and Rudwick (1964) in placing primacy on biomechanical models. Models emphasizing phylogeny (e.g., Coddington, 1988), are criticized, but the more favored “paradigm approach” of Rudwick (1964) emphasizing biomechanics, has been criticized elsewhere (e.g., Lauder, 1995). We do not understand biological systems in sufficient detail to “retrodict” behavior from a few biomechanical principles. But the authors are right to urge that inferences about behavior must be consistent with biomechanical principles or observations.

Hylander and Johnson’s description of the highly influential and often cited oeuvre on in vivo bone strain patterns in primate faces is a useful introduction to the topic. This experimental approach makes clear the limitations of biomechanical optimization models. Strain patterns in the bones of the faces of primates do not correspond to patterns predicted by an optimization of bone mass in response to masticatory stress. Despite this, Hylander and Johnson endorse an optimization model in which bone design includes a response to both routine and exceptional (rare or traumatic) loads. The problem with optimization is that it is difficult to test. There is more bone than one would expect in the supraorbital tori of many primates because they experience occasional potentially traumatic loads in a highly sensitive region of the cranium (between the brain case and the eye sockets). Maybe, but how can this be tested ethically? Hylander and Johnson note that features enhanced in male primates in response to sexual selection, like elk antlers, are impossible to predict from a purely mechanistic approach. In the end it makes sense that facial structures of unusual size result from a combination of mechanical responses (mastication), structural constraints (face-neurocranial-orbital relations) and non-mechanical responses (sexual selection). The trick will be to work out the relative contributions of each, and until we learn to do that trick, application to the fossil record will continue to be problematic.

Ravosa and Vinyard continue in a similar vein in their review of ontogeny and function in primates. As they note, the data needed to carry out the research protocols they endorse are never available from fossils, but it is important nonetheless to consider the effect of growth on the relationship between form and function in primates. I have to take issue with the two premises that ontogenetic data are “superior” to data from adults, and that growth stage comparisons can test hypotheses of homology. Data relevant to the analysis of fossils cannot be superior to other data if they are absent from the fossil record. The solution they propose is to use a living close relative, but this has two problems: uncertain phylogenetic relations and the likelihood that fossil evidence will consist of such small samples that growth trend comparisons will be limited (see their Figure 1). In addition, similarity in growth pattern or timing is not proof of homology (Hall, 1994). Ravosa and Vinyard endorse a criterion of subtraction in comparisons of growth trajectories, which makes sense to me. Ross et al. reject criteria of subtraction, arguing correctly that scaling
relationships are also functional. Ross et al. are
talking about interspecific scaling, which can be
problematic with regard to function, and Ravosa
and Vinyard are talking about ontogenetic scaling.
Ravosa and Vinyard’s survey of ontogenetic scal-
ing relationships in primate skulls is a very good
introduction to the subject, even if the methods are
difficult, or impossible, to apply to most fossil
primates.

Godfrey et al. explore life history and behavior
in extinct primates. Their comprehensive survey of
growth and development, life history, and mor-
phology leads to an analysis of “sloth” lemurs.
Their methods, such as modularity of traits,
requires a detailed knowledge of functional,
structural, and developmental integration within
character complexes, and an understanding of
the effects of character decoupling. Population
growth-rate elasticities require a knowledge of the
inter-relationships among population growth and
life cycle stages, and information about the pertur-
bations of both. Unfortunately these methods
are only applicable to rare samples preserving
relatively intact ontogenetic series.

Godfrey et al. note that Propithecus and its
fossil relatives have a remarkably fast rate of
dental development, leading to a completed adult
dentition at very early chronological ages. This
helps to account for different looking crania and
mandibles that all appear to be the same “age”
based on the dentition. In other words, different
parts of the skull take different amounts of time to
catch up to the teeth. Godfrey et al. use modularity
analysis to describe growth patterns in sloth le-
murs, and elasticity analysis to describe population
parameters. They assume that subsets of extant
skeletal populations accurately reflect age distri-
butions in living populations, a problem that is
significantly amplified by taphonomy in fossil
samples.

What did these authors discover about sloth
lemurs? Paleopropithecids resemble extant indriids
in life history strategies, and placed a premium on
adult survival, while archaeolemurs, also related to
indriids, do not. The latter grew more slowly, like
other lemurs, and placed a higher survival pre-
mium on juveniles. Using similar but simpler
observations on dental development, Kordos and
Begun (2001) and Dean et al. (2003) concluded
that Anapithecus, the primitive catarrhine found
with Dryopithecus at the late Miocene of Rudabánya, grew its dentition extremely rapidly,
possibly to achieve adult sizes as quickly as poss-
ible. This may have been to avoid predation
(maybe from Dryopithecus) that targeted smaller
individuals. These conclusions were based on ob-
servations of associated deciduous and permanent
teeth and percentages of broadly defined age
classes, and an analysis of dental growth indicators
(perikymata). I am not sure that the complex
analysis of Godfrey et al. provides more reliable
conclusions, though surely the most rigorous poss-
ible approaches need to be used to assess behavior
in fossils. If we had adequate samples of Ana-
pithecus and Dryopithecus, perhaps this kind of
analysis would represent a comprehensive test of
our results and on that basis alone we would do it
(or, more likely, ask Godfrey et al. to do it).

Nunn and van Schaik explore the comparative
socioecology of extinct primates in an interesting
and innovative chapter. Their approach is more
applicable to the fossil record. Nunn and van
Schaik recognize that many aspects of socio-
ecology are not recoverable directly from fossil
evidence, and while they suggest that cladistic
approaches (ancestral morphotypes and parsi-
mony, see above) can help, it would be most
useful if it were possible to assess the degree to
which unknowable (U) variables can be predicted
from more knowable (K) variables from the
fossil record. Knowable variables include activity
period, substrate preference, diet, body mass, and
habitat. Unknowable variables include popu-
lation and foraging group sizes, home range, day
journey length, and defensibility. The decision
about which are K variables (e.g., nocturnal-
diurnal, wooded-open, etc.) could be criticized,
but the authors’ choices are realistic given the
limitations of the fossil record. K variables occur
in characteristic combinations or syndromes, and
the elegant analysis (which includes a consider-
ation of complicating factors like phylogeny or
spurious correlations) results in a relatively small
number of syndromes with predictable relation-
ships to U variables. Matching fossil primate K
variables with syndromes with some or all of the
same K variables produces a clear set of broadly defined but reasonable estimates of otherwise unknowable aspects of the behavior of a fossil primate taxon. But it is not all plain sailing. Some primates sets of K variables that are compatible with more than one syndrome. This says something about behavioral flexibility and the difficulties this poses for attempts to reconstruct behavior. On the other hand, *Gorilla* is assigned only one syndrome (diurnal-arboreal-wooded-fovires), though the degree of frugivory in this taxon is substantial (Tutin and Fernandez, 1993). Nevertheless, the authors suggest that most fossil primates should fall into one or more of their syndromes. However, as the sloth lemur example illustrates, there may be quite a few fossil primates that fall into categories not observed among living species, or that fall into K syndromes with different relationships to U variables than are observed in extant primates. Autapomorphic taxa like *Oreopithecus* and *Gigantopithecus* may well present challenges to this approach. They would likely be classified as diurnal-arboreal-fovires (D-A-Fo) and diurnal-terrestrial-open?-frugivores (D-T-O-Fr), respectively, but it would surprise me if they had many U variables in the range of living apes in those categories. Nevertheless, for “normal” looking fossil primates this approach should be useful.

*Dryopithecus* closely resembles juvenile African apes in many features of craniodental anatomy, whereas it resembles orangutans to some extent in postcranial morphology (Moya`-Sola` and Köhler, 1996; Begun, 2002). It can confidently be classified as a D-A-Frugivore (D-A-Fr), and the predicted U variables are provided in Table 1. While these ranges are large, we could hypothesize that *Dryopithecus* values are closer to those of *Pongo* than...
Hylobates, which is much smaller and more distantly related (body mass has an effect in this analysis). On the other hand, Pongo is so specialized and isolated that it may not be the best model for Dryopithecus socioecology. Despite these uncertainties, this approach generates insights about Dryopithecus that I frankly had never considered (and I have thought a lot about Dryopithecus). Dryopithecus may have lived and foraged in small groups, and had short day ranges, intermediate-sized home ranges (larger than gibbons and many foliviore but smaller than other African apes and many frugiviore) and low defense indices. While qualitative, to use the authors’ own term, these methods are informative both in terms of behavior and in the interpretation of the preservation of individuals at fossil localities (taphonomy), which is the focus of the next chapter.

Reed takes on the difficult task of assessing the role of paleoecology and taphonomy in reconstructing behavior in fossil primates. Much of the first part of her chapter is a comprehensive summary of extant community ecological classification that is a useful resource for non-specialists. It is based on frequencies of different kinds of mammalian adaptations (ecomorphology) rather than taxonomy. The latter assumes similar adaptations among related fossil and extant organisms, a clearly indefensible idea for many mammal lineages. Having shown that these methods reliably predict ecology from modern death assemblages, despite a few taphonomic concerns, Reed reconstructs the paleoecology of the southern African australopithecine locality of Makapansgat as bushland with riverine forest, while noting some important differences from modern settings. One of the difficulties here is that reasons for the differences are all post hoc (such as productivity differences, unique taphonomic factors in fossil localities, or recent historical effects in modern Africa), and we cannot know how this could have affected the behavioral ecology of the fossil primates. This leads to an inverted pyramid. A reasonable description of the paleoecology along with the ecomorphology of the primates, which is less secure, leads to behavioral ecological statements that have to be qualified (e.g., fossil species were “probably” similar to an extant analogue; “likely” lived in riparian regions, and “perhaps” had unique behavioral adaptations). The rigor of the analysis reveals, paradoxically, the difficulties of making precise statements about behavioral ecology. In addition, a mosaic setting such as that reconstructed for Makapansgat could be used to support multiple reconstructions of behavior, such as arboreal (riverine forest) or terrestrial (bushland) substrate preferences for Australopithecus. Finally, I have to wonder about treating fossil species in the same way as living species for the purpose of comparing species diversities between fossil and modern communities. Paleontological species concepts differ from biological species concepts, and it is dangerous to place too much emphasis on a comparison between paleocommunities and modern ones at the species level. This does not detract from the clear and important message of this chapter, which is that in order to understand behavioral ecology you need to understand paleoecology. And to understand paleoecology in an effective and reproducible way you need a comparative and actualistic approach.

Ungar surveys the methods available for reconstructing fossil primate diets. A comprehensive survey that will be of use to students and colleagues unacquainted with this type of research, it is unlike other chapters in that little it contains is new. I was disappointed to not have seen mention of the use of GIS to model teeth, a method that Ungar has pioneered, or the use of digital morphometrics to describe subtle aspects of tooth form, particularly crown form, and their relationship to function. Ungar emphasizes the importance of multiple lines of evidence and points to uncertainty in the reconstruction of behavior, but new techniques and ideas, some only touched upon at the end of the chapter, would have put it more in line with the other chapters.

Sexual dimorphism and social behavior in the fossil record is the topic tackled by Plavcan. The problems are similar to those covered by Nunn and van Schaik in their attention to social factors, but Plavcan focuses on two “knowable” attributes, sexual dimorphism in body mass and canine morphology, and several “unknowable” variables related to mating systems and competition.
Plavcan notes that sexual dimorphism is difficult to estimate in fossils for a variety of reasons. There is another problem he does not mention. To identify fossils by sex, there must be something dimorphic preserved, and it is usually assumed, variability in the morphology of this structure (usually the canine or a surrogate for body mass) will be within the limits of extant taxa, with perhaps some rare exceptions (e.g., Kelley and Xu, 1991). It is intriguing that most Miocene hominids known from enough specimens appear to come close to maximum levels of dimorphism observed in extant anthropoids. This level of sexual dimorphism is relatively rare in other anthropoids. What is going on with the late Miocene hominids in particular, in which nearly all have a 2:1 level of body mass dimorphism? Is this primitive for hominids and retained by all late Miocene taxa regardless of body mass or ecological preferences? Are body mass differences exaggerated due to various errors? Or, are we exaggerating body mass sexual dimorphism in fossils because of the methodological requirement that if the range of variation in dimensions does not exceed that observed in extant primates, and if there are no morphological differences we interpret as taxonomically significant, we opt for our null hypothesis, which is that there is only one species? In essence, by failing to find more effective ways of identifying species in fossil assemblages, we are constructing them all from the same model, which is a species that is maximally sexually dimorphic. If this is the case, how can we really be sure about levels of sexual dimorphism, a relatively “knowable” attribute, in the fossil record? One possibility is to look at finer levels of morphological diversity, using digital morphometrics of surfaces, curvatures and proportions, or 3-D techniques.

Plavcan’s analysis relating body mass dimorphism to mating system and competition levels shows that the generally assumed straight-forward relationship between sexual dimorphism and social behavior does not survive close scrutiny. Most levels of dimorphism are consistent with several mating systems or competition levels, and different measurements (mesiodistal vs. buccolingual diameter) result in different predictions for the same fossil taxon. Plavcan notes that we are probably less confident in inferring social behavior from the fossil record than in Darwin’s time. Of course, the same could be said about phylogeny reconstruction, but it is particularly striking in the context of sexual dimorphism and mating systems, and it also communicates an underlying message of this book: the more complex the analysis, the less confidence in the results. This is a little depressing, but honest, and surely a challenge for the future.

Only the last two chapters focus on fossil taxa, making the book heavy on theory and light on application. Illustrative examples are given throughout the book, but usually using information on fossil taxa plucked from the literature (an exception is Godfrey et al.). Kay et al. on the early platyrrhine Branisella and Jungers et al. on giant subfossil lemurs buck this trend. I would have liked to have seen a few more chapters in this vein, explicitly testing as many of the ideas from as many of the chapters as possible by the researchers who know the fossil material best. Kay et al. begin their chapter with a lengthy discussion of adaptation, much of which is covered in Ross et al. In the end I am not sure that a preoccupation with the meaning of the word has a real impact on research about adaptation. We notice parts on fossils and seek to explain their function, whatever we want to call them, no matter how they got to be the way they are. In fact, Kay et al.’s analysis of Branisella is interesting and plausible, but it is not specifically informed by a particular understanding of adaptation. Kay et al. consider many reasons for evolutionary change in morphology apart from “adaptation,” including various sources of structural and phylogenetic constraint. However, these concepts probably more usefuly inform hypotheses of phylogeny (e.g., in suggesting more likely pathways of change) than hypotheses of function and behavior in fossils.

With regard to Branisella, Kay et al. consider the phylogeny, paleoecology, taphonomy, and ecomorphology of this taxon. They illustrate the practical limitations of using some of the methods outlined by various authors for most primate fossil samples. The paleoecology at Salla (the locality) was analyzed by ecomorphological and taphonomic approaches together with some
geochemistry, along with a number of comparisons to other high altitude communities, but not with the statistical rigor or detailed comparative analysis endorsed by Reed. However, this is a ca. 27 Ma relatively high altitude locality with significant ecological differences from well documented modern communities. Personally I have as much confidence in their reconstruction of Salla as I do in Reed’s reconstruction of Makapansgat; both are convincing. But it would be useful in the future to assess Kay et al.’s paleoecology of Salla using the more comprehensive tests of Reed.

Kay et al. combine their paleoecological inference that Salla was open woodland with seasonal rainfall with the morphology of *Branisella* to propose a niche for this primate. Based on craniodental evidence, Kay et al. describe *Branisella* as a 720–760 g, diurnal, terrestrial frugivore with powerful jaws, lacking the adaptations of many platyrrhines for exploiting a variety of embedded forest resources (e.g., gum, bark, tough or hard fruits). While they briefly consider a number of the same caveats discussed in detail this book, these do not really affect their analysis. This is a state-of-the-art analysis of the paleobiology of a fossil primate that is a model for all researchers who can focus on a few taxa at specific localities. It is not especially informed by much of the discussion in this book, except perhaps that the authors limit themselves to a broad outline of the behavior of *Branisella*. I was especially interested that molar crown height in *Branisella* was compared to extant cercopithecoids to suggest terrestriality, without a consideration of the phylogenetic effects of the type noted by Kay and Ungar (1997). The conclusion that *Branisella* was terrestrial is striking because no other platyrrhine is terrestrial, and as the oldest one *Branisella* could have been assumed to have resembled the ancestral morphotype for platyrrhines, which was probably arboreal. Does this behavioral reconstruction call into question an arboreal ancestry for platyrrhines, or, conversely, does the phylogeny call into question the behavioral reconstruction? No to both. *Branisella* predates the last common ancestor (LCA) of platyrrhines, so it could have been anything. But how do we know it predates the LCA? Kay et al. says it lacks characters found in the LCA, which is hypothetical and based on shared features of all the descendent. *Branisella* is a stem platyrrhine that was quite different from all crown platyrrhines and represents a hitherto undocumented phase of platyrrhine evolution. This is fascinating but it means that, at least in this case, neither phylogeny nor function informs each other in very significant ways.

Finally, the giant lemurs of Madagascar are examined by Jungers and colleagues. Their first paragraph expresses a sentiment I hold dear as well, and one that is apparent in the previous chapter. Inferring the behavior of fossil taxa is the only way to understand them as whole organisms, and we need to attempt this wherever possible despite the difficulties. Jungers et al. have a practical view of adaptation that I endorse as well. They consider body mass, sexual dimorphism, and skeletal attributes and attempt to relate these to activity pattern, oral behavior, and positional behavior. The analysis is elegant and convincing and once again a model for others, but it does not specifically address many of the caveats or recommendations noted repeatedly in this book. The inferences that extinct subfossil lemurs ranged in size between about 10 to 200 kg, were all probably minimally sexually dimorphic and diurnal, are based on traditional but comprehensive analyses of morphology and the relationships between form and function. Diet and positional behavior is variable in subfossil lemurs, but all reconstructions are based on correlations between cranial and dental anatomy, microwear, biomechanic, and direct form-function analogies to extant animals. The strength or reliability of these correlations is not questioned. Interestingly, they found an almost complete displacement of shearing quotient values between fossil and extant forms. Kay and Ungar (1997) propose a historical, non-functional explanation for this phenomenon in Miocene hominoids, while Jungers et al. see this in functional terms as evidence of extreme specialization. Kay and Ungar’s fossils were less specialized, while the subfossil lemurs were more specialized. However, in the context of this book it is interesting that an alternative explanation for the discrepancy between fossil and living Malagasy lemurs was not explored.
The message of this book is valuable for all students of the primate fossil record, but it is not entirely new [see Thomason (1995) for a view from vertebrate paleontology and Russell (1916) for many of the intellectual roots of the analysis of form and function]. Nevertheless, the interpretation of fossil primate behavior is explored here in more detail than in any other volume of which I am aware, and Table 1 summarizes aspects of the behavioral reconstruction of a few well known fossil primates along the lines suggested by a number of authors in this book.

Overall the authors are more optimistic about being able to reliably reconstruct behavior from the fossil record than some recent scholars (Lauder, 1995). I share their optimism, and also their concern for analytical rigor. At the same time, despite the warnings of the many authors, the two chapters on the reconstruction of behavior in specific fossil taxa provide excellent but “traditional” comparative functional analyses. They skirt problems with traditional methods for correlating form with function, and avoid the problems associated with the reconstruction of complex social behaviors by ignoring them altogether. This is not a criticism. It is a realistic choice about what to expect from the fossil record, and represents a stage in the progression of the field that is important to document. We must accept that until new techniques are devised we should limit ourselves to reconstructing functions that have strong correlations with morphology in extant organisms. We must also recognize that many aspects of form are not directly related to function, and that many important functions and behaviors will not be revealed by the structures that are well represented in the primate fossil record. The next advances are likely to be the approaches described by Reed and Nunn and van Schaik. These involve incorporating ecological data to expand what we can say about fossil primate socioecology (Table 1).

At the student level, readers of this book will learn a great deal about the methods and limitations of reconstructing behavior in fossil taxa. Researchers at all levels would be well advised to apply as many of the innovative approaches to reconstructing behavior in fossil primates as are feasible. They should also heed the warnings of most authors about the complexity of the interplay between morphology and behavior. This book is an invaluable resource for students and researchers in vertebrate paleobiology generally, and it would also make an excellent text for an advanced course in paleobiology.

And the three “Cs”? Careful analysis, cautious interpretation, and keep it simple.

References


David R. Begun
Department of Anthropology
University of Toronto
Toronto
ON M5S 3G3
Canada
Evolution - Evolution - The fossil record: Paleontologists have recovered and studied the fossil remains of many thousands of organisms that lived in the past. This fossil record shows that many kinds of extinct organisms were very different in form from any now living. Evolution of the horse: Evolution of the horse over the past 55 million years. The present-day Przewalski's horse is believed to be the only remaining example of a wild horse—i.e., the last remaining modern horse to have evolved by natural selection. Numbered bones in the forefoot illustrations trace the gradual transition from a four-toed to a one-toed animal. Encyclopædia Britannica, Inc. Using recovered fossils, paleontologists have reconstructed examples of radical evolutionary transitions in form and function.