

Ecological polarities of mid-Cenozoic fossil plants and animals from central Oregon

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Abstract.—Ecological polarities are theoretical roles of organisms, reflected in evolved behaviors and characters. Ecological polarity includes what has been called life history strategies, functional types, habitat templates, and r and K selection. Three common ecological polarities emphasize reproduction, agonistic behavior, and withstanding harsh conditions. Such organisms can be called breeders, competitors, and tolerators, respectively. Polarities of ecospace can be envisaged graphically as apices of a triangular diagram within which each species occupies a particular region. Quantitative studies of ecological polarities rely on proxy measurements of specific morphological features, such as the proportional functional area of canines (for competitors), molars (for tolerators), and incisors (for breeders) among mammals. Such proxy measures of morphospace or chemospace are traditionally judged successful by the degree to which they reveal adaptive differences between species. This approach to approximating ecological polarity is here applied to modern soils, plants, snails, and mammals, as well as to comparable fossils of the Clarno and John Day Formations (Eocene and Oligocene) of central Oregon. An advantage of this approach is that adaptive similarities can be tested quantitatively, as shown here for Oligocene oaks and maples, rather than assuming that extinct species were comparable to related living plants. Paleosols that supported fossil creatures provide useful supporting evidence of past selection pressures for ecologically significant adaptations. Degree of hardship can also be quantified from paleosol features. For example, fossil snails had narrower apertures in paleosols of drier climates as revealed by their shallower calcic horizons, and leaves of extinct relatives of *Meliosma* and *Oreomunnea* were sclerophyllous in paleosols showing evidence of waterlogging, nutrient-deficiency, and metal toxicity. Evolutionary trends of ecological specialization revealed by this approach include molarization (interpreted as evolution toward the tolerator pole) in ungulates. Adaptive breakthroughs that initiated evolutionary radiations also can be reassessed by using these approximations of ecospace, for example, the convergent evolution by bears of degree of caninization previously evolved in an extinct creodont (*Hemiposalodon*). Ecological polarities provide new concepts and metrics for ordering morphological, chemical, and ecological characters of fossil and modern organisms, and for reassessing evolutionary trends.

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Introduction

An ecological polarity is a theoretical role toward which organisms and ecosystems evolve by means of a variety of behavioral, chemical, and morphological adaptations. Three theoretical polarities are widely recognized (Schad 1977; Grime 1979, 2001; Southwood 1988; Westoby et al. 2002) and are here called breeders (with emphasis on reproduction), competitors (with emphasis on agonistic behavior), and tolerators (with emphasis on coping with resource shortages). All organisms breed, compete, and suffer shortages to some extent within their lives, but organisms differ widely in the proportion of resources devoted to each (Fig. 1). Some organisms show a balance between the demands of

breeding, competition, and toleration, and can be regarded as generalists (within the 50% line for each polarity measure in Fig. 1). Other organisms are more effective in all categories. Even so, organisms evolve with a particular orientation within ecological polarities, and these adaptations differentiate them from other organisms. Qualitative assessment of organisms as breeders, competitors, or tolerators tends to enshrine boundaries, which may not be natural. In contrast, quantitative studies along axes of measurement chosen to represent ecological polarities can reveal grades of adaptational compromise and adaptive differences between organisms.

Theoretical ecological polarities are quantified by specific measurements, called variables, "axes" (Westoby 1998), or "dimensions"

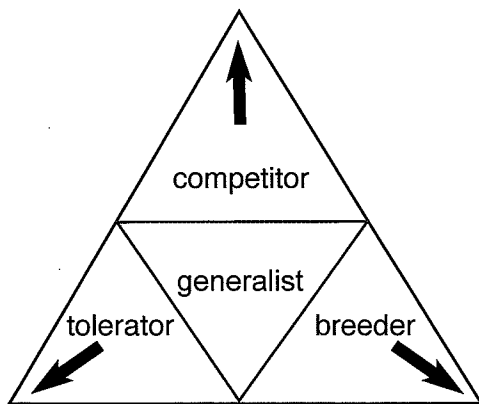


FIGURE 1. Idealized ecological polarity for organisms, applying a simplified new nomenclature of breeder, competitor, and tolerator to general concepts developed by Ramenskii (1938: "explorer, violent, and patient"), Schad (1977: "nerve-sense, respiratory-circulatory, and metabolic-limb"), Grime (1979: "ruderal, competitor, and stress tolerant"), and Southwood (1988: "disturbance, biotic interaction, adversity"). These theoretical ecological polarities are approximated by a variety of measurements (Figs. 2, 4, 6, 7) (Westoby et al. 2002).

(Westoby et al. 2002). For example, Grime (1979, 2001) characterized what are here called breeder species by field measurements of maximum growth rate (weekly dry weight gain normalized to total dry weight). Grime characterized competitor species by measures of canopy height and spread, and by accumulation depth of persistent litter. Grime did not measure tolerator adaptations, using only growth and canopy axes to determine the position of species within his triangular ecospace. Neither of his measurements are applicable to fossils, for which this concept requires preservable morphological or chemical proxies of ecological polarities from among many potential proxies (Tables 1–3). Few of the many potential ecological indicators are preserved in fossils, but there are many studies of such ecologically significant features of fossils, such as proxies of body size through time (Gingerich 1980; MacFadden 1992; Alroy 1998). Bivariate morphospaces also have been applied to fossils, such as Walker and Teaford's (1989) characterization of Miocene apes as frugivorous versus folivorous based on the proportion of pits versus scratches visible on SEM images of the surface of their teeth. Trivariate analysis of modern and fossil carnivore guilds by Van Valkenburgh (1985) used

measures of body weight (estimated from tooth size), cursoriality (from femur/metatarsal ratio), and scansoriality (from metacarpal/phalangeal ratio), and a three-dimensional representation. In a comparable trivariate analysis, Gatesy and Middleton (1997; see also Carrano and Sidor 1999) used triangular diagrams to assess relative importance of theropod and bird tarsometatarsus, femur, and tibiotarsus for interpreting cursoriality and terrestriality. Multivariate analyses of fossils also have used principal components or polar ordination analysis of ecologically significant measurements, though only two significant axes are usually shown at any one time (Andrews 1981; DiMichele et al. 2001). Instead of such a posteriori procedures and specific locomotor or dietary studies, I have selected a priori measures that independent research indicates as approximating an ecological polarity model. My approach is thus simply a modification of the Grime (1979, 2001) triangle (Fig. 1) for application to the fossil record of plants and animals. The Eocene and Oligocene Clarno and John Day Formations of Oregon were chosen for study because they are well known for fossil plants (Chaney 1951; Manchester 1986, 1994; Meyer and Manchester 1997; Wheeler and Manchester 2002), snails (Roth 1986), and mammals (Fremd et al. 1994). In addition, the paleosols of these formations have also been monographed (Retallack et al. 2000; Retallack 2004).

Historical Development of Ecological Polarity Theory

Ecological polarity is a new term for old concepts. The cornerstone of Charles Darwin's (1869) insight of evolution by natural selection was that the natural propensity of organisms to reproduce cannot be sustained by resources of the environment. In the conventional notation of population biology (MacArthur and Wilson 1967; Hutchinson 1978), the intrinsic rate of increase of a population (r) is eventually curtailed at the carrying capacity (K) of the environment, to create the characteristic sigmoid curve of population increase to equilibrium, seen, for example, during plant successional colonization of disturbed ground (Rees et al. 2001). Individual species differ

TABLE 1. Theoretical ecological polarity indicators in living plants. Grime (1979) group in parentheses.

Category	Breeder (Ruderal)	Competitor (Competitive)	Tolerator (Tolerant)
Seeds	Small, numerous	Large, few	Large, few
Flowering	Early peak	Seasonal	Intermittent
Pollen	Small, numerous	Large, few	Large, few
Pollination	Wind, water	Insects, birds	Mammals, birds
Dispersal	Wind, water	Insects, mammals	Insects, birds
Perennation	Dormant seeds	Dormant buds and seeds	Tolerant roots and leaves
Regeneration	Seeds	Seeds and vegetative	Seeds and vegetative
Maximum growth rate	Rapid	Intermediate	Slow
Photosynthate storage	Seeds only	Leaf, stem, seed, root	Leaf, stem, seed, root
Plant size	Small	Large	Very large
Canopy height	Low	High	Medium
Tissues	Herbaceous	Woody	Resinous, sclerophyllous, succulent, thorny
Life form	Herb	Tree, shrub, herb	Lichen, herb, shrub, tree
Shoot	Small, limited lateral spread	Dense leafy canopy, laterally spreading	Succulent, columnar, cushion, and others
Leaf form	Various	Robust mesomorphic	Small, coriaceous, needle
Leaf mass/twig size	Medium	High	Low
Leaf phenology	Early leafing out	Seasonally deciduous	Evergreen
Leaf longevity	Low	Medium	High
Life span	Annual	Perennial	Perennial
Horticultural	Weed	Shade	Hardy
Palatability	Various, often high	Various	Low
Habitat	Disturbed	Stable, fertile, moist	Stable, infertile, frigid, dry
Litter	Sparse, nonpersistent	Copious, persistent	Sparse, persistent
Soils	Entisol, Inceptisol, Andisol	Alfisol, Mollisol	Oxisol, Histosol, Vertisol, Spodosol, Aridisol, Ultisol
Non-vascular plants	Liverworts (Marchantiales)	Hornworts (Anthocerotales)	Mosses (Sphagnales)
Vascular plants	Horsetails (Equisetales)	Angiosperms (Angiospermae)	Conifers (Coniferales)
Pteridophytes	Horsetails (Equisetaceae)	Tree ferns (Cyatheaceae)	Clubmosses (Lycopodiaceae)
Conifers	Pine (<i>Pinus contorta</i>)	Redwood (<i>Sequoia sempervirens</i>)	Juniper (<i>Juniperus occidentalis</i>)
Pines	Lodgepole (<i>Pinus contorta</i>)	Ponderosa (<i>Pinus ponderosa</i>)	Bristlecone (<i>Pinus aristata</i>)
Angiosperms	Grasses (Gramineae)	Oaks (<i>Quercus</i>)	Cacti (<i>Opuntia</i>)
Grasses	<i>Hyparrhenia</i>	<i>Themeda</i>	<i>Chloris</i>
<i>Eucalyptus</i>	<i>E. piperita</i>	<i>E. regnans</i>	<i>E. pauciflora</i>

Sources: Grime (1979, 2001), Keeley and Zedler (1998), Westoby et al. (2002).

widely in their capacity for reproduction and for nutrient acquisition, with species emphasizing reproduction (r-selected) dominating communities early in plant succession and those emphasizing resource acquisition (K-selected) dominating late in ecological succession (Tilman 1988). Among animals, crickets (*Gryllus rubens*) show an inverse relationship (and implied resource trade-off) between wing size and ovarian growth that reflect underlying r-selection for wing size versus K-selection for ovarian growth (Zera and Denno 1997). Alternative terms for r-selected and K-selected plants include proletarians and capitalists of MacLeod (1894) and Niobe and Leto

strategists (Krassilov 2003), respectively. In the simplified terminology advocated here, some species are breeders and others are competitors.

In addition to r and K polarities, a widespread third evolutionary polarity is adaptation to nutrient or other resource shortage, as in cacti of deserts or wind-swept conifers of the montane tree line. Ramenskii (1938) was first to recognize explorers, violents, and patients among plants. This tripolar ecological analysis was later popularized by Grime (1979, 2001), who considers plants according to their "ruderal" (r-selected, weedy, or breeder), "competitive" (K-selected, "climax

TABLE 2. Theoretical ecological polarity indicators in living placental mammals.

Category	Breeder	Competitor	Tolerator
Schad (1977) groups	Nerve-sense	Respiratory-circulatory	Metabolic-limb
Newborn	Very altricial	Altricial	Precocial
Litter size	Large	Moderate	Small
Placenta	Discoidal	Zonary	Enveloping, diffuse, and cotyledonary
Placental shedding	Yes	Yes	No
Placental nutrition	Blood (hemochorial)	Clotted blood (endotheliochorial)	Uterine "milk" (epitheliochorial, syndesmochorial)
Sexual dimorphism	Little	Modest	Marked
Life span	Months	Years	Decades
Food chemistry	Fats, oils, starch	Protein	Cellulose
Food	Nuts, seeds, fruits	Meat	Plants
Food quality	Energy-rich	Similar to animal	Difficult
Chewing direction	Backward-forward	Vertical	Side-to-side
Dung quality	Dry pellets	Moist turds	Wet cakes
Tooth emphasis	Incisors	Canines	Molars
Head emphasis	Whiskers, eyes, ears	Nose, tongue	Horns, antlers, tusks
Emphasized postcrania	Clavicle	Retractile claws	Hooves, monodactyl
Body center of gravity	Posterior	Balance	Anterior
Body size	Small	Medium	Large
Color patterning	Dark on top, light below	Spotted, striped or pied	Whole colored
Psychic profile	Timid	Active, balanced	Placid, phlegmatic
Habitat quality	Disturbed	Stable	Difficult
Habitat	Ground surface, burrows, river banks, cliffs, towns	Forest trees, permanent water	Mountains, poles, open plains, swamps, deserts
Mammals	Rodents	Carnivores	Ungulates
Carnivores	Civet (<i>Civettictis civetta</i>)	Lion (<i>Panthera leo</i>)	Wolf (<i>Canis lupus</i>)
Mustelidae	Weasel (<i>Mustela nivalis</i>)	Marten (<i>Martes martes</i>)	Badger (<i>Meles meles</i>)
Weasels	Least (<i>M. rixosa</i>)	Common (<i>M. nivalis</i>)	Ermine (<i>M. erminea</i>)
Voies	Bank (<i>Clethrionomys glareolus</i>)	Common (<i>Microtus arvalis</i>)	Water (<i>Arvicola terrestris</i>)
Cetaceans	Porpoise (<i>Phocaena phocaena</i>)	Killer whale (<i>Orcinus orca</i>)	Blue whale (<i>Balaenoptera musculus</i>)
Perissodactyls	Horses (Equidae)	Tapirs (Tapiridae)	Rhinos (Rhinocerotidae)
Rhinoceroses	Javan (<i>Rhinoceros sondaicus</i>)	Sumatran (<i>Didermoceras sumatrensis</i>)	White (<i>Ceratotherium simium</i>)
Bovids	Aurochs (<i>Bos taurus</i>)	Yak (<i>Bos mutus</i>)	Bison (<i>Bison bison</i>)
Caprids	Chamois (<i>Rupicapra rupicapra</i>)	Sheep (<i>Ovis ammon</i>)	Muskox (<i>Ovibos moschatus</i>)
Apes	Bonobo (<i>Pan paniscus</i>)	Chimpanzee (<i>Pan troglodytes</i>)	Gorilla (<i>Gorilla gorilla</i>)

Source: Schad (1997).

dominant," or competitor), or "stress tolerant" (withstanding, stunted, or tolerator) characteristics (Table 1). Individual species can be ordered within an ecospace between these poles by using a variety of measurements. Grime (1979), followed by Tilman (1988), Westoby et al. (2002), and Krassilov (2003), called these underlying emphases reflected in adaptive features of plants evolutionary "strategies," but strategy has connotations of foresight contrary to both evolutionary theory and common experience with plants. The features of the plants quantified

are also mainly inherited characteristics, which individual plants cannot change. Recognizing these difficulties, Grime (2001) has acquiesced in the alternative term "functional types" (of Smith et al. 1996). But this term suggests ecological taxonomies of life form like those of Raunkiaer (1937) and Hallé et al. (1978), quite different from the vision of Grime (1979) to discover underlying rules of ecology by measurement and correlation. Functional types are many and can be considered indicators of ecological niches, but ecological polarities are broader axes along which

TABLE 3. Theoretical ecological polarity indicators in communities.

Category	Breeder	Competitor	Tolerator
Microbial communities	Microbial mats	Microbial earth, freshwater stromatolites	Sabkha stromatolites, phytokarst
Trophic class	Early successional	Eutrophic	Oligotrophic
Plant formations	Weedy, pole woodland	Forest, grassland	Rain forest, swamp, desert
Community biomass	Low	High	High-moderate
Community productivity	High	Moderate	Low-moderate
Community diversity	Low	Moderate	High
Community stability	Low	High	Moderate
Soil fertility	High (N limited)	High	Low (P limited)
Soil clays	Illite	Smectite	Kaolinite, palygorskite
Other soil minerals	Pyroxene, plagioclase	Hematite, goethite	Halite, calcite, dolomite, gypsum, pyrite
Soil development	Weak	Moderate	Strong
Soil thickness	Thin	Thick	Intermediate
Soil humus	Moderate	Mull	Mor
Soil moisture	Moderate	Moderate	Arid or perhumid
Soil pH	Moderately alkaline	Near neutral	Acidic or alkaline
Soil Eh	Mild oxidizing-reducing	Mildly oxidizing	Very oxidizing-reducing
U.S. soil taxonomy	Entisol, Inceptisol, Andisol	Alfisol, Mollisol	Oxisol, Spodosol, Histosol, Ultisol, Vertisol
FAO soil classification	Fluvisol, Cambisol, Regosol	Luvisol, Chernozem, Phaeozem	Nitrosol, Ferralsol, Podzol Podzoluvisol, Histosol, Yermosol, Solonchak

Sources: FAO (1974), Retallack (1990, 1997b, 2001b).

functional types are ordinated. The habitat template model (Southwood 1988; Schoonhoven et al. 1998) is a comparable idea, but also an unfortunate metaphor, because it implies an unrealistically good fit between selection and adaptation, and between theory and practice. Such a concept denies assessment of maladaptation, which is attempted here by comparing plants, animals, and snails with soils assessed independently. The alternative phrase "life history evolution" (Keeley and Zedler 1998) is misleading because it emphasizes behavior and development rather than adaptations and characters visible in fossils that give a truly evolutionary perspective. Grime's (1979) term "stress tolerant" is also problematic, because stress is so temporally and spatially variable. For both living and fossil plants, the result of the stress is examined, such as succulence or sclerophylly. In physical terms, this is strain, produced as a result of stress. In biological terms, it is an adaptation to natural selection, not selection itself, that can be quantified by ecological polarity proxies. Selective pressures in turn can be assessed from ecological polarity proxies of the soils

and paleosols, which supported the plants and animals.

For animals, the most comprehensive scheme of ecological polarity is Schad's (1977) "threefoldness" of mammals (Table 2), according to adaptive emphasis on anatomical and physiological systems of nerve-sense (as in rodents), respiratory-circulatory (as in carnivores), or metabolic-limb (as in ungulates). These categories of animals have a direct parallel in Grime's (1979, 2001) evolutionary "strategies" of plants, here restated as breeder, competitor, and tolerator (Table 1). Schad's term "threefoldness" suggests there are only three poles, but trivariate analysis is only one of several useful conventions. In theory, as well as in the practical selection of proxy measures, there are many ecological polarities, "axes" (Westoby 1998), or "dimensions" (Westoby et al. 2002). Selection of three evolutionary polarities and particular trivariate axes by Schad (1977), Grime (1979, 2001), Southwood (1988), and Westoby (1998) is a manageable and revealing convention. For fossils, because of taphonomic limitations, three axes also prove a practical convention.

Ecological polarities are also apparent in ecosystems as a whole (Table 3), even though individual species within ecosystems show a variety of ecological polarities (Westoby et al. 2002). These can be assessed by study of soils, and for ancient communities, from associated paleosols. Several distinct kinds of soil difficulties are tolerated by ecosystems: stagnation (in Gleysols of swamps), aridity (in Pedocals of deserts), and acidity (in Pedalfers of rain forests). These different groups of soils also have different developmental tracks, beginning with communities in each case dominated by weedy plants and r-selected animals, here called breeders. Plant and animal competition is most marked on fertile soils of eutrophic forests and grasslands (Retallack 2001). It may be objected that soils are merely altered rocks and sediments, and so not comparable with evolving organisms, but that is a nineteenth-century view effectively disproved by Dokuchaev (1883) in a monograph widely regarded to mark the birth of modern soil science and its separation from chemical geology (Tandarich and Sprecher 1994). Dokuchaev showed that grassland soils had high organic content and fine crumb peds from earthworms and grass roots, regardless of parent material, and also that this organic-crumb layer was not simply a loessic geological deposit. Furthermore, grassland soils have evolved over the past 40 million years with coevolution of grasses and grazers (Retallack 2001). Like grassland Mollisols, many soils strongly reflect their living ecosystems. Joint consideration of ecological polarities of organisms and of soils that support them may reveal selection pressures for evolutionary change.

An Ecological Proxy Morphospace for Plants

Grime (1979, 2001) approximated ecospace of plant species within triangular diagrams using only two axes: growth rate and a morphological index of dominance, thus creating a physiomorphospace. My attempt here to apply his general concept to the fossil record cannot include such variables as growth rate unobtainable from fossils, so his particular growth-dominance ordination cannot be used with fossils. Many other features for quanti-

fying morphospace of plants are listed in Table 1, but most are difficult to use with fossils. Plant height would be a feasible alternative to seed size (Niklas 1997) if fossil stumps were more completely preserved and attributable to fossil leaves, fruits, and seeds than is usually the case (Retallack et al. 2000; Wheeler and Manchester 2002). Thus Westoby's (1998) leaf-height-seed ordination also is difficult to apply to the fossil record. My ordination that most closely followed the spirit, if not the letter, of Grime's (1979, 2001) and Westoby's (1998) ordinations is a seed-endosperm-sclerophylly morphospace.

The new morphospace for fossils (Fig. 2) used seed size as a proxy for the competitor pole. Many studies (Salisbury 1974; Westoby et al. 2002) have shown that this is proportional to the amount of endosperm that fuels seedling growth through leaf litter and shade inhibition of closed canopy vegetation thriving in the high-fertility and well-watered sites where plant competition prevails.

To approximate the breeder pole, seed number per cone or fruit was used. Again numerous studies (Salisbury 1942; Rees et al. 2001) reveal a weedy reproductive syndrome, which blankets the landscape with many small propagules in the expectation that some will find an open or disturbed patch of ground in which to take root.

To approximate the tolerator pole, vein density was used, as a measure of sclerophylly, which has been shown to reduce palatability of leaves to insects in sites where mineral nutrients are so scarce as to make leaf construction metabolically expensive (Bolton and Brown 1980; Kämpf and Lange 1983; Hill 1998). Other factors also come into play for these measures (Grime 1979; Hill 1998; Uhl and Mosbrugger 1999), particularly water shortage and full exposure to sun as a selection for high vein density (Napp-Zinn 1984, 1988; Uhl et al. 2002). These latter variables are not as extreme as they could be for fossil leaves, which because of taphonomic bias are largely from wetland environments and humid climates (May 1996; Retallack 1998; Retallack et al. 2000).

Methods.—Venation density is the sum of linear measurements ($\text{mm}\cdot\text{mm}^{-2}$) of fossil and

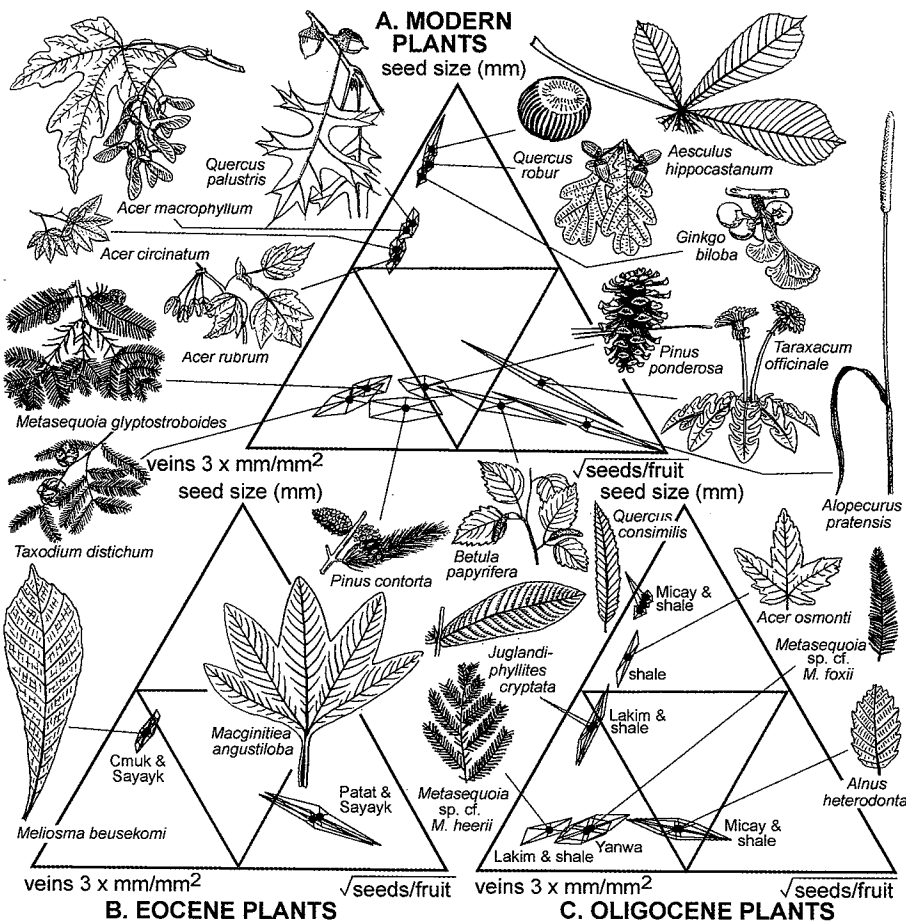


FIGURE 2. Seed-endosperm-sclerophylly morphospace for living plants from the campus of the University of Oregon, and for Eocene and Oligocene fossil plants from the Clarno and John Day Formations of central Oregon. Annotations beside error envelopes explain the kind of paleosol or lacustrine shale in which the fossils were found. Error envelopes are one standard deviation. Data are from Tables 5 and 6, and pole values are explained in Table 4.

extant plant leaves measured with digital calipers within a 1-cm-square window cut into a cover card. Percent vein area was also calculated by multiplying vein lengths by vein widths, but because vein width is difficult to measure accurately with digital calipers, this measure in percent is not as reliable as simple length measures (Uhl and Mosbrugger 1999). For univeined conifer needles, both vein density measures were calculated from measurements of needle width and midrib width. Unlike all the other leaves measured, dandelion leaves wilted under my magnifying lamp within hours of picking, in a dramatic demonstration of why so few herbaceous angiosperm leaves enter the fossil record.

Seeds per fruit of modern cones and fruits

was determined by pulling them apart and counting. For fossils the number of seeds per cone or fruiting head is an estimate based on visible cone units, as well as those inferred from phyllotaxy to be on the covered side of compression fossils.

The maximum length of the seed endocarp was measured, which is smaller than the diameter of the entire seed with fleshy, stylar, or winged extensions. Although winged fruits and seeds are often found in the fossil record, fleshy parts of seeds and fruits are rarely preserved. For comparison with fossils, modern plant material was all collected from partly rotted debris fallen to the ground from trees during the winters of 2001 and 2003.

The relative importance of each axis was

TABLE 4. Equations used to determine ecological polarity proxy morphospaces and chemospaces.

Plant seed size axis = $(S/(S+N+V)) \cdot 100$
Plant seed abundance axis = $(V/(S+N+V)) \cdot 100$
Plant vein density axis = $(N/(S+N+V)) \cdot 100$
Mammal canine area axis = $(C/(C+I+M)) \cdot 100$
Mammal molar area axis = $(M/(C+I+M)) \cdot 100$
Mammal incisor area axis = $(I/(C+I+M)) \cdot 100$
Snail shell thickness axis = $(T/((D/A)+(1/P)+T)) \cdot 100$
Snail aperture size axis = $((D/A)/((D/A)+(1/P)+T)) \cdot 100$
Snail protoconch smallness axis = $((1/P)/((D/A)+(1/P)+T)) \cdot 100$
Calcareous soil fertility axis = $(100F/(100F+(10,000(1/K))+(100-Y))) \cdot 100$
Calcareous soil aridity axis = $(10,000(1/K)/(100F+(10,000(1/K))+(100-Y))) \cdot 100$
Calcareous soil development axis = $((100-Y)/(100F+(10,000(1/K))+(100-Y))) \cdot 100$
Non-calcareous soil fertility axis = $(100F/(100F+100W+(100-Y))) \cdot 100$
Non-calcareous soil acidity axis = $(100W/(100F+100W+(100-Y))) \cdot 100$
Non-calcareous soil development axis = $((100-Y)/(100F+100W+(100-Y))) \cdot 100$
Peaty soil fertility axis = $(100F/(100F+L+(100-Y))) \cdot 100$
Peaty soil stagnation axis = $(L/(100F+L+(100-Y))) \cdot 100$
Peaty soil development axis = $((100-Y)/(100F+L+(100-Y))) \cdot 100$

A = mean aperture altitude (mm)
C = mean labial area of canine tooth (mm²)
D = mean shell diameter at last whorl (mm)
F = mean molar ratio of bases/alumina in Bt horizon: mole/mole = $(CaO+MgO+K_2O+Na_2O)/Al_2O_3$
K = mean depth in soil profile to calcic horizon (cm, compaction corrected for paleosols)
I = mean labial area of incisor tooth (mm²)
L = mean thickness of peat, lignite or coal (mm, compaction corrected for paleosols)
M = mean occlusal area of molar tooth (mm²)
N = square root of mean number of seeds per cone or fruit
P = mean protoconch diameter (mm)
S = mean seed length with sclerotesta, but without sarcotesta or wing (mm)
T = mean shell thickness at aperture (mm)
W = mean molar ratio of sesquioxides/silica in Bt horizon: mole/mole = $(Al_2O_3+Fe_2O_3)/SiO_2$
V = $3 \times$ mean vein density of leaf (mm \cdot mm⁻²)
Y = mean relative soil development (1–100; e.g., moderate 50)

calculated as the percentage of the sum of these measures represented by each of the measures individually (Table 4). Standard deviations of each measure were converted to percentages for an error envelope around each plot position (Fig. 2). Because the number of seeds per fruit extended over several orders of magnitude, unlike the other measures, the square root of this ratio was used. Comparability of the three measures was also achieved by multiplying vein density measurements by a factor of three, which gave a distribution in the morphospace most like that predicted by Grime (1979, 2001).

Materials.—The living plants studied are all planted on or near the University of Oregon campus, Eugene (Table 5) (May 1996). Most grow on Steiner soils, which are Ultic Haploxerolls, but the bald cypress (*Taxodium distichum*) was on Hazelair soils, which are Aquultic Haploxerolls (Patching 1987). The fossil plants measured were collected during a re-

cent study of the Eocene Clarno Formation, near Clarno, and the Eocene–Miocene John Day Formation in the Painted Hills, both in Oregon (Retallack et al. 2000). These fossils are all located precisely within stratigraphic sections, and in some cases were in leaf litters of different kinds of paleosols (Table 6). They are in collections of the John Day Fossil Beds National Monument, Kimberly, Oregon (catalog online at <http://www.museum.nps.gov/>). Measurements of fossil fruits were supplemented by published data (Manchester 1986, 1994; Wolfe and Tanai 1987; Meyer and Manchester 1997). The rarity of fossil leaves to which reproductive structures can be attributed is why so few fossil plants were studied.

A taxonomic problem arose during measurement of dawn redwood (*Metasequoia*) fossils, which confirmed suspicions of Meyer and Manchester (1997) that there are at least two species in the Oligocene John Day Formation. *Metasequoia* sp. cf. *M. heerii* (Lesquereux) Cha-

TABLE 5. Modern plant specimens studied at and near University of Oregon, Eugene.

Taxon	Fruit (n)	Seed (n)	Leaf (n)	Seeds/fruit	Seed size (mm)	Venation density (%)	Venation density (mm ² ·gmm ⁻²)
<i>Acer circinatum</i>	77	77	30	2.0 ± 0	9.8 ± 0.9	57.8 ± 4.7	2.19 ± 0.21
<i>Acer macrophyllum</i>	70	70	31	2.0 ± 0	11.7 ± 1.3	47.9 ± 4.9	2.11 ± 0.24
<i>Acer rubrum</i>	97	77	30	2.0 ± 0	8.2 ± 0.8	49.8 ± 4.6	1.99 ± 1.19
<i>Aesculus hippocastanum</i>	49	49	30	1.5 ± 0.5	35.9 ± 4.3	39.5 ± 3.4	2.17 ± 0.24
<i>Alopecurus pratensis</i>	111	30	31	454.5 ± 61.0	1.7 ± 0.2	26.8 ± 2.3	1.44 ± 0.12
<i>Betula papyrifera</i>	20	55	32	211.2 ± 26.5	3.2 ± 0.4	67.9 ± 9.5	2.97 ± 0.45
<i>Ginkgo biloba</i>	61	61	34	2.0 ± 0	20.9 ± 1.4	60.1 ± 7.5	2.0 ± 0.03
<i>Metasequoia glyptostroboides</i>	12	79	104	26.6 ± 1.1	4.2 ± 0.5	17.3 ± 0.4	5.3 ± 0.6
<i>Pinus contorta</i>	21	59	114	164.0 ± 15.4	4.5 ± 0.9	26.4 ± 7.6	7.5 ± 1.1
<i>Pinus ponderosa</i>	7	56	116	183.6 ± 12.1	6.7 ± 0.6	39.4 ± 7.6	6.4 ± 0.7
<i>Quercus palustris</i>	198	198	30	2.0 ± 0	11.5 ± 0.8	45.7 ± 3.8	1.83 ± 0.15
<i>Quercus robur</i>	68	68	32	1.0 ± 0	28.3 ± 5.1	47.3 ± 4.8	2.15 ± 0.24
<i>Taraxacum officinale</i>	110	34	31	119.1 ± 21.6	3.3 ± 0.3	27.4 ± 4.1	1.20 ± 0.16
<i>Taxodium distichum</i>	20	95	102	25.8 ± 3.3	6.4 ± 1.0	30.4 ± 5.8	8.7 ± 1.4

ney (in Hu and Cheng 1948) has small, near-spherical, seed cones (Chaney 1951: Plate 12, Fig. 1; Meyer and Manchester 1997: Plate 2, Fig. 6), whereas *M. sp. cf. M. foxii* Stockey et al. (2001) has large, subcylindrical cones (Chaney 1951: Plate 7, Fig. 3; Meyer and Manchester 1997: Plate 2, Fig. 5). Seed size and seeds per cone can be used to discriminate these taxa (Table 5), but the simplest criterion from the material measured for this project is leaflet width, which is 0.9 ± 0.1 mm for *M. sp. cf. M. heerii* and 1.7 ± 0.3 for *M. sp. cf. M. foxii*. Although *Metasequoia* is widely regarded as a living fossil, and traditionally referred to a single highly variable species (*Metasequoia occidentalis*), none of the fossil leaves from the John Day Formation are comparable to the apically round and wide leaflets of type specimens of *M. occidentalis* from the Eocene, Chuckanut Formation at Birch Bay, Washington (Chaney 1951). This study confirms diversity of dawn redwood (Meyer and Manchester 1997), but is not the place for systematic treatment of this taxonomic problem.

Results.—The seed-endosperm-sclerophylly morphospace chosen can be considered a success to the extent that it discriminates different taxa significantly beyond error envelopes (Fig. 2). Furthermore, the living species plot in areas comparable to those in the triangular diagrams of Grime (1979, 2001), for whom dandelions (*Taraxacum officinale*) and grasses (*Alopecurus pratensis*) are breeders (his "ruderals"), oaks (*Quercus*) and maples (*Acer*) are competitors, and conifers (*Pinus*, *Metasequoia*, *Taxodium*) are tolerators (his "stress tolerant"). Thus the seed-endosperm-sclerophylly ordination provides a reasonable proxy for Grime's (1979, 2001) ecological triangle approach, though differing in detail from his growth-dominance physiormorphospace, and from Westoby's (1998) leaf-height-seed morphospace.

This study also reveals that the measured variables are genetically determined adaptations, rather than features of plants acquired due to local environmental conditions. The modern plants studied as a training set are cultivated, and not in the soils to which they were originally adapted or might naturally occupy. Furthermore, fossil species gave iden-

TABLE 6. Fossil fruits (F), seeds (S), and leaves (L) studied from measured sections in Oligocene rocks of the Painted Hills (P) and Eocene rocks of Clarno (C), Oregon.

Taxon	Paleosol, section and level (m)	F (n)	S (n)	L (n)	Seed/fruit	Seed size (mm)	Venation density (%)	Venation density (mm-mm ⁻²)
<i>Acer osmonti</i>	Shale, P115.0	7	7	6	2 ± 0	12.8 ± 1.8	59.1 ± 5.9	26.1 ± 3.0
<i>Alnus heterodonta</i>	Micay, P115.6	4	14	9	55.8 ± 5.6	2.0 ± 0.4	56.1 ± 4.5	26.2 ± 2.2
<i>Alnus heterodonta</i>	Shale, P116	4	14	16	55.8 ± 5.6	2.0 ± 0.4	62.0 ± 3.9	29.1 ± 2.7
<i>Juglandiphyllites cryptata</i>	Shale, P115.0	5	5	7	1 ± 0	5.1 ± 1.7	50.3 ± 3.9	23.6 ± 2.0
<i>Juglandiphyllites cryptata</i>	Lakim, P114.0	5	5	11	1 ± 0	5.1 ± 1.7	50.1 ± 4.1	23.4 ± 2.2
<i>Macginitiea angustiloba</i>	Patat, C38.0	7	7	9	200.0 ± 20.7	3.5 ± 0.5	42.5 ± 2.2	17.6 ± 1.2
<i>Macginitiea angustiloba</i>	Sayayk, C37.0	7	7	8	200.0 ± 20.7	3.5 ± 0.5	46.5 ± 3.0	19.4 ± 1.2
<i>Meliosma beusekornii</i>	Sayayk, C53.0	31	31	10	1 ± 0	4.2 ± 0.6	46.3 ± 2.5	20.7 ± 1.2
<i>Meliosma beusekornii</i>	Crnk, C28.0	31	31	4	1 ± 0	4.2 ± 0.6	46.0 ± 2.6	20.7 ± 1.1
<i>Metasequoia sp. cf. M. foxii</i>	Yanwa, P131.4	2	7	18	31.0 ± 1.4	2.8 ± 0.9	20.1 ± 7.5	6.3 ± 0.8
<i>Metasequoia sp. cf. M. foxii</i>	Yanwa, P125.0	2	7	59	31.0 ± 1.4	2.8 ± 0.9	17.3 ± 4.1	5.9 ± 1.0
<i>Metasequoia sp. cf. M. foxii</i>	Yanwa, P121.0	2	7	43	31.0 ± 1.4	2.8 ± 0.9	15.3 ± 6.8	5.9 ± 0.9
<i>Metasequoia sp. cf. M. heerii</i>	Lakim, P114.0	3	5	15	24.3 ± 4.7	4.5 ± 0.1	19.3 ± 4.5	11.1 ± 1.2
<i>Metasequoia sp. cf. M. heerii</i>	Shale, P116.0	3	5	33	24.3 ± 4.7	4.5 ± 0.1	17.6 ± 6.3	11.1 ± 2.5
<i>Quercus consimilis</i>	Shale, P116.0	4	4	12	1 ± 0	22.3 ± 0.1	59.4 ± 3.1	26.2 ± 1.5
<i>Quercus consimilis</i>	Micay, P115.6	4	4	4	1 ± 0	22.3 ± 0.1	59.2 ± 4.4	25.0 ± 1.5
<i>Quercus consimilis</i>	Shale, P115.0	4	4	8	1 ± 0	22.3 ± 0.1	54.5 ± 3.2	21.9 ± 1.8

tical results regardless of the paleosol type or lacustrine shale in which they were found (see annotations to Fig. 2 of paleosol names from Retallack et al. 2000). Other experimental studies (Stanton et al. 2000), show that application of stresses such as high boron, high salt, low light, low water, or low nutrients do not elicit tolerator adaptations, but rather stress avoidance changes in phenology or disfiguring pathology. The characters measured and their natural variation appear to be adaptations, genetically determined at least at the taxonomic level of species.

Interpretation.—The seed-endosperm-sclerophylly morphospace (Fig. 2) confirms Keeley and Zedler's (1998) interpretation of ponderosa pine (*Pinus ponderosa*) as a better competitor than lodgepole pine (*P. contorta*), but not their view that lodgepole is a breeder. Both pines are sclerophyllous like tolerators, as are dawn redwood (*Metasequoia glyptostroboides*) and bald cypress (*Taxodium distichum*). Among fossil *Metasequoia*, one species (*M. sp. cf. M. heeri*) is most like living bald cypress, and the other species (*Metasequoia sp. cf. M. foxii*) more like living dawn redwood. Remnant stump fields and associated flora of *M. glyptostroboides* in China suggested to Bartholomew et al. (1983) that this famous "living fossil" was a swamp cypress like *Taxodium distichum* before human logging to create rice paddy. Other visitors to relict populations of dawn redwood in China have observed isolated trees on levees of rice paddies and other human-disturbed habitats typical of weedy or breeder species, and regarded *Metasequoia glyptostroboides* as a part of a mixed mesophytic forest of well-drained fertile soils (Chaney 1951). This study supports neither a breeder nor competitor polarity for dawn redwood. Both Oligocene species are sclerophyllous and can be interpreted as tolerators. Dawn redwood (*M. sp. cf. M. foxii*) of peaty Oligocene (Yanwa) paleosols is less sclerophyllous than *Metasequoia sp. cf. M. heerii* of waterlogged clayey (Lakim) paleosols and of most of the lacustrine shales (except Fossil and Twickenham localities of Meyer and Manchester 1997). Yanwa paleosols include many clastic bands within the peat and were thus frequently disturbed by flooding, which would

have introduced nutrients, whereas Lakim paleosols have drab colors of persistent waterlogging and nodules indicating iron-manganese toxicity (Retallack et al. 2000). In this and other cases discussed above, evidence from paleosols and ecological polarity are concordant, so that maladaptation was not detected, although there is potential to do so. The two extinct species of *Metasequoia* were adapted to distinctly different swamp habitats, as are living dawn redwood (Bartholomew et al. 1983) compared with swamp cypress (Ewel and Odum 1984).

This analysis supports interpretations that the Oligocene fossil oak (*Quercus consimilis*) was like living competitors, especially white oaks such as English oak (*Quercus robur*) rather than black oaks such as pin oak (*Quercus palustris*). Also generally near the competitor pole are maples, especially bigleaf maple (*Acer macrophyllum*), but vine maple (*A. circinatum*) and red maple (*A. rubrum*) are more centrally placed in the seed-endosperm-sclerophylly triangle (Fig. 2). Oligocene *Acer osmonti* is more like living bigleaf than red or vine maple, but these differences are not significant considering error envelopes of the chosen convention (Fig. 2). Wolfe and Tanai (1987) have used a variety of other characters to argue that *Acer osmonti* is taxonomically closer to bigleaf than to red maples. The Oligocene alder (*Alnus heterodonta*) is similar to generalist-breeders, such as paper birch (*Betula papyrifera*). Also supported is past interpretation of a breeder syndrome like that of living sycamore (*Platanus occidentalis*) for the extinct Eocene plane tree *Macginitiea angustiloba* (Manchester 1986; Retallack et al. 1996). These results confirm that the fossil plants were comparable in ecological polarity to their nearest living relatives. This is not a surprising conclusion, but it has been reached by measurement and testing, rather than assumed.

Inferences from nearest living relatives are not confirmed by other fossils studied. The Eocene aguacatilla (*Meliosma beusekomii*) plots in a region that can be interpreted as a tolerator (Fig. 2), which is only one of a diversity of ecological roles of living Malaysian and central American *Meliosma* (Gentry 1980). This matches well the chemical infertility of the wa-

terlogged paleosols in which it has been found (Cmuk Histosols and Sayayk Entisols of Retallack et al. 2000). This study thus resolves ecological polarity of extinct species from a variety of roles that could be inferred by using taxonomic uniformitarianism alone.

The extinct walnut-relative *Juglandiphyllites cryptatus* also plots as a marginal sclerophyll, and its paleosol (Lakim Inceptisol) indicates that it tolerated lowland waterlogging and iron-manganese toxicity (Retallack et al. 2000). Two species of *Oreomunnea* in central America are its closest living relatives (Meyer and Manchester 1997). Both are large, rain forest trees of varied habitats ranging from deep ravines to steep hillsides and fog-shrouded ridges at elevations of 200–2600 m (Stone 1972). This study indicates a habitat and ecological polarity of this extinct species different from its nearest living relatives.

An Ecological Proxy Morphospace for Mammals

Ecological polarities of mammals would best be approximated by population biological or reproductive physiology data (Table 2), which are rarely and incompletely known for fossil mammals. A variety of morphological features for each of the three ecological polarities also have been outlined by Schad (1977), including sense organs and color patterns (Table 2). These are not preserved in fossils but are often inferred during their reconstruction, for which ecological polarity considerations provide a new theoretical framework. For fossils, the most practical choice of axes is relative emphasis of different kinds of teeth. Skulls and teeth are the only precisely identifiable remains of most fossil mammals.

Carnivores, with their large threatening canines, can be considered competitors for the most valued form of food. The relationship between canine size and both intraspecific and interspecific aggression is best known among primates (Kay et al. 1988; Manning and Chamberlain 1993), although the correlation is not necessarily strong (Kappeler 1996).

Ungulates, with their large molars for grinding large amounts of low-quality food, can be considered tolerators. Molar occlusal area is strongly correlated with body mass,

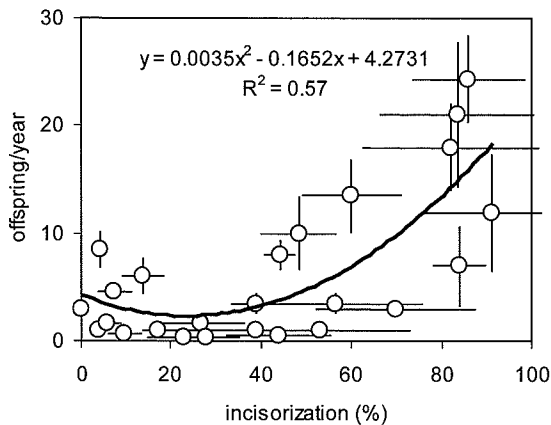


FIGURE 3. Correlation between relative incisorization (% from Tables 4, 7) and fecundity (offspring/year from Nowak and Paradiso 1983; Tyndale-Biscoe and Renfree 1987).

home range size, basal metabolic rate, life span, gestation time, and age at first parturition, and inversely correlated with fecundity and population density (Martin 1990; Janis and Carrano 1992). Body mass is to some extent factored out of my analysis by normalizing functional areas of molars relative to those of canines and incisors, so that this leaves metabolic and population implications of molarization, which are part of ecological polarity models (Maiorana 1990).

Rodents and lagomorphs are prime examples of breeders among mammals and have enormous incisors for their body size. Furthermore, incisor size is correlated with fecundity (Fig. 3). This relationship is striking in buck-toothed mammals (relative incisorization of Table 4 >50%), such as rodents, lagomorphs, and some insectivores and primates, in which small species tend not to have proportionally small incisors. Schad (1977) argued that fecundity is promoted by a diet of oily yet tough-coated seeds of small size scaled to rodent body size. Similarly, young elk (*Cervus elephas*) have greater incisorization for cropping young spring foliage compared with older animals who cope with more fibrous and siliceous forage of fall and winter (Illius and Gordon 1990). Incisorization is also an aspect of a sclerocarpy syndrome in apes adapted for eating large fruits with tough rinds (McCrossin and Benefit 1997). These are energy-rich foods gained by incisorized apes

by means other than competition for rare but universally desirable foods, or by tolerance for unpalatable parts of foods.

Methods.—Measurements of the functional area of mammal teeth were done only on upper dentition of skulls with a full complement of teeth. Individual measurements included apical incisor width, labial enameled incisor height, anteroposterior basal canine width, labial enameled canine height, labial anteroposterior molar length, and linguolabial maximal molar width. The labial area of incisors was calculated from these measures as an approximating rectangle, and the labial area of canines as an approximating right triangle. The occlusal area of molars was calculated from these measures as an approximating rectangle, but in possums, mustelids, and fissioned carnivores it was approximated as a right triangle. The carnassial (upper P4) occlusal area of carnivores was also approximated as a right triangle; it was included as if it were a molar because it is a major cheek tooth distinct in function from canines and incisors, and because it occludes with bladed lower molars. In creodont carnivores, such as *Hemiposalodon* studied here, upper molars have carnassial blades as well. The relative importance of each tooth type was calculated as a percent for each of the sum of the average areas of each tooth type (Table 4). Standard deviations of each measured quantity are plotted as an error envelope (Fig. 4).

Materials.—Modern, Eocene, and Oligocene skulls and a Pleistocene saber-toothed cat were measured in the collections of the Museum of Paleontology, University of California, Berkeley, but a few fossil skulls were measured from the collections of the John Day Fossil Beds National Monument (Tables 7, 8). Modern rodent and lagomorph skulls were mainly from the Condon Museum, University of Oregon. Modern primate skulls were principally from collections of the Department of Anthropology, University of Oregon, curated by J. R. Lukacs, who provided dental casts of a living population of the Chenchu tribe from India, representative of *Homo sapiens*. The exact location and stratigraphic level of most of the fossil mammals skulls is not known, but Oligocene fossil mammals from the John Day

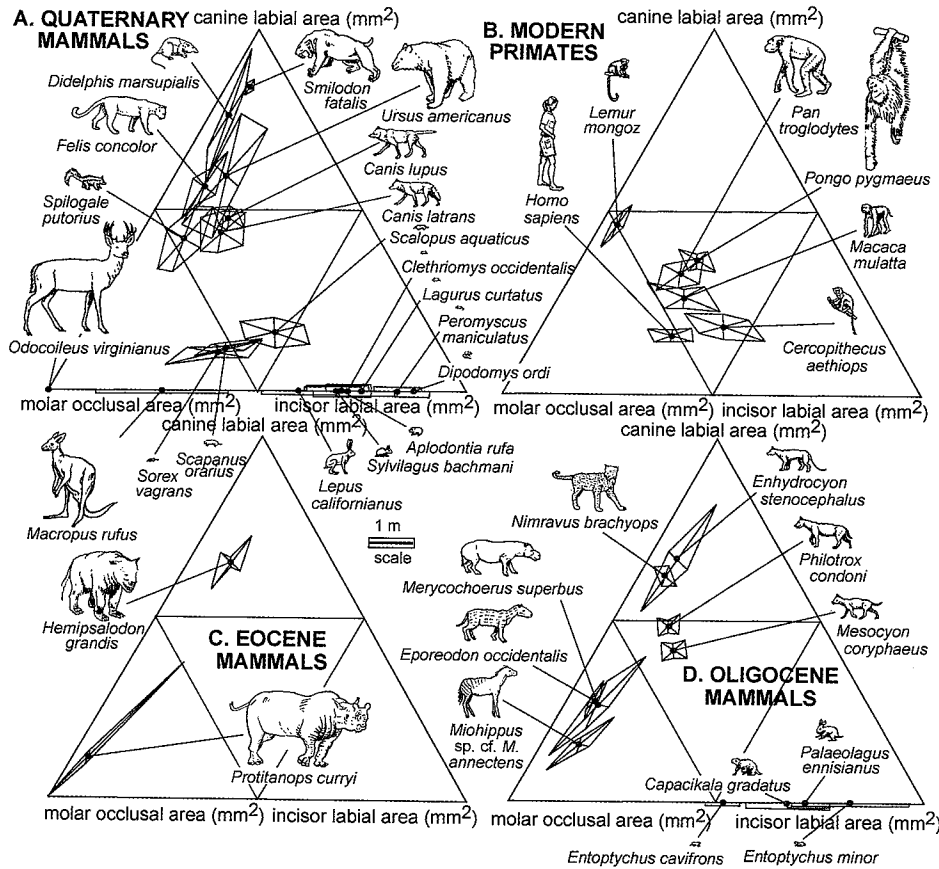


FIGURE 4. Tooth emphasis morphospace for living mammals, and for Eocene and Oligocene fossil mammals from the Clarno and John Day Formations of central Oregon. Error envelopes are one standard deviation. Data are from Tables 7 and 8, and pole values are explained in Table 4.

Formation were largely from Xaxus paleosols and Eocene fossil mammals from the Clarno Formation were largely from Micay paleosols (Retallack et al. 2000). The chief limitation on the number of fossil species studied was the rarity in museum collections of skulls with complete dentition, especially incisors.

Results.—The relative positions of each species within the tooth emphasis morphospace effectively discriminates between a variety of mammals, both fossil and living (Fig. 4). In addition, the fossil species plot in positions comparable to those of living relatives.

Practical limitations also are apparent. The selected tooth functional areas are not effective in discriminating between taxa belonging to groups with only one kind of tooth, such as the upper dentition of many ungulates, which plots at the molarization apex (e.g., *Odocoileus*

virginianus). Other measures, such as horn-antler elaboration, cursoriality, and body mass may be more useful in future analysis of ungulates (Table 2). Kangaroos, rodents, and lagomorphs, lacking canines, are spread along incisorization-molarization axes, which does not do justice to differences in their competitor adaptations, such as the large body size and small litters of red kangaroo (*Macropus rufa*) and sewellel (*Aplodontia rufa*). Other measures such as size of the orbit and auditory bulla and body mass may be more useful in their future analysis (Table 2). Saber-toothed cats are highly caninized, but so are mustelids and possums. The particular tooth emphasis morphospace chosen here works best for primates, carnivores, mustelids, and primitive ungulates.

Interpretation.—Unexpectedly large vari-

TABLE 7. Modern and Pleistocene mammal skulls (S), incisors (I), canines (C), and molars (M) studied.

Taxon	Locality	S (n)	I (n)	C (n)	M (n)	Incisor area (mm ²)	Canine area (mm ²)	Molar area (mm ²)
<i>Aplodontia rufa</i>	Grays Harbor, Wash.	4	8	0	32	44.2 ± 11.1	0	19.0 ± 4.9
<i>Canis latrans</i>	Kaibab Forest, Ariz.	3	18	6	12	49.3 ± 16.7	113.6 ± 16.0	197.5 ± 20.6
<i>Canis lupus</i>	Hart River, Ala.	2	12	2	7	95.6 ± 23.9	249.2 ± 15.9	352.8 ± 16.4
<i>Cercoptihicus aethiops</i>	Kenya	3	6	12	14	42.2 ± 11.5	18.5 ± 3.1	38.2 ± 6.4
<i>Clethrionomys occidentalis</i>	Eugene, Ore.	16	32	0	91	4.57 ± 0.51	0	1.69 ± 0.39
<i>Didelphis marsupialis</i>	Orinda, Calif.	3	26	5	18	4.7 ± 1.9	71.7 ± 16.3	36.9 ± 9.9
<i>Dipodomys ordi</i>	Boardman, Ore.	4	8	0	29	12.4 ± 0.72	0	1.71 ± 0.50
<i>Felis concolor</i>	Tehama Co., Calif.	3	12	6	6	30.1 ± 14.8	215.7 ± 14.5	271.9 ± 35.7
<i>Homo sapiens</i>	Chenchu, India	22	84	44	99	64.8 ± 13.2	31.0 ± 2.6	103.6 ± 10.0
<i>Lagurus curtatus</i>	Madras, Ore.	8	16	0	48	5.98 ± 0.48	0	1.88 ± 0.51
<i>Pan troglodytes</i>	Africa	2	7	4	9	77.84 ± 21.6	111.8 ± 16.4	118.3 ± 32.6
<i>Pongo pygmaeus</i>	Indonesia	1	4	2	6	132.3 ± 35.0	172.7 ± 5.3	169.0 ± 21.1
<i>Lemur mongoz</i>	Madagascar	2	4	8	16	1.90 ± 0.50	29.8 ± 2.5	31.1 ± 4.8
<i>Lepus californianus</i>	Meade Co., Kans.	5	8	0	21	24.5 ± 4.4	0	16.3 ± 4.1
<i>Macaca mulatta</i>	India	11	44	22	66	43.1 ± 16.7	40.6 ± 3.7	60.0 ± 9.0
<i>Macropus rufus</i>	Coopers Ck, Australia	5	26	0	34	42.0 ± 15.6	0	116.3 ± 26.7
<i>Odocoileus virginianus</i>	Wyo. and N.Y.	3	0	0	18	0	0	240.8 ± 31.8
<i>Peromyscus maniculatus</i>	Sisters, Ore.	2	4	0	12	2.97 ± 0.29	0	0.57 ± 0.11
<i>Sorex vagrans</i>	Eugene, Ore.	5	9	10	30	0.51 ± 0.06	0.19 ± 0.01	0.74 ± 0.14
<i>Scalopus aquaticus</i>	Ann Arbor, Mich.	3	6	6	18	3.44 ± 0.81	1.10 ± 0.28	2.75 ± 0.63
<i>Scapanus orarius</i>	Eugene, Ore.	7	11	13	42	1.88 ± 0.19	0.61 ± 0.08	2.96 ± 0.76
<i>Smilodon fatalis</i>	La Brea, Calif.	1	6	2	2	177.2 ± 36.0	2461.0 ± 3.2	639.9 ± 83.1
<i>Spilogale putorius</i>	North America	3	17	6	12	3.0 ± 1.5	11.7 ± 2.6	26.4 ± 3.1
<i>Sylvilagus bachmani</i>	Clarno, Ore.	3	6	0	29	16.1 ± 2.2	0	7.02 ± 1.3
<i>Ursus americanus</i>	Shasta Co., Calif.	5	27	10	20	64.0 ± 23.4	306.2 ± 90.5	291.6 ± 83.5

TABLE 8. Eocene and Oligocene mammal skulls (S), incisors (I), canines (C), and molars (M) studied.

Taxon	Locality	S (n)	I (n)	C (n)	M (n)	Incisor area (mm ²)	Canine area (mm ²)	Molar area (mm ²)
<i>Capacikala gradatus</i>	Rudio Creek, Ore.	1	2	0	4	17.3 ± 1.0	0	8.7 ± 2.8
<i>Enhydrocyon stenocephalus</i>	Kimberly, Ore.	1	4	1	2	25.5 ± 15.5	271.0 ± 0	217.0 ± 62.0
<i>Entoptychus capifrons</i>	Rudio Creek, Ore.	3	5	0	15	18.0 ± 1.6	0	16.6 ± 5.4
<i>Entoptychus minor</i>	Rudio Creek, Ore.	4	6	0	15	17.9 ± 3.1	0	3.8 ± 1.0
<i>Eporeodon occidentalis</i>	Kimberly, Ore.	11	41	17	41	35.2 ± 11.8	121.0 ± 29.8	291.0 ± 82.1
<i>Hemipsalodon grandis</i>	Clarno, Ore.	1	2	2	2	133.8 ± 48.2	839.2 ± 3.3	635.9 ± 105
<i>Merycochoerus superbis</i>	Kimberly, Ore.	6	17	5	17	72.3 ± 21.0	301.6 ± 74.3	701.9 ± 21.0
<i>Mesocyon coryphaeus</i>	Kimberly, Ore.	2	4	3	8	33.4 ± 6.3	74.3 ± 0	143.5 ± 7.7
<i>Miohippus</i> sp. cf. <i>M. annectens</i>	Logan Butte, Ore.	2	12	4	23	23.8 ± 7.1	41.1 ± 7.7	198.0 ± 34.8
<i>Nimravus brachyops</i>	Kimberly, Ore.	1	6	2	1	34.8 ± 19.6	331.3 ± 15.6	335.9 ± 0
<i>Palaeolagus ennisianus</i>	Camp Creek, Ore.	1	2	0	7	17.3 ± 1.0	0	6.8 ± 1.0
<i>Philotrox condoni</i>	Logan Butte, Ore.	1	1	1	4	35.0 ± 8.3	119.3 ± 4.6	183.2 ± 9.0
<i>Protitanops</i> sp. cf. <i>P. curryi</i>	Clarno, Ore.	1	1	2	9	116.6 ± 0	379.5 ± 48.1	2924 ± 1267

ance in tooth dimensions of some taxa (Fig. 4) can be interpreted as due to canine sexual dimorphism and molar polymorphism. Large variance within canines in black bears (*Ursus americanus*) and oreodonts (*Eporeodon occidentalis*, *Merycochoerus superbis*) is probably due to sexual dimorphism, because in each case two significantly different canine sizes are involved. Large variance in size and shape of molars of possums (*Didelphis marsupialis*), skunks (*Spilogale putorius*), and titanotheres (*Protitanops* sp. cf. *P. curryi*) is not due to sexual or population variation, because the titanother teeth are in a single skull, and single skulls of possums and skunks also show great variation in molar size. Molar polymorphism is probably a primitive mammalian character, conserved in marsupials and mustelids.

Another surprise is caninization compatible with a competitor role for primitive dentitions, such as that of the possum (*Didelphis marsupialis*). In contrast, oreodonts (*Eporeodon occidentalis*, *Merycochoerus superbis*) have less prominent canines. The two skulls of three-toed horses (*Miohippus* sp. cf. *M. annectens*) studied both had small canines and were presumably males. Females may have lacked canines as in living horses, but no comparably complete female skulls were available. Most modern ungulates lack canines and upper incisors, having evolved to only molars in the upper dentition, which can be interpreted as evolution toward a tolerator polarity by some early member of their clade.

In tooth emphasis the gracile oreodont (*Eporeodon occidentalis*) is not significantly different from the robust oreodont (*Merycochoerus superbis*). Both taxa are similar in molarization and presumed browsing diet, even though *Merycochoerus superbis* was larger and had more marked sexual dimorphism. By the competitive exclusion principle, they would not be expected to have shared the same habitat, and indeed one replaced the other in a succeeding biostratigraphic zone. Modest paleoclimatic drying and a change to less productive desertic vegetation is evident from studies of paleosols across the transition from Geringian assemblages dominated by *E. occidentalis* to Monroecreekian assemblages dominated by

M. superbus (Retallack 1997b, 2004; Retallack et al. 2000).

The creodont *Hemipsalodon grandis* has been compared to a big cat and a bear (Retallack et al. 1996), but its tooth emphasis (Fig. 4) supports the bearlike interpretation. The saber-toothed cat *Nimravus brachyops* has tooth emphasis similar to that of a mountain lion (*Felis concolor*). The doglike carnivores are discriminated by their tooth emphasis. *Mesocyon coryphaeus* is similar to a coyote (*Canis latrans*), whereas *Philotrox condoni* has more prominent canines like modern wolves (*Canis lupus*). *Enhydrocyon stenocephalus* has been called a hypercarnivore (Wang and Tedford 1996), and its tooth emphasis is more like that of primitive mammals and saber-toothed cats, rather than wolves or coyotes. Both primates and carnivores are centrally placed in the tooth-emphasis morphospace, with few species showing marked caninization.

An Ecological Proxy Morphospace for Snails

Snail population biology could be a guide to ecological polarity, but is unlikely to be easily applicable to the fossil record of their shells. Among marine snails, massive production of small eggs forms clouds of planktotrophic larvae that disperse widely, and small larvae form a small protoconch (Vermeij 1987). The ecological role of egg size among nonmarine snails is comparable, because egg size, protoconch size, and mature shell size are all positively correlated with each other (Fig. 5). Small eggs are scattered over the ground in great numbers, but large eggs are laid in large clutches (Fig. 5A), which may be an adaptation to predator satiation comparable to mast seeding in plants (Kelly and Sork 2002). Nevertheless, land-snail egg-size as a proportion of adult body size is inversely correlated with adult body size (Peake 1978), and protoconch and adult body size is inversely correlated with natural population density (Oosterhoff 1977). These are both predictions of Grime's (1979, 2001) concept of the breeder-competitor continuum. Lacking fossil or modern snail eggs, I have used the inverse of protoconch size as a proxy for breeder adaptations among living and fossil land snails.

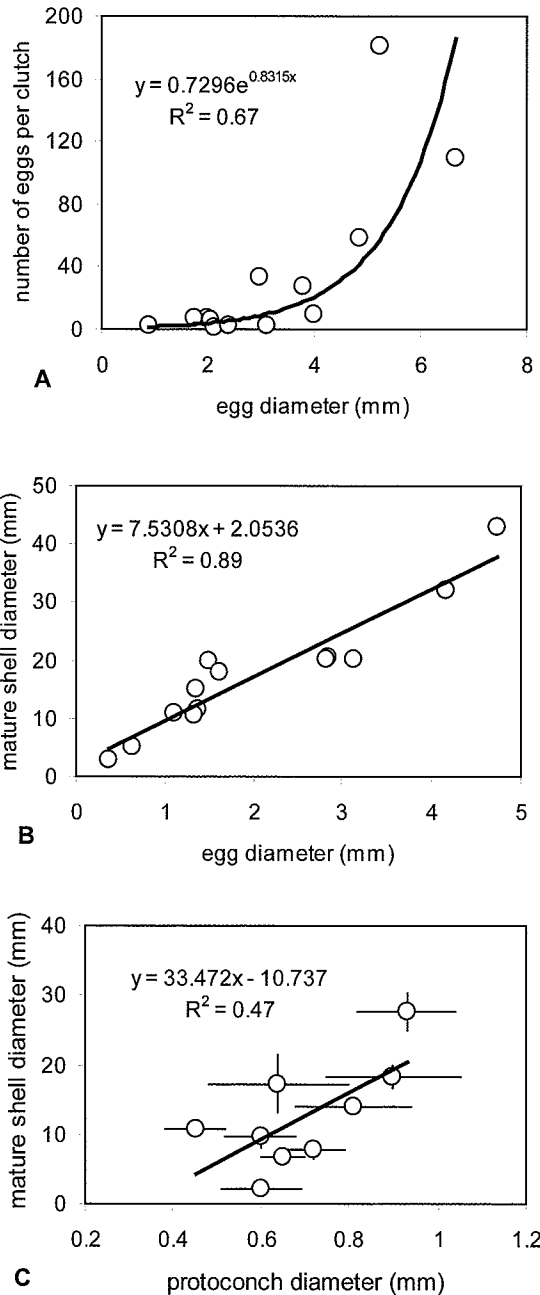


FIGURE 5. Relationships between land-snail egg diameter, protoconch diameter, mature shell diameter, and eggs per clutch. Data for A are from Ingram (1944) and Peake (1978), for B from Peake (1978), and for C from Table 9.

Also among marine snails, thick, nodose, spiny, or otherwise ornamented shells are competitive in the sense that they foil predators (Vermeij 1987). Nonmarine snails do not show such diversity of ornament as marine

shells, but shell thickness in the Bahamian land snail *Cerion* has been shown to be related to effectiveness in resisting land crab predation (Quensen and Woodruff 1997). Some snails have apertural lips that are thickened with respect to the rest of the shell, or have apertural flaps and teeth (Pilsbry 1939–1948), but these plausible defensive structures are distinct from general shell thickness considered as defensive armor here.

An important environmental stress for land snails is desiccation, and many land snails of dry climates have narrow apertures (Pilsbry 1939–1948). Variation in apertural ellipticity and size has been documented in clines of related land snail species from humid to dry climatic regions, as well as by comparison of full glacial (18 Ka) dry and cold-adapted fossil snails with modern humid and warm-adapted snails of related species (Baker 1934; Chiba 1996). The aperture becomes narrower and smaller, giving more effective shelter as climate becomes drier and colder. The question before us, then, is whether shell initiation, armor, and shelter are reasonable proxies of breeder, competitor, and tolerator ecological roles.

Methods.—Land snails were measured for protoconch diameter and shell thickness away from the apertural lips or teeth. Also measured was maximum diameter of the shell (width of the body whorl perpendicular to helical axis) and aperture altitude (distance between upper and lower part of aperture coplanar with axis of helix), as defined by Baker (1934). The measure chosen as a proxy for the tolerator pole was the inverse of aperture altitude normalized to maximum shell diameter. This normalization removes considerable variation in adult shell size. Protoconch diameter and shell thickness showed much less variation in diameter and were not normalized for size. Only a few shells measured had teeth or conspicuous apertural thickening, and these features were not measured in this study. The relative importance of each pole was calculated as percentage of each relative to the sum of these measures (Table 4).

Materials.—Modern snails were collected from various localities in North America (Table 9) and identified from the manuals of Pils-

bry (1939–1948). The fossil snails were all collected in a measured section of the late Oligocene upper Turtle Cove Member of the John Day Formation, on Longview Ranch, south of Kimberly, Oregon (Table 10). They were identified following the scheme of Roth (1986) and are curated by the John Day Fossil Beds National Monument (catalog online at <http://www.museum.nps.gov/>). The exact stratigraphic level of each fossil snail is known. Some were in *Xaxus* paleosols with deep (>50 cm) calcic horizons, but others in *Xaxuspa* paleosols with shallow (<50 cm) calcic horizons (Retallack 2004). Study of fossil snails was limited by the need for specimens with original shell including a complete apex and well-preserved lip.

Results.—Modern snail shells can be differentiated by this initiation-armor-shelter morphospace (Fig. 4). There is relatively little variance in the measures chosen. The three species of snails found in a single road cut near Bend, Texas, each fall in a different area of the morphospace (Table 9, Fig. 6), again supporting the observation of Westoby et al. (2002) that ecosystems contain organisms with a variety of ecological polarities. Co-occurring species of Oligocene snails are clustered, yet in significantly different areas of the morphospace, in support of other indications that they were distinct species (Roth 1986).

Interpretation.—Living species with substantial apertural thickening, teeth, and constriction (*Polygyra septemvolva*) plot in an area of morphospace that could be interpreted as tolerators, and species with thin shells, open apertures, and small protoconchs (*Bulimulus alternatus*, *B. dealbatus*) could be interpreted as breeders. Other species with less-marked apertural thickening and teeth (*Gastrocopta arnifera*, *Triodopsis tridentata*, *Mesodon roemeri*) plot more centrally, so that these features show little correlation with apertural constriction or shell thickness. Teeth and thickened apertures may be adaptations to other hazards, such as predator and pathogen deterrence, as well as to desiccation.

The fossil snail shells all cluster within the restricted aperture area of the initiation-armor-shelter morphospace, but each species is also separated by at least one standard devi-

TABLE 9. Modern snails studied.

Taxon	Locality	Specimens	Protoconch diameter (mm)	Shell thickness (mm)	Aperture altitude/shell diameter
<i>Bulimulus alternatus</i>	Bend, Tex.	4	0.60 ± 0.08	0.47 ± 0.12	0.95 ± 0.04
<i>Bulimulus dealbatus</i>	Camp Classen, Okla.	4	0.45 ± 0.07	0.41 ± 0.24	0.98 ± 0.03
<i>Gastrocopta armifera</i>	Belle Valley, Ohio	5	0.60 ± 0.09	0.36 ± 0.08	0.76 ± 0.06
<i>Megomphix hemphilli</i>	Florence, Ore.	16	0.64 ± 0.16	3.93 ± 0.11	0.44 ± 0.05
<i>Mesodon roemeri</i>	Bend, Tex.	2	0.90 ± 0.15	1.02 ± 0.07	0.46 ± 0.01
<i>Monadenia fidelis</i>	Cottage Grove, Ore.	37	0.93 ± 0.11	0.57 ± 0.16	0.42 ± 0.04
<i>Polygyra septemroloa</i>	Dougherty, Okla.	5	0.65 ± 0.05	0.69 ± 0.09	0.14 ± 0.05
<i>Praticollera campi</i>	Bend, Tex.	6	0.72 ± 0.07	1.03 ± 0.11	0.67 ± 0.06
<i>Triodopsis tridentata</i>	Bloomington, Ind.	2	0.81 ± 0.13	0.36 ± 0.08	0.25 ± 0.05

ation (Fig. 6B). *Monadenia* and *Vespericola* (probably including "*Polygyra*" *expansa* [Roth 1986]) each have a pair of species with significant differences on what can be interpreted as an aridity-toleration axis. Placement of the fossil snails in the shell-initiation-armor-shelter morphospace agrees well with evidence from paleosols in which they are found. *Monadenia marginicola* and *Vespericola dalli* are found in Xaxus paleosols, whereas *Monadenia dubiosa* and "*Polygyra*" *expansa* are found in Xaxus paleosols. Depth to calcic horizon in soils is related to mean annual precipitation (MAP), and use of a transfer function (from Retallack 1994, 2000, 2004a; Royer 1999) on decompacted paleosols (using method of Sheldon and Retallack 2000), gives MAP 366 ± 141 mm for 215 Xaxus paleosols and MAP 493 ± 141 mm for 110 Xaxus paleosols of the upper Turtle Cove Member (Retallack 2004; Retallack et al. 2000). Both snail genera include a wide- and a narrow-apertured species, and these species migrated back and forth into the local section with climatic variation. The wet-dry cycles had a duration of Milankovitch scale (41–100 Kyr) and were repeated 105 times in the stratigraphic interval between Turtle Cove Member tuff H (28.7 Ma) and the top of the Kimberly Member (24.5 Ma). Trace fossil and mammal assemblages also varied with this wet-dry climatic fluctuation (Retallack et al. 2004).

Monadenia fidelis now lives in humid, Douglas fir (*Pseudotsuga menziesii*) forests, on infertile clayey soils (Ultisols) of western Oregon, and is more centrally placed in the morphospace than either fossil species. Here is another case of different habitats and adaptations of fossils and their living relatives, but because humid forested paleosols do not preserve land snails (Retallack 1998), it is likely to remain forever unknown whether *Monadenia* lived in Oligocene Ultisols. No modern species of *Monadenia* lives in habitats as dry as the Oligocene species (Pilsbry 1939–1948).

An Ecological Proxy Chemomorphospace for Ecosystems

Communities also show breeder, competitor, and tolerator ecological polarities (Table 3), independent of their species (Westoby et al.

TABLE 10. Oligocene fossil snails studied.

Taxon	Paleosol	Locality	n	Protoconch diameter (mm)	Shell thickness (mm)	Aperture altitude/diameter
<i>Monadenia dubiosa</i>	Xaxuspa	Kimberly, Ore.	5	1.02 ± 0.22	0.39 ± 0.07	0.41 ± 0.05
<i>Monadenia marginicola</i>	Xaxus	Kimberly, Ore.	7	1.12 ± 0.11	0.42 ± 0.07	0.56 ± 0.08
" <i>Polygyra</i> " <i>expansa</i>	Xaxuspa	Kimberly, Ore.	6	0.89 ± 0.35	0.29 ± 0.06	0.42 ± 0.05
<i>Vespericola dalli</i>	Xaxus	Kimberly, Ore.	17	0.74 ± 0.14	0.35 ± 0.08	0.45 ± 0.06

2002). A breeder community would be one early in the ecological succession of disturbed ground, such as the red alder (*Alnus rubra*) community that colonizes flood deposits in western Oregon. A competitor community consists of longer-term plant associations of fertile, stable sites, sometimes called "climax vegetation," such as hemlock (*Tsuga heterophylla*) forests on Cascade and Holland soils (Fig. 7) of western Oregon. A tolerator community is adapted to resource scarcity, such as the juniper-sage (*Juniperus occidentalis-Artemisia tridentata*) shrublands and Norad soils (Fig. 7) of eastern Oregon deserts (Franklin and Dryness 1973). Soils of these communities reflect a variety of ecosystem differences; for example, soils of breeder communities are weakly developed and retain abundant relict bedding from floods that laid their parent material (Entisols), whereas soils of competitor communities are thick, clayey, red, and humic (Alfisols), and soils of tolerator communities are thin, silty, and calcareous (Aridisols) (Dyksterhuis 1981; Patching 1987). In other regions tolerator soils are acidic with metal toxicity (Spodosols), or stagnant with anoxic peaty substrates (Histosols) (Retallack 2001). Thus measures of soil youth, fertility, and a variety of growth-inhibiting hardships can be considered proxies for breeder, competitor, and tolerator communities. Soil assessment could give insights into evolutionary selection pressures on the organisms associated with particular soils and paleosols.

Methods.—My quantification of soil age modified a previously published five-point scale of soil development (Retallack 1997a, 2001) to moderate development at 50 and a maximum of 100. Relict bedding defines young soils, but the development scale proceeds on three separate tracks away from that origin: (1) thicker more massive clayey subsurface horizons in humid climates (pedalfers of Marbut 1935), (2) larger and more laterally extensive carbonate nodules in dry climates (pedocals of Marbut 1935), and (3) thicker peats in waterlogged sites (Histosols of Soil Survey Staff 1999). Underclay development (as in pedalfers) is added to development based on peat thickness in the case of Histosols of woody vegetation. The soil development in-

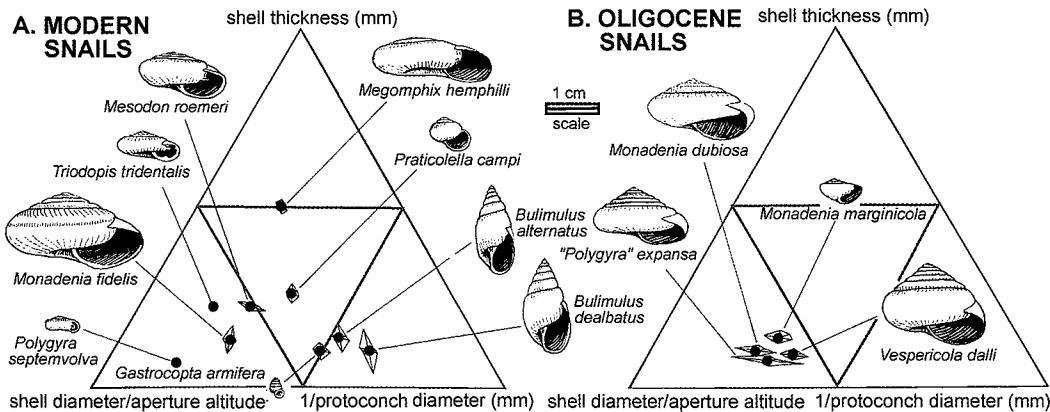


FIGURE 6. Shell initiation-armor-shelter morphospace for living land snails, and for Oligocene fossil snails from the John Day Formation of central Oregon. Error envelopes are one standard deviation. Data are from Tables 9 and 10, and pole values are explained in Table 4.

dex was subtracted from 100 to give a value for youthfulness, because the development index has low values for weakly developed soils.

For soil fertility, I used bases/alumina molar ratios as a chemical index of soil fertility suitable for paleosols (Retallack 1997a, 2001). Soil fertility is directly related to the abundance of cationic plant nutrients: Ca^{2+} used in plant cell walls, bones, and shells; Mg^{2+} critical for chlorophyll; and K^+ and Na^+ , which are important cytoplasmic electrolytes. Availability of these nutrients is approximated by chemical analysis of oxides of these elements normalized on a molar basis to alumina as a relatively stable constituent in soils.

Three different proxies were used for the three different kinds of hardship presented by excessively humid, arid, and waterlogged soils. Sesquioxide/silica molar ratios reflect the increased abundance of sesquioxides (Al_2O_3 and Fe_2O_3) compared with silica (SiO_2) as weathering proceeds to break down silicate minerals and leaves clay, hematite, and gibbsite of nutrient-poor spodic horizons of Spodosols, and oxic horizons of Oxisols (Sanford 1987). As peat thickness increases, plants growing in it are increasingly isolated from mineral nutrition of underclays (Ewel and Odum 1984). This thickness was corrected in paleosols for burial compaction (using method of Sheldon and Retallack 2000). As depth to carbonate nodules decreases, soils have lower mean annual precipitation (Retallack 1994, 2000a; Royer 1999). This latter depth was

corrected in paleosols for burial compaction (Sheldon and Retallack 2000) and recast as a reciprocal in order to obtain values that increase with soil aridity.

Materials.—The modern soils used (Table 11) were described by Marbut (1935) in a comprehensive survey of soils of the United States, and their modern taxonomy and soil-forming factors were tabulated by Sheldon et al. (2002). This is the most thorough existing grain size and major-element description of soils on a continent-wide scale, because much subsequent soil science abandoned whole-soil analysis in favor of partial analyses, such as cation exchange capacity. One Hawaiian soil (Pooku silty clay loam) also has been added (Soil Survey Staff 1975: p. 692) as an example of an Oxisol. Fossil soils of the Clarno and John Day Formations of central Oregon (Table 12) were described by Retallack et al. (2000), using similar petrographic and whole rock chemical approaches. Unlike the few stratigraphic levels of fossil plants, snails, and mammals suitably preserved for ecological polarity studies, there are 1195 measured paleosol levels in the Clarno and John Day Formations of Oregon (Retallack 2004; Retallack et al. 2000), and their study is limited not by lack of suitable preservation, but by the expense of chemical analysis.

Results.—Modern soils of the United States are discriminated well by the youth-fertility-hardship chemomorphospace. Furthermore, the modern soils plot in similar places to pa-

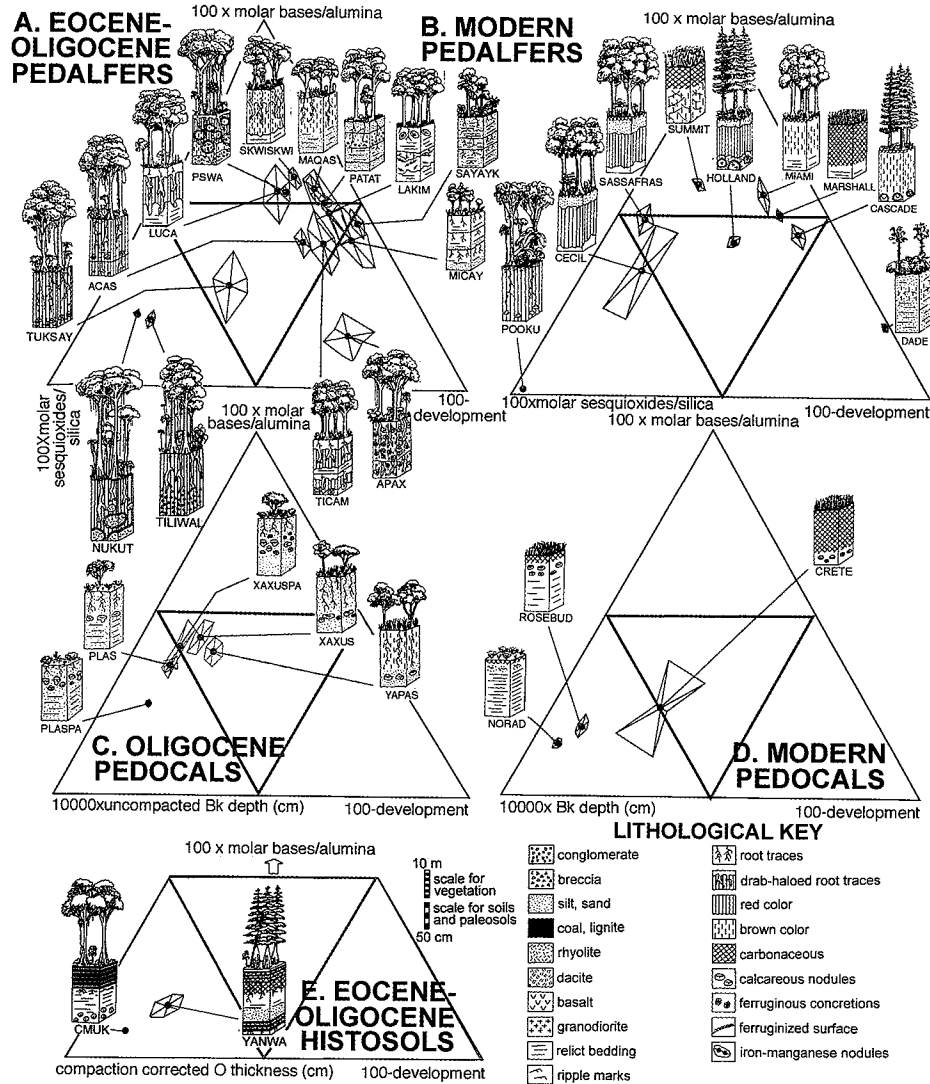


FIGURE 7. Soil youth-fertility-hardship chemomorphospace for North American soils, and for Eocene and Oligocene paleosols from the Clarno and John Day Formations of central Oregon. Error envelopes are one standard deviation, data are from Tables 11 and 12, and pole values are explained in Table 4.

leols with similar profile horization, soil structure, and other soil characteristics (Fig. 7). Semiarid grassland and desert calcareous soils (Crete Mollisol, and Norad and Rosebud Aridisols) plot toward the tolerator field like comparably calcareous Oligocene paleosols (Plas, Plaspa, and Xaxuspa Aridosols). Subhumid grassland and broadleaf woodland soils of the Great Plains (Summit and Marshall Mollisols and Miami Alfisol) and of Oligocene age in the Painted Hills (Luca Alfisol and Skwiskwi and Maqas Andisols) plot in the competitor field, reflecting in part their

nutrient-rich parent material of vitric, rhyodacitic, airfall ash. A tropical, rain forest soil from Hawaii (Pooku Oxisol) is more deeply leached of nutrients and more sesquioxidic than Eocene, subtropical, rain forest paleosols of the Painted Hills (Tiliwal Oxisol and Nukut Ultisol). An early successional saw-palmetto and pine woodland soil from Florida (Dade Entisol) is broadly comparable to early successional paleosols of Eocene mudflows (Apax Inceptisol) in being poor in both cationic nutrients and sesquioxides. Other Eocene paleosols with abundant relict bedding (Sayayx and

TABLE 11. Modern soils studied.

Plant formation	Soil series	Soil taxonomy	County, State	n	Development	Bases/ alumina	Depth to Bk (cm) sesquioxides/ silica ratio
Conifer forest	Cascade	Humic Fragixerept	Multnomah, Ore.	1	20 ± 0	0.81 ± 0.11	0.168 ± 0.010
Deciduous forest	Cecil	Typic Kanhapludult	Rutherford & Yadkin, N.C.; Anderson, S.C.; Chambers, DeKalb, Habersham, Hall, Lamar, & Wilkes, Ga.	10	89.5 ± 10	0.15 ± 0.06	0.278 ± 0.070
	Sassafras	Typic Hapudult	Dorchester & Talbot, Md.; Accomack, Va.	4	60 + 0	0.51 ± 0.08	0.099 ± 0.027
Grassland	Summit	Vertic Arguidoll	Sumner & Republic, Kans.	2	70 ± 0	0.66 ± 0.07	0.156 ± 0.014
Oak forest	Holland	Ulitic Haploxeralf	Josephine, Ore.	2	80 ± 0	0.24 ± 0.01	0.344 ± 0.010
Oak woodland	Miami	Oxyaquic Hapludalf	Decatur, Wayne, & Hancock, Ind.	4	60 ± 0	0.73 ± 0.23	0.161 ± 0.025
Pole woodland	Dade	Spodic Quartzipsamment	Collier, Fla.	1	1 ± 0	2.22 ± 0.61	0.014 ± 0.008
Sagebrush desert	Norad	Xerollic Haplargid	Harney, Ore.	2	48 ± 5	1.23 ± 0.27	16 ± 4 cm
	Rosebud	Calcic Argiustoll	Cheyenne, Nebr.; Fall River, S.D.	2	59 ± 6	0.80 ± 0.08	35 ± 2 cm
Semi-arid grassland	Crete	Pachic Argiustoll	Fillmore & Lancaster, Nebr.	2	50 ± 5	0.53 ± 0.32	97 ± 22 cm
Subhumid							
grassland	Marshall	Typic Hapludoll	Fremont, Iowa	2	50 ± 0	0.81 ± 0.11	0.149 ± 0.002
Tropical rain forest	Pooku	Typic Acrudox	Kauai, Hawaii	1	80 ± 0	0.007 ± 0.005	21.48 ± 11.77

Micay clayey Entisols) are marginally within the breeder field because they are relatively rich in cationic nutrients.

Interpretation.—Eocene Oxisols and Ultisols are rich in sesquioxides, which lead to aluminum toxicity and other hardships for ecosystems (Retallack 2001), as in the Hawaiian soil, which formed in tropical, humid, and deeply weathering climates (Fig. 7). The sequence of paleosols in the Painted Hills shows a geologically abrupt (within 200 Kyr) shift in soil fertility and development at the Eocene/Oligocene boundary with paleoclimatic change from warm and humid, to paleoclimate at least 5°C cooler and 500 mm drier in mean annual precipitation (Retallack et al. 2000). The magnitude of this shift is indicated by separation of Tuksay and Tiliwal paleosols on the one hand, from Luca, Lakim, and Ticam paleosols on the other hand (Fig. 7). By mid-Oligocene time, calcareous paleosols appear with continued paleoclimatic drying. These paleosols show increased aridity from mid-Oligocene Yapas, Xaxus, and Xaxuspa paleosols, to Oligocene-Miocene Plas and Plaspaleosols. From this it can be inferred that central Oregon Eocene ecosystems were tolerators because they were infertile and waterlogged. Early Oligocene ecosystems were generalists with improved fertility, although tolerator ecosystems persisted in waterlogged parts of the landscape. Late Oligocene ecosystems returned slightly toward the tolerator pole as paleoclimate became drier. Details of this paleoenvironmental change from paleosols have been documented elsewhere (Retallack et al. 2000), but comparable environmental histories cannot be gained from the few fossil plants or animals suitably preserved for ecological polarity analysis.

Xaxuspa paleosols interpreted to represent tolerator desert shrubland of the Oligocene Turtle Cove Member include snails with narrow apertures, rodents and lagomorphs with hypsodont teeth, and mammals of small body size, whereas Xaxus paleosols include more open-mouthed snails, less hypsodont teeth, and larger mammals (Retallack et al. 2004). Xaxuspa paleosols are dominated by cicada burrows (ichnogenus *Taenidium*), which are characteristic of sagebrush steppe (O'Geen

TABLE 12. Fossil soils studied near Clarno (C), Longview Ranch (R), and Painted Hills (P), Oregon.

Presumed plant formations	Pedotypes	Soil taxonomy	Locality and meter level	n	Development	Bases/ alumina	Depth Bk corrected (cm), thickness O corrected (mm) or sesquioxides/silica
Broadleaf swamp	Cmuk	Hemist	C12	1	45 ± 0	0.42 ± 0	413 ± 0 mm
Bunch grassland	Xaxus	Aquic Ustivitrandid	L200-220	15	64 ± 7	1.28 ± 0.08	90 ± 20 cm
	Yapas	Mollic Haplustand	P360-425	4	57 ± 2	0.97 ± 0.19	110 ± 24 cm
Dry grassland	Plas	Typic Haplocalcid	L236-277	6	66 ± 6	1.16 ± 0.02	65 ± 5 cm
Forest	Pswa	Lithic Haplustalf	C16-17	2	68 ± 60	0.58 ± 0.03	0.198 ± 0.004
Grassy woodland	Maqas	Vitric Haplustand	P293-424	2	38 ± 4	0.93 ± 0.11	0.175 ± 0.008
	Skwiskwi	Eutric Fulvudand	P221-271	5	57 ± 3	0.82 ± 0.09	0.199 ± 0.013
Lowland forest	Acas	Plinthic Haplohumult	C113, P62	2	56 ± 1	0.43 ± 0.06	0.222 ± 0.002
	Lakim	Aquandic Plaquept	C124, P115	6	29 ± 13	0.93 ± 0.61	0.062 ± 0.023
Pole woodland	Apax	Andic Dystropept	P52-61	4	18 ± 2	0.18 ± 0.09	0.273 ± 0.032
	Micay	Aquandic Fluvaquent	P278	3	2 ± 0.2	1.17 ± 0	0.146 ± 0.030
Rain forest	Sayayk	Tropofluent	C54-55	4	1.0 ± 2	0.87 ± 0.11	0.080 ± 0.034
	Nukut	Lithic Kanhapludult	P-5	2	95 ± 0	0.10 ± 0.001	0.345 ± 0.001
	Tiliwal	Plinthic Kandudox	P0-1	2	93 ± 0	0.09 ± 0.02	0.334 ± 0.018
	Tuksay	Plinthic Paleudult	P8-P60	5	80 ± 1	0.20 ± 0.09	0.304 ± 0.024
Sagebrush	Xaxuspa	Aquic Haplocalcid	L100-141	2	57 ± 1	1.74 ± 0.54	51 ± 3 cm
Sagebrush desert	Plaspa	Ustic Haplocalcid	L234-277	2	57 ± 0	1.17 ± 0	38 ± 0 cm
Swamp	Yanwa	Histic Humaquept	P122-134	2	34 ± 3	0.62 ± 0.04	259 ± 46 mm
Woodland	Luca	Hapludalf	C87-P250	15	67 ± 4	0.65 ± 0.18	0.219 ± 0.028
	Patat	Psammentic Eutrochrept	C30	2	22 ± 0	0.92 ± 0.05	0.179 ± 0.019
	Ticam	Andic Eutrochrept	P65-243	4	36 ± 1	0.58 ± 0.19	0.248 ± 0.020

and Busacca 2001), whereas *Xaxus* paleosols have abundant dung beetle boli (*Pallichnus* of Retallack 1984) and earthworm fecal casts (*Edaphichnium* of Bown and Kraus 1983), characteristic of grasslands, probably wooded grasslands considering the common large, calcareous rhizoconcretions (Retallack et al. 2004). Such ecosystem differences are reflected in the distribution of four fossil snail species of two different genera, distinct within the shell initiation-armor-thickness morphospace (Fig. 6).

Paleosol-related differences in plant communities also are apparent. Thin, impure lignites and underclays of Oligocene Yanwa paleosols were poor in nutrients and waterlogged as in a tolerator ecosystem, and associated leaves and cones of dawn redwood (*Metasequoia* sp. cf. *M. foxii*) are also interpretable as from a tolerator plant (Fig. 2). Coals and nutrient-poor underclays of Eocene Cmuk paleosols were even more challenged by waterlogging and nutrient deficiency, as in a tolerator ecosystem (Fig. 7E), and their leaf litter includes aguacatilla (*Meliosma beusekomii*), which is sclerophyllous, but less so than dawn redwood (Fig. 2B). Fossil aguacatilla leaves and fruits also were found in leaf litters of Sayayk paleosols, which are centrally placed in the youth-fertility-hardship diagram principally because of relict bedding and other evidence of soil youth. Fossil aguacatilla thus had a broader environmental tolerance than is apparent from its seed-endosperm-sclerophylly placement (Fig. 2). Generalist and breeder plants within the seed-endosperm-sclerophylly triangle, such as the Clarno plane (*Macginitiea angustiloba*), are found in fossil leaf litters of Sayayk and Patat paleosols, which are placed in breeder and generalist fields, respectively, close to the youth-fertility axis. Lakim paleosols are also generalists close to the youth-fertility axis. The leaf litter of one of the Lakim paleosols contained leaves of both *Juglandiphyllites cryptatus*, a moderate sclerophyll, and *Metasequoia* sp. cf. *M. heerii*, a marked sclerophyll (Fig. 2). Such variation in ecological polarity of species within ecosystems is widespread today and may be interpreted as ecological niche partitioning. Ecological polarity of an ecosystem is not neces-

sarily identical to that of its individual, averaged, or common species, because of incumbency, biogeography, seasonality, and other reasons (Westoby et al. 2002).

From an evolutionary perspective, particular soils provide particular challenges to which different species adapt at different rates. Both Eocene *Meliosma* and Oligocene *Juglandiphyllites* were adapted to the hardship of waterlogging, whereas their living relatives are mainly adapted to the nutrient shortages of rain forest Oxisols. Living *Meliosma* has diversified into a variety of habitats including river margins that give its common name of aguacatilla (Gentry 1980), whereas the two living *Oreomunnea* species most closely related to *Juglandiphyllites* are upland evolutionary relicts of a once-diverse group of lowland plants (Stone 1972; Manchester 1987). Unfortunately the evolutionary study of plants evolving into and out of swamp habitats is compromised by the taphonomic limitation that fossil plants are well preserved only in swamp and disturbed sedimentary habitats (Retallack 1998). Nevertheless, this study supports suggestions from the fossil record of Australian angiosperms (Hill 1998) that sclerophylly evolved for tolerating waterlogging may later serve for tolerating infertility (particularly low phosphorus), and even aridity.

Taphonomic limitations extend to all the fossils found in paleosols. Their fossil record would be complete if each paleosol preserved fossil leaves, wood, fruits, snails, and bones, and if all the different parts of fossil plants were easily reconstructed. However, fossils of any kind are extremely rare in well-drained tropical Oxisols and Ultisols. Bones and snail shells are mostly found in calcareous Inceptisols and Mollisols, and fossil plants in non-calcareous Entisols and Inceptisols (Retallack 1998). Thus hardships for fossil plants preservable in the fossil record are mostly related to soil waterlogging and stagnation, and hardships for fossil snails and mammals preservable in the fossil record are mainly related to soil aridity and saltiness.

Other Applications of Ecological Polarity

Ecological polarity studies are most effective when applied to closely related organ-

isms, such as swamp cypresses (Fig. 2) and canids (Fig. 4). This pilot study explored a wide application of these concepts, finding both successes and limitations. Applying the concept of ecological polarity well back into geological time and to other kinds of organisms will require new measures and proxies. The proxy morphospaces suggested here could be applied at least as far back as the earliest angiosperms (Wing and Boucher 1998), and probably back to the late Devonian origin of seed and leaves. For example, the Pennsylvanian seed fern *Callospermation pusillum* produced enormous numbers of small ovules and great clouds of wind-dispersed pollen, and had a weakly woody, scrambling habit like living breeders. Contemporaneous *Pachytesta illinoensis*, on the other hand, was a small tree that produced only a few large seeds, and large, complex pollen organs with enormous (500 μm) prepollen probably dispersed by insects, as in competitor plants today. Mid-Carboniferous *Lagenostoma lomaxi* was a small shrub with almost all exposed parts of the plants covered in glandular hairs of presumed defensive function, a tolerator characteristic (Retallack and Dilcher 1988). Before the late Devonian, land plants had photosynthetic axes rather than leaves and also lacked seeds (Kenrick and Crane 1997), so that the ecospace proxies chosen here would not work. Nevertheless, changes both in spore size and number and in sclerenchyma of leaves of Pennsylvanian tree lycopsids parallel trends in seed size and number, and in vein density, though at different scales (Bateman et al. 1992). Early Paleozoic land plants, land animals, and paleosols have been considered in terms of the breeder-competitor-tolerator trichotomy in nonquantitative terms (Beerbower 1985; Retallack 2000b, 2001). Quantitative study of Early Paleozoic and Precambrian terrestrial ecosystems will require new proxy ordinations, perhaps including carbon isotopic indicators of ecosystem type.

Ecological polarity could also be applied to human cultures. Plausible examples of breeder cultures are represented by Lapita pottery distributed widely through Polynesia as birds became extinct around 6 Ka, and by Clovis spear points that littered North America as

large mammals became extinct at 10 Ka (Flannery 1994). The traditional Inuit of Alaska and Koori of central Australia are cultures well adapted to scarcity, as in tolerators. The martial emphasis of Imperial Roman society and its domination of the most fertile regions of Europe and North Africa are similar to competitor adaptations and habitats. Quantification of cultural ecospace may require proxies based on material artifacts.

Conclusions

Ecological polarities can be defined as general communal roles, reflected by adaptations or suites of adaptations, toward which organisms, communities, and societies evolve. There are many ecological polarities, but much morphological and ecological diversity can be explained by just three: breeders, competitors and tolerators. Breeders emphasize reproduction, competitors emphasize resource acquisition and tolerators emphasize survival of hardship. Environments that select for breeders have abundant little-exploited resources, whereas competitors are favored in fertile environments in which nutrient supply does not meet demand, and tolerators are favored by environments lacking in important resources. Breeders, competitors and tolerators are useful as categories (Tables 1–3), but are more informative as quantified axes, or polarities (Grime 2001; Westoby et al. 2002). These polarities can be recognized among plants, animals, and communities, living and fossil (Figs. 2, 4, 6, 7).

Ecological polarities have a fractal character, in the sense that they are independent of taxonomic scale, and implied evolutionary divergence time. Breeder, competitor, and tolerator species can be found within genera, within families, and within larger groups of organisms (Grime 2001). Breeder, competitor, and tolerator components can be recognized within, as well as between, different communities. Different proxy measures may be needed to resolve differences between taxa at different taxonomic levels (Westoby 1998).

Although ecological polarities of living creatures and ecosystems are many and varied (Tables 1–3), the options for such studies of fossils are limited. The few species of fossil

plants, mammals, and snails studied (Tables 8–10) are the only ones out of hundreds of fossil species known from the Clarno and John Day Formations (Fremd et al. 1994; Retallack et al. 2000) for which there are adequately preserved fossil seeds and fruits, snail shell apices and apertures, and skulls with most incisors as well as molars and canines. In contrast, this approach could be applied to all 1195 successive paleosols now logged in the Clarno and John Day Formation (Retallack 2004; Retallack et al. 2000), as well as to thousands of paleosols off that line of measured section, if it were not for the expense of all the chemical analyses needed. Thus the few fossil taxa and paleosols analyzed here are all that are currently suitable or affordable for study.

Quantitative studies of adaptations for ecological polarities allow assessment and ordination of inferred ecological preferences of living and extinct organisms. Paleosols that supported the fossil creatures provide useful supporting evidence of past ecological conditions, such as the narrower apertures of snails in paleosols of drier climates with shallower calcic horizons (Retallack 2004), and the sclerophyllous leaves of *Meliosma* and *Juglandiphyllites* leaves in nutrient-poor swamp paleosols (Retallack et al. 2000). Furthermore, ecological preferences can be demonstrated, as in the case of Oligocene oaks and maples, rather than assuming paleoecological roles comparable to those of related living plants.

Ecological polarities can be approximated by a variety of morphospaces and chemospaces within which adaptations can be quantified (Westoby et al. 2002). Evolutionary trends of specialization toward breeder, competitor, or tolerator poles can be inferred from the fossil record, for example the evolutionary trend toward molarization in herbivorous mammals. New adaptive breakthroughs and evolutionary radiations also are apparent from such morphospace analysis, such as the reoccupation of creodont niches by nimravids, canids, and felids. Evolutionary polarities thus suggest a new system of metrics for ordering morphological and ecological data, and for reassessing the process of evolution.

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