The dietary adaptations of European Miocene catarrhines

(Hominoidea/Pliopithecidae/dietary evolution)

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ABSTRACT   European Miocene "apes" have been known for nearly a century and a half but their phylogenetic significance is only now becoming apparent with the recent discovery of many relatively complete remains. Some appear to be close in time and morphology to the last common ancestor of modern great apes and humans. The current study is an attempt to reconstruct the diets of these fossils on the basis of quantitative data. Results suggest that these primates varied more greatly in their diets than modern apes, with adaptations ranging from hard-object feeding to soft-object frugivory to folivory.

Ape-like primates from the middle and late Miocene of Europe have been known for more than a century (1, 2) and new finds continue to improve the record of these important taxa. A substantial diversity of European primates are now known. These include the hominoids *Dryopithecus*, *Oreopithecus*, and *Ouranopithecus*, some known since the middle of the 19th century but better documented since the 1970s with many finds from Greece, Spain, Hungary, and Italy. Recent proposals suggest that *Dryopithecus* or *Ouranopithecus* may be a sister group to all extant great apes (3, 4), "African" apes (5), or even hominids (6). The phylogenetic position of *Oreopithecus* remains enigmatic, but recent opinion suggests it to be a hominoid with a highly derived dentition (7). Small-bodied forms, the Pliopithecidae—with two subfamilies, crouzelines and pliopithecines—likewise known for more than a century, also are represented by many newly discovered remains. They most likely represent a primitive sister group to all living catarrhines (Old World monkeys, gibbons, great apes, and humans).

Here we reconstruct the diets of European Miocene hominoids and pliopithecids by analysis of molar shearing-crest development. Results suggest that these primates showed a wider range of dietary adaptation than modern apes that probably included hard-object feeding, soft-object frugivory, and folivory.

Several researchers have demonstrated a relationship between diet and the development of shearing blades on molar teeth of living catarrhines (8–11). Folivorous apes, for example, show relatively longer shearing crests than do frugivorous ones because leaf fibers form resistant, almost two-dimensional sheets and rods more easily broken by shearing than by crushing, whereas frugivores consume more crushable three-dimensional fruits. In this study we use this relationship between crest development and diet in living hominoids to infer trophic adaptations in the Miocene European taxa, using methods similar to those of previous studies (12–15).

Original specimens or high-resolution replicas representing 10 species of living hominoids and 7 Miocene taxa were examined. The fossils represent all available European hominoids and pliopithecids with unworn or nearly unworn lower second molars (M_2s) (Table 1). Extant hominoids were used as

Table 1. Fossil specimens used in this analysis

Specimen	Taxon	MN*	Location of recovery
Pliopithecidae			
RUD 89	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 91	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 98	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 100	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 106	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 108	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 122	*Anapithecus hernyaki*	9	Rudabánya, Hungary
RUD 128	*Anapithecus hernyaki*	9	Rudabánya, Hungary
OE 303	*Pliopithecus platydon*	6	Göriach, Austria
IPS Plio 1	*Pliopithecus* sp.	8	Castell de Barbera, Spain
IPS Plio 2	*Pliopithecus* sp.	8	Castell de Barbera, Spain
Hominoidea			
Type	*Dryopithecus fontani*	8	St. Gaudens, France
IPS 1782	*Dryopithecus laietanus*	9	Can Llobateres, Spain
IPS 1796	*Dryopithecus laietanus*	9	Can Llobateres, Spain
IPS 1797	*Dryopithecus laietanus*	9	Can Llobateres, Spain
IPS 9001	*Dryopithecus laietanus*	9	Can Llobateres, Spain
IPS 1808	*Dryopithecus laietanus*	10	La Tarumba I, Spain
IGF 4335	*Oreopithecus bambolii*	12	Monte Bamboli, Italy
IGF 11778	*Oreopithecus bambolii*	11	Baccinello, Italy
RPL 54	*Ouranopithecus macedoniensis*	10	Ravin de la Pluie, Greece
RPL 75	*Ouranopithecus macedoniensis*	10	Ravin de la Pluie, Greece

*MN numbers refer to the biostratigraphic scale of Neogene Mediterranean mammals (16). Museum identifications: RUD, Magyar Geologiai Szolgalat, Budapest, Hungary; IPS, El Institut de Paleontologia "Miquel Crusafont" de Sabadell, Spain; IGF, Istituto e Museo di Geologia e Paleontologia dell'Università di Firenze; RPL, Aristotle University of Thessaloniki, Greece; OE, Naturhistorisches Museum Basel (examined at Anthropologisches Institut und Museum der Universität Zürich-Irchel).

a baseline for interpretation of relative crest lengths in the fossils because living apes are conservative in their molar morphology (14). Extant species examined include 8 frugivorous taxa and 2 that eat substantial amounts of leaves (Table 2).

The mesiodistal lengths of the occlusal surfaces and shearing crests 1–8 were measured on unworn or nearly unworn M_2s by following previous protocols (8, 12, 17) (Table 2). Data were log-transformed, and a least-squares regression line was fit to the frugivorous extant species with M_2 length as the independent variable and total crest length as the dependent variable. We used frugivorous species alone to control for allometric changes in animals with similar adaptations (18). Deviations from the frugivore regression are expressed as shearing quotients (SQs), measures of differences between the observed and "expected" shearing crest lengths. A positive SQ indicates relatively long shearing crests compared with the typical frugivorous extant

Abbreviations: M_2, lower second molar; SQ, shearing quotient.

Table 2. Shearing-crest descriptive statistics

Species	n	M₂ length, mm Mean	SD	T_shear, mm Mean	SD
Extant					
*Pongo pygmaeus**	5	12.77	0.92	28.98	1.92
*Pan troglodytes**	10	11.68	1.05	24.74	1.84
*Pan paniscus**	11	9.90	0.35	21.50	1.06
Gorilla gorilla	14	18.25	1.74	41.95	3.66
*Hylobates lar**	5	5.85	0.34	13.64	1.60
*Hylobates agilis**	5	6.53	0.19	14.72	1.55
*Hylobates klossii**	5	5.85	0.34	12.96	0.71
*Hylobates moloch**	5	6.32	0.63	14.06	1.14
*Hylobates hoolock**	5	7.70	0.32	17.71	1.32
Hylobates syndactylus	6	8.71	0.63	20.49	1.30
Miocene					
Anapithecus hernyaki	8	8.70	0.34	19.48	0.55
Dryopithecus fontani	1	11.38	—	25.38	—
Dryopithecus laietanus	5	10.50	0.39	22.94	0.94
Oreopithecus bambolii	2	9.88	—	29.53	—
Ouranopithecus macedoniensis	2	15.94	—	31.69	—
Pliopithecus sp. (Spain)	2	6.00	—	14.53	—
Pliopithecus platydon	1	7.94	—	16.88	—

Means and standard deviations are provided for M₂ occlusal surface mesiodistal diameter and summed lengths of shearing crests 1–8 (T_shear) (see text for details). Dietary data for living species have been summarized (13). Taxa marked with an asterisk were used in computing the shearing-crest regression equation. Other extant species (i.e., *Hylobates syndactylus*, and *Gorilla gorilla*) are considered more folivorous.

ape; a negative SQ denotes less crest development. SQs for living and fossil taxa are summarized in Fig. 1.

More folivorous extant apes (siamang and gorilla) show the highest SQs, indicating that these species have better developed shearing crests than do frugivorous taxa. Further, orangutans consume more leaves than other frugivores examined and show a higher SQ than these species. This confirms that shearing-crest development accurately tracks diet in living hominoids. Similar results are evident when other groups of extant primates are considered (8, 9, 15).

Some researchers (19) identify differences in shearing-crest development (and infer dietary differences) between pliopithecid subfamilies Crouzelinae and Pliopithecinae, but others suggest that pliopithecids in general had a more folivorous diet (20). Our results show that SQs for the pliopithecids exceed the range for extant hominoids, implying substantial dietary heterogeneity. Spanish and Austrian *Pliopithecus* specimens show respectively higher and lower SQs than any living ape. While *Pliopithecus* from Spain is likely to have been extremely folivorous, *P. platydon* may have been more frugivorous than the other pliopithecids. *Anapithecus hernyaki* was evidently intermediate between the *Pliopithecus* species.

Among the fossil hominoids, *Oreopithecus bambolii* has a higher mean SQ than has any extant hominoid suggesting an extremely specialized folivorous diet. In contrast, *Ouranopithecus macedoniensis* has a lower SQ than has any living ape (Figs. 1 and 2). Because hard-object feeding primates show lower SQ values than closely related soft-fruit specialists (15), *O. macedoniensis* may have habitually consumed harder food items than did other European Miocene apes. Its remarkably thick dental enamel is consistent with this notion (21). *Dryopithecus fontani* and *Dryopithecus laietanus* have shearing crests similar to extant frugivorous gibbons and chimpanzees, suggesting a softer fruit diet lacking specializations for either hard-object feeding or extreme folivory.
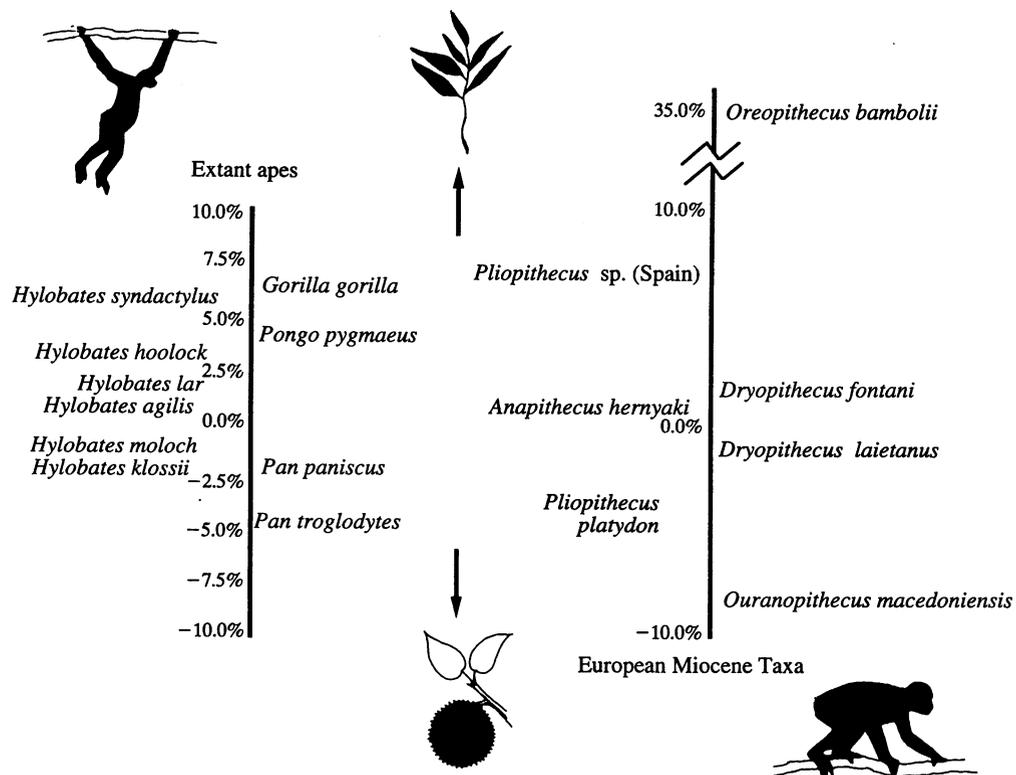

FIG. 1. SQs of Miocene apes and living hominoids compared. "Expected" shearing-crest lengths are computed from the M₂ mesiodistal diameters for all taxa by using the regression equation for the frugivorous living apes: $\log_{10}$ SE $= 0.959 \log_{10}$ M₂ length $+ 0.386$, where SE is the expected summed shearing-crest length for a given M₂ length. SQs express the difference between the observed and expected shearing-crest lengths as $100 \times$ (observed $-$ expected)/expected. A positive SQ value indicates relatively long shearing crests compared with that of the average frugivorous extant ape, whereas a negative SQ value denotes less crest development.
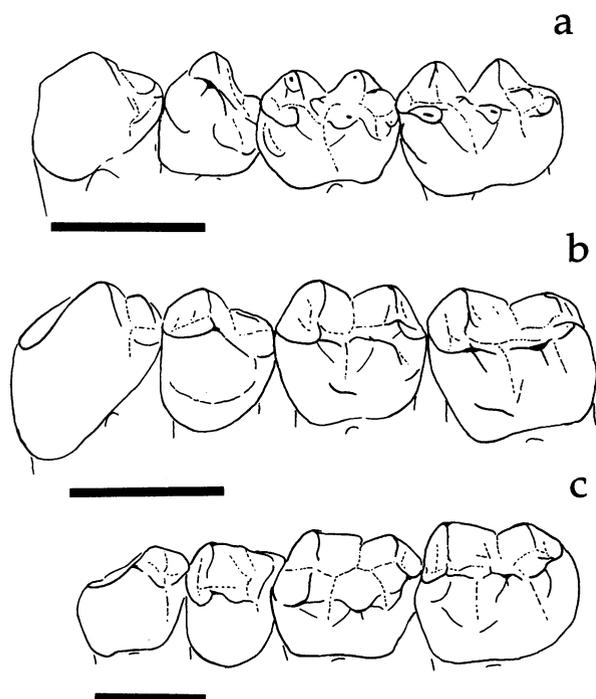
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FIG. 2. Occlusolateral views of the right lower third premolar (P3) through M2 of *Oreopithecus bambolii* (IGF 11778) (*a*), *Dryopithecus fontani* (type) (*b*), and *Ouranopithecus macedoniensis* (RPL 54) (*c*) exemplifying the differing degree of development of shearing crests, as reflected in the SQs in Fig. 1. (Bars = 2 cm.)

In sum then, this study provides a glimpse of the remarkable variation that probably characterized the diets of middle and late Miocene catarrhines in Europe. Our data suggest that these taxa exhibited an even broader range of dietary adaptations than their modern counterparts. To find a suitable modern analog for *Ouranopithecus*, we may have to include hard-object-feeding platyrrhines from South America and perhaps even consider analogies with forest-dwelling peccaries (22). At the other extreme, the best modern diet analogs for *Pliopithecus* from Spain and *Oreopithecus* may be colobines and howler monkeys (15, 23). Perhaps extant apes have experienced trophic restriction compared with their middle and late Miocene European counterparts as a consequence of the modern taxa being in competition with Old World monkeys (24), a group that is not found in sympatry with European Miocene hominoids. Other factors likely to affect niche diversity include a greater possible range of habitats, especially open country for *Ouranopithecus*, in which European Miocene primates lived (25).

A reconstruction of the dietary adaptations of late Miocene hominoids from Europe is especially important given that most authors now agree that two of these forms, *Dryopithecus* and *Ouranopithecus*, possess morphological characteristics suggesting that they are close to the divergence of modern great apes. The precise phylogenetic position of these taxa with respect to that split is, however, a matter of some debate, with inferences of phylogenetic affinities ranging from basal great ape to hominid ancestor (3–6, 26–28). Given that our data indicate

that European Miocene hominoids show substantial dental variation as a probable consequence of trophic specialization, it may be well to ask whether the adaptive dietary signal may confound phylogenetic analyses.

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