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Faunal Approaches in Early Hominin Paleoecology

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The paleoecology of early hominin species is more than simply reconstructing the habitats in which they existed. Ultimately we would like to know the ecological context before and after speciation and extinction events, and about the interactions of hominins with their environment, including other species. A first step toward this goal is to discover as much information as possible regarding the climate, geomorphology, vegetation physiognomy (habitat structure), and the faunal community. These factors build on one another such that climate, soil properties, and geomorphology are responsible for the vegetation, which, in turn, plays a fundamental role in controlling what other life forms can be supported. An understanding of extant African habitats is necessary to reconstruct ancient vegetation physiognomy for early Pliocene hominins. An appreciation of living mammals is also important in interpreting Pliocene environments when using faunal techniques. The most common data recovered with early hominins are other mammalian fossils, and these are targeted here for explaining how reconstructions of habitat and community ecology can be approached. Faunal analyses can be compared with other types of research such as palynology, fossil botanical studies, and isotopic analyses of soils and teeth to arrive at a better understanding of hominin paleoecology.

Fossil mammals found within the same deposits as early hominins can be used to answer a variety of questions relating to evolutionary paleoecology. First, fossil

mammals have been used as indicators of habitats since early paleontological studies (e.g., Ewer 1958; Brain 1967; Leakey and Harris 1987). More recent work on this topic has emphasized the importance of determining taphonomic histories before reconstructions are attempted (e.g., Behrensmeyer and Hill 1980; Brain 1981; Behrensmeyer 1991; Soligo and Andrews 2005; Andrews 2006), but this caveat is still only rarely addressed. The majority of African hominin paleoecological work falls into the category of using faunal analyses for reconstructing ancient habitats, and forms the bulk of the work reviewed here. Second, studies of contemporaneous fauna are critical for investigating aspects of community ecology, such as guild structure. This avenue of research can be also used to determine possible differences between ancient Plio-Pleistocene and extant communities (e.g., Janis et al. 2004). Third, faunal studies can give insights into how hominins might have interacted with specific members of their shared community. For example, study of the members of the carnivoran guild (Marean 1989; Lewis 1997) can lead to hypotheses about how hominins might have avoided predation or competed with predators for access to meat. Finally, faunal studies can be used to answer questions of patterns and processes in the evolution of both hominins and other mammalian lineages (e.g., Vrba 1988, 1995; Behrensmeyer et al. 1997; Potts 1998; Bonnefille et al. 2004).

Faunal approaches in hominin paleoecology can be assigned to two types of studies. The first is analyzing individual fossil species of mammals and other fauna found at particular localities. This information can be used to reconstruct habitats and to look at species interactions with hominins. It is also a critical precursor for community studies. The second type of study examines communities as a whole, which is necessary for studies of community ecology and also for investigating evolutionary patterns in hominin lineages.

A second dichotomy exists between the taxonomic and ecological/functional approaches to faunal research. In taxonomic analyses, phylogeny plays an important role. Taxonomic methodologies are used occasionally to reconstruct environments (e.g., Vrba 1980), but the usual focus using these methods is to examine biogeographic and species-turnover patterns (Behrensmeyer et al. 1997; Bobe and Eck 2001). The second approach is often referred to as taxon free because species diversity, ecological diversity, or the results of functional studies are ecological representations of each species. Damuth (1992) has argued that results derived from these types of taxon-free data transform species-specific fauna, and by extension assemblages or communities, into parameters to be incorporated into ecological patterns that can then be compared with any other faunal community in space and time since the parameters used are not taxon specific. For example, it might be difficult to compare an

Fossil Assemblages

TAXONOMIC	TAXON FREE
• Environmental reconstruction based on single species	• Ecomorphology of a single species to reconstruct diet, locomotion, or substrate use
• Environmental reconstruction based on groups of species (e.g., Bovidae)	• Groups of species in communities or guilds to reconstruct habitats using ecological diversity patterns
• Species–turnover patterns	• Groups of species compared with living communities to find community structure differences

Modern Assemblages

FIGURE 1.1. *Taxonomic and taxon-free methodologies are used to study modern and fossil assemblages.*

Australian *Macropoda* (kangaroo) to an African *Damaliscus* (topi) on a phylogenetic level, but to compare them as terrestrial grazers of similar body size is possible. Both phylogenetic and taxon-free approaches have been important in understanding hominin paleoecology as well as in developing evolutionary scenarios (Figure 1.1).

As mammal species are most often recovered in the greatest numbers from hominin fossil localities, much of our discussion is devoted to analyses of mammalian fauna. However, the results of any research using mammals should be compared with other types of analyses—such as the study of amphibian, bird, and reptile fossils; research on paleoclimate, pollen, and depositional environments; and isotopic analyses—depending on the ultimate goals of the research. In this chapter, we present a brief overview of existing African habitats and African mammal communities. We then discuss issues of taphonomy such as time-averaging, collection bias, and other factors that may bias faunal assemblages such that they obscure paleoecological reconstructions. Faunal analyses are only as good as the data derived from the fossil localities. Third, we provide an overview of the types of analyses mentioned above—those focusing on individual species and those focusing on the community from phylogenetic and taxon-free perspectives. We then survey research that has been used to investigate three areas in hominin paleoecology: reconstructing habitats, reconstructing

community ecology, and investigating species interactions between hominins and other mammals.

AFRICAN HABITATS

Reconstructing past African habitats is usually based on comparisons to extant habitats. Today, ecologists often refer to existing habitats by the dominant plant species, such as miombo woodland. Usually the best that can be accomplished for ancient vegetation, however, is to reconstruct the habitat physiognomy (structure) in which fossil hominins have been recovered. Actual plant-species identification can only be done through palynological and paleobotanical studies when these types of remains are present. Habitat structure simply refers to the architecture of the floral species—for example, forest or bushland—rather than to the actual species. Within Africa the assumption is that the fundamental architecture of past and extant habitats is similar. Habitats from different continents may be inappropriate for comparison to fossil localities in Africa because vegetation structure can be labeled the same (e.g., forests) but exhibit significant differences (Archibold 1995). For this reason, habitats that are present in Africa today are probably the best analogs (but see Andrews et al. 1979; Andrews and Humphrey 1999; Mendoza et al. 2005). Mendoza et al. (2005) have shown that terrestrial ecosystems can be separated best if placed into three categories: arid habitats with no trees, humid evergreen forests, and wooded savannas. While this is undoubtedly true, almost all of the early hominin localities in Africa would likely fall into the wooded savanna category.

Extant African habitats range from primary rain forests to deserts. The amount of rainfall, temperature, sunlight, evapotranspiration, soil type, landscape, and weather patterns/seasonality are thus indicative of these habitats, and habitats can, in return, inform on these climatic conditions. In the tropical belt, however, the seasonal pattern and the amount of rainfall are the critical determining factors of the vegetation structure (Archibold 1995). Identifying ancient habitats will thus provide limited information on these aspects of the climate.

African forests consist of tall trees with multiple canopies (White 1983). Forests need mean annual rainfall of greater than 1500 mm and/or consistent groundwater, and long wet seasons if the moisture is derived from rain. These conditions create a closed architecture. Deserts usually have stunted trees, if any, and small, succulent plants and/or bushes. The mean annual rainfall is usually less than 200 mm. Deserts have extreme seasonality, that is, long periods without rainfall. The desert habitat is open.

Every other habitat in Africa today is savanna, covering 65 percent of the continent (Archibold 1995). This does not mean that all savanna habitats are the same or that they cannot be differentiated from one another: the nature of the physiognomy depends on the amount and seasonality of rainfall. Thus, when attempting to understand human (and broader mammalian) evolution, conceptually separating savannas from other terrestrial ecosystems is better for understanding the habitats in which hominins existed, and the community relationships within the environment. Many classifications of savannas have been made, but we follow White (1983) and utilize classifications that may be meaningful in reconstructing past habitats. Savannas characteristically have grasses as ground cover and other arid-adapted plants that can survive long dry seasons. Unlike on other continents, in Africa most of the woodland trees are deciduous (Archibold 1995). This means that leaf development will occur in the wet season and leaves will fall during the driest months of the year (Hopkins 1970). This contrasts with evergreen species in which leaf production occurs in the dry season. See Table 1.1 for subdivisions of savanna habitats.

The broad-based structural definitions of habitats are often the overall biomes of particular biogeographic regions, although there may be other habitats within them (White 1983), such as the Southern Savanna Grassland of South Africa (Rautenbach 1978). Various habitat structures often occur together in mosaic patterns within regions because of changes in soil types, subterranean water, and so on. River courses and lacustrine environments cause much of the mosaicism as they provide subterranean water that alters the general habitat close to the water. Thus it is possible to have riverine forests abutting almost desertlike habitats, such as along the Awash River that travels through extremely arid environs in Ethiopia. As most regions in Africa today possess a mosaic of habitats, it is reasonable to assume that ancient habitats were likely distributed in a similar manner. In eastern Africa, where the majority of hominin fossil localities occur within lacustrine and fluvial depositional environments, the vertical facies associations observed in the stratigraphy reflect ancient horizontal landscape associations (Miall 2000). That is, types of habitats across the landscape move horizontally through time due to common channel migration, change in fluvial regime (e.g., from meandering to braided), lake transgressions and regressions, and tectonic events.

ISSUES THAT CONFOUND THE RECONSTRUCTION OF HABITATS FOR FOSSIL LOCALITIES

The success of faunal analysis is related to the accurate estimation of taphonomic processes that contributed to the resultant fossil assemblages. If these

TABLE 1.1. Modern savanna habitat descriptions. While all of these are considered to be savannas as they have grass as a ground cover, finer descriptions better describe individual habitat structures.

Habitat Structure	Mean Annual Rainfall (mm)	Description	Examples of Modern Localities
Savanna	450–1100	Grass ground cover is ubiquitous; fires occasionally occur; main growth closely related to wet and dry seasons.[1]	
Closed Woodland	850–1100	Trees of between 8 and 20 m, crowns can contact but are not interlaced; less-developed grass cover; can have understory of bushes and shrubs.[2]	Guinea Woodland, Rwenzori National Park
Bushland	250–500	Bushes (multiple stems and ~3–7 m in height); cover at least 40% of ground surface; grasses secondary to bushes; can possess thickets of impassable bushes.[2]	Lake Mweru National Park, Rukwa Vally, Serengeti Bushland
Woodland	500–850	Trees (between 8 and 20 m in height); cover 30–40% of ground surface; some bushes, but these are often reduced by fire.[2]	Kapama Game Reserve, Sudan Woodland, Hluhluwe National Park, Kafue National Park
Wooded Grassland	450–500	Land mostly covered with grasses and occasional woody plants (10–40%), which may or may not include trees.[2]	Northern Senegal, parts of Kruger National Park
Shrubland	140–450	Shrubs of 10 cm to 2 m in height; plant structure caused by low rainfall, summer droughts.[2]	Kgalagadi Transfrontier Park; Modern Hadar
Scrub Woodland/ Transition Woodland	400–600	Transitional between woodland and bushland in which tree species are stunted due to poor soil, less rainfall, or both.[2]	Chobe National Park, Tarangire National Park, Amboseli National Park
Edaphic Grassland	600–800	Grasses associated with permanent or seasonally water-logged soils.[2]	Kafue Flats, Okavango Delta (grassland area)
Grassland	250–500	Grasses dominant with < 10% woody vegetation.[2]	Serengeti Plains, Southern Savanna Grassland
Ecotones	750–1200	Forests adjacent to grassland or heath.	Tongwe National Park, Aberdare National Park, Masai Mara

1. Bourliere and Haley (1983).
2. White (1983).

factors are not considered, the paleoecological reconstruction and subsequent evolutionary analyses derived from these comparisons may be inaccurate.

Taphonomy, strictly speaking, refers to the laws of burial (Efremov 1940). The term now usually refers to any alteration that may have occurred to a fossil at any time between the death of the animal and the fossil's placement in a museum. The taphonomic processes that have affected a fossil or a fossil assemblage may dictate that particular methods of analysis are inappropriate (Gifford 1981; Behrensmeyer 1991; Behrensmeyer et al. 2000). Therefore, it is important to discover the taphonomic information derived from both fossil fauna and other sources, such as the depositional environment, so that any incongruities resulting from these biases can be identified. Taphonomic processes that have influenced fossil localities can then be considered in the selection of methods to analyze the assemblage further (Behrensmeyer 1991). Taphonomy can be the focus of research and can therefore answer questions regarding modes of accumulation and pre- and postdepositional processes. However, we are more concerned in this chapter with briefly describing various confounding factors that may affect faunal analyses. When we explain methods of faunal analysis, we note which of these confounding aspects can be overcome as there are analytical methods that can minimize taphonomic overprint in faunal assemblages.

Time-averaging refers to the fact that most fossil deposits have accumulated over hundreds, if not thousands, of years. It is difficult to reconstruct a slice of time environment when the faunal accumulation used to predict the habitat is the result of some 10 kyr (thousand years) of deposition. We can never avoid this problem altogether, but analyses of particular species and their differences, if any, within deposits and also through time will help in this regard. That is, if species at the bottom of a section vary in dental dimensions from the same species at the top of the deposit, for example, then it is possible that what we have deemed as a single deposit is in fact more than one.

It is also necessary to determine if the fossil assemblage has been transported. An *autochthonous assemblage* is one in which no transport of specimens has occurred. *Allochthonous assemblages* refer to fossil deposits that have come from different habitats and yet appear to be a unified accumulation. These deposits would most likely be the result of fast-moving fluvial systems that wash many animals downstream during high-energy situations. These assemblages have a particular signature that can be interpreted before any ecological reconstruction is attempted. Lyman (1994) outlined taphonomic criteria with which to judge assemblages for identifying these biases, such as degree of abrasion and skeletal-part representation.

The *accumulating agent* refers to what or who was responsible for the fossil deposit—that is, animals dragging carcasses into caves, tar pits trapping animals, fluvial systems gathering up carcasses during flooding, hominin hunting or butchery practices, and so on. If one is interested in whether hominins were the hunters or the hunted (Brain 1975), then discerning the accumulating agent is the most important endeavor. Collection bias sometimes occurs when researchers are recovering fossils. It may be that there is no room in a museum for very large mammals, such as elephants, so they are left behind, or that the mode of collection (e.g., a walking survey) does not allow for the recovery of micromammals. Bone modification is the analysis of various alterations on the bone surface and can determine if the bones have been modified by carnivores, rodents, and/or hominins or if they have lain on the ground and weathered, or if they have been rolled or transported in fluvial settings (Behrensmeyer and Hill 1980; Behrensmeyer 1991; Lyman 1994).

Once the biases have been identified, researchers can select methods for reconstructing environments, identifying community structure, and examining species-turnover patterns that will minimize the effects of these biases. For example, if a fossil locality is depauperate in micromammals, it is likely that a comparison with extant faunal communities would be made only with macromammals. If hyenas have collected material of a certain size in the fossil record, then an extant database of animals should be created that takes this into consideration for subsequent comparisons with the fossil faunal assemblage. In other words, if one compares fossil communities with living communities to determine habitat, the comparison will work only if the same types of animals are being compared—that is, those of the same body size, such as micro-, mid-range, or macromammals, or those of the same mammalian orders, such as Artiodactyla or Primates (again of similar body sizes). Comparisons of recently deposited material—for example, assemblages acquired from hyena dens (Brain 1980) or fluvial flood remains, in which the originating habitat is known—will also minimize problems with reconstructing habitats when accumulating agents have modified the selection of fauna.

RECONSTRUCTING HABITATS

Taxonomic uniformitarianism

The taxonomic uniformitarian approach has been used most frequently in the reconstruction of environments (Dodd and Stanton 1990). Using this method, the ecology of a fossil species is reconstructed as similar to its closest living

relatives. For example, a fossil bovid species is a member of a tribe that contains extant bovids, and the ranges of ecological parameters found in the living members of that tribe, such as tolerance to aridity, are attributed to the fossil species. While this taxonomic methodology can be accurate in reconstructing the paleobiology of some fossil taxa (Reed 1998), and therefore useful for subsequently reconstructing habitats, problems with this technique include an ecological bias that may result from the use of only one or two taxonomic groups (Cooke 1978), failure to consider morphological indicators of paleobiology in the fossil taxa (Spencer 1997), or failure to use the full range of extant behaviors for comparison of communities. Using taxonomic analogy, WoldeGabriel et al. (1994) suggested that the high abundances of an undescribed species of tragelaphin bovid and the numerous specimens of a colobine species at the *Ardipithecus* site of Aramis indicated the ancient habitat was wooded and closed. These suggestions are based on the fact that many extant tragelaphins, such as the bushbuck, *Tragelaphus scriptus,* and the bongo, *T. eurycerus*, are found in closed habitats, and most extant colobines are arboreal or at the least spend a great deal of time in trees (Fleagle 1999). However, extant tragelaphins also range into habitats of medium- and open-density woodlands and thus can be found in more arid environments (e.g., *T. imberbis*, lesser kudu, and *Taurotragus oryx*, eland). Several fossil colobine species were terrestrial and thus possibly lived in more open environments (Jablonski 2002; Frost and Delson 2002). While the habitat at Aramis may have been closed with many trees, taxonomic analogy does not definitively suggest this.

In an example of comparing species as if comparing actual habitats, Leakey et al. (2001) demonstrated that the Upper Lomekwi Member at West Turkana, from which the hominin *Kenyanthropus platyops* derives, differed in species composition from the Hadar site at a similar time period, and thus suggested that the Lomekwi habitat was more wet and closed than Hadar. The argument hinged on the fact that the extinct gelada baboon *Theropithecus darti* was recovered from Hadar, while *T. brumpti* was found at West Turkana. *Theropithecus brumpti* is frequently associated with more closed habitats (Krentz 1993). It is possible that the Upper Lomekwi Member is more closed and wet than Hadar, but an analysis of all of the fauna would provide more secure conclusions.

In the same vein as single-species taxonomic uniformitarianism, but using broader analogies, Vrba (1974) argued that members of the extant bovid tribes Alcelaphini and Antelopini (A & A) could be used to reconstruct habitats. Living members of these extant tribes are tolerant of arid conditions and are the majority of animals in open plains or grassland habitats. Vrba suggested

that the presence of extinct members of these groups in similarly high proportions from Plio-Pleistocene fossil assemblages (either in high numbers of the same species or in high relative proportions of the tribe) would be indicative of similar habitats existing in the past.

Vrba (1980) and Greenacre and Vrba (1984) further used modern abundance data to calculate bovid tribal representation in order to determine a criterion for reconstructing habitats. In modern African game parks, when the percentage of antilopine and alcelaphin bovids contribute to more than 50 percent of the bovids on the landscape, inevitably these derive from an open woodland or grassland habitat. Percentages of bovids in these two tribes were then computed from the Plio-Pleistocene hominin sites of Sterkfontein, Swartkrans, and Kromdraai in South Africa. The results of the percentages of the A & A specimens suggested that Sterkfontein was the most closed of these localities with percentages of roughly 50 percent whereas the other sites had between 70 percent and 80 percent A & A bovids. Shipman and Harris (1988) extended this method to examine other bovid tribal representations at *Paranthropus* sites in East Africa. They suggested that high percentages of tragelaphin and aepycerotin bovids indicate closed, dry habitats, while high abundances of reduncin and bovin bovids signal closed, wet habitats. Their results suggested that robust australopithecines possibly preferred closed, wet habitats.

Taxonomic analogy is likely less effective the further back in time it is used because many artiodactyls, perissodactyls, and primates have undergone radiations in the last 2 myr (million years) (Vrba 1995). Nevertheless, as mentioned above this technique can be somewhat effective and is a baseline method for estimating the habitat of early hominins (WoldeGabriel et al. 1994; Leakey et al. 2001). Taphonomic considerations for all of the above examples would include understanding biases toward high abundances of any of the taxa (e.g., tragelaphins caught in a flood) or in the level of identification for collection of each species (e.g., collection of primate limb bones versus noncollection of bovid limb bones).

Taxon-free methodologies

Taxon-free methods depend on analyzing species or communities of fauna in such a way as to reconstruct ecological adaptations in individual species and ecological patterns in communities. The first method involves ecological or functional morphology in which individual species adaptations are analyzed from measurements of various functional systems and compared with modern taxa with similar adaptations (Kappelman 1988; Benefit and McCrossin 1990;

Plummer and Bishop 1994; Kappelman et al. 1997; Lewis 1997; Spencer 1997; Sponheimer et al. 1999; DeGusta and Vrba 2003, 2005a, 2005b). Habitats in which these species lived are thus derived from their adaptations. The second method is ecological-diversity analysis, in which distributions of the various adaptations in fossil communities are compared with extant communities of known habitats (Andrews et al. 1979; Reed 1997, 1998, 2008; Reed and Rector 2006; Rector and Reed 2010).

Ecological or functional morphology

Ecological morphology (also known as *ecomorphology*) links the fields of ecology and morphology (Wainwright and Reilly 1994). This discipline was formally defined in 1948 by Van der Klaauw as the study of the relationship between the morphology of an organism and its environments. Ecomorphological analyses operate under the assumption that the functional design of organisms can be related to their ecology (Wake 1992; Damuth 1992; Ricklefs and Miles 1994; Losos and Miles 1994).

A discussion of ecomorphology by Ricklefs and Miles (1994) articulated the limitations and advantages of this type of research. An important limitation is that morphology provides only a general indication of the possible range of behaviors available to an organism. This caution is especially relevant for bovids, as observations have documented a wide range of intraspecific variation in their diets despite similar morphology. Another limitation is that other aspects of an organism, such as physiology and behavior, are more responsive to short-term changes in the environment than is morphology. Therefore, it is important to combine morphological studies with analyses that are responsive to short-term changes such as microwear and isotope analysis of teeth. A final caveat is that morphologies can be difficult to compare between different classes of organisms: the morphology of a bird is not comparable with that of a mammal, for example.

In spite of these limitations, ecomorphology provides a number of advantages for addressing questions relevant to both ecologists and anatomists. Studies of ecomorphology may be used to address questions of convergence, evolution of function, community organization and evolution, and adaptive significance of morphological design (Losos and Miles 1994). The morphological characters used in an ecomorphological study are usually straightforward measurements that have high repeatability (Ricklefs and Miles 1994). Generally measurements are chosen to reflect biomechanical principles, which serve to strengthen the link between structure and function.

There is one major assumption on which ecomorphology is based: that the morphological phenotype provides information about the relationship between an organism and its environment (Wing and DiMichele 1992; Losos and Miles 1994; Ricklefs and Miles 1994). Though there have been criticisms of the automatic assumption that form is only related to function (Gould and Lewontin 1979), this premise is still prevalent in many studies of morphology. However, in the wake of Gould and Lewontin's criticism, this assumption has been used in a more rigorous and testable fashion (Wake 1992), and support for it has come from two different types of study: the correlation of ecological and morphological relationships, and the concordance of ecomorphological correlations between different species assemblages (Ricklefs and Miles 1994). It is widely accepted among biologists that a high degree of convergence between unrelated organisms indicates "a substantial role for natural selection in shaping or channeling functional attributes" (Wing and DiMichele 1992:140), and therefore the inference of function from form is justified.

The application of ecomorphology to paleontology is easily understood (Van Valkenburgh 1994). Most of paleontology is the study of morphology, because skeletal remains are often the only surviving evidence of extinct animals. The morphology of extinct animals is often used by paleontologists to address paleoecological questions about the relationships between particular morphologies and environments (Van Valkenburgh 1994).

Ecomorphological studies of extinct animals often consist of investigations of morphological adaptations within a single species or closely related groups of species. These studies are usually directed at reconstructing the lifeways (e.g., diet, locomotion, body size) of extinct animals, and can be used to address questions of convergence, morphological evolution through time, and the tempo and mode of evolution. Reconstructions at this level can be based on analogies with living relatives, but they are strengthened when based on physical laws that are equally applicable to past organisms as well as present, using the principles of uniformitarianism and analogy (Gould 1965; Janis 1994). For example, Sanson (1991) noted that inferring diet in extinct organisms is facilitated by the fact that convergence of the feeding apparatus is common across many animal groups, suggesting that there are constraints provided by the nature of the food type.

Faunal analysis at hominin sites has only relatively recently included the functional analysis of various taxa recovered with hominins to further understand their habitat and community ecology (Kappelman 1988; Benefit and McCrossin 1990; Plummer and Bishop 1994; Kappelman et al. 1997; Lewis 1997; Spencer 1997; Sponheimer et al. 1999; DeGusta and Vrba 2003, 2005a, 2005b). Functional morphology is useful for reconstructing the genetic potential of fos-

sil taxa; that is, if the morphology of a particular bovid indicates that it was a mixed feeder (eating both leaves and grasses) then it had the *ability* to ingest both foods. Comparing these data with analyses of epigenetic data such as isotope analysis or micro- and mesowear of teeth can lead to better insights into actual and potential behavioral ecology.

The results of morphological analyses are often extended to infer the likely habitat in which the animals might have existed. For example, Benefit and McCrossin (1990) measured the molar shearing crests of both extant and extinct cercopithecine monkeys to examine trophic behavior. Using the resultant information, they argued that the proportion of foods eaten by each species is correlated with species habitat. They therefore suggested various habitats for hominid sites based on the presence of particular cercopithecines eating various percentages of fruits and leaves.

Spencer (1997) sought to determine morphological correlates in bovids to feeding in secondary grasslands to determine when this habitat became prevalent in Africa. Morphometric analyses of living bovids identified a number of cranial and mandibular traits that were correlated with diet (Figure 1.2). These results allowed reconstructions of diet in a variety of extinct bovids. Dietary reconstructions led to habitat reconstructions at a number of hominin sites. An important result from this study was the demonstration that diets and dietary morphology can differ within a tribe. An extinct reduncin, *Menelikia lyrocera*, did not resemble its close relatives. Also, one of the earliest members of the tribe Alcelaphini was reconstructed as a mixed feeder rather than a grass feeder (Spencer 1995). Finally, strong evidence for the presence of secondary grasslands does not appear until after 2 myr, coincident with the appearance of *Homo ergaster*. This result has implications for understanding the ecological transition from *Australopithecus* species to *Homo habilis sensu lato* and then to *Homo ergaster*.

Other analyses have examined postcranial elements in quadrupedal large mammals (Kappelman 1988, 1991; Kappelman et al. 1997; Plummer and Bishop 1994; Lewis 1997; DeGusta and Vrba 2003, 2005a, 2005b). Kappelman was the first to identify traits of the femur that could be related to locomotor behavior and thus to habitat preference. Plummer and Bishop (1994) extended this work to bovid metapodials, and showed that remains from Olduvai Bed I document a range of habitat types. Many of these studies used Discriminant Function Analysis (DFA) in order to assign fossil taxa to various categories of habitat cover. DFA is also useful for providing quantitative data regarding the ability of the method to classify the extant taxa correctly (DeGusta and Vrba 2003, 2005a, 2005b).
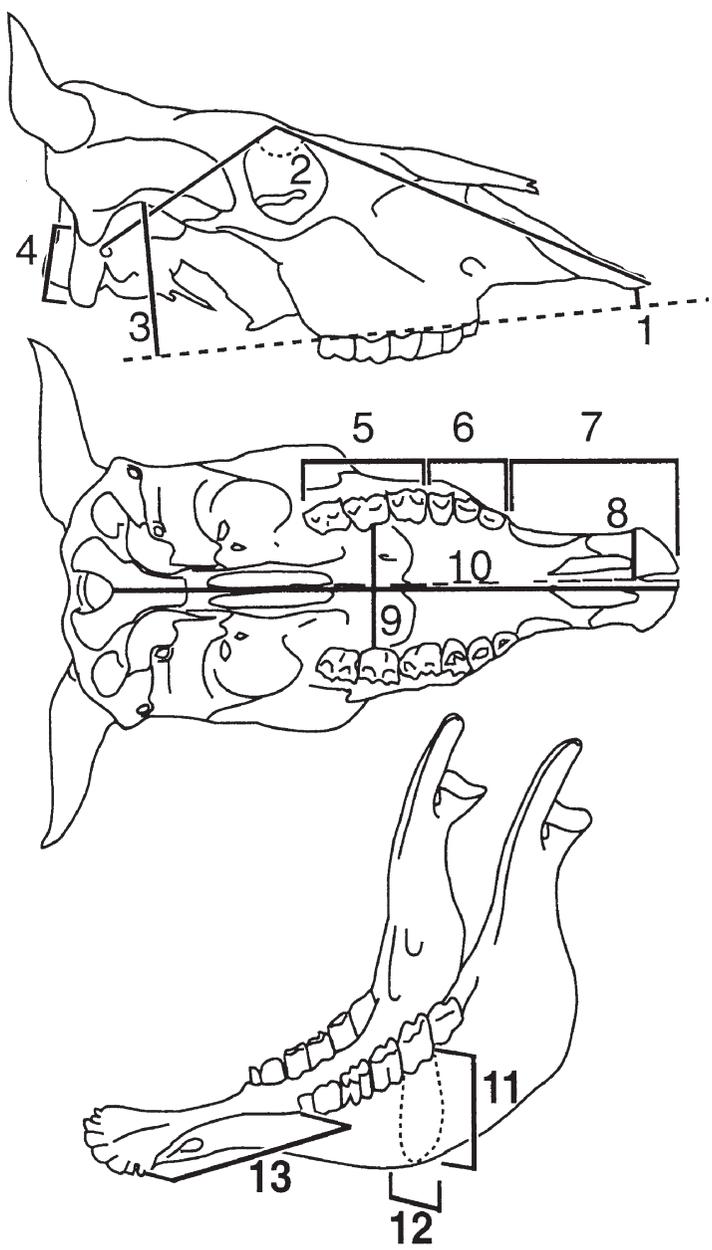
Figure 1.2. *Example of ecomorphological measurements made on bovid skulls to reconstruct dietary adaptations. Numbers indicate where measurements of the masticatory apparatus were taken. See Spencer (1997) for details. (After Spencer, 1995.)*

Some of the more interesting aspects of reconstructing the behavioral ecology of fossil taxa have been the results that show some taxa do not share a diet or substrate use with their extant relatives (e.g., Spencer 1997; Sponheimer et al. 1999; Frost and Delson 2002). Indeed, some taxa may have occupied a trophic niche for which there is no extant counterpart. These types of results enable the study of evolutionary patterns in particular lineages especially when compared with epigenetic data as available. They also show that taxonomic analogy may not be as reliable as one would like for reconstructing behavioral ecology in fossil taxa. Functional morphology and the use of the comparative method is an excellent means to infer the potential behavioral ecology of the organism being examined. However, an extension of this method to environmental reconstruction is possibly limited by the inclusion of only one taxonomic group, and, in the case of the cercopithecine trophic study mentioned above, the assumption that particular trophic resources represent definitive habitats. Taphonomic biases are limited when recreating the diet or locomotor behavior of particular species. However, reconstructing habitats by relying on the reconstructed behavior of a single species or a group of species merits review of collection and accumulating biases, differences in depositional environments, and so on.

Ecological structure or diversity analysis

This taxon-free faunal approach, usually used to reconstruct paleoenvironments, is concerned with the faunal community that existed with early hominins. Mammalian species exist cohesively in the various types of African habitats outlined above, and they partition resources such that the ecological adaptations exhibited by these mammals are somewhat predictable depending on the habitat structure (Andrews et al. 1979; Andrews 1989; Reed 1997, 1998; Mendoza et al. 2005). Each taxon is represented as an ecological entity and these behaviors are examined at the community level. For example, *Panthera pardus*, the leopard, is the ecological entity: "90 kg, terrestrial/arboreal, meat-eating animal." After all of the mammals from the community are assigned to various categories of trophic and substrate use, body-size categories, and so on, the numbers and/or percentages of each adaptation are calculated for the entire community, or in the case of fossil fauna, the relevant assemblage (i.e., single cave deposit, single stratigraphic level, or spatial location). Specific patterns of adaptations are equated with different African habitats. Of the many adaptations that mammals exhibit, six are significantly different among several types of habitats: aquatic, arboreal, and terrestrial locomotion; frugivory (combined with leaf or insect consumption); grazing; and fresh-grass grazing diets (Reed
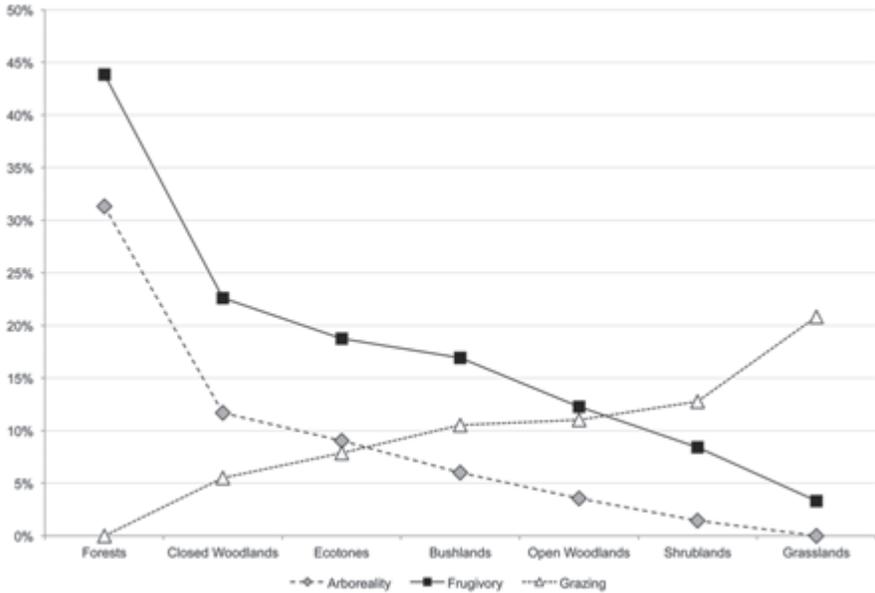
FIGURE 1.3. *Mean proportions of arboreal substrate use, frugivory, and grazing in groups of modern African habitats (forests through grasslands). Mammals included have a body mass greater than 500 grams. (Data from Reed, 1997)*

1998, 2008; Reed and Rector 2006; Rector and Reed 2010). The mammals that live together within a forest community, for example, exhibit higher proportions of arboreal substrate use than is found in any other habitat (Figures 1.3 and 1.4). Open grasslands have no arboreal animals but have high proportions of grazers. Wetland ecosystems also have high proportions of grazers and specialized fresh grass grazers—those mammals that focus on floodplain grasses. Sites that are near lakes and/or rivers have higher proportions of aquatic and fresh-grass grazing animals than sites that do not (Figure 1.5). Thus, the structure of the mammal communities as represented by trophic and substrate use is indicative of vegetation.

Analyzing fauna from a fossil assemblage using this approach requires several steps. First, fossils are assigned to categories using functional morphology if at all possible to discern dietary category, and in the case of carnivores, primates, and a few ungulates, to identify substrate use as well. Second, the fossil assemblage is contrasted with an extant comparative sample of communities from different habitats. Comparing fossil sites with extant communities has ranged from spectral analyses in which histograms of various adaptations have
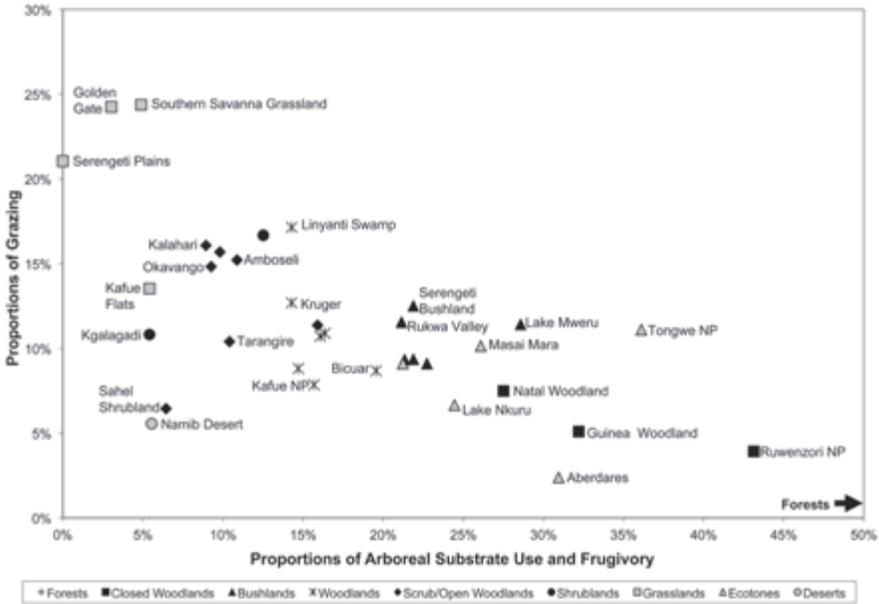
FIGURE 1.4. *Bivariate plot of arboreal substrate use and frugivory (percentages added together) vs. grazing mammals for modern sites of identifiable habitats. Wet, closed habitats are positioned toward the right, while more open, dry, and seasonal habitats are toward the left.*

particular shapes dependant on the habitat (Andrews et al. 1979; Andrews 1989; Gagnon 1997), bivariate plots of two adaptations (e.g., arboreality and frugivory; Reed 1997; Andrews and Humphrey 1999), to multivariate analyses, including principal components (PCA), discriminant function (DFA), and correspondence (CA) analyses of some or all adaptations in each community (Reed 1997, 1998, 2005, 2008; Sponheimer et al. 1999; Mendoza et al. 2005: Reed and Rector 2006; Rector and Reed 2010). Using ecological diversity analyses, habitats have been reconstructed for early hominin sites in eastern and southern Africa (Reed 1997).

RECONSTRUCTING COMMUNITY ECOLOGY

Guild structure

A *guild* is defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967: 335). While being strictly defined in ecology, guilds and communities often represent the same group of species. For example, when discussing groups of primate species living in the same place,
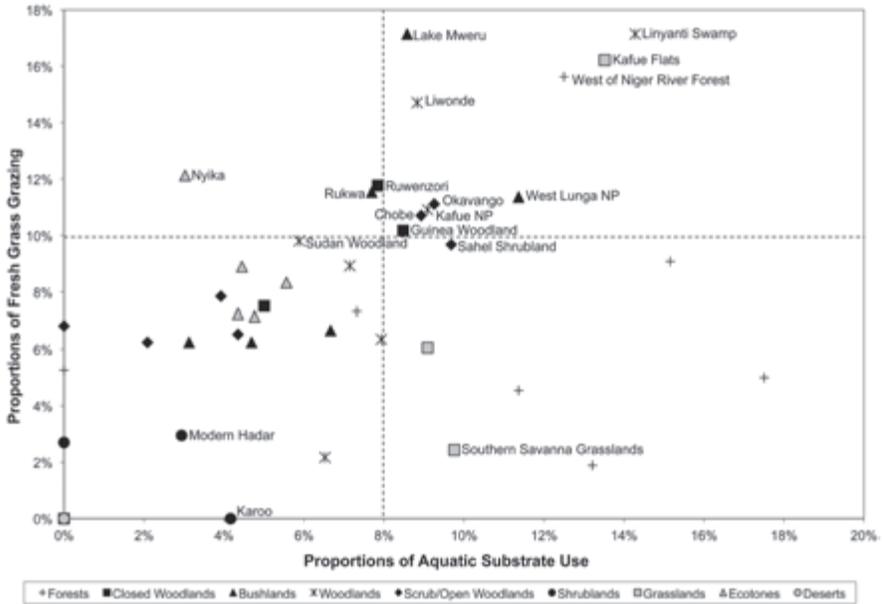
FIGURE 1.5. *Bivariate plot of aquatic substrate use vs. fresh-grass grazing animals for modern sites of identifiable habitats. Habitats in which there are wetlands, swamps, floodplains, and so on are located in the upper-right quadrant irrespective of overall habitat physiognomy and are labeled for reference.*

the term *primate community* is often used (Fleagle and Reed 1996). On the other hand, Lewis (1997) discussed *Homo* species as members of the carnivoran guild—that is, those mammals, irrespective of lineage, that consume meat. For our purposes, the concept of guild and community are defined by the focus of the researcher. For fossil assemblages, guilds usually refer to a subset of a community, unless community is preceded by a grouping adjective, such as *mammal* community or *carnivore* community. Fossil assemblages are usually considered to be samples of a living community or guild and as such need appropriate living analogs for comparisons. If a researcher is interested in a carnivoran guild, then extant samples are based on that concept.

TROPHIC, LOCOMOTOR AND BODY-SIZE PATTERNS
IN GUILDS AND COMMUNITIES

All of the ecological information derived from the fossil assemblage is used to examine the ecological structure of the community. First, it is important to

analyze the fossil assemblage taphonomically. Is there a particular body mass (trophic, substrate, etc.) class that is missing? Why is it missing? Are there both crania and postcrania available for study? Once the answers to these questions are determined, the second step is to develop an appropriate data set from modern communities so that the taphonomic biases are minimized (Soligo and Andrews 2005).

There are two primary questions to investigate regarding fossil communities. First, are the ecological patterns for a particular habitat (e.g., bushland) the same in the past? Second, if these patterns are not the same, what influences might have caused the differences and would those have affected hominins? The difference in the numbers of browsing mammals in modern and fossil communities provides an example. Browsers eat the leaves of dicot plants to the exclusion of other types of plants. Despite the fact that we might predict that there would be higher numbers of browsers in regions with more bushes and trees (forests, closed woodlands, and bushlands), modern browsers do not increase in numbers of species in these habitat types compared to others. We conclude that the distribution of browsing species across the modern African landscape is independent of habitat type. In fact, browsing is one of the few adaptations that is not significantly different between habitats (Reed 2008). Figure 1.6 illustrates an interesting phenomenon: in Pliocene fossil assemblages, browsers represent higher proportions of the faunal assemblages than is the case in extant habitats. This is also the case in the communities of the Miocene of North America (Janis et al. 2004). Is there something fundamentally different about past communities or habitats that allowed higher percentages of browsers? Janis et al. (2004) suggest higher plant productivity and/or higher levels of CO_2 in the atmosphere as possible reasons for the higher number of browsers in the Miocene. If this is the case in the African Pliocene, how would higher leafing productivity have affected early hominins? On the other hand, Soligo and Andrews (2005) suggested that taphonomic processes might inflate the numbers of large browsing species unless the correct modern comparative material is used in analyses. Further investigation into differences between modern and fossil communities will enable better understanding of the communities in which early hominins existed.

In another example, there are primate communities across the African continent today such that higher numbers of primates usually indicate more wet, forested habitats. These forest communities contain high numbers of cercopithecins and low numbers of colobines, papionins, and possibly great apes. In more open woodlands, there is usually just one papionin and cercopithecine species, with occasional colobines along river courses. In the more arid
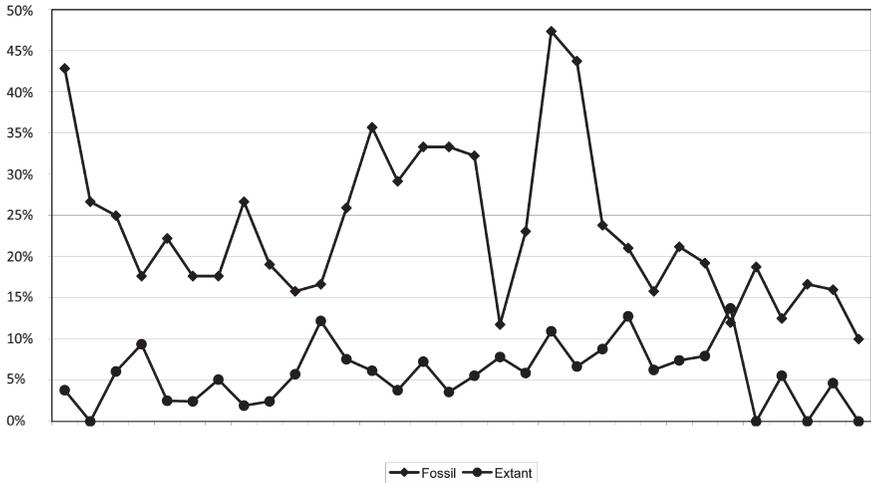
Figure 1.6. *Plot of proportions of browsers in modern communities compared with browsers in fossil assemblages. There is no pattern to the proportions of browsers by habitat, although almost all of the fossil assemblages possess higher proportions of browsers than are found in modern sites.*

woodland habitats of fossil assemblages there are sometimes several papionins, several colobines, and no cercopithecins. In other words, an extinct primate community of nine species (e.g., Makapansgat) does not necessarily indicate a forest as it would in the present. In addition, Reed (2002) has shown that the body-size distribution pattern of primates at Makapansgat does not compare with any living primate community. Thus, an examination of community structure contrasted with habitat reconstructions provides additional information about possible differences between modern and extinct communities.

RECONSTRUCTING EVOLUTIONARY AND BIOGEOGRAPHIC CHANGES

Much research has been devoted to discerning an African faunal response to global climate change hypothesized to have occurred between 2.8 and 2.5 mya (million years ago) (deMenocal 2004). Habitat change due to climatic change has been proposed as the responsible agent for pulses of rapid and varied speciation in the hominin and other lineages (Vrba 1988). More recently, however, researchers are focusing on refining paleoecological data provided by the fauna

of individual localities in order to examine localized environmental changes and how they might be associated with the appearance of various hominin taxa (Bobe and Eck 2001; Bobe et al. 2002; Alemseged 2003). This phenomenon is in response to the hypothesis that the major adaptation of hominins is their ability to adapt to variable environments in contrast to the turnover-pulse hypothesis of Vrba (Potts 1998). While other methods of reconstructing the past environments are also used to address these hypotheses (e.g., depositional environments, Feibel 1999; pollen, Bonnefille et al. 2004), other mammals presumably respond in similar ways as hominins to various ecological changes, and as such, they can be used to compare evolutionary scenarios with early hominins. Fortunately, mammals also provide fairly large sample sizes with which to examine species diversity at various sites as well as species-turnover patterns within sites. In this section we explain various methods of faunal analysis that have been and could be used to understand the paleoecology of early hominins.

SPECIES DIVERSITY AND SPECIES ABUNDANCE

Paleocommunity structure is often represented by diversity and dominance of species (Cruz-Uribe 1988; Dodd and Stanton 1990). This methodology can be as simple as using the number of species in an assemblage: for example, the Denen Dora Member 1 (DD1) of Hadar has a total of sixteen species while the Makapansgat Member 3 assemblage has a total of fifty species. In this example, the Makapansgat faunal assemblage appears to be more diverse than that of the DD1. Of course the taphonomic issues and time-averaging at each site have not been considered, and as such we cannot really say much about the diversity of the fauna with the number of species recovered.

More complex techniques in species diversity and abundance analyses usually entail the derivation of the relative abundance of each of species—that is, the percentages of the number of individuals in each taxon with respect to the total assemblage, and the calculation of species (beta) diversity indices (Peet 1974; Magurran 1988; Cruz-Uribe 1988). It has been argued that a high species-diversity index is equated with an environment that is mesic, warm, and structurally varied (i.e., having animals that utilize various substrates). A low faunal-diversity index would indicate cooler or more arid, open environments with limited structure (Cousins 1991). Marean et al. (1994) used this index to compare diversity through time and relate it to colder climate in small-mammal fauna from Enkapune Ya Muto Rockshelter in Kenya, a Holocene *Homo sapiens* locality.

Analyses of this type do not provide a reconstruction of the habitat of a particular site but quantitatively show the similarity of one site to another. The use of similarity coefficients or faunal resemblance indices (FRIs) facilitates the comparison of the fauna between two sites by examining a resultant index that ranges from 0 (no similarity) to 1 (total similarity). Originally developed by Simpson, this type of index is often used to detect taxonomically distinct biogeographic areas (Flynn 1986). High similarity between assemblages has also been used to suggest that communities were environmentally analogous, such as one study of Miocene hominoid sites (Van Couvering and Van Couvering 1976). While this may be true with geographically penecontemporaneous sites, these comparisons may not be accurate when examining sites over time and space, because the indices may reflect differences in chronology or geography rather than ecology. In fact, Flynn (1986) argued that the Simpson Similarity Coefficient, in particular, was designed to minimize ecological differences and therefore it is erroneous to suggest environmental similarity using this type of index. Similarity coefficients can be used to examine mammalian communities of changing taxa over time (i.e., relative chronology; Flynn 1986) and across space (i.e., biogeographical differences).

Indices can be used solely between two sites giving a percentage of similarity, or indices can be calculated between many pairs of habitats and examined through cluster analyses and other multivariate analyses (Reed and Lockwood 2001). Taxonomic similarity measures among members (strata) of the same site will either reflect change in species composition or show that faunal assemblages are similar through time. Similar faunal groups in a sedimentary sequence may mean that there was little habitat change through time and mammals remained the same over long periods. As can be seen in Figure 1.7, the early part of the Hadar sequence from which *Australopithecus afarensis* has been recovered is fairly similar with the same species of animals uniting the Basal, Sidi Hakoma, Denen Dora, and basal Kada Hadar Members. The differences among these units could be the result of taphonomic or depositional differences during each particular period or indicate slight habitat changes back and forth through time. The Kada Hadar 2 Member (KH2), however, is in a fairly isolated cluster with a large jump in dissimilarity from the other members and represents a species turnover (Reed 2008). Similarly, the Makaamitalu (MAKA) area from which *Homo* has been recovered shows a major species turnover from the rest of the deposit. When sites are compared across geographic regions using similarity coefficients, possible contemporaneous localities can be identified, although
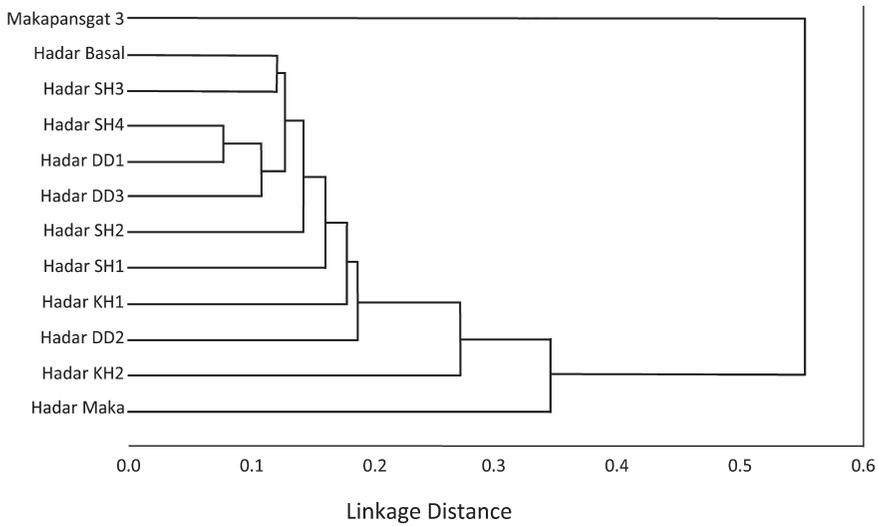
FIGURE 1.7. *Results of a cluster analysis of the submembers of Hadar (Ethiopia) and Makapansgat (South Africa), demonstrating faunal-turnover patterns.*

this can be complicated by biogeography. This can also be seen in Figure 1.7 as Makapansgat Member 3, despite sharing several taxa with the Hadar assemblages, is very distinct, likely indicating a different biogeographic realm and/or a possible difference in age.

The advantage to examining species turnover using more than one taxonomic group is that minor discrepancies that may result from using single higher taxa, such as Cercopithecoidea (e.g., Delson 1984), are minimized. Sites that are found to be chronologically similar through radiometric techniques and relative dating methods can be further compared both ecologically and biogeographically. Ecological reconstructions of communities that are based on other methods of faunal analysis can then be interpreted with reference to the chronology of fossil assemblages. This chronology, along with ecological and biogeographical analyses, will allow ecological patterns to be studied through time and across space.

Bobe and Eck (2001) used this methodology on the American collection of the Shungura Formation of Omo in Southern Ethiopia and discovered a rapid turnover in bovid taxa that occurred between 2.9 and 2.7 mya, which likely indicated a change from wet to drier environments. These researchers proposed that changes of relative abundances in various taxa across time are more likely to reflect environmental alterations than speciation and extinction events. It is

important in light of this statement to have research that considers changes in species abundances as well as species representations across the landscape in order to understand their associations with depositional environments with respect to the principle that vertical facies associations observed in the stratigraphy reflect horizontal landscape associations (Miall 2000). Alemseged (2003) used abundance data from roughly the same region collected by the French paleontological team and found a species-abundance turnover at approximately 2.3 mya, possibly coinciding with the appearance of *P. boisei*. These studies used both the analysis of abundances of bovids over time as well as correspondence analyses to examine the relationships of various tribes of bovid taxa with extant and extinct habitats.

SPECIES INTERACTIONS BETWEEN HOMININS AND OTHER MAMMALS

As discussed above, an important facet of the paleoecology of early hominin species is elucidating the interaction between hominins and contemporary large mammals. This information is important for understanding the ecological context of hominin evolution. Unfortunately, this is one of the most difficult aspects of paleoecology for reconstructing the fossil record. Previous efforts in this arena have focused on the possible interactions between hominins and large carnivores. Archaeological studies have concentrated on hominin carcass acquisition and processing abilities, since these data are readily available in the fossil record. Therefore, it has been pointed out that it is necessary to understand how carnivores would have influenced hominin dietary strategies, both as competitors for prey and as providers of carcasses for scavenging (Blumenschine 1987; Marean 1989; Lewis 1997; Domínguez-Rodrigo 2001).

Studies of modern carnivore behaviors in the context of the East African savanna habitats have demonstrated riparian woodlands are the habitat in which carcasses are likely to survive the longest (Blumenschine 1987; Domínguez-Rodrigo 2001). Using these modern communities as an analog for the past, it has been suggested that early hominins would have found a niche in the carnivore guild that consisted of inhabiting riparian woodlands to exploit both food and the relative safety provided by trees. Efforts to strengthen this analogy by analysis of the paleobiology of the extinct carnivores, especially the sabertoothed felids, indicated that there was a niche available for exploitation of hominins that consisted of scavenging sabertooth kills in closed woodlands (Marean 1989). However, more detailed analyses of the entire carnivoran guild of the east African Plio-Pleistocene by Lewis (1997) suggested that there were

fewer scavenging opportunities available to hominins than previously thought because of the large number of carnivores filling the ecomorphospace. Lewis indicated that scavenging opportunities would have been greater in East Africa relative to South Africa, because of the lack of a large bone-cracking carnivore in the East African carnivoran paleoguild.

The basic interactions of carnivores with the earliest hominins, however, are probably those of predator and prey. Brain (1981) refined the art of taphonomic analyses by showing that australopithecines were the hunted (or at least scavenged) rather than the hunters. Behrensmeyer (2008) noted that the AL–333 assemblage from Hadar was likely the result of carnivore attack on a group of early hominins. These studies do not focus on competition, but rather indicate the difficulty of early hominin survival in savanna mosaic habitats.

CONCLUSION

Faunal analyses that explore paleoecological patterns are critical to understanding hominin evolution. Faunal analyses are used as secondary indicators of habitat because it has been shown that mammalian adaptations correlate with various types of vegetation (i.e., habitats). Ecomorphological studies allow predictions of adaptations, based on taxonomic analyses, to be tested against modern comparative samples for better understanding of life in the past. Species-turnover patterns, combined with climatic information, assist in understanding how mammals of particular groups and early hominins may have been affected by climate-induced habitat change. No faunal analyses are complete without a consideration of taphonomy, because alterations to fossil assemblages are the norm. Without understanding taphonomic processes, any faunal analysis used to reconstruct environments or examine species turnovers is likely flawed. We hope that future faunal analyses will be able to build on the past and offer more refinements to reconstructing diets, habitats, and patterns of eurytopic and stenotopic species through time, and to provide valuable insight into hominin evolution.

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