

# Late Pliocene Faunal Turnover in the Turkana Basin, Kenya and Ethiopia

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Analysis of a large sample of well-dated fossil mammals from localities in the Turkana Basin of Kenya and Ethiopia revealed sampling biases that affect patterns of faunal turnover during the late Pliocene. When these biases were accounted for, results indicated that 58 to 77 percent of the mammal species were replaced between 3.0 and 1.8 million years ago (Ma). Overall diversity increased from 3.0 to 2.0 Ma but then declined. No distinct turnover pulse is seen between 2.8 and 2.5 Ma; instead, the most significant period of faunal change began after 2.5 Ma and continued through 1.8 Ma.

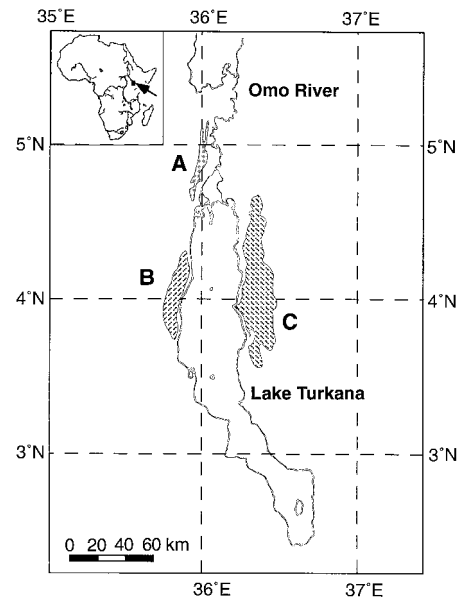
A major biotic turnover event for African land mammals has been proposed for the time interval from 2.8 to 2.5 Ma and linked to a global change toward cooler, drier, and more variable climates associated with the onset of Northern Hemisphere glaciation (1–6). The late Pliocene radiation of hominid species and the emergence of the genus *Homo* have also been attributed to global climate forcing (2, 4, 5, 7). The African turnover event can be viewed as part of a broader “turnover pulse” hypothesis, in which climate change results in brief periods of significant evolutionary change (1–4, 8). In this article, we provide evidence that faunal turnover between 2.5 and 1.8 Ma was a prolonged rather than pulsed response to late Pliocene climate change in East Africa.

Central issues in demonstrating climate forcing in the geological record are (i) whether observed changes in faunas or floras can be linked to climate change and (ii) whether information from the preserved organisms is sufficient to allow biological signals coincident with climate change to be distinguished from sampling biases. Previous studies of late Pliocene faunal change in Africa have focused on individual groups such as bovids (1–4), suids (9, 10), equids (11), cercopithecids (12), and hominids (4, 9) or provided multilineage overviews (13, 14) with biostratigraphic range data of varying quality and resolution for the continent as a whole. Here, we use the published records of all mammal groups from one African late Pliocene basin to separate sampling biases from original biological signals

and to examine evolutionary patterns in relation to climate change.

**The Turkana Basin fauna.** We focused our study on the Turkana Basin because the Pliocene-Pleistocene strata there are well dated and highly fossiliferous and the timing of faunal change elsewhere in Africa has been correlated to these strata (4, 14–17). We compiled and analyzed a data set consisting of 425 referenced fossil localities from three regions in the northern Turkana Basin from 4.4 to 0 Ma. This data set provides 3574 records of fossil mammal occurrences based on over 10,000 specimens (Fig. 1 and Table 1), representing 246 named taxa (18).

The three regions in the Turkana Basin are the Omo Valley, Ethiopia (Shungura Formation); East Turkana, Kenya (Koobi Fora Formation); and West Turkana, Kenya (Nachukui Formation) (Fig. 1 and Table 1). The geochronology of these deposits is primarily based on radiometric dates on volcanic strata that mark the boundaries between stratigraphic members or submembers. The conservative estimate of maximum and minimum ages for fossil localities is the same as for the stratigraphic member or submember in which they occur, and these dates provide the first appearance datums



**Fig. 1.** Map showing the Turkana Basin and the locations of the three major fossil producing formations spanning the late Pliocene (3.0 to 1.8 Ma). A, Omo Valley; B, West Turkana; and C, East Turkana. The paleo-Omo River was a major agent of deposition in all three areas during much of this interval (16, 17, 41).

(FADs) and last appearance datums (LADs) used in this article (19). The only exception is the fossiliferous portion of the upper Burgi Member of East Turkana, which lies unconformably above a major erosion surface and thus is likely to be significantly younger than the Lokalalei Tuff (dated at 2.52 Ma) at the boundary between the upper and lower Burgi members (15). The upper Burgi fauna is generally accepted as close to, if not slightly younger than, 2.0 Ma (20), and we use a maximum date of 2.0 Ma for this fauna.

In our analysis, it was necessary to decide how to use published identifications (21–27) of the mammal taxa to create range charts that could be analyzed for sampling biases. Most of the named taxa provide adequate range information at the species level, but for some we used the generic level. For example, the range for *Potomo-*

**Table 1.** Summary results for the northern Turkana Basin data set, which consists of 3574 mammal records from localities dated between 4.4 and 0.0 Ma. This data set includes faunal data from all localities that can be assigned to stratigraphic members on the basis of published information for this time interval. The number of specimens (NISP) includes a minimum estimate of 1 for locality records that otherwise included no data on number of specimens.

Region	Total number of localities	Percentage in basin	Total NISP	Percentage in basin
Omo Valley, Ethiopia	254	60	5,218	52
East Turkana, Kenya	120	28	3,731	37
West Turkana, Kenya	51	12	1,173	12
Total	425		10,092	

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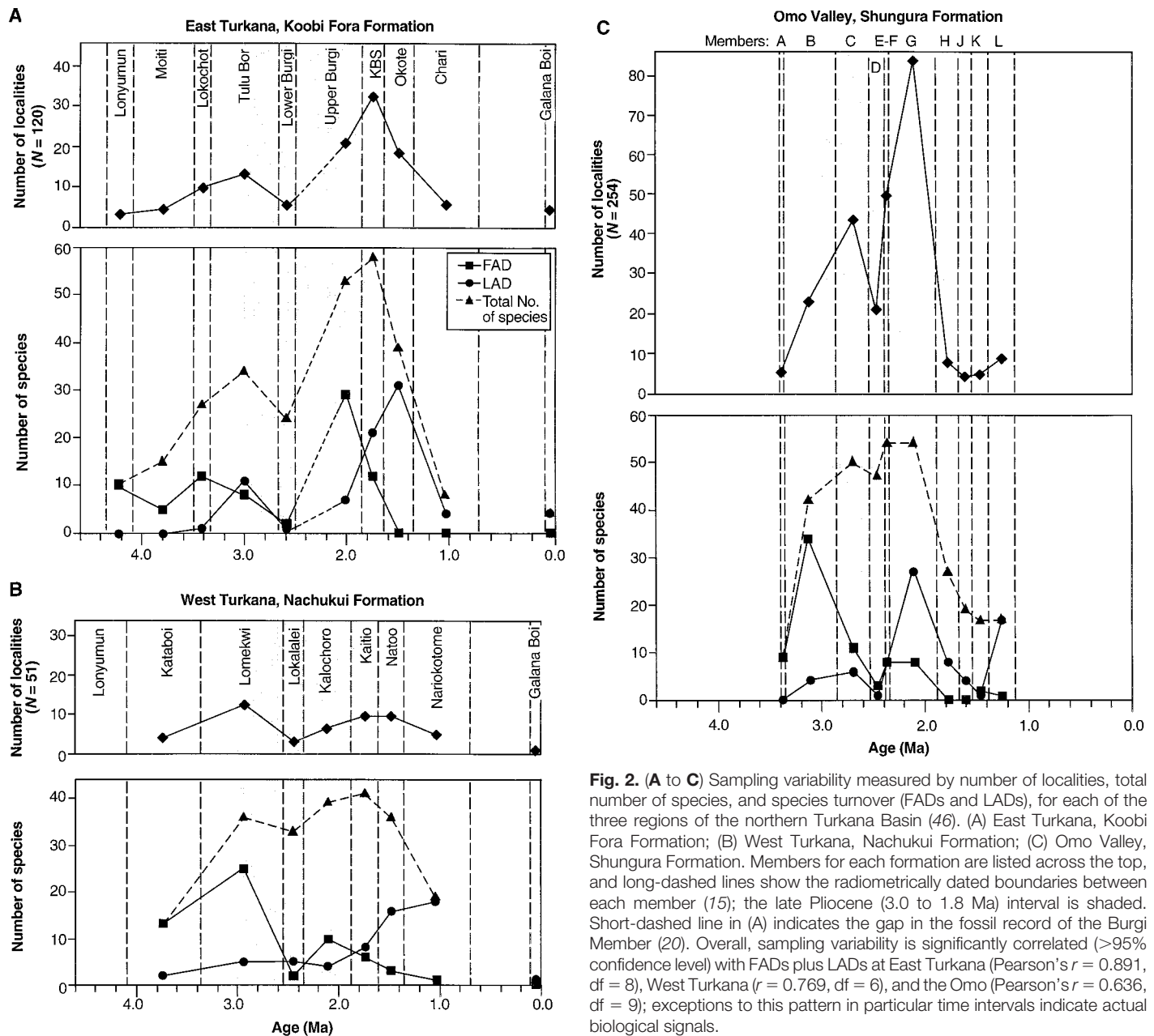
*choerus* sp. combines *P. porcus* (three localities at East Turkana, dated from 4.35 to 2.68 Ma) and *Potomochoerus* sp. (two localities at West Turkana, dated from 3.36 to 1.6 Ma). This approach thus combines some taxa that might be recognized as distinct but results in better documented ranges that permit more comprehensive analysis of sampling biases.

To establish outside limits on the number of appearances and extinctions in the Turkana Basin record, we adopted an approach that provided "maximized" and "minimized" estimates of turnover (28) based on criteria for deciding which taxa to retain, combine, or eliminate from the analysis. The maximizing approach yielded 144

taxa, and the minimizing approach reduced the sample to 74 taxa. Stratigraphic ranges were plotted for both data sets, and the number of FADs, LADs, and total species were counted for specified intervals (29).

Sampling variability can have serious effects on inferred patterns of faunal turnover (4, 8, 9, 30, 31). We looked for times when the number of FADs and LADs was not correlated with this variability as evidence for actual biological turnover or lack of turnover. For the Turkana Basin sequence, the number of localities per time unit (referred to subsequently as "fossil abundance") can be used as a measure of sampling variability (32). When the different regions of the Turkana Basin are examined

separately, this measure of sampling is correlated significantly with faunal turnover (Fig. 2). Changes from low to high fossil abundance coincide with FAD peaks in the Lokochot and upper Burgi members (about 3.4 and 2.0 Ma) in the East Turkana record, in the Lomekwi and Kalachoro members (about 3.0 and 2.1 Ma) in the West Turkana record, and in Members B and E-F (about 3.1 and 2.4 Ma) in the Omo record. Likewise, high followed by low fossil abundance coincides with LAD peaks in the Tulu Bor and Okote members (about 3.0 and 1.5 Ma) at East Turkana and in Member G (about 2.1 Ma) at Omo. Because of these correlations, we cannot rule out that sampling variability, rather than a biological



**Fig. 2. (A to C)** Sampling variability measured by number of localities, total number of species, and species turnover (FADs and LADs), for each of the three regions of the northern Turkana Basin (46). (A) East Turkana, Koobi Fora Formation; (B) West Turkana, Nachukui Formation; (C) Omo Valley, Shungura Formation. Members for each formation are listed across the top, and long-dashed lines show the radiometrically dated boundaries between each member (15); the late Pliocene (3.0 to 1.8 Ma) interval is shaded. Short-dashed line in (A) indicates the gap in the fossil record of the Burgi Member (20). Overall, sampling variability is significantly correlated (>95% confidence level) with FADs plus LADs at East Turkana (Pearson's  $r = 0.891$ ,  $df = 8$ ), West Turkana ( $r = 0.769$ ,  $df = 6$ ), and the Omo (Pearson's  $r = 0.636$ ,  $df = 9$ ); exceptions to this pattern in particular time intervals indicate actual biological signals.

cally mediated increase or decrease in species, is responsible for the turnover peaks. However, in the Omo record, the number of FADs per member is relatively constant from 3.0 to 2.0 Ma (with the exception of Member D) in spite of the wide fluctuations in the sample sizes, indicating a consistent level of faunal turnover throughout this interval. In the East Turkana record, the overall increase in number of species could result primarily from increased fossil abundance up to about 2.0 Ma, but between 2.0 and about 1.8 Ma, continued high productivity in the KBS Member accompanied by decreased FADs and increased LADs indicates a period of real faunal turnover. This turnover is also evident between about 2.1 and 1.8 Ma at West Turkana.

When the data for each region were combined in 200,000-year intervals, the effects of uneven sampling were reduced but not eliminated (Figs. 3 and 4). For the interval between 3.3 and 1.5 Ma, which is relatively well sampled with >15 localities per 200,000-year interval, there is no overall correlation between fossil abundance and total FADs plus LADs for either the maximizing or minimizing approach (Fig. 4), indicating that the turnover pattern represents a biological signal rather than sampling variability. However, the marked increase in fossil abundance between 2.5 and 2.1 Ma, which reflects increased numbers of

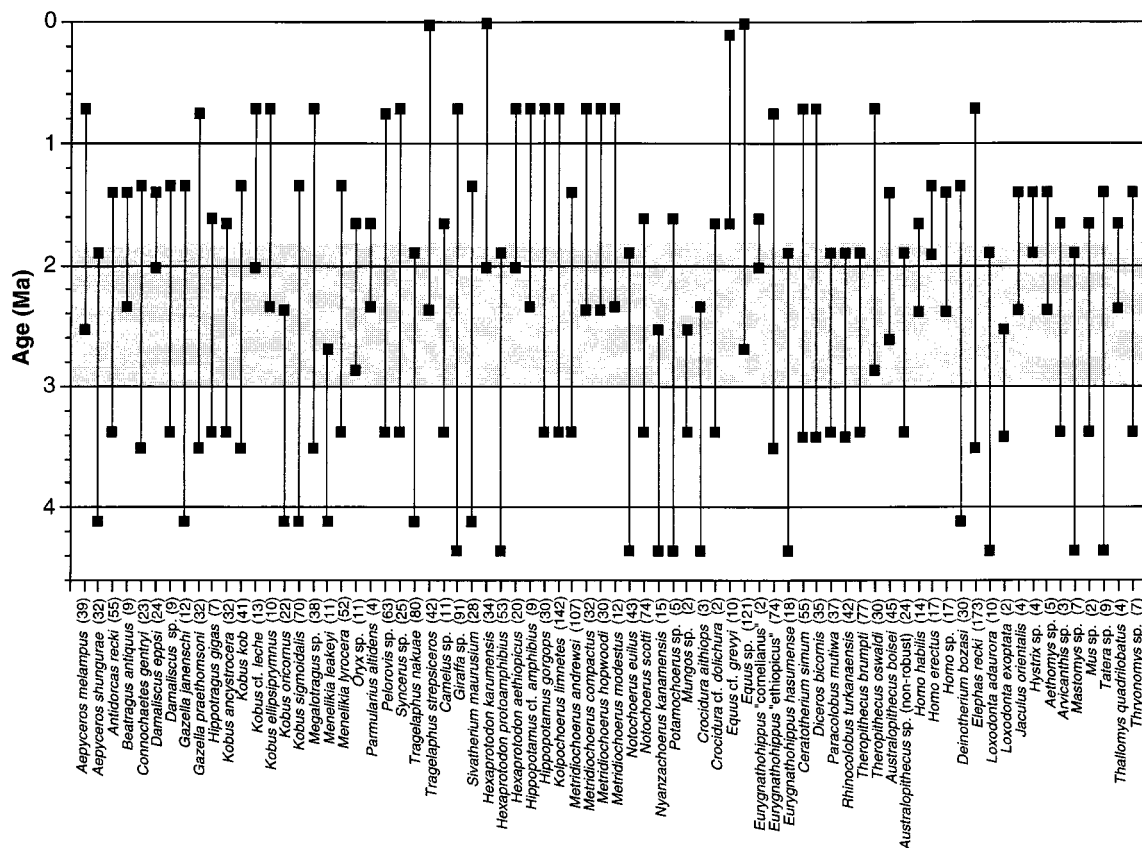
localities from Omo Members E through G, corresponds to the peaks in FADs and LADs between 2.4 and 2.2 Ma (Figs. 2C and 4), and it is not possible to resolve a finer scale pattern of biological turnover because of this sampling effect.

**Patterns of fauna change.** Vrba (4, 8) has specified criteria for testing the turnover pulse hypothesis that can be applied to the African fauna, including (i) significant and synchronous increases in the number of FADs and LADs of species, with the existence of a turnover pulse determined by a statistically significant change in the turnover rate during a specified, relatively short time interval between 2.8 and 2.5 Ma; (ii) concurrent increase in turnover rate across different taxonomic groups; (iii) differential timing of turnover depending on ecological tolerances of the group(s); and (iv) correspondence in time with independently documented environmental change, that is, the onset of Northern Hemisphere glaciation.

The Turkana Basin data show that although significant species turnover occurred during the 3.0- to 1.8-Ma interval, there is no marked pulse affecting different taxonomic groups between 2.8 and 2.5 Ma. The highest turnover [represented here as (FADs + LADs/total number of species) × 100 (%)] for any 200,000-year interval between 3.0 and 1.8 Ma is 24 to 32% for the interval from 2.4 to 2.2 Ma (the range is for

the minimizing versus maximizing approaches, respectively) and 19 to 28% for the interval from 2.0 to 1.8 Ma. The change in turnover is significant between 2.5 and 2.1 Ma but not between 2.9 and 2.5 Ma (Fig. 5). The peak in turnover between 2.4 and 2.2 Ma is about 15% above that of the previous interval (based on the increase relative to the total number of species in each interval for both approaches) (Fig. 5). However, because of the sharp increase in fossil abundance (Fig. 4), species appearances that may have occurred before 2.2 and 2.4 Ma were concentrated in this interval, and it is not possible to distinguish the pattern of faunal change from this sampling bias for the interval from 2.5 to 2.1 Ma. This sampling effect may also extend before 2.5 Ma and include species that actually appeared between 2.8 and 2.5 Ma (4), but the pattern of relative faunal stability in the well-sampled Omo fauna (Fig. 2C) as well in the combined data (Fig. 4) indicates no major turnover event between 3.0 and 2.5 Ma. Between about 2.1 and 1.7 Ma, during a period of continuing high fossil productivity, the pattern of FADs and LADs provides evidence for accelerated faunal turnover. The duration of this period of increased turnover is uncertain because of the sharp drop-off in fossil abundance after 1.7 Ma.

From 3.0 to 2.0 Ma, total species turn-



**Fig. 3.** Species range chart for the northern Turkana Basin fauna, based on the minimizing approach (see text) (28, 47) and organized alphabetically by order and then by family and genus. The late Pliocene time interval (3.0 to 1.8 Ma) is shaded. Numbers after the species names are the total number of localities at which the species was recorded. Tabular data for both the minimizing and maximizing approaches are available at [etweb.lscf.uscb.edu](http://etweb.lscf.uscb.edu) and [www.sciencemag.org/feature/data/973775.shl](http://www.sciencemag.org/feature/data/973775.shl)

over was between 41 and 59% (minimizing and maximizing approaches, respectively) (Fig. 4 and Table 2). This rate is similar to the estimate of about 42%/Ma for North American Pliocene-Pleistocene mammals (31). First appearances represent 82% of the total turnover in the minimizing approach, and total diversity increases by about 35%, from 48 species before 3.0 Ma to 65 species at 2.0 Ma. This increase represents the addition of 23 species in seven different families and the loss of 5 species in four families (Table 2). Most of this change appears to have occurred from 2.5 to 2.0 Ma. At the end of the Pliocene, between 2.0 and 1.8 Ma, the rate of turnover per 200,000-year interval increased, and disappearances outnumbered appearances. Thus, overall, FADs increased between 2.5 and 2.0 Ma, leading to higher species diversity, followed by a period of turnover with low FADs and increased LADs resulting in a diversity decline by 1.8 Ma.

Vrba (4) has suggested that responses to environmental change toward cooler and drier climatic conditions from 2.8 to 2.5 Ma promoted more open habitats in tropical Africa and led to a turnover pulse repre-

sented in the records of the Bovidae, Rodentia, and Homnidae. A number of bovid species (8 out of a total of 25 in the minimizing approach and 17 out of 46 in the maximizing approach) appeared between 3 and 2 Ma in the Turkana Basin, but these appearances were not clustered between 2.8 and 2.5 Ma (Fig. 3). The bovid tribes Antilopini and Alcelaphini are generally regarded as indicative of open habitats, and their increase has been used as an index of vegetational change toward grasslands (1, 2). The maximizing approach includes 15 species in these two tribes; 7 have FADs between 3 and 2 Ma, and 5 of these appear between 2.5 and 2.0 Ma. The minimizing approach includes nine species in these groups, with three FADs, all between 2.5 and 2.0 Ma (Fig. 3). The presence of dry or open (or both) habitats is indicated by a number of species that originated before 3 Ma and survived through 2 Ma, such as the antilopines *Gazella praethomsoni* and *G. janenschii*, as well as the alcelaphine genera *Connochaetes* and *Damaliscus* (1, 33). The range data for these two bovid tribes indicate that open or dry (or both) habitats provided opportunities for new species throughout the

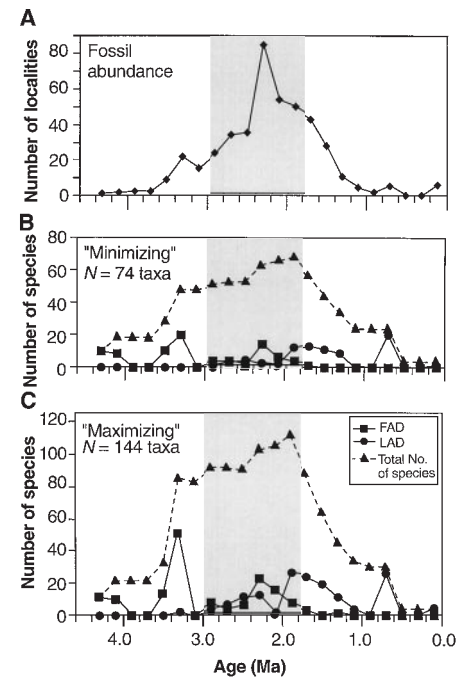
interval from 3 to 2 Ma and support the hypothesis that ecological change was prolonged in the Turkana Basin.

The persistence of woodland to forest species from 3 to 2 Ma provides further evidence of stability in some parts of the ecosystem. Primate species requiring arboreal substrates in woodlands or forests, such as *Paracolobus mutiwa* and *Rhinocolobus turkanaensis* (34), were present from about 3.4 to 1.9 Ma. The extinct baboon *Theropithecus* was abundant in the basin, and *Theropithecus brumpti*, which was associated with woodland habitats, appeared at 3.4 and disappeared at about 2.0 Ma (35). *Tragelaphus strepsiceros* (greater kudu), which today prefers woodland and bush habitats, appeared between 2.5 and 2.3 Ma and was present at many localities in all three regions.

In the northern Turkana Basin, the

**Table 2.** Summary of late Pliocene faunal turnover in the northern Turkana Basin, showing overall turnover rates and species diversity for the maximizing and minimizing approaches and breakdown of species turnover and continuity in the fossil record of different mammal groups for the time interval between 3 and 2 Ma (Fig. 3) (18, 19, 28, 29, 36).

	3.0 to 2.0 Ma				Species diversity at 3.0 Ma	Species diversity at 2.0 Ma	Species diversity at 1.8 Ma
	FAD	LAD	Total number of species	Percentage of turnover FAD + LAD			
Maximizing	50	28	132	59	82	104	86
Minimizing	23	6	71	41	48	65	56
	Maximizing			Minimizing			
	FAD	LAD	Total number of species	FAD	LAD	Total number of species	
Artiodactyla							
Bovidae		17	46	8	2	25	
Camelidae	0	0	1	0	0	1	
Giraffidae	0	0	4	0	0	2	
Hippopotamidae	5	1	7	3	0	5	
Suidae	4	2	12	3	1	9	
Carnivora	3	3	8	0	1	1	
Chiroptera	0	1	1	0	0	0	
Hyracoidea	0	2	1	0	0	0	
Insectivora	0	1	2	0	1	2	
Lagomorpha	1	0	1	0	0	0	
Perissodactyla							
Chalicotheriidae	1	0	1	0	0	0	
Equidae	6	0	9	2	0	4	
Rhinocerotidae	0	1	3	0	0	2	
Primates							
Cercopithecidae	2	1	8	1	0	4	
Hominidae	5	0	6	3	0	4	
Lorisidae	0	1	1	0	0	0	
Proboscidea	1	2	5	0	1	4	
Rodentia	5	8	16	3	0	8	



**Fig. 4.** Number of localities representing fossil abundance (A) and the results of the minimizing and maximizing approaches (B and C), showing the turnover pattern through time and total numbers of species, combined for all three regions (46, 48). FAD or LAD records that fall precisely on the time lines in Fig. 3 are counted in the older interval to derive the totals plotted here. The correlation between fossil abundance and turnover between 3.3 and 1.5 Ma is not significant at the 95% confidence level [Pearson's  $r = 0.271$  (maximizing) and  $r = 0.355$  (minimizing), 9 df in both cases]. The sharp peak in (A) between 2.5 and 2.1 Ma primarily reflects an increase in fossil abundance in Members E to G in the Omo (Fig. 2C), which is centered at 2.3 Ma in this figure as a result of the method for distributing localities in 200,000-year intervals (48). Totals for FADs, LADs, and continuing taxa for each interval were counted directly from the maximizing and minimizing range charts.

record for rodents and lagomorphs is documented by 362 published specimens at only 18 localities, 13 of which are in the Omo deposits (27). Some species that indicate drier habitats, such as *Jaculus orientalis* (jerboa), *Heterocephalus atikoi* (naked mole rat), and *Lepus capensis* (Cape hare), appeared at about 2.5 Ma, but sampling of microfauna before that time is sparse (seven localities in the whole northern basin, only two of which have multiple taxa). As with the Bovidae, taxa affiliated with open or drier habitats were present before 3 Ma and persisted through 2 Ma [such as *Tatera inclusa* (large naked-soled gerbil) and *Xerus erythropus* (African ground squirrel)], but closed habitat to mesic savanna species [such as *Crociodura cf. dolichura* (white-toothed shrew) and *Thryonomys gregorianus* (cane rat)] also continued through this interval. In general, however, the microfaunal record is too incomplete to provide adequate evidence for turnover patterns in the late Pliocene.

Six hominid taxa were represented in the region from 3 to 2 Ma: *Australopithecus* (*Paranthropus*) *boisei*, *A. cf. boisei* [including *A. (P.) aethiopicus*], a "nonrobust" *Australopithecus* species less megadont than *A. boisei*, *Homo habilis*, *H. cf. habilis* (including *H. rudolfensis*), and *Homo sp.* (36). We counted all six in the maximizing approach, and, in the minimizing approach, we combined *A. cf. boisei* with *A. boisei* and *H. cf. habilis* with *H. habilis*, for a total of four taxa. Five of the six (maximizing) or three of the four (minimizing) taxa first appeared during the 3- to 2-Ma interval, with FADs for *H. habilis* and

*Homo sp.* between 2.4 and 2.2 Ma (Fig. 3). Because of the region's ecological diversity, the first appearances of *Homo* and robust australopithecines do not necessarily imply that these hominids preferred open habitats. Global (37) and regional (38, 39) climate records indicate that the period between 3 and 2 Ma was cooler and drier but was also characterized by wide environmental fluctuations. On the basis of the temporal correlation alone, it is not possible to determine whether turnover and adaptive change in hominids were a response to the overall environmental change or to the long series of high-amplitude habitat variations in the vegetational mosaic (40).

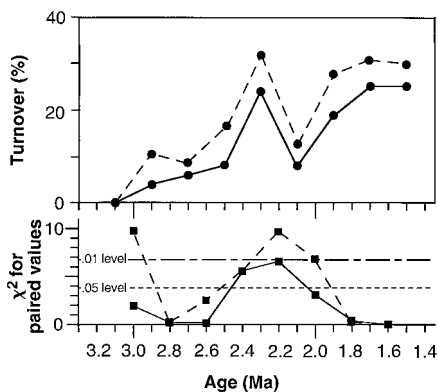
The different records of faunal turnover in the three regions of the Turkana Basin (Fig. 2) thus result from a mix of sampling effects and actual biological stasis and change. Combined records for the three parts of the basin (Figs. 4 and 5) reflect faunal change as well as the persistence of species representing a spectrum of open to closed habitats. We propose that a fluctuating but overall expansion of open habitats combined with the persistence of woodland and forest initially provided increased opportunities for mammals and led to a rise in diversity from 3.0 to 2.0 Ma, followed by a diversity decline as open habitats became more dominant at the end of the Pliocene. This two-part interval of turnover lasted about 0.7 million years.

Feibel *et al.* (41) have attributed the apparent absence of a turnover pulse around 2.5 Ma in the Turkana Basin to the effect of permanent water supplied by the ancestral Omo River, implying that riverine and lacustrine environments in the basin were buffered from continental-scale changes by regional conditions. Between 3 and 2 Ma, there were shifts in abundance within some groups of mammals within the Omo sequence (42), suggesting that habitat changes affected local populations but were not severe enough to cause their extinction. The basin included a range of habitats from forest to bushland and grassland, some of which were considerably drier than areas proximal to the paleo-Omo River (38, 41), but species representing the drier habitats do not provide evidence for a short-term turnover event. Thus, although a pulse of species turnover may have occurred elsewhere on the continent between 2.8 and 2.5 Ma, the absence of evidence for such a pulse from the best calibrated, fossil-rich deposits for this time period weakens the case for rapid climatic forcing of continent-scale ecological change and faunal turnover. Instead, our data indicate that late Pliocene evolution in East Africa was affected by the cumulative ecological con-

sequences of cooler, drier, and more variable climatic conditions rather than by a sudden change toward open habitats.

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18. We included available published information on identifications of mammals from Pliocene–Pleistocene localities of the northern Turkana Basin but excluded information on biostratigraphic ranges from other regions (we recognize that in some cases these ranges provide different FADs or LADs for Africa as a whole). Some taxonomic groups, such as the Elephantidae [N. Todd, thesis, George Washington University, Washington, DC (1997)], the Suidae (10), and the Equidae (11), are being revised, and ongoing work was incorporated where there is reference to northern Turkana Basin localities and specimens. The Evolution of Terrestrial Ecosystems (ETE) Program database is explained by J. Damuth [ETE Database Manual (ETE Consortium, Washington, DC, 1997)], and data relevant to this report are available at [eteweb.lscf.ucsb.edu](http://eteweb.lscf.ucsb.edu) and [www.sciencemag.org/feature/data/973775.shl](http://www.sciencemag.org/feature/data/973775.shl)
19. The end points of each species range were established as follows: (i) a table of taxa was constructed with the use of all northern Turkana Basin locality records in the ETE database, (ii) bounding dates for the age of a locality were transferred to the table as minimum and maximum dates for each taxonomic record, and (iii) all the records for each taxon from multiple localities were sorted, and the oldest and youngest dates were used to establish the biostratigraphic range; thus, range lines in Fig. 3 are plotted between the maximum older date for the stratigraphic member or submember of first occurrence and the minimum younger date for the member or submember of last occurrence. These dates represent the oldest date at which a taxon could have appeared and the youngest date at which it could have disappeared based on currently available information. Nearly all species have continuous records through the members in each region between their FAD and LAD; that is, there are few breaks in the biostratigraphic records based on this data set. Species first recorded in the upper, middle, or lower parts of the same member are assigned the same FAD age based on the date for the lower boundary or, for species last recorded in a member, a LAD age based on the date for the upper boundary (unless there are intermediate dated horizons within the member). We did not interpolate dates for localities on the basis of stratigraphic distance below or above dated tuffs because of the variability of sediment accumulation rates in fluvial and lacustrine deposits [P. M. Sadler, *J. Geol.* **89**, 569 (1981)] and because the deposits in



**Fig. 5.** Plot of percentage of turnover (FADs plus LADs divided by the total number of species for each interval) for the late Pliocene of the Turkana Basin for the minimizing (solid line) and maximizing (dashed line) approaches.  $\chi^2$  values for each pair of points are shown below the turnover plots, with the relative significance of changes in turnover indicated by the horizontal dashed lines. The marked peak between 2.5 and 2.1 Ma is at least partly a result of increased fossil abundance (Fig. 4), but, between 2.1 and 1.7 Ma, the pattern represents faunal turnover during a period of continuing high fossil abundance.

- the Turkana Basin have major disconformities representing significant periods of time that may not be apparent in any particular stratigraphic section (15).
20. Geological and paleomagnetic analysis shows that 120 m of lacustrine deposits below the KBS Tuff (dated at  $1.88 \pm 0.02$  Ma) and above the unconformity are normally magnetized and thus younger than the base of the Olduvai Subchron (1.91 Ma). Feibel *et al.* (15) also correlate these lacustrine deposits to the Shungura Formation in the Omo region, where lacustrine sedimentation begins around 2.0 Ma. On the basis of both lines of evidence, they place the base of the lacustrine deposits at East Turkana at 2.0 Ma, which then requires a gap on the order of 450,000 years between the upper and lower Burgi members [this interpretation was reconfirmed by C. S. Feibel (personal communication)].
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  28. The maximizing approach (Table 2) gives reasonable benefit of doubt to all published taxonomic designations and thereby maximizes the sample of ranges contributing to the analysis of faunal turnover. The maximizing approach (i) treats each named taxon with a distinct range as a separate entity but combines "Genus species" with Genus cf. species (same names) if the range of one completely includes the range of the other; (ii) includes taxa designated by tribe or genus as species "A," "B," and so forth (for example, *Kobus* sp. D, West Turkana); (iii) excludes records referred to only as "indet. sp." under a family or tribe name (for example, "indet. sp. Cercopithecidae"); (iv) retains taxa designated only as Genus "sp." if this taxon provides unique range information, even when there are other named species of the same genus; and (v) includes taxa from any of the three regions. The minimizing approach represents our conservative assessment of the actual numbers of distinct taxa. The minimizing approach (i) combines named taxa that are likely to represent the same species (for example, one range for *Connochaetes gentryi* and *Connochaetes cf. gentryi*); (ii) eliminates all taxa referred to only as "sp. nov. A"; (iii) retains taxa identified only to genus (for example, *Oryx* sp.) if it is the only occurrence of that genus or if it provides unique range information; (iv) combines records for a genus under "Genus sp." if this genus provides a unique record of the range of that genus (for example, if the genus occurs in more than one region, but none of the species do); and (v) includes only taxa that occur in more than one of the three fossiliferous regions (to reduce the effects of regional sedimentation and taphonomy on FADs and LADs). [Similar conventions for the use of taxonomic information have been described by B. Van Valkenburgh and C. Janis [in *Species Diversity in Ecological Communities*, R. E. Ricklefs and D. Schluter, Eds. (Univ. of Chicago Press, Chicago, IL, 1993), pp. 330–340], A. Turner and B. Wood (14), and J. Alroy (31).] In spite of the differences between the maximizing and minimizing approaches, both approaches show essentially the same pattern between 3.3 and 1.5 Ma; correlation between the turnover percentages was significant at the 99% confidence interval [Pearson's correlation coefficient  $r = 0.958$  with 9 degrees of freedom (df)].
  29. The range charts do not include taxa that were represented at only one locality in the Turkana Basin (amounting to 80 out of the original 246 taxa in the raw data) because a sample size of one occurrence is too small to contribute reliable information on the beginning or end of a species' range. To test whether this omission biased the analysis against FADs caused by short-lived migrations or evolutionary events connected with a turnover pulse between 2.8 and 2.5 Ma, we analyzed turnover in the subset of 80 single-locality taxa. Although there is a peak of 70% in FADs between 2.4 and 2.2 Ma (primarily the result of rare taxa occurring in Omo Members E through G), there is an even distribution of 15 to 20% FADs from 2.4 Ma back to 3 Ma. This even distribution argues against a bias affecting turnover between 2.8 and 2.5 Ma.
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  36. Taxonomic designations follow B. A. Wood [Koobi Fora Research Project, vol. IV, *Hominid Cranial Remains* (Clarendon, Oxford, UK, 1991); G. Suwa, T. D. White, and F. C. Howell *Am. J. Phys. Anthropol.* **101**, 247 (1996)]; and B. Wood *et al.* (45). Although *A. (P.) aethiopicus* and *H. rudolfensis* are represented by unusually complete crania, almost all other taxonomically identified specimens in the 3- to 2-Ma interval are fragmentary maxillae or mandibulae or isolated teeth. On the basis of the latter specimens, these two taxa cannot easily be distinguished from *A. boisei* and *H. habilis*, respectively. In the range charts used for this study, *H. rudolfensis* was thus placed in *H. cf. habilis*, and, following Wood *et al.* (45), megadont hominid specimens older than 2.3 Ma, most of which could represent *A. (P.) aethiopicus*, were placed in *A. (P.) cf. boisei*. In Table 2, *A. aethiopicus* would represent an additional LAD within the Hominidae at about 2.3 Ma, when it is replaced by *A. boisei*, if it were not included in the taxon "*A. (P.) cf. boisei*" (maximizing) or in "*A. (P.) boisei*" (minimizing) to facilitate analysis of sampling biases.
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  46. In plotting the pattern of FADs and LADs through time, we used the midpoint of each member (Fig. 2) and the midpoint of each 200,000-year interval (Fig. 4) as the most objective representation of summed data that are scattered throughout the time represented by these intervals. This convention compensates in part for the clustering of FADs and LADs at the beginnings and ends of members, which results from the use of member boundaries as estimates on species ranges. The total number of species for each member is based on counts of the continuing species plus any that appear or disappear in that member; species with a FAD and a LAD in the same member are counted once. The same method applies to the 200,000-year intervals in Fig. 4. Total turnover was calculated with the cumulative records of FADs and LADs compared with the total number of species for the entire time interval under consideration (3.0 to 1.8 Ma or 3.0 to 2.0 Ma) (Table 2).
  47. The FAD for *Equus* sp. is based on a lower first or second molar from Area 102, East Turkana, which is reported to be from "Zone C," between the Hasuma Tuff ( $2.85 \pm 0.08$  Ma) and the Lokalele Tuff ( $2.52 \pm 0.05$  Ma) [V. Eisenmann, in (24), pp. 156–214]. This early date for *Equus* disagrees with other evidence that places the FAD at about 2.3 Ma [Member G, Omo sequence (22)].
  48. Member boundaries in each area do not fall at 200,000-year intervals or at the same absolute times, and to construct the running fossil abundance totals on the basis of numbers of localities, we used the proportion of total time spanned by a member for each 200,000-year interval that it crossed. Thus, a member with 30 localities that covers 1/3 of one 200,000-year interval and 2/3 of the adjacent interval contributes 10 localities to the first and 20 to the second of these intervals. The total for each interval is then the sum of localities contributed by each of the three regions.
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