

Evolution of Grasses and Grassland Ecosystems

Caroline A.E. Strömberg

Department of Biology and the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington 98195; email: caestrom@u.washington.edu

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Abstract

The evolution and subsequent ecological expansion of grasses (Poaceae) since the Late Cretaceous have resulted in the establishment of one of Earth's dominant biomes, the temperate and tropical grasslands, at the expense of forests. In the past decades, several new approaches have been applied to the fossil record of grasses to elucidate the patterns and processes of this ecosystem transformation. The data indicate that the development of grassland ecosystems on most continents was a multistage process involving the Paleogene appearance of (C₃ and C₄) open-habitat grasses, the mid-late Cenozoic spread of C₃ grass-dominated habitats, and, finally, the Late Neogene expansion of C₄ grasses at tropical-subtropical latitudes. The evolution of herbivores adapted to grasslands did not necessarily coincide with the spread of open-habitat grasses. In addition, the timing of these evolutionary and ecological events varied between regions. Consequently, region-by-region investigations using both direct (plant fossils) and indirect (e.g., stable carbon isotopes, faunas) evidence are required for a full understanding of the tempo and mode of grass and grassland evolution.

Phytolith:

microscopic silica body produced in the tissues of many plants

Macroflora:

assemblage of fossilized leaves, stems, and/or fruits and seeds

Paleosol: fossilized soil

Palynoflora:

assemblage of fossilized pollen and spores (so-called palynomorphs)

INTRODUCTION

Grasses, the family Poaceae, are among the most important extant clades of vascular plants. The group, which now inhabits all major landmasses, exhibits tremendous taxonomic richness (~11,000 species), ranges from herbs to the tree-like bamboos, and occupies warm and cold deserts to rainforests (Gibson 2009). Grasses are Earth's most important crop plant (e.g., rice, corn, cereals) and supply humans with important building material (bamboo) and biofuels (e.g., switchgrass). Grass-dominated habitats, which encompass temperate grasslands, tropical savannas, and cropland, cover up to 40% of Earth's land surface (Gibson 2009). Through unique ecosystem properties (e.g., high albedo, low carbon storage capability, high silica reservoir), grasslands exert strong influence on global climate as well as the carbon and silica cycles (Kidder & Gierlowski-Kordesch 2005, Sage 2004). The Cenozoic rise to dominance of grasses undoubtedly influenced climate systems and was central to the evolution of grass-eating animals (Jacobs et al. 1999, Pagani et al. 2009). Understanding this ecological transformation provides the evolutionary context for today's grass-dominated ecosystems and may help us disentangle their complex controls—as well as predict how they will respond to ongoing anthropogenic climate change.

Not surprisingly, therefore, the origin and subsequent evolution of grasses and grasslands continue to be major foci in evolutionary biology and paleontology (e.g., Edwards et al. 2010, Jacobs et al. 1999, Osborne 2008, Thomasson 1987, Tiplle & Pagani 2007). In the past decade, the use of new types of grass fossils (e.g., phytoliths) and proxies for grasses and grasslands in the fossil record (e.g., compound-specific isotope analyses) (Huang et al. 2007, Strömberg 2004), development of large paleontological databases (Fortelius 2010), application of novel analytical methods to new and old data (Mendoza & Palmqvist 2008), and the explicit incorporation of a phylogenetic framework into grassland research (Edwards & Smith 2010, Osborne & Freckleton 2009) have vastly expanded our insights into grassland ecosystem evolution. As a result, we have a different and substantially more nuanced perspective on the ecosystem changes to which grasses significantly contributed.

This review outlines our current understanding of when and where grasses evolved and when and where grasslands (both C₃ and C₄ dominated) spread. Different hypotheses for which factors influenced these major evolutionary and ecological developments are also assessed.

THE RECORD OF ANCIENT GRASSES AND GRASSLANDS

Both direct and indirect records have contributed to shaping our view of ancient grasses and grasslands. The direct record of grasses, including macrofossils (fossilized leaves, stems, reproductive structures) and microfossils [pollen, plant silica bodies (phytoliths)], is notoriously spotty and suffers from several biases. First, the arid, well-drained, highly oxidative, “upland” environments that open-habitat grasses typically occupy rarely preserve organic fossils (pollen and macrofossils) (Retallack 1990a). Second, herbaceous plants such as grasses are generally underrepresented in macrofloras. Third, Poaceae macroremains seldom show cellular preservation and can therefore be hard to distinguish from other, closely related monocotyledonous plants. Fourth, even though grasses are wind pollinated, and consequently, their abundant pollen is usually well represented in modern pollen assemblages (10–94%, but regularly >>25%) (Leopold et al. 1992, Vincens et al. 2006a), a potential bias exists against grasses in paleosol palynofloras because grass pollen preferentially degrades with time under typical arid land soil conditions (Bryant et al. 1994). Finally, pollen morphology is uniform within Poaceae, prohibiting taxonomic distinctions below the family level and making it difficult to estimate species diversity. This is especially important because the most abundant plant fossils are pollen grains.

Phytoliths, microscopic silica bodies formed in the tissues of many plants, have recently started providing direct evidence for Cenozoic grasses. They are taxonomically diagnostic, sometimes down to the genus level, within Poaceae (Piperno 2006) and have proven reliable indicators of the proportion of grasses versus trees in many ecosystems (Strömberg 2004). Because they can preserve in the well-oxidated sediment types that are often devoid of pollen and macrofossils (Retallack 1990a), phytoliths have helped close vast gaps in the fossil record of grasses (Strömberg 2005).

Several indirect proxies have also been applied to track the evolutionary history of grasses. For example, mammalian functional morphology has long been used to infer grass-dominated habitats, based on the assumption that traits common in mammals that eat grasses or live in grasslands today (powerful chewing muscles, long legs, large body size, tooth morphology) evolved in response to the spread of this new vegetation type (Jacobs et al. 1999). In particular, high-crowned (hypsodont) cheek teeth were regarded as an adaptation to feeding in grasslands, where silica-rich grasses and dust wear down herbivore teeth (MacFadden 1997). However, modern faunal studies indicate that hypsodonty correlates more closely with habitat openness, feeding height, and levels of aridity than with proportion of grass consumed (Eronen et al. 2010a, Mainland 2003, Mendoza & Palmqvist 2008). Therefore, various measures of hypsodonty—for example, mean faunal hypsodonty (the sum of hypsodonty scores for an herbivore fauna divided by the number of taxa) (Fortelius et al. 2002)—are today used to infer generally open habitats and dry climates rather than grasslands per se (Flynn et al. 2003, Janis et al. 2004). Faunal body-size distribution (e.g., cenograms) is another proxy for vegetation type, relying on the observation that faunas occupying open habitats tend to lack medium-sized species (Travouillon et al. 2009).

Study of mammalian tooth wear focuses at the scale of microwear (the pits and scratches that hard particles in/on food items leave on the enamel surface during mastication) and mesowear (the effect of food abrasion and attrition on the shape and height of molar cusp apices). The dental enamel of modern grazing ungulates tends to have more and coarser scratches than that of browsers. Modern grazers also have deep gouges produced by grit (Solounias & Semperebon 2002) and develop blunter cusps and low molar crown relief (Fortelius & Solounias 2000). Although these patterns are used to distinguish grazers from browsers and, indirectly, infer vegetation type, several factors complicate the interpretation of tooth wear. Microwear records only the last day(s) of an animal's life, providing a potentially biased view of its diet ("the last supper syndrome," Solounias et al. 1994). Also, horizontal (shearing) jaw movement may distort gouges from grit to resemble scratches typical of grasses (Billet et al. 2009).

Analysis of fossil soils (paleosols) provides another indirect way of detecting ancient grasslands. Modern grassland soils are characterized by granular structures called mollic epipedons, which are also preserved in geologic strata (Retallack 1997). This information has been combined with rainfall estimates based on the depth to the calcic horizon within the paleosol to help characterize the grassland type (Retallack 2007).

Finally, stable carbon isotopes permit reconstruction of the evolution and spread of grasses that utilize C_4 photosynthesis (see below). These grasses fractionate carbon differently from C_3 plants (over half of grasses and most other plants) and C_4 grass tissues have heavier, or more positive isotopic ratios ($\delta^{13}C$) than C_3 tissues (Cerling et al. 1997b). This difference in $\delta^{13}C$ is preserved in grass pollen (Urban et al. 2010), carbonates that form in grassland soils (Quade et al. 1989), and the teeth and bones of herbivores (Cerling et al. 1997b). Because aridity affects the isotopic signal of plants, variation within the spectrum of isotopic ratios representative of C_3 vegetation can help distinguish plants or vertebrates living in more open (arid) habitats from those under a forest canopy (Zanazzi & Kohn 2008).

Continued development of these diverse lines of evidence has allowed us to increasingly dissect the complex evolutionary history of grasses and grasslands. Below I outline our current

Hypsodont

dentition: having high-crowned cheek teeth

BEP: clade of grasses that includes grass subfamilies

Bambusoideae, Ehrhartoideae, and Pooideae

PACMAD: clade of grasses that includes grass subfamilies

Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae

understanding of the tempo and mode of Poaceae diversification and the spread of grass-dominated habitats.

OVERVIEW OF ORIGIN AND DIVERSIFICATION OF POACEAE

The past two decades of phylogenetic work using molecular and morphological data have revolutionized our understanding of Poaceae relationships. A growing consensus holds that the vast majority of grass diversity falls in either of two clades, the so-called BEP (Bambusoideae, Ehrhartoideae, Pooideae) and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae), although the relationships within these groups remain somewhat unclear (Christin et al. 2008, GPWG 2001, Vicentini et al. 2008). Basal grasses and bambusoids are primarily forest dwelling, and Ehrhartoideae are found in moist, closed or open habitats (Bouchenak-Khelladi et al. 2010). The ability to tolerate the (often arid) conditions in grassland habitats evolved in members (heretofore referred to as open-habitat grasses) of the Pooideae and the PACMADs independently, either near (or below) the base of these clades (Kellogg 2001, Osborne & Freckleton 2009) or, in the case of Pooideae, potentially multiple times within the clade (Bouchenak-Khelladi et al. 2010). Within the PACMAD clade, grasses evolved C₄ photosynthesis at least 9 and perhaps up to 20 times (Edwards & Smith 2010). C₄ photosynthesis allows grasses to fix carbon efficiently under conditions of high temperatures, aridity, low atmospheric CO₂, high salinity, and waterlogging; as a result, C₄ grasses are favored in tropical-subtropical lowlands and also in regions with warm-season precipitation (Sage 2004). In contrast, grasses with the ancestral C₃ pathway dominate at high latitudes/altitudes and under high pCO₂ as well as in climates with cool-season precipitation.

Although still poor, the pre-Miocene record of grasses has started to reveal the broad patterns of Poaceae diversification. Whereas many Cretaceous and Paleocene fossil grass pollen initially assigned to the grasses have now been assigned to sister taxa of the Poaceae (e.g., Restionaceae) on the basis of details of pollen wall structure (Linder 1986), currently accepted pollen and macrofossil records reveal that grasses were established in northern South America, northern Africa, and India in the latest Cretaceous and Paleocene (**Figure 1a**). Cuticles with phytoliths of several major modern Poaceae clades (Ehrhartoideae, BEP, PACMAD) have been found on the Indian subcontinent in the latest Cretaceous (Prasad et al. 2005), implying that by this time the BEP and PACMAD lineages had split and that at least the BEP clade had diversified further (**Figure 1b**). Moreover, highly hypsodont, gondwanatherian mammals from the Late Cretaceous of South America, Madagascar, and India and the Paleogene of South America and Antarctica may represent the earliest evolution of grazers (Prasad et al. 2005, Wilson et al. 2007).

The Eocene saw a nearly worldwide distribution of grasses with Early Eocene records ranging from Great Britain and the United States to Australia (**Figure 1c**). During the Middle Eocene–earliest Oligocene, members of more derived Poaceae subclades began to appear, including poods and potential chloridoids (Patagonia, Argentina) (Zucol et al. 2010), bamboos with affinity to the genus *Chusquea* and stipoid poods (North America) (Manchester 2001, Strömberg 2005), and the first C₄ PACMADs (western Europe) (Urban et al. 2010). These early records show that open-habitat grasses had started diversifying by the Middle Eocene, up to ten million years earlier than previous estimates based on molecular dating of grass phylogenies (e.g., Bouchenak-Khelladi et al. 2010, Bremer 2002).

The rich record of Miocene grass fossils, much richer than the pre-Neogene fossil record, demonstrates that Poaceae, especially open-habitat grasses, had become abundant in many regions. Several fossils resemble modern genera, pointing to further radiation within Pooideae and PACMAD (**Figure 1c**).

Where and in what context did grasses evolve? Fossil data and phylogenetic inference place the Late Cretaceous common ancestor of Poaceae in northern Gondwana (South America or Africa) (Bouchenak-Khelladi et al. 2010, Bremer 2002). However, it is unclear how crown group Poaceae achieved a nearly worldwide distribution by the Eocene. In light of the early presence of grasses in India, Prasad et al. (2005) suggested that the BEP and PACMAD clades spread within Gondwana before India became geographically isolated in the Late Cretaceous (~80 Ma), either through vicariance or dispersal via available land bridges (e.g., the Kerguelen Plateau, southern Indian Ocean) (Hay et al. 1999). This scenario is consistent with an African origin for the BEP clade inferred from phylogenetic analysis (Bouchenak-Khelladi et al. 2010). Alternatively, the modern subclades may have evolved in India and reached all other continents after India's Early Eocene collision with Asia (55–50 Ma) (Clyde et al. 2003). Both scenarios are problematic—the first implies earlier than predicted diversification of Poaceae; the second requires rapid migration across hypothesized dispersal barriers—and discriminating between them is difficult with available data (Rana & Wilson 2003).

Consistent with phylogenetic comparative analyses indicating that Poaceae was ancestrally adapted to warm, relatively mesic, closed environments (Edwards & Smith 2010, Osborne & Freckleton 2009), most Cretaceous-Paleocene grass fossils are found in tropical areas (**Figure 1a**) in floras that indicate wet forests or mangrove vegetation (Macphail & Hill 2002). An exception is the Late Cretaceous grasses from India, where sedimentology indicates seasonally arid climates (Samant & Mohabey 2009). Eocene grasses ranged from tropical to warm temperate climate zones (**Figure 1c**), suggesting expanded climatic tolerances during this time.

ASSEMBLY OF THE GRASSLAND BIOME: CONTINENT-SPECIFIC PATTERNS

The evolutionary history of grasslands can be broken down into several distinct stages: (*a*) the Paleogene appearance of C₃ open-habitat grasses; (*b*) the Paleogene appearance of C₄ open-habitat grasses; (*c*) the mid-late Cenozoic emergence of open, C₃ grass-dominated habitats; and finally, in some regions, (*d*) the late Neogene shift to C₄-dominated grass-dominated habitats. In reviewing continental patterns of grassland biome assembly below, I show that the time separating these stages most likely varied widely between continents and regions. I also argue that the evolution of hypsodonty and the grazing habit signify two additional steps in the formation of grassland ecosystems that did not necessarily occur simultaneously with each other or any of the four steps outlined above.

North America

Analysis of the exceptionally rich Cenozoic fossil record of North America has revealed that grassland evolution was complex. Whereas the earliest grasses on the continent are known from earliest


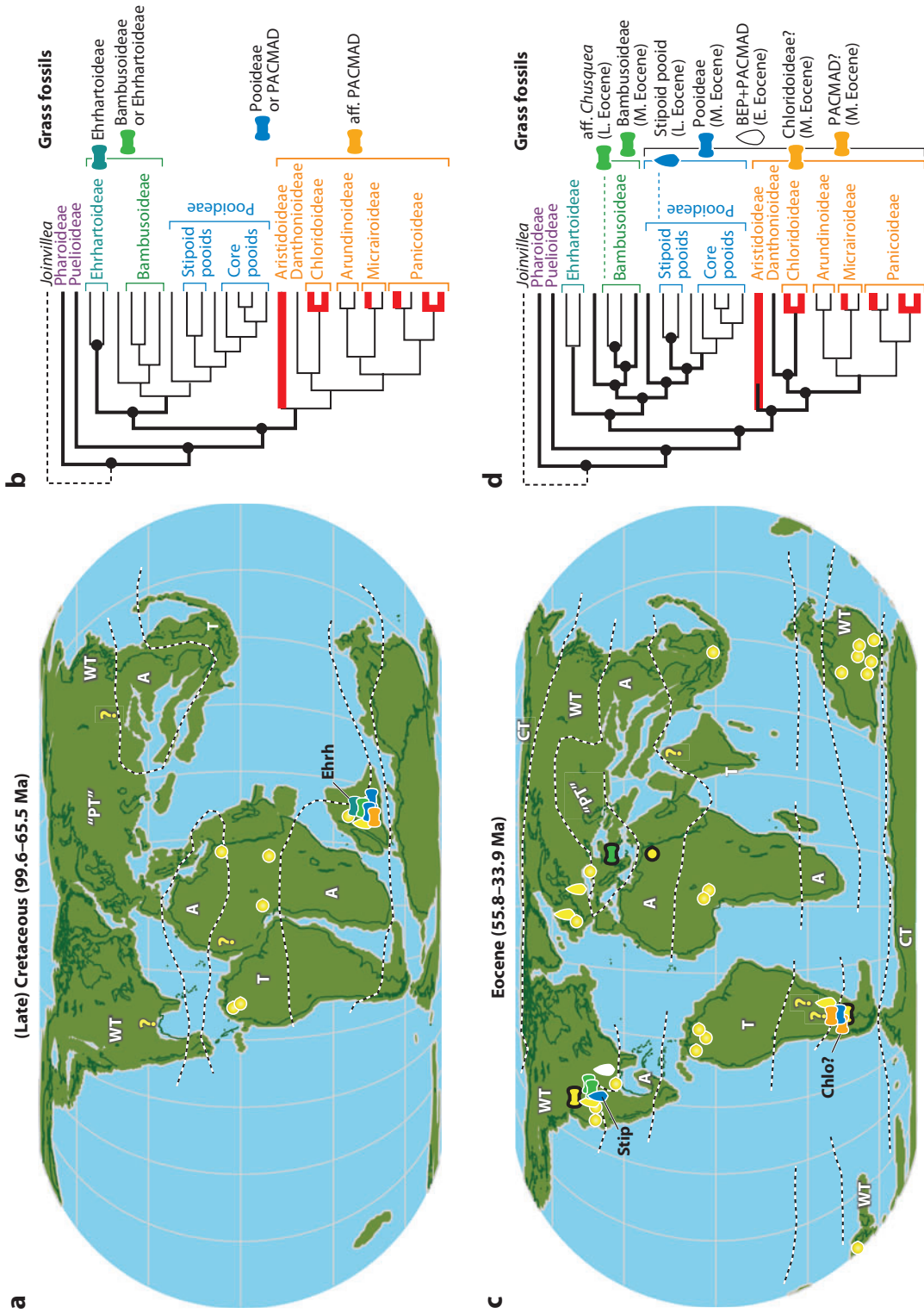
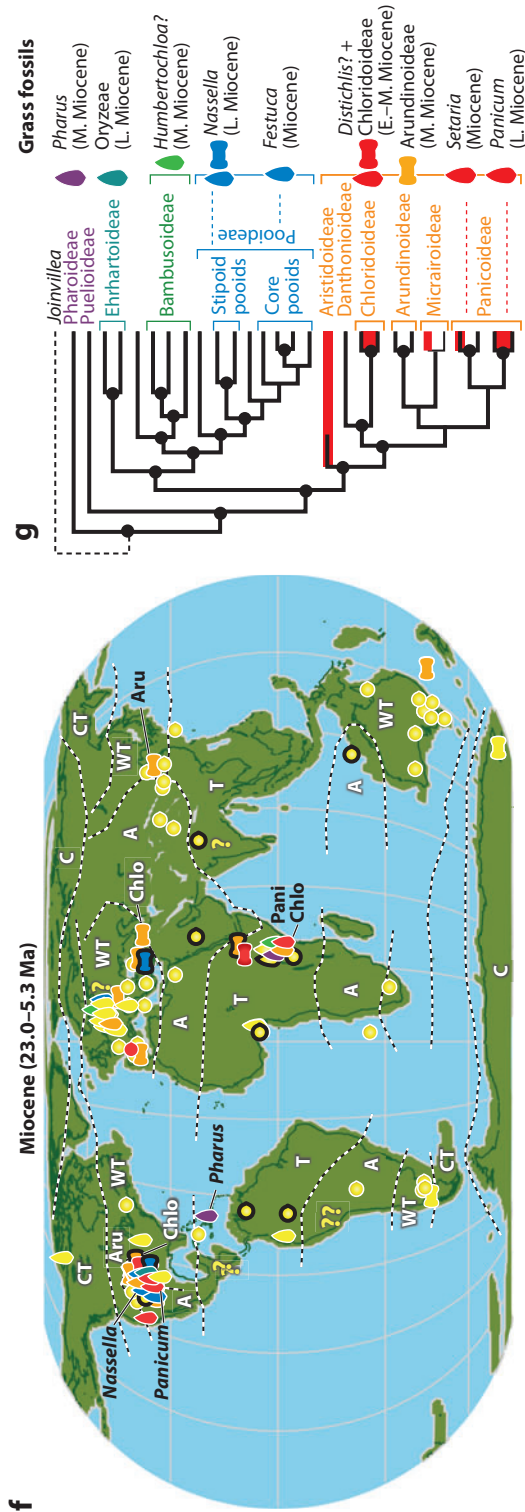
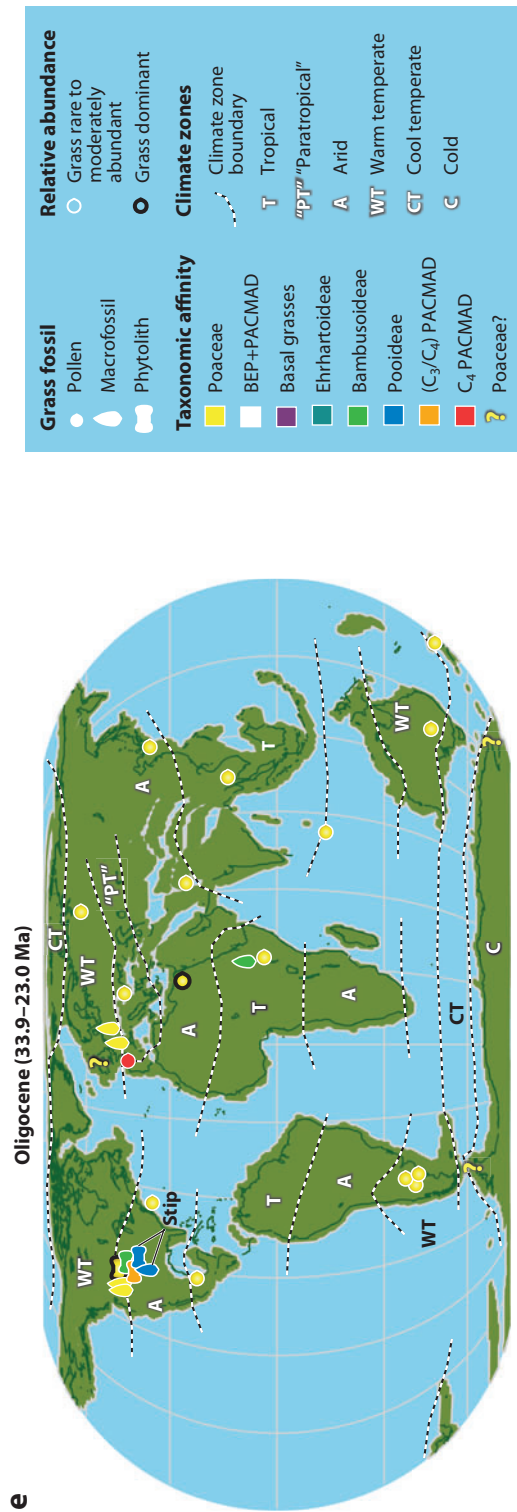
 Supplemental Material

Figure 1

Grass fossils through time: biogeographical distribution relative to climate (*a, c, e, f*) and phylogenetic distribution (*b, d, g*). (*a, b*) Late Cretaceous (Maastrichtian), (*c, d*) Eocene, (*e*) Oligocene, (*f, g*) Early-Middle Miocene. Maps: Aru, Arundinoideae; Chlo, Chloridoideae; Ehrh, Ehrhartoideae; Pani, Panicoideae; Stip, stipoid pooid. Phylogenies: Bold red lines represent C₄ lineages; bold black lines and black filled circles represent lineages and divergencies inferred to have occurred on the basis of fossils present in that time slice (only). See **Supplemental Material** for data sources, and for Paleocene grass fossil distribution, see **Supplemental Figure 1** (follow the **Supplemental Materials link** from the Annual Reviews home page at <http://www.annualreviews.org>). Other abbreviations: BEP, clade of grasses that includes grass subfamilies Bambusoideae, Ehrhartoideae, and Pooideae; PACMAD, clade of grasses that includes grass subfamilies Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae.





Eocene (55 Ma) macrofossils (Crepet & Feldman 1991), different lines of evidence have suggested three competing scenarios for when and how open, grass-dominated vegetation spread. Macrofossils and palynofloras point to a scenario whereby North America was covered with subtropical-tropical evergreen or semideciduous dicotyledonous forests during the Early-Middle Eocene (Graham 1999); grasses were widespread, if rare, during this time (**Figure 1c**). In the Middle Eocene, the continental interior saw the formation of open, dry savanna woodlands, which, based on the scarcity of grass pollen and macrofossils, are reconstructed as consisting exclusively of small trees and shrubs (Leopold et al. 1992). These open, but largely grass-free habitats apparently persisted in central North America throughout the Oligocene; however, note that grasses may have been more abundant (13%) in arid land vegetation farther south, judging by Early Oligocene palynofloras from southern Mexico (Ramirez-Arriaga et al. 2006). Open-habitat grasses appeared in North America during the Late Eocene–Early Oligocene, as indicated by stipoid poid fruits from Colorado (e.g., Manchester 2001). Nevertheless, Great Plains macrofloras and pollen suggest that open, grass-dominated habitats did not spread until the Middle-Late Miocene (e.g., Bolick et al. 1995, Thomasson 1990).

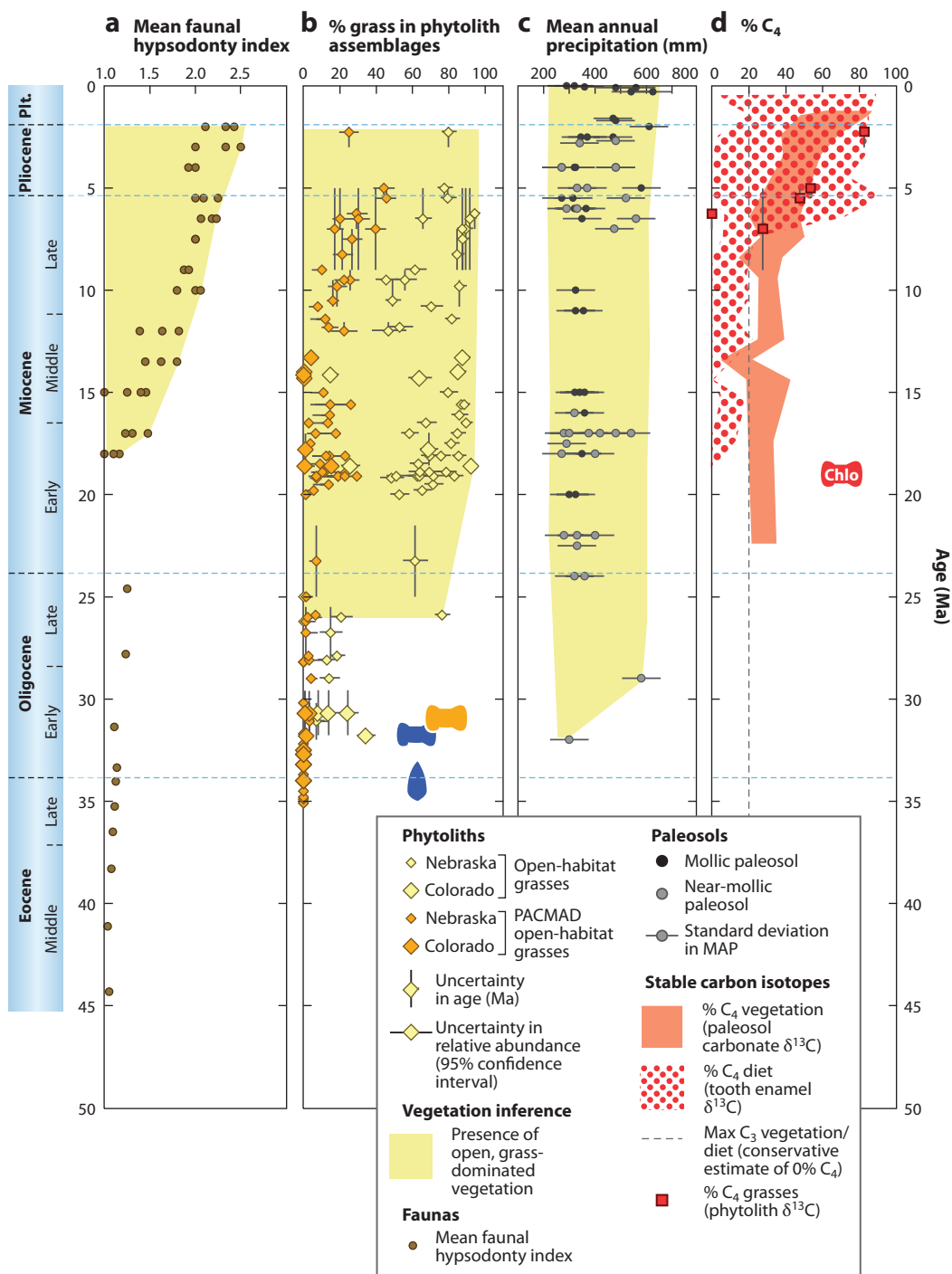
In a second scenario, phytolith assemblages from the central Great Plains indicate that (stipoid) poid and PACMAD open-habitat grasses that had originated by at least 42–38 Ma (see South America, below) migrated into subtropical, closed forest with abundant palms and bamboos (Strömberg 2005) by the earliest Oligocene (~33 Ma). They persisted as minor elements in forest openings or in the understory until the Late Oligocene–Early Miocene, when they expanded at the expense of trees and bamboos to form poid-dominated savanna woodlands (**Figure 2b**). Phytoliths indicate a mix of grassy and more wooded patches throughout the Early-Middle Miocene until the latest Miocene, when more uniformly open grasslands apparently spread (Strömberg & McInerney 2011). A similar change from forests to savanna woodlands occurred somewhat later (late Early Miocene) in the northern Rocky Mountains (Strömberg 2005). However, the Eocene–Oligocene vegetation preceding this shift differed from vegetation farther south in having fewer palms, and in grass-community composition. Rather than being dominated by bamboos, these northern grass communities had high abundances of grasses of unknown ecology but with potential affinities to open-habitat grasses. Occasionally, the unknown grasses also dominated vegetation overall; however, it is unclear whether these signify open, arid habitats.

Paleosol data from the central Great Plains, northern Rocky Mountains, and Pacific Northwest offer a third scenario for grassland evolution (**Figure 2c**). The appearance of near-mollic paleosols suggests that open-habitat grasses expanded ecologically by the Earliest Oligocene, resulting in a mix of humid-dry woodlands, shrublands, and bunch grasslands in these areas (Retallack 1997, Retallack 2007). The presence of open grasslands to woodlands in the Late Eocene–Early Oligocene is supported by paleosol root traces and burrowing structures typical of grasslands from northeastern Colorado (Hembree & Hasiotis 2007). Presumably C₃-dominated, short-sod

▶ Supplemental Material

Figure 2

Grassland biome assembly, Great Plains, USA. (a) Faunal record. (b) Phytolith assemblages (earliest poid and PACMAD fossils marked). (c) Paleosol record, plotted against mean annual precipitation (MAP, in mm) inferred from depth to calcic horizon. (d) Evidence for C₄ grasses (earliest grass fossil, ranges of stable carbon isotope ratios from paleosol carbonates, ungulate tooth enamel, phytoliths). See **Figure 1** for grass fossil symbols and systematic affinities. Max C₃ vegetation/diet: The maximum isotopic value for C₃ vegetation/diet under arid climates is identical to isotopic values corresponding to 20% C₄ grasses. See **Supplemental Material** for data sources (follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>). Abbreviations: Chlo, Chloridoideae; PACMAD, Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae; Plt., Pleistocene.



grasslands are thought to have spread in drier habitats in the Early Miocene (20 Ma) on the basis of the occurrence of typical mollic epipedons in soils indicating arid conditions (Retallack 2007).

The succession of mammalian faunas in North America, particularly from the Great Plains, provides a detailed view into faunal response to Cenozoic vegetation change. *Stenomyline* camels and leptauchiniine oreodonts evolved hypsodonty in the Oligocene, but given other morphological aspects, they are believed to have been adapted to life in rocky habitats, rather than grasslands (Janis et al. 1998). The increasing numbers of mesodont and hypsodont ungulate taxa (e.g., horses) starting in the late Early Miocene (**Figure 2a**) (e.g., Janis et al. 2000) have classically been interpreted as marking the spread of grass-dominated vegetation (Jacobs et al. 1999). However, recent work shows that faunas may have started responding to the opening-up of landscapes even earlier. During the Late Oligocene–Early Miocene, many of the features relating to a pacing gait—viewed as adaptive in open habitats—appeared in several lineages of camelids (Janis et al. 2002). Additionally, mesowear analysis indicates that oreodonts adopted more abrasive diets during the same time frame, although wear consistent with a grazing habit did not occur until the late Early Miocene (Mihlbachler & Solounias 2006). Micro- and mesowear similarly suggest that brachydont Great Plains horses started consuming some grass (or grit) in the earliest Miocene, well before hypsodonty evolved in horses (Mihlbachler et al. 2011, Semperebon 2005).

The spread of C₄ grasses is also richly documented in North America. Middle Miocene silicified shoots displaying “Krantz” anatomy typical of many C₄ grasses constitute the earliest unequivocal C₄ grass fossils (Nambudiri et al. 1978), but rare phytoliths of likely C₄ chloridoids occur in the central Great Plains by ~19 Ma (Strömberg 2005). Whereas phytolith assemblages show that PACMADs were moderately abundant in pooid-dominated grass communities through most of the Miocene, chloridoids and other potential C₄ PACMADs became dominant 5.5 Ma; these changes are also mirrored in phytolith $\delta^{13}\text{C}$ values (McInerney et al. 2011). This scenario of moderately abundant C₄ grasses preceding a latest Miocene–Pliocene C₃–C₄ shift is consistent with carbon isotope data from soil carbonate nodules (**Figure 2d**). Both phytoliths and paleosol carbonate $\delta^{13}\text{C}$ also point to significant heterogeneity in plant community composition (tree cover, C₃ versus C₄ grasses) before and during the C₃–C₄ shift (Fox & Koch 2003, Strömberg & McInerney 2011). In contrast, the expansion of grasses into more humid paleosols (**Figure 2c**) has been used to infer that C₄ grasslands formed by 7–6 Ma and were likely dominated by mesic C₄ grasses rather than the xeric chloridoids. Stable carbon isotope ratios from horse tooth enamel indicate that some animals were feeding mainly on C₄ grasses by 6.6 Ma, that is, before all parts of the landscape were C₄ dominated (**Figure 2d**) (e.g., Passey et al. 2002).

South America

Much of what is known about South America’s ancient grasslands comes from faunal and floral sites in Patagonia. Macrofossil and palynological evidence from this region indicates that, although some types of grasses were present by at least the Early Eocene (e.g., Berry 1937), they remained sparse in Eocene–Oligocene tropical to temperate forests (Barreda & Palazzesi 2007, Gayó et al. 2005). Arid-adapted taxa (e.g., composites) indicative of more open environments appeared in the Late Oligocene. By the Early Miocene, shrubby and herbaceous elements, including rare grass pollen, increased slightly in abundance, marking the presence of open, dry habitats (Barreda & Palazzesi 2007). This open, shrubby or herbaceous vegetation remained relatively rare in Patagonia until the Late Miocene and, judging from grass pollen frequency, they did not contain abundant grasses, indicating that grasslands were not widespread in southern South America during most of the Cenozoic (Barreda & Palazzesi 2007). Grasses may have been more prevalent in northern Argentina and Brazil, where pollen assemblages point to the presence of Late Miocene grassy

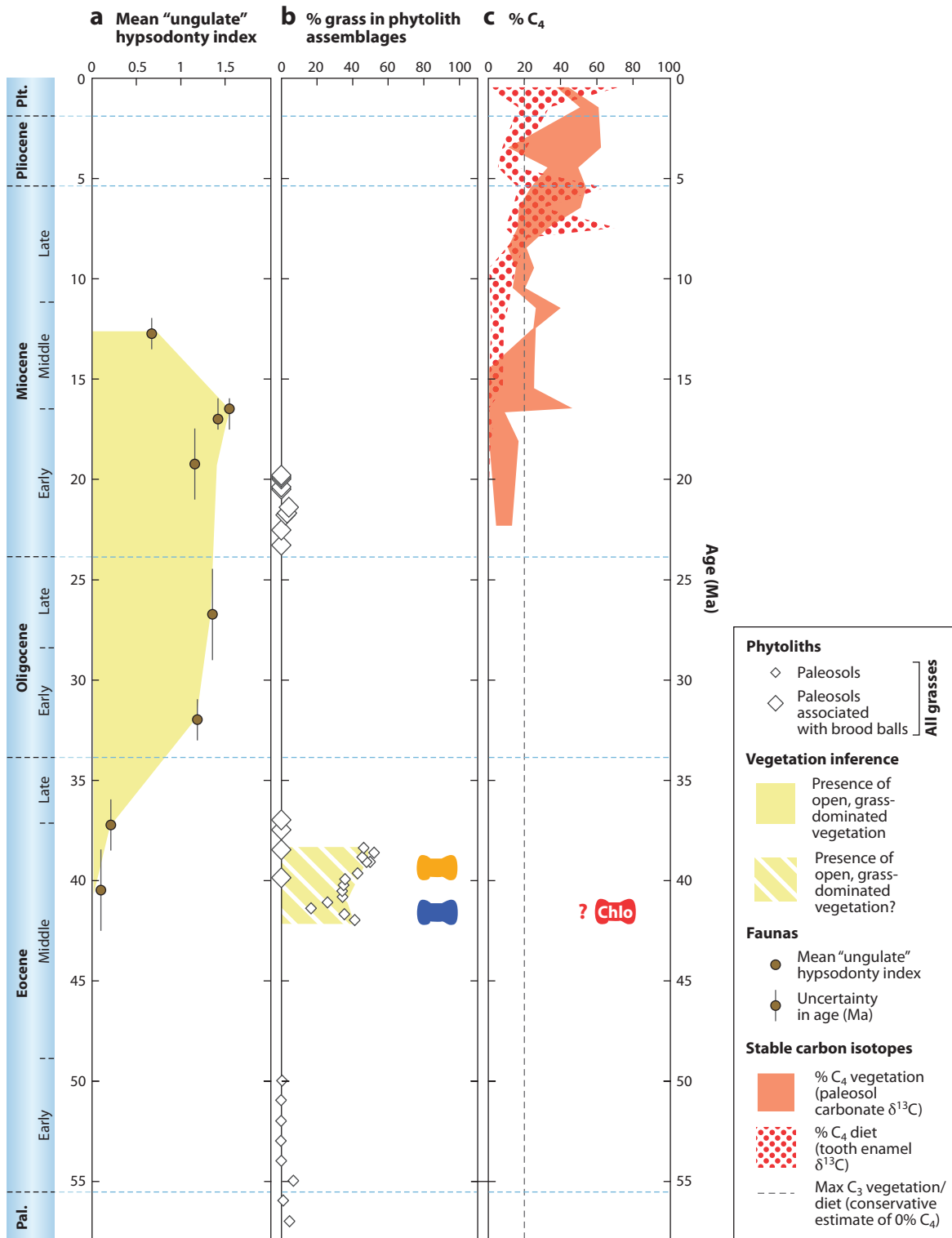
savannas (Latrubesse et al. 2010, Mautino & Anzótegui 2002). Similarly, Venezuelan palynofloras show that grasses became dominant ($\geq 50\%$) by the Early Miocene (Lorente 1986). These comparisons point to latitude as an important consideration when tracking the expansion of open-habitat grasses in South America.

Phytoliths add vital, if contradictory, data to the grassland story in Patagonia (**Figure 3b**). Grasses were apparently rare in the Paleocene–Early Eocene, but by the Middle Eocene, grass forms comprise $> 50\%$ of phytoliths, indicating that grasses were important in vegetation. Most of these grass phytolith morphotypes are not clearly assignable to grass subclades (e.g., truncated rondels) (Piperno 2006), making it hard to evaluate whether the assemblages reflect typical open, grass-dominated vegetation. However, forms diagnostic of pooids, chloridoids, and other PACMADs occur in low abundances, signaling the presence of open-habitat grasses by 42–38 Ma (Zucol et al. 2010). Middle Eocene–Early Miocene paleosols associated with dung beetle brood ball remains from the same stratigraphic sections have produced a very different phytolith assemblage pattern (Sánchez et al. 2010, Strömberg & Stidham 2001) that agrees more closely with pollen and macrofloral data. Accordingly, grasses were very rare in the areas where these brood balls were deposited. In addition, the diet of the dung producers, presumably large, herbivorous meridiungulates, did not include much grass. These results question the traditional assumption, based on the modern association between brood ball accumulations and herding grassland herbivores, that the massive, Eocene–Miocene dung beetle brood ball deposits in Patagonia necessarily reflect savanna habitats (Retallack 1990b).

Rare high-crowned herbivores first appeared in the latest Paleocene–Early Eocene of Patagonia (Reguero et al. 2010), and during the Middle–Late Eocene, hypsodont taxa increased in diversity in dominantly brachydont faunas (**Figure 3a**) (Ortiz-Jaureguizar & Cladera 2006). Nevertheless, cenogram analyses indicate closed, moist forest habitats (Croft 2001). In the Tinguirirican fauna, spanning the Eocene–Oligocene boundary, hypsodont taxa became dominant owing to immigration (e.g., rodents) and in situ crown-height evolution in several endemic groups (Flynn et al. 2003, Reguero et al. 2010). Ecological diversity analysis and cenograms suggest that this fauna inhabited open environments (Flynn et al. 2003, Kay & Madden 1997). Further development of hypsodonty or hypselodonty (ever-growing teeth) in herbivore lineages as well as diversification of already high-crowned taxa have been interpreted as signaling widespread, open vegetation in Patagonia by the Late Oligocene (Ortiz-Jaureguizar & Cladera 2006). However, the continued presence of frugivores, insectivores, and omnivores, including platyrrhine primates, indicates that forested patches persisted on the landscape. By the Late Miocene, herbivore communities consisted largely of hypselodont taxa, whereas groups indicative of subtropical woodlands became rare or extinct (Ortiz-Jaureguizar & Cladera 2006).

The Late Oligocene diversity of hypsodont rodents and the absence of primates in Patagonia compared with sites farther north imply more open habitats at higher latitudes (Ortiz-Jaureguizar & Cladera 2006, Vucetich 1991). Similarly, mammals from northern South and Central America contrast with Patagonian faunas, thereby suggesting predominantly closed Miocene forests or woodlands (MacFadden 2006). Nevertheless, the Late Oligocene fauna at Salla, Bolivia, with its mix of hypsodont notoungulates and brachydont rodents, appear to reflect at least partly open vegetation (Croft 2001, Vucetich 1991). Open habitats at Salla are also supported by tooth-wear analysis of notoungulates, showing that some taxa ingested a substantial amount of abrasives (Billet et al. 2009).

Stable carbon isotope data from soil carbonates from Argentina demonstrate that by 16.5 Ma C_4 grasses were present, and initially relatively abundant, but they did not become dominant until after 7 Ma (**Figure 3c**) (e.g., Kleinert & Strecker 2001). Some herbivores started feeding dominantly on C_4 grasses at about the same time or slightly earlier (~ 8 Ma) (MacFadden et al. 1996).



After their Late Miocene expansion, C₄ grasses were more important in herbivore diets at lower latitudes, indicating a latitudinal gradient in C₄ grass abundance (MacFadden et al. 1996).

Eurasia

Eurasia boasts a rich, well-studied Neogene fossil record. I review the three regions—Europe and Asia Minor (Western Eurasia); Pakistan, Nepal, and India (South Asia); and China—that have received the most intense study over the past several decades.

Western Eurasia. Grass macrofossils and pollen are known from the Early Eocene of England but remain rare in Western Eurasia during most of the Cenozoic (Jacobs 1999). Although northern and central Europe stayed fairly forested throughout the Cenozoic (Kovar-Eder et al. 2008), grasses gained importance in southern Europe and Asia Minor starting in the Miocene. In Spain, palynofloras containing ~30% grass pollen point to open, arid steppe and woodland environments during the Early and Middle Miocene (e.g., Jiménez-Moreno et al. 2007); faunal hypsodonty indices and tooth-wear analyses are consistent with this environmental reconstruction (DeMiguel et al. 2008, Eronen et al. 2010b). A resumption to primarily closed habitats occurred in the Middle Miocene, judging from pollen, phytolith, and faunal data (Barrón et al. 2006, Eronen et al. 2010b, Pinilla & Bustillo 1997). Pollen evidence for open vegetation with abundant grasses and increasingly dry-adapted trees in the eastern Mediterranean comes from the Late Miocene (~10–7 Ma) of Greece (Ioakim et al. 2005) and Anatolia, Turkey, where grass, composite, and chenopod pollen thought to reflect grassy patches expand during the Middle-Late Miocene (e.g., Akgün et al. 2007). Phytolith assemblages from Turkey and surrounding areas suggest that the rise to dominance of (primarily C₃ pooid) open-habitat grasses occurred somewhat earlier, by the Early Miocene, although the exact timing of this event is obscured by the lack of Oligocene data from this area (**Figure 4b**). During most of the Miocene, considerable variation in tree cover is implied by phytoliths, consistent with a mosaic of grass-dominated and more forested habitats, but habitats overall seem to have become more uniformly open toward the Late Miocene (Strömberg et al. 2007). Fossil soil data are rare for Western Eurasia, but paleosols from the Middle Miocene (~15 Ma) locality Pasalar, Turkey, are interpreted as reflecting deciduous dry woodland (Bestland 1990), consistent with the idea of more open, arid habitats by at least the Middle Miocene.

Faunal hypsodonty patterns in Western Eurasia reveal that Early Miocene faunas consisted dominantly of brachyodont ungulates, indicative of subtropical forests (Eronen et al. 2010b). During the Middle Miocene, these were gradually replaced in the eastern Mediterranean by faunas containing more mesodont and hypsodont taxa, typical of open, arid habitats (**Figure 4a**). The Late Miocene (11.1–10.7 Ma) immigration and subsequent adaptive radiation of North American hypsodont hipparionine horses in Western Eurasia coincided with diversification of native ungulates (e.g., bovids) and added substantially to the pattern of increasing hypsodonty among herbivores (Fortelius et al. 2002). The resulting faunal communities, which ranged from the Balkans to Afghanistan during the Late Miocene, featured highly diverse large ungulates and other animals (e.g., giraffids, antelopes, rhinos, hyenas) reminiscent of modern East African savanna faunas (Eronen et al. 2009). However, meso- and microwear analyses of eastern

Figure 3

Grassland biome assembly, Argentina. (a) Faunal record. (b) Phytolith assemblages. (c) Evidence for C₄ grasses. See **Figure 1** for grass fossil symbols and systematic affinities. Abbreviations: Chlo, Chloridoideae; Pal., Paleocene; Plt., Pleistocene.

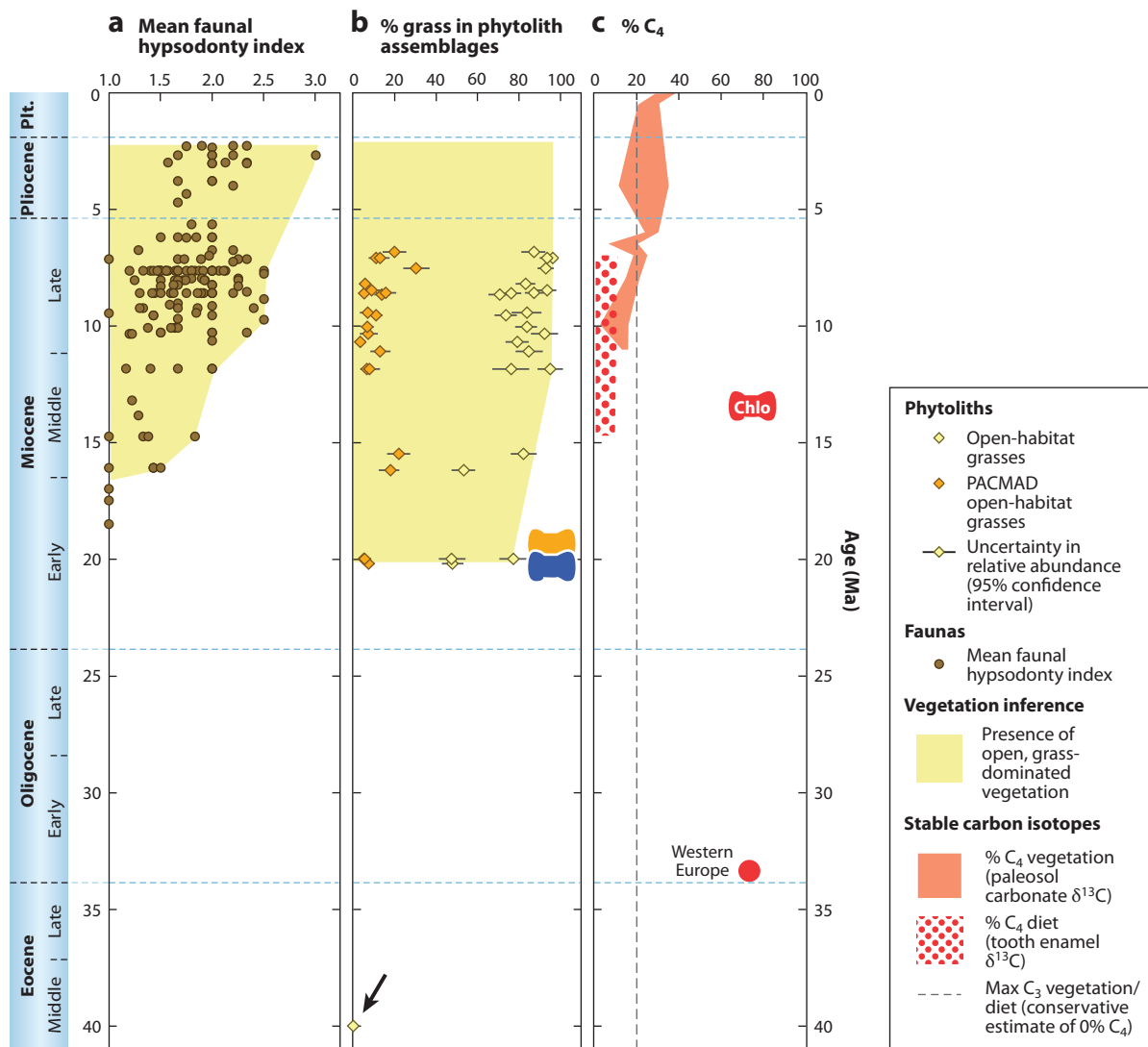


Figure 4

Grassland biome assembly, Greece-Afghanistan, Western Eurasia. (a) Faunal record. (b) Phytolith assemblages. (c) Evidence for C_4 grasses. Arrow in panel *b* highlights outlier. See **Figure 1** for grass fossil symbols and systematic affinities. Abbreviations: Chlo, Chloridoideae; PACMAD, Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae; Plt., Pleistocene.

Mediterranean herbivores have identified a spectrum of diets, from browse to graze, suggesting that Middle-Late Miocene faunas may have occupied a mix of grass-dominated and wooded habitats, rather than typical savanna vegetation (e.g., Merceron et al. 2004, Solounias et al. 2010); faunal composition and diversity comparisons also point to significant heterogeneity in vegetation across the region (Kostopoulos 2009).

Grass pollen with a C_4 signature make up 26–62% of the relatively rare grass pollen (10–15% of the total count) in palynofloras from the earliest Oligocene of southwestern Europe (Urban et al. 2010). Nevertheless, stable carbon isotope data from paleosols and ungulate tooth enamel show

a predominantly C₃ vegetation in Western Eurasia throughout the Neogene (**Figure 4c**) (e.g., Quade et al. 1994). Consistent with this pattern, phytolith data indicate that PACMAD grasses, including in some instances rare C₄ chloridoids, formed a very minor component of the eastern Mediterranean grass communities since the Early Miocene.

China. Although northeastern and southern China remained largely covered in humid, temperate-subtropical forests, palynofloras indicate that open habitats with abundant dry-adapted shrubs (e.g., *Ephedra*) developed in the northwestern and central regions during the Paleogene (Leopold et al. 1992, Sun & Wang 2005). Grasses, however, were rare until the Early Miocene (**Figure 1**). During the Middle-Late Miocene, steppe or grassland vegetation seems to have spread south and east (Jiang & Ding 2009).

The earliest mammal evidence for open habitats is at the Eocene-Oligocene boundary, when faunas dominated by hypsodont rodents and lagomorphs replaced perissodactyl-dominated faunas (Wang et al. 2007). In the Early Miocene, faunas in west-central China were more high crowned than elsewhere in Eurasia, and high levels of hypsodonty persisted in northern and western China and Mongolia throughout the Miocene (Eronen et al. 2010b). In the Pliocene, faunas displayed a substantial increase in mean faunal hypsodonty, pointing to increasingly open habitats.

$\delta^{13}\text{C}$ values for soil carbonates and ungulate tooth enamel from northern China show that C₄ grasses first rose to dominance in vegetation 8–7 Ma, roughly simultaneously becoming abundant in certain ungulates' diets (e.g., Edwards et al. 2010, Passey et al. 2009).

South Asia. Macrofossils and palynofloras from the Oligocene of central Pakistan point to tropical forested habitats with rare grasses (De Franceschi et al. 2008). Forest vegetation has also been reconstructed for the Early–early Late Miocene (18–11 Ma) of northwestern India on the basis of macrofossils and pollen; however, there is evidence for drying or increased seasonality in younger floras (Jacobs 1999). Grass pollen make up 10–35% of palynofloras during the early Late Miocene of central Nepal, suggesting that grasses were present in moderate abundances or in some parts of the landscape; between 8.5 and 6.5 Ma, they increase to >90%, signaling the establishment of grasslands across the landscape (Hoorn et al. 2000). Faunal functional morphology, tooth-wear data, and $\delta^{13}\text{C}$ from tooth enamel (e.g., Badgley et al. 2008) all indicate that parts of the landscape were open and potentially grass dominated by 9.3 Ma (Edwards et al. 2010).

$\delta^{13}\text{C}$ values for fossil soils indicate that C₄ grasses did not rise to dominance in ecosystems until ~7.5 Ma (Behrensmeyer et al. 2007, Sanyal et al. 2010); this timing is consistent with carbon isotopes in *n*-alkanes from marine sediments in the Arabian Sea (Huang et al. 2007). Analysis of stable carbon isotopes of ungulate tooth enamel shows that some herbivores started eating dominantly C₄ grasses approximately one million years earlier (e.g., Badgley et al. 2008). During the C₃–C₄ transition, vegetation was highly heterogeneous, with C₄ grasses primarily inhabiting drier patches (Behrensmeyer et al. 2007).

Africa

The African terrestrial fossil record of the Cenozoic is spotty, but it is complemented by marine and deltaic cores that provide more continuous temporal coverage (Jacobs et al. 1999). Pollen data suggest that grasses were present in northern Africa since the Maastrichtian and may have become dominant in certain habitats by the Late Eocene (**Figure 1**); however, it is unclear whether this pattern reflects aridification of Africa's tropical forests or grass-dominated wetlands (Jacobs & Herendeen 2004). Middle Eocene floras from northern Africa and central Tanzania support the idea that relatively open habitats developed in the continent's interior, but evidence for grasses is

lacking (Jacobs & Herendeen 2004). By the Middle Oligocene, floras in coastal northern Africa similarly point to drier and possibly open habitats (Bown et al. 1982).

The Late Oligocene–Early Miocene paleobotanical record of Eastern Africa is thought to reflect mosaic dry to wet forests and woodlands (e.g., García Massini et al. 2010, Vincens et al. 2006b). An exception is the Early Miocene Mount Elgon paleoflora in Uganda, where abundant *in situ* grasses and seemingly dry-adapted dicotyledons, paleosols, and terrestrial gastropods indicate grasslands mixed with more closed forest woodland (Jacobs 2004, Pickford 2002). The Middle Miocene Fort Ternan site, Kenya, provides clear evidence for a heterogeneous landscape that included relatively open wooded grasslands with predominantly C₃ grasses, on the basis of a palynoflora, anatomically preserved grass leaves, faunal functional morphology, microwear, paleosols, and carbon isotopes of soil carbonates and ungulate tooth enamel (Cerling et al. 1997a, Jacobs et al. 1999). However, paleobotanical evidence for fully open African grasslands is lacking until the Late Miocene–Pliocene, when grass pollen from Niger Delta core samples increase from 2% in the Early Miocene to in some cases >50% after 8.2 Ma (Morley & Richards 1993). By the Pliocene, pollen data imply widespread grasslands in East Africa (Bonnefille 1995).

Whereas Eocene–early Middle Miocene faunas in north Africa and Kenya appear to reflect forest environments (e.g., Bown et al. 1982), Middle Miocene faunas in Kenya, such as Fort Ternan (see above), as well as Maboko and Nyakach Formations, indicate grassland-to-forest mosaic, consistent with paleosol information (e.g., Retallack et al. 2002). Hypsodont hipparionine horses and murine rodents, both classically linked to grassland vegetation, immigrated into Africa in the Late Miocene (hipparionines at 10.5 Ma) (Garcés et al. 1997). Nevertheless, faunal communities typical of modern savanna ecosystems did not become established in East Africa until the latest Miocene, through migration and *in situ* diversification of taxa such as elephants, true giraffes, and hypsodont antelopes (Leakey & Harris 2003). In the Turkana Basin, Kenya, hypsodont ungulates increased to 47% of species between 7 and 1 Ma, likewise pointing to an opening-up of the landscape; still, other areas provide evidence for persisting forests in East Africa until at least 1.8 Ma (Bobe 2006). Faunal structure and tooth wear indicate that relatively open habitats were also in place in Chad by 7 Ma (e.g., Blondel et al. 2010). A pattern similar to that seen in East Africa is evident in southern Africa, with herbivores, particularly rodents, pointing to some opening-up of the landscape by the Early Miocene and spread of open, fire-prone grass-dominated habitats in the Late Miocene (5–4 Ma) (Jacobs et al. 1999).

Carbon isotope ratios of fossil soils and leaf waxes in marine sediments suggest that C₄ grasses formed minor parts of East African vegetation as early as 16 Ma, but they did not become dominant until after 5 Ma (e.g., Feakins et al. 2005, Levin et al. 2004). The presence of likely (C₄) chloridoid phytoliths in Ethiopia at 4.4 Ma supports this scenario (WoldeGabriel et al. 2009). In contrast, certain East African ungulate taxa switched to mainly C₄ grazing as early as 9 Ma, judging by isotopic data (e.g., Cerling et al. 1997a; see Edwards et al. 2010). $\delta^{13}\text{C}$ of ungulate tooth enamel and ratite eggshells from other parts of Africa show that vertebrate herbivores in southern Africa made this dietary shift 4–5 million years later than in eastern and central Africa, implying a latitudinal gradient in the expansion of C₄ grasses (Segalen et al. 2007).

Australia

No reliable grass macrofossils have been reported from Australia (Macphail & Hill 2002), but rare grass pollen occurs in Early-Middle Eocene palynofloras reflecting rainforest to sclerophyllous forest in northwestern, central, and southeastern Australia (**Figure 1c**), suggesting that grasses had become widely established in inland regions (Martin 2006). Following the cool, wet Oligocene, floras indicative of increasing seasonal aridity appear in Australia during the Miocene

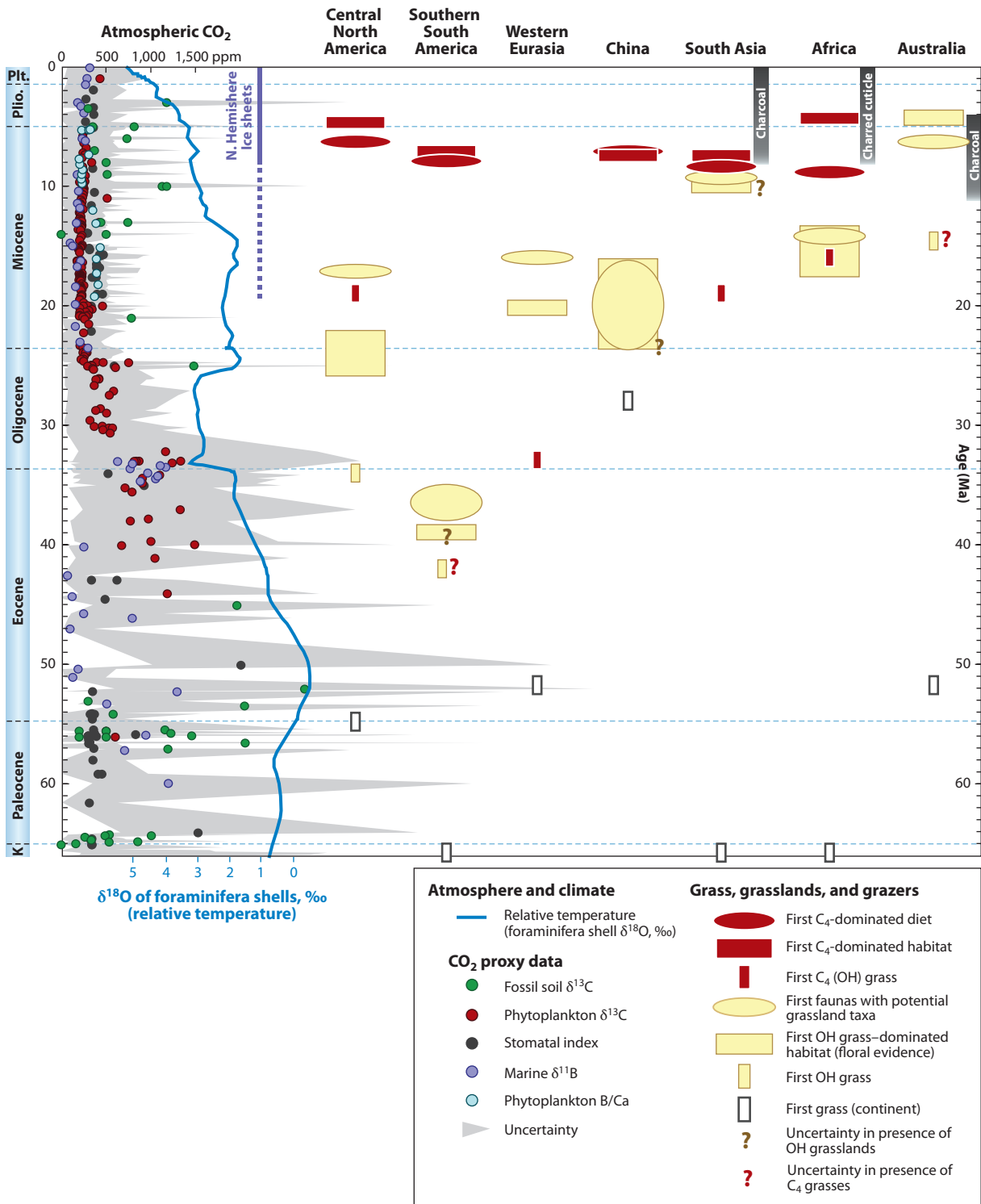
(Martin 2006). Grass pollen is found in moderate abundances (4–11%) at certain Miocene sites but has generally been interpreted as representing grasses adapted to wetland habitats rather than open, dry vegetation (Kershaw et al. 1994, Macphail & Hill 2002). In contrast, abundant grasses (~30%) in a Late Miocene palynoflora from Ocean Drilling Program (ODP) Site 765 have been used to infer the presence of sclerophyllous forest with grassy understory in northwestern Australia. Pliocene floras with >40% grass pollen from the same core are the earliest evidence for grasslands and desert chenopod shrublands (Martin & McMinn 1994). By the latest Pliocene–Early Pleistocene, relatively open woodland grasslands had spread to southeastern Australia as well (Kershaw et al. 1994, Macphail & Hill 2002).

Grass phytoliths, including potential PACMAD forms, have been recovered at Deep Sea Drilling Project (DSDP) Site 591 (14.4–0.9 Ma) (Locker & Martini 1986), east of Australia. They remain fairly sparse throughout the Miocene part of the core but increase drastically after 4 Ma, peaking at ~2.5 Ma. Given the long distance traveled by the phytoliths from Australia's east coast (>1,000 km), Locker & Martini (1986) interpreted the Pliocene increase in grass phytolith abundance as evidence for the spread of grasslands in inland Australia, but they note that an increase in wind strength associated with the expansion of the Antarctic ice sheet may have also influenced the pattern.

Paleogene mammals are scarce in Australia and the more continuous Neogene faunal record has been the subject of few paleoecological studies. Using cenogram and body-mass distribution analysis, Travouillon et al. (2009) proposed that Late Oligocene and late Early Miocene vegetation at Riversleigh, northwest Queensland, consisted of relatively open forest. Oligocene–Miocene faunas from central Australia, although dominated by browsers, contain few arboreal species and are thought to reflect more open woodland in addition to forest (Archer et al. 1994). Fossils of comparatively high-crowned kangaroos and wombat relatives from the early Middle Miocene of northern Australia constitute the earliest potential adaptations to more abrasive diets, and the first hypselodont taxon, a wombatid, occurs in the Late Miocene of Riversleigh (Archer et al. 1999, Dawson & Dawson 2006). Nevertheless, taxa interpreted as grassland adapted (e.g., kangaroos and wombats) did not undergo radiation until the Pliocene and did not spread from northern areas (e.g., Queensland) to the rest of the continent until the Early–Middle Pleistocene; during the same time, many browsers went extinct (Dawson & Dawson 2006).

STAGES OF GRASSLAND BIOME ASSEMBLY: GENERAL PATTERNS

Several general observations can be made about the stages of grass and grassland history proposed above. First, currently available fossil data, as well as the dating of grass molecular phylogenies, indicate that open-habitat grasses in the Pooideae and PACMAD clades diversified and were present in many areas long before (~10 myr) they became vegetation dominants (**Figure 5**). A temporal offset between radiation and ecological expansion is even clearer for the C₄ grasses, which originated by the Early Oligocene, ≥25 myr before their rise to ecological dominance in the Late Miocene–Pliocene and were present on several continents before this time. It is conceivable that these time lags are preservational artifacts and that open-habitat grasses evolved and rose to dominance in parallel in areas that have not yet been sampled—and that the same was true for C₄ grasses, only somewhat later in time. The arid habitats with rare to moderately abundant grasses that seem to have existed in, for example, Mexico and China in the Paleogene may be examples of such environments (Ramirez-Arriaga et al. 2006, Sun & Wang 2005). However, if real, the pattern of temporal decoupling suggests that the factors promoting the evolution of open-habitat grasses and C₄ grasses differed from the factors triggering their ecological expansion (Edwards et al. 2010, Strömberg 2005).



Another general finding is that the emergence of (C₃) grass-dominated habitats preceded the spread of C₄ grasslands by up to 20 million years, supporting the idea of two distinct stages in grassland evolution on most continents (Australia may be an exception) (Edwards et al. 2010). On the basis of variation in tree cover estimated from phytoliths (**Figures 2 and 4**) and the presence of diverse sets of mammals that depended on woody vegetation in at least North America, Western Eurasia, South Asia, and Africa, the earliest (C₃) grass-dominated habitats seem to have originated as part of mosaic landscapes that included both more closed habitats (e.g., forest) and more open woodland-grassland elements. The spread of open-habitat grasses may therefore have occurred through expansion of grass-dominated patches within highly heterogeneous ecosystems rather than as a gradual thinning-out of trees across the landscape. This distinction may in part explain why the pollen record, with its distinct preservational biases, points to a later date for the expansion of open-habitat grasses than does the phytolith record. Phytoliths often preserve in dry, “upland” habitats, whereas pollen is preferentially recorded from lowland swamps; in addition, the phytolith record is typically more spatially resolved than that of pollen and spores, which provide a regionally mixed vegetation signal (e.g., Piperno 2006). Thus, a signal of patchy grasslands would be evident in phytolith assemblages reflecting local habitats but would be overwhelmed by forest tree pollen in the spatially averaged pollen record. Several lines of evidence, including diet variation among Late Neogene herbivores (Edwards et al. 2010, Janis et al. 2004), indicate that some tree-cover heterogeneity persisted until and during the rise to dominance of C₄ grasses. Therefore, fully open grasslands, whether C₃ or C₄, were likely a Late Miocene–Pliocene phenomenon.

Although the records are incomplete, they indicate variation among continents in the timing of the two suggested stages of grassland evolution, the spread of, respectively, C₃ and C₄ grass-dominated vegetation (**Figure 5**). For example, although open, grass-dominated habitats had appeared by the Early Miocene in North America, there is currently no compelling evidence for grassland vegetation in Australia until the Late Miocene or Pliocene. Likewise, the expansion of C₄ grasses is not synchronous across continents, even at comparable latitudes (Edwards et al. 2010). These differences indicate that regional or local conditions, perhaps in addition to global factors, must have influenced the Cenozoic development of grass-dominated ecosystems.

The data also show that the evolution of hypsodonty did not necessarily coincide with the spread of open-grass-dominated habitats. In North America and Western Eurasia, hypsodonty evolved or became common in faunas several million years after open-habitat grasses expanded (Strömberg 2006, Strömberg et al. 2007). The South American case is less clear, but data from dung beetle balls and associated paleosols indicate the reverse pattern, i.e., that grass-dominated habitats developed well after high-crowned herbivores emerged (**Figure 3**). These patterns suggest that several case-dependent factors other than the ecological expansion of grasses contributed to determining the timing of hypsodonty evolution, including changes in habitat openness, nutritional quality of the food, soil erosion, and general aridity (Eronen et al. 2010a, Madden 1999). In addition, mammals are subject to behavioral, developmental, and physical constraints that likely influenced the rate of tooth crown-height evolution in response to increased abundances of environmental abrasives (Strömberg 2006). For example, herbivores could have avoided feeding in open grassy patches as long as there was sufficient browse, thereby delaying adaptive evolution. The advent of hypsodonty


 Supplemental Material

Figure 5

Summary of the evidence for grassland biome assembly in different regions, in the context of Cenozoic trends in average temperature and atmospheric CO₂. See **Supplemental Material** for data sources (follow the **Supplemental Materials link** from the Annual Reviews home page at <http://www.annualreviews.org>). Abbreviations: K, Cretaceous; OH, open habitat; Plio., Pliocene; Plt., Pleistocene.

should therefore be a good marker of a dietary shift to abrasives in a lineage, but it is less reliable as an indicator of habitat change. Also, once evolved, tooth crown-height seems to no longer precisely reflect diet (Mihlbachler & Solounias 2006).

The acquisition of C₄-rich diets provides another example of the decoupling between vegetation alteration and faunal change. In many regions, certain ungulate taxa apparently specialized on C₄ grasses that had not yet gained vegetation dominance, whereas others remained mainly C₃ feeders (**Figure 5**). This pattern points to niche partitioning among ungulates inhabiting a landscape consisting of grassy patches dominated by C₃ or C₄ grasses mixed with more wooded areas (Edwards et al. 2010).

In sum, the assembly of grassland ecosystem consisted of a series of four stages (appearance of C₃ and C₄ grasses, spread of C₃ and C₄ grasslands), each of which requires a causal explanation. The variation in timing and nature of changes among regions and continents implies not only that the factors involved in these four stages differ, but also that the drivers determining a particular stage may vary among regions.

ECOLOGICAL TRIGGERS

It is often assumed that open-habitat grasses evolved or diversified in response to enhanced higher latitude aridity and global cooling during the Cenozoic. However, the role of cooling in the advent of open-habitat tolerance is dubious. PACMADs were never adapted to cool climates (Edwards & Smith 2010), and at least some key adaptations to cold stress recognized in Pooideae are restricted to core pooids (**Figure 1**) (Sandve & Fjellheim 2010), indicating that basal pooids were not necessarily cold tolerant. Also, pooids (and PACMADs) originated by the Middle Eocene, >7 myr before the Eocene-Oligocene drop in global temperatures (**Figure 5**). The Eocene (or earlier) ancestors of open-habitat grasses therefore more likely inhabited areas with evidence of aridity (**Figure 1**). Alternatively, because certain structures (e.g., intercalary meristems) are advantageous under extreme aridity as well as in nutrient-deficient, water-saturated conditions, traits conferring drought resistance in open-habitat grasses may initially have been adaptations to swampy habitats (Bredenkamp et al. 2002).

It has recently been proposed that the first C₄ grasses evolved in response to a sudden Early-Oligocene decrease in atmospheric CO₂, which would have favored C₄ photosynthesis (Christin et al. 2008, Vicentini et al. 2008). However, the appearance of C₄ grasses by the earliest Oligocene (Urban et al. 2010, Zucol et al. 2010), while pCO₂ was still high, challenges this explanation. Instead, a shift to open, hence more arid, habitats may have provided key selective pressure in the already warm-adapted PACMADs (Edwards & Smith 2010, Osborne & Freckleton 2009). Thus, it can be hypothesized that the earliest C₄ grasses will be found at latitudes where seasonal drying promoted the development of open vegetation during the exceptionally warm Eocene, conferring a competitive edge to grasses with C₄ photosynthesis even at elevated CO₂ levels (see also Lunt et al. 2007).

What triggered the opening-up of vegetation that allowed (C₃) open-habitat grasses to expand at the expense of trees? Modern ecological studies investigating the controls of tree-grass interactions point to a complex relationship between the abiotic/biotic environment and vegetation structure in which different processes vary in importance depending on the temporal and spatial scale (Mills et al. 2006). Grass dominance appears to be controlled in part by climate (e.g., precipitation, temperature seasonality), soil type, as well as disturbance (e.g., fire, herbivory). In Africa, mean annual precipitation (MAP) determines the maximum tree cover in dry climates (200–700 mm MAP), whereas soil characteristics (e.g., nitrogen mineralization), fire, and herbivory act to reduce woody cover below the upper limit set by MAP in both dry and wet climates (Bond 2008,

Sankaran et al. 2007). Other studies have indicated that seasonality and, specifically, stochasticity in rainfall may be instrumental in limiting tree growth (Fensham et al. 2005). In addition, lowered CO₂ may act to favor grasses over trees even at high rainfall by suppressing tree postfire growth rates and herbivory defenses (Bond 2008).

In South Asia, records of oxygen isotope ratios ($\delta^{18}\text{O}$) suggest that monsoonal climates with summer rainfall developed by 11–10 Ma, one million or so years before the presence of (C₃) open habitats in this region (**Figure 5**). In addition, an overall decrease in MAP, rather than a change in seasonality, has been inferred on the basis of $\delta^{18}\text{O}$ and leaf-wax hydrogen isotope ratios (δD) for the same region and time frame (Huang et al. 2007). These changes may have promoted the spread of C₄-dominated grasslands in South Asia, but they could also have had an influence on the abundance of C₃ grasses prior to the C₃–C₄ shift. Unfortunately, the uncertainty regarding when grass-dominated habitats appeared in most other areas makes it hard to speculate about causal factors in these cases. For example, in central North America, the spread of grass-dominated habitats may have coincided either with relatively high pCO₂ and global warming at the end of the Oligocene or with near-modern CO₂ levels, global cooling, and reduced seasonality at the Oligocene–Miocene boundary (Zachos et al. 2001). Although dramatic cooling or drying can be ruled out for North America given the survival of relatively frost-intolerant palms and moisture-dependent gingers (Strömberg 2005), the inability to correlate the vegetation shift to climate data prevents a rigorous evaluation of process. Another obstacle with inferring mechanisms is that it is unclear whether conclusions drawn from studies of tropical, C₄-grass-dominated ecosystems apply to the nonanalog mix of C₃ pooid grasses, palms, and woody dicotyledons that typified some of the earliest grass-dominated habitats (Strömberg 2005, Strömberg et al. 2007).

A latest Miocene drop in pCO₂ was previously regarded as the likely cause of the C₃–C₄ shift (Cerling et al. 1997a) but has fallen out of favor as the Cenozoic history of CO₂ has become clearer, for the most part indicating stable, low CO₂ levels throughout the Miocene (**Figure 5**). The focus now lies on more region-specific climatic factors and disturbance (fire, herbivory) predicted by modern ecological work in C₄ savannas and grasslands (with low CO₂ as a possible necessary precondition). For example, the Late Miocene increase in charcoal in marine and terrestrial deposits in South Asia, West Africa, and Australia (**Figure 5**) is viewed as evidence that intensified fire regime promoted the spread of C₄ grasses in these regions (Keeley & Rundel 2005). In contrast, phytolith assemblages and $\delta^{18}\text{O}$ records from central North America and South Asia, respectively, indicate that increased overall aridity during the latest Miocene favored a C₃–C₄ shift (Dettman et al. 2001, Strömberg & McInerney 2011). Until each region has been investigated separately in terms of Late Miocene environmental changes, we cannot gain a full understanding of what drove the rise to ecological dominance of C₄ grasses. Furthermore, because different C₄ lineages respond differently to climatic and disturbance factors, information about the specific grasses involved in C₄ expansion is vital for evaluating the rise of C₄ grasses (Edwards et al. 2010, Osborne 2008). The same holds true for the (earlier) spread of C₃-grass-dominated habitats. Hence, detailed work involving both direct and indirect lines of evidence on all continents is essential if we are to make any generalizations about the Cenozoic assembly of Earth's grassland ecosystems. Understanding these general rules may provide additional insight into the processes that maintain today's grasslands and allow us to assess better how they will change in the future.

DISCLOSURE STATEMENT

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