

Eurasian Hominoid Evolution

The European Science Foundation recently sponsored its third in a series of workshops on hominoid evolution and environmental change in the Neogene of Europe. This workshop, devoted to the phylogeny of Eurasian Neogene hominoid primates, was held October 21–25 in Nikiti, Greece. It was a fitting location, within sight of sediments bearing the fossilized remains of one of the most famous of Eurasian hominoids, *Ouranopithecus* (or *Graecopithecus*) *macedoniensis*.¹ Hosted by Louis de Bonis of the University of Poitiers and George D. Koufos of the University of Thessaloniki, the workshop included 21 participants from 13 countries. Papers covered diverse subjects related to Eurasian hominoid evolution, ranging from geological history and stratigraphy to systematics, functional morphology, development, and paleobiogeography.

The workshop began with three papers on the geology of fossil hominoid localities. Spyros B. Pavlides kicked off the workshop with an impressive synopsis of the large-scale geological structure of central Macedonia, currently one of the most geodynamically active areas in the Mediterranean. George E. Syrides followed with a synthesis of the last decade of research on the stratigraphy of the Lower Miocene to Holocene sediments of the Chalkidiki peninsula. These sediments contain numerous fossiliferous localities that are rich in a variety of mollusk and mammal, including micromammal, faunas. Of particular interest is the discovery of Paratethyan-type faunas in the Upper Miocene “Trilophos For-

mation.” These faunas promise to shed light on the transitional zone between the Tethys and Paratethys. Pavlides’ and Syrides’ presentations also prepared the participants for an informative field trip to fossil localities such as Ravin de la Pluie² and Xirochori.³

In the third of the geological papers, Jorge Agustí, Lluís Cabrera, and Miguel Garces compiled stratigraphic evidence of hominoid-bearing sites in Europe. They proposed new age estimates for a variety of important localities, including a range of 9.64 to 9.74 Mya (Chron C4Ar) for the *Dryopithecus* remains at Can Llobateres 1, an age of about 9.6 Mya for Can Llobateres 2 (the site that recently yielded the partial *Dryopithecus* skeleton CL2-18000), and a range of 9.2 to 9.6 Mya (bottom of Chron C4Ar.2r) for *Ouranopithecus macedoniensis* from Ravin de la Pluie, Greece.

The majority of papers concentrated on phylogenetic and functional issues in hominoid evolution. Bernard Wood and Mark Collard attempted to test cladistic methodology by assessing whether or not any of a variety of cladistic analyses employing morphological traits of hominoids and papionins can reproduce the relatively well-established cladograms derived from molecular data. They argue that most descriptive character states (e.g., “strong,” “reduced,” or “absent”) are unavoidably subjective. Using quantitative metric features, they were unable to reproduce molecular phylogenies. Thus, they argued that, using only morphological data, our attempts to recover phylogenetic relationships

in the fossil record are not likely to be correct.

José Braga investigated the variation in “discrete” traits typically described as being present or absent. With an enormous database of 1,453 great ape specimens, Braga found differences in trait frequencies among orangutans, chimpanzees, and gorillas in features associated with ossification of the skull base and cranial venous drainage. Some features successfully distinguish chimpanzee taxa at the species or subspecies level, matching patterns found with mitochondrial DNA polymorphisms.

Peter Andrews and Bernard Wood joined forces to investigate whether or not there is any evidence of a “grade shift” between fossil hominoids and fossil hominids. As a first approximation, dietary grade was assessed by molar crown area relative to body mass. Using these criteria, there is currently little evidence for a grade shift between fossil hominoids and hominids. The first evidence of a grade shift in the fossil record occurs with the appearance of *Homo ergaster*, or early African *Homo erectus*.

Jay Kelley re-examined the evidence supporting the claim that *Ouranopithecus macedoniensis* exhibits canine, especially male canine, reduction, a characteristic purportedly linking *Ouranopithecus* with the human lineage to the exclusion of *Pan* and *Gorilla*. Kelley noted that the canine/molar ratios typically employed are potentially complicated by variation in molar size. Using orbit dimensions as an alternative estimator of body mass, Kelley found that relative male

canine size (height) appears to be at least as great as that in common chimpanzees, suggesting that molar megadontia rather than canine reduction characterizes *Ouranopithecus*.

In reply to Kelley's analysis, Louis de Bonis and George Koufos suggested that perhaps the relevant canine measure for sexually dimorphic primates is the height of the canines visible to a competitor; that is, the height of the canines relative to the cheek teeth. They also noted that honing facets are not found on the canines of *Ouranopithecus*. Whatever the merits of the canine evidence, de Bonis and Koufos argued that other features such as thick enamel, relative tooth sizes, and cusp patterns support a close relationship between *Ouranopithecus* and australopithecines.

Extending their research into the paleobiology of *Oreopithecus*, Terry Harrison and Lorenzo Rook investigated the suite of autapomorphies (unique, derived features) that have confounded early attempts at resolving the relationships of *Oreopithecus*. This, they contend, is the first step toward understanding which features may be interpreted as being homologous with morphology in other taxa or part of autapomorphic complexes. Focusing on cranial morphology, they condensed a list of traits into three potential structural-functional complexes: a large, anteriorly placed masticatory musculature; a short, robust lower face and mandible; and a small neurocranium. Harrison and Rook then integrated these complexes with the paleoecological context to generate an adaptive scenario for *Oreopithecus*.

Peter Andrews treated the newly discovered *Ankarapithecus* cranium to a similar functional analysis.⁴ Andrews argued that this skull exhibits two functional complexes related to diet: The large, thick-enameled teeth and the strongly developed jaw and zygomatic region appear to reflect an adaptation for crushing and grinding, while the large incisors and premaxilla are adaptations for preparation of large food items. Andrews concluded that an understanding of cranial adaptations and identification of functional complexes must precede a phylogenetic analysis in order to avoid fla-

grant violations of the assumption of character independence.

Tania King presented a wealth of data on molar enamel microwear to reconstruct diet and feeding behavior in a diverse sample of extant and fossil hominoids. She concluded that the large ratio of pits to striations in the molars of *Graecopithecus freybergi* reflects hard-object feeding, while low pit percentages reflect a highly folivorous diet for *Oreopithecus*. Other taxa such as *Sivapithecus*, *Dryopithecus*, *Anapithecus*, and *Pliopithecus* appear to have preferred soft fruit. King noted that the dietary diversity in extinct Miocene catarrhines exceeds that among apes today.

Using quantitative metric features, they were unable to reproduce molecular phylogenies. Thus, they argued that, using only morphological data, our attempts to recover phylogenetic relationships in the fossil record are not likely to be correct.

Moving into the realm of postcranial adaptations, Brian Richmond quantified the shape of the humeral shaft in a variety of extant and fossil anthropoids including *Dryopithecus* and *Sivapithecus*. The humeral morphology of both *S. parvada* and *S. indicus* reflects pronograde quadrupedalism and lack the modern ape-like suspensory adaptations purportedly linking *Sivapithecus* with *Dryopithecus*. However, Richmond argued that the locomotor homoplasy required for a close relationship between *Sivapithecus* and *Pongo* is more likely than convergence in the derived craniofacial morphology unique to them, citing other examples of postcranial convergence and biomechanical data on activity-induced remodeling of long-bone shaft morphology.⁵

Roberto Macchiarelli, Lorenzo Rook, and Leca Bondioli presented their research on trabecular bone structure and density in the pelvis of living and fossil primates. By virtue of the sensitivity of trabecular bone to the magnitude and direction of biomechanical stresses, such bone provides a record of the loads sustained by an individual. A sample of australopithecine pelvises from southern Africa lack the distinctive human trabecular bundles, suggesting that the early hominid bipedal gait was not entirely like that of modern humans. Pelvic remains of *Oreopithecus* show more well-developed trabecular bundles than do those of extant apes. This evidence is compatible with some form of bipedal postural and locomotor support.

Imaging technology and computer-assisted methods have developed rapidly in recent years, leading Christoph Zollikofer and Marcia Ponce de Leon to offer a synthesis of currently available methods and potential applications in paleoanthropology.⁶ Among these are promising new methods for noninvasive fossil preparation and reconstructions. Possibilities for morphometric analyses are limited only by the imagination; for example, one can create contour maps of cranial vault thickness and examine the volumes and shapes of internal structures and spaces such as the frontal sinus.

Two papers focused on heterochrony in hominoid evolution. Brian Shea reviewed fundamental heterochronic theory, presenting illustrative cranial and postcranial examples of heterochronic change between both sexes and species of modern hominoids. He argued that the pygmy chimpanzee and *Oreopithecus* may be examples of neotenic reduction in facial morphology, perhaps related to a decrease in sexual dimorphism. Heterochronic approaches clearly have value in assessing character covariation and proportional changes in size (allometry) that are important in phylogenetic decisions and, more generally, understanding interspecific morphological differences.

D. M. Alba, S. Moya-Sola, M. Kohler, and L. Rook examined the craniofacial anatomy of *Oreopithecus* from a heterochronic perspective and concurred that *Oreopithecus* has a neo-

tenous cranial form. Relative to its putative ancestor *Dryopithecus*, *Oreopithecus* has a paedomorphic cranium with a rounded braincase and an anteriorly positioned zygomatic root. This example underscores the need for phylogenetic analyses to incorporate a heterochronic approach to provide better understanding of character interdependence.

The final three papers concerned Eurasian faunal biogeography. L. Gabunia, D. Lordkipanidze, and A. Vekua discussed the paleobiological significance of the relatively poorly known *Udabnopithecus garedjensis* from lower Turolian sediments (MN11, roughly 8.5 Mya) of eastern Georgia.⁷ The only known fossil of *Udabnopithecus* is a right maxillary fragment containing two worn teeth (P4-M1) that most closely resemble those of *Dryopithecus*. This may be one of the latest known appearances of Dryopithecines and extends their geographic range.

The last two papers investigated large-scale paleobiogeographic patterns of Eurasian Neogene faunas, but using very different approaches. Mikael Fortelius and Arja Hokkannen employed their Neogene Old World mammal database to examine spatio-temporal distribution and changes in the trophic structure of mammalian communities of western Eurasia during the mid-late Miocene. This publicly available database currently consists of 776 species and 450 localities, with 37 hominoid and 28 cercopithecoïd localities. Among a host of inter-

esting trends, Fortelius and Hokkannen suggested that mammalian migrations appear to have occurred in an east-west direction. Primates depart from the pattern and disappear from the north by 9 Mya. However, Fortelius and Hokkannen cautioned that this result may be influenced by sampling bias.

David Begun applied a cladistic approach to the problem of hominoid biogeography, taking advantage of the fact that a given set of relationships implies a set of likely migration events. In his presentation, Begun⁸ suggested that the ancestor of the true hominoids (a monophyletic group including the ancestor of living apes and their fossil relatives) migrated out of Africa around MN5/6 (~16–14Mya) and that the ancestor of African apes and humans migrated back into Africa around MN8–11 (~12–8Mya). Drawing on postcranial and craniodental evidence, Begun argued that *Ouranopithecus* and *Dryopithecus* are likely to be the closest known sister taxa of the African ape and human clade, and suggested this clade most parsimoniously originated in Europe.

Workshops such as this one are useful in assessing progress in the field of hominoid evolution. From the diversity of research topics presented, as well as from open discussions within the workshop, it was clear that studies of hominoid evolution have moved well beyond the descriptive stage and have begun drawing on powerful analytical methods. Now seems to be the

time to focus energies on developing methods to integrate ontogenetic, biomechanical, and systematic studies to arrive at more secure phylogenetic hypotheses that ultimately will lead to a better understanding of the evolutionary history of apes and humans.

REFERENCES

- 1 Koufos GD. 1993. A mandible of *Ouranopithecus macedoniensis* from a new late Miocene locality of Macedonia (Greece). *Am J Phys Anthropol* 91:225–234.
- 2 de Bonis L, Bouvrain G, Geraads D, Melentis J. 1974. Première découverte d'un primate hominoïde dans le Miocène supérieur de Macédoine (Grèce). *CR Acad Sci Paris, ser. D* 278:3063–3066.
- 3 de Bonis L, Bouvrain G, Geraads D, Koufos G. 1990. New hominoid skull material from the late Miocene of Macedonia in Northern Greece. *Nature* 345:712–714.
- 4 Alpagut B, Andrews P, Fortelius M, Kappelman J, Temizsoy I, Celebi H, Lindsay W. 1996. A new specimen of *Ankarapithecus meteai* from the Sinap Formation of central Anatolia. *Nature* 382:349–351.
- 5 Larson SG. 1998. Parallel evolution in the hominoid trunk and forelimb. *Evol Anthropol* 6:87–99.
- 6 Zollikofer CPE, Ponce de Leon MS, Martin RD. 1998. Computer-assisted paleoanthropology. *Evol Anthropol* 6:41–54.
- 7 Burtshak-Abramovitsch NO, Gabachvili EG. 1945. Anthropoid ape from the upper Tertiary deposits of eastern Georgia. *Comm Acad Nat Georgia* 6.
- 8 Begun DR, Ward CV, Rose MD. 1997. Function, phylogeny, and fossils: miocene hominoid evolution and adaptations. New York: Plenum Press.

Brian G. Richmond
Department of Anthropology
George Washington University
2110 G. St., NW
Washington, DC 20052
© 1999 Wiley-Liss, Inc.

