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Evolution and importance of wetlands in earth history

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ABSTRACT

The fossil record of wetlands documents unique and long-persistent floras and faunas with wetland habitats spawning or at least preserving novel evolutionary characteristics and, at other times, acting as refugia. In addition, there has been an evolution of wetland types since their appearance in the Paleozoic. The first land plants, beginning in the Late Ordovician or Early Silurian, were obligate dwellers of wet substrates. As land plants evolved and diversified, different wetland types began to appear. The first marshes developed in the mid-Devonian, and forest swamps originated in the Late Devonian. Adaptations to low-oxygen, low-nutrient conditions allowed for the evolution of fens (peat marshes) and forest mires (peat forests) in the Late Devonian. The differentiation of wetland habitats created varied niches that influenced the terrestrialization of arthropods in the Silurian and the terrestrialization of tetrapods in the Devonian (and later), and dramatically altered the way sedimentological, hydrological, and various biogeochemical cycles operated globally.

Widespread peatlands evolved in the Carboniferous, with the earliest ombrotrophic tropical mires arising by the early Late Carboniferous. Carboniferous wetland-plant communities were complex, and although the taxonomic composition of these wetlands was vastly different from those of the Mesozoic and Cenozoic, these communities were essentially structurally, and probably dynamically, modern. By the Late Permian, the spread of the *Glossopteris* flora and its adaptations to more temperate or cooler climates allowed the development of mires at higher latitudes, where peats are most common today. Although widespread at the end of the Paleozoic, peat-forming wetlands virtually disappeared following the end-Permian extinction.

The initial associations of crocodylomorphs, mammals, and birds with wetlands are well recorded in the Mesozoic. The radiation of Isoetales in the Early Triassic may have included a submerged lifestyle and hence, the expansion of aquatic wetlands. The evolution of heterosporous ferns introduced a floating vascular habit to aquatic wetlands. The evolution of angiosperms in the Cretaceous led to further expansion of aquatic species and the first true mangroves. Increasing diversification of angiosperms in the Tertiary led to increased floral partitioning in wetlands and a wide

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variety of specialized wetland subcommunities. During the Tertiary, the spread of grasses, rushes, and sedges into wetlands allowed for the evolution of freshwater and salt-water reed marshes. Additionally, the spread of *Sphagnum* sp. in the Cenozoic allowed bryophytes, an ancient wetland clade, to dominate high-latitude mires, creating some of the most widespread mires of all time. Recognition of the evolution of wetland types and inherent framework positions and niches of both the flora and fauna is critical to understanding both the evolution of wetland functions and food webs and the paleoecology of surrounding ecotones, and is necessary if meaningful analogues are to be made with extant wetland habitats.

Keywords: paleobotany, paleoecology, paleoflora, earth history, wetlands, coal, swamp, mire, marsh, fen, bog.

INTRODUCTION

Modern wetlands are characterized by water at or near the soil surface for some part of the year, soils that are influenced by water saturation all or part of the year, and plants that are adapted to living in conditions of water saturation all or part of the year (National Research Council, 1995; Keddy, 2000; Mitsch and Gosselink, 2000). Many wetlands occupy lowlands and natural depressions, so have a relatively high preservational potential. It is not surprising, then, that a large part of the fossil record of terrestrial flora and fauna (especially in the Paleozoic) is found within wetlands or wetland-associated habitats. These deposits provide windows into ancient biodiversity, but frequently represent a mix of allochthonous and autochthonous material from different ecosystems. In order to examine the importance of wetlands through time, it is important to recognize that there are many different types of wetlands and wetland functions, and that both have changed through time.

Types of Wetlands

Holocene wetlands have been classified variously over the past several decades, with workers on different continents and in different hemispheres using a range of terms to classify wetlands on the basis of hydrology, geography, and flora, among other criteria. Unfortunately, variable definitions and terminology can lead to uncertain or mistaken use of analogues when interpreting the paleoecology of ancient wetlands. For the purposes of this investigation, we use the following general terminology adapted from Keddy (2000): *aquatic* (or *shallow water*) *wetland* for wetlands dominated by submerged vegetation under continually inundated conditions; *marsh* for wetlands dominated by herbaceous, emergent vegetation rooted in mineral (non-peat) substrates; *swamp* for forested wetlands on mineral (non-peat) substrates; *fen* or *nonforested mire* for wetlands dominated by herbaceous or shrub vegetation on peat substrates. Because there is considerable variability in the use of the term *bog* (Keddy, 2000; Mitsch and Gosselink, 2000), the term *forest mire* is used herein for forested peats. These general terms can have a wide array of meanings (Mitsch and Gosselink, 2000) but serve as a starting point for discussion of paleowetlands. The terms are similar to wetland classes in the hierarchical Canadian wetland system (Zoltai and Pollett, 1983). Such hierarchical classifications are commonly used to describe modern wetlands. In the context of characterizing paleowetlands on the basis of standardized wetland classifications, additional modifiers such as marine, estuarine, riverine, palustrine, and lacustrine are used where appropriate for comparison to the U.S. Fish and Wildlife wetland classification (Cowardin et al., 1979). Modifiers such as marine/coastal and inland are used where appropriate to indicate relative equivalence to wetlands in the Ramsar Convention classification. Modifiers also are used to describe wetland forms, types, and varieties as described in the Canadian system or to describe form, hydrology, or nutrient status for peat-producing wetlands (Gore, 1983; Moore, 1989, 1995; Mitsch and Gosselink, 2000). Each of the modern systems is designed for different purposes, so varied modifiers from each are used to describe clearly paleowetlands discussed in this report.

Wetland Functions

Modern wetlands provide many critical functions in global ecology, including providing habitat and food for diverse species, and aiding in groundwater recharge and water retention and detention, which allows for maintenance of high water tables in wetlands as well as reduced flooding in adjacent ecosystems. They also provide erosion and sedimentation controls between adjacent ecosystems, improve water quality through filtering sediment and metals from groundwater, and cycle nutrients to terrestrial and aqueous environments within the wetland and between ecotones (National Research Council, 1995; Keddy, 2000; Mitsch and Gosselink, 2000). Wetlands are also important global sources, sinks, and transformers of various elements in the earth's various biogeochemical cycles (National Research Council, 1995; Keddy, 2000; Mitsch and Gosselink, 2000). As full or part-time habitats, they function as a significant repository of the world's biodiversity (Bacon, 1997; Keddy, 2000; Mitsch and Gosselink, 2000). These functions are important not only within the wetlands themselves, but also to surrounding ecosystems. Not all functions are equally distributed through the different types of wetlands, and many are influenced by particular floras and faunas. Because the floras, faunas, and types of wetlands have evolved through time, wetland functions have changed through time, as well.

Wetland Niches and Associations

The variety of organisms adapted to various wetland habitats is large and includes all major groups of animals and plants (Bacon, 1997). Herein, we examine the evolution of some common wetland faunal and floral associations. Changes in wetland niches and associations have occurred as the various adaptive strategies of plants and animals have evolved. In some cases, the extant wetland biota lives under conditions similar to those of ancient wetland plants and animals. In others, framework positions or habitats have evolved through specialization, resulting in new wetland types and functions.

Analyses of Paleowetlands

There has been extensive research on ancient wetlands, mostly centered on coals because of their economic value. Several papers have specifically examined floral change in coal-forming floras through time, sometimes concentrating on a particular era (e.g., Shearer et al., 1995) or region (e.g., Cross and Phillips, 1990). Some reports also have used various aspects of coal distribution through time to further understanding of global changes in tectonics, climate, and eustasy (e.g., Scotese, 2001). In terms of wetlands, such reviews tend to be focused on peat-forming mires, which represent a subset of wetland types. In fact, coals are often generalized as representing wetlands, which has the unfortunate result of marginalizing the significance of non-coal facies as wetlands of importance. The understanding that coal floras and "roof" shale floras represent different types of wetlands (e.g., Gastaldo, 1987), emphasizes that non-peat producing wetlands are well represented in the fossil record. In some cases, at different times in earth history, these non-peat producing wetlands may have been more important, in terms of their functions and influences on ecotones, than mires.

Numerous botanical and biogeographical studies have demonstrated how changing climate or timing of tectonic movements changed the composition of Tertiary floras (including wetland inhabitants) in different areas (e.g., Aaron et al., 1999). In terms of climate, it also is important to understand the bias imposed by the present global climate on wetlands and wetland floras. Pfefferkorn (1995) noted the need for a reorientation of a perceived north-temperate perspective and search strategy for interpreting ancient mire ecosystems. Likewise, Collinson and Scott (1987) pointed out the importance of understanding differences in a flora through time when attempting to reconstruct ancient mires. Similarly, it is important to understand changes in specific types of wetland ecosystems. Extant floras and faunas occupy specific niches in different types of wetlands, some of which entail unique physiological adaptations and ecological interactions. These adaptations have changed through time. In some cases, novel floral adaptations have led to new types of wetlands, wetland functions, and wetland faunal niches.

Purpose

Herein the evolution of wetland ecosystems through time is analyzed. We focus on the development of new and changing wetland ecosystems, which accompanied the evolution of the terrestrial flora and, in turn, influenced the evolution of numerous animal groups through the evolution of new niche space, food sources, and habitat. The unusual chemistry and sedimentology of wetland systems resulted in a wide variety of traps in which both fauna and flora are preserved. Significant wetland fossil sites that offer snapshots of ancient biodiversity and paleoecology are also highlighted in order to illustrate the importance of wetland ecosystems to our understanding of earth history. Likewise, we examine the origins and changing influences of specific wetland functions through time to illustrate the potential importance of wetland ecosystems on neighboring ecosystems and in some cases, global paleoecology. The fossil record is our best tool for understanding how changes in wetland distribution, type, niches, and functions influence non-wetland ecosystems, which is particularly important when trying to understand potential long-term natural and anthropogenic influences on global ecology.

ORDOVICIAN-SILURIAN

Prevascular Wetlands

The origin of land plants appears to have occurred in the Late Ordovician to Middle Silurian, involving pre-tracheophyte, embrophytic or bryophytic (moss, lichen) plants that were obligate dwellers of wet substrates (Gray et al., 1982; Gensel and Andrews, 1984; Taylor, 1988; Stewart and Rothwell, 1993; Tomescu and Rothwell, this volume*)*. Whether these prevascular plant-vegetated substrates can be considered wetlands depends on the definition used, and Retallack (1992) has proposed a separate terminology for the associated paleosols. If a "wetland" can be defined simply as consisting of vegetation on a wet substrate, then this habitat has its origin with these vascular precursors. Using the classification scheme of Cowardin et al. (1979), these habitats come closest to representing fluvial and paludal moss-lichen wetlands in which mosses or lichens cover a saturated mineral substrate, other than rock, and dominate the vegetation. They obviously would have differed significantly from extant moss-lichen wetlands in not being associated with any vegetation of taller stature. Pre-Devonian moss-like wetlands also were non-peat-accumulating and therefore would not be termed bogs or fens, nor would they be expected to have similar ecology and functions to those of extant *Sphagnum* moss-dominated mires. If wetlands are defined by the presence of hydrophytic vascular plants, then, by definition, wetland origins are tied to the origin of vascular plants in the Middle Silurian.

SILURIAN

The Oldest Vascular Plants in Wetlands

By many accounts, *Cooksonia* (Wenlockian) is considered the oldest vascular plant (Edwards, 1980; Edwards and Fanning, 1985). *Cooksonia* is a rhyniophyte, a group of small, simple, stick-like vascular plants. It is found mostly in autochthonous deposits associated with fluvial sandstones and floodplains. Edwards (1980) inferred *Cooksonia* habitats along large rivers, which might indicate inland fluvial wetlands according to the Cowardin et al. (1979) classification. The term "riparian wetland," which describes wetlands and associated upstream areas influenced by the river, also would apply, although there would be few functional similarities to extant riparian settings because of the small stature of these rhyniophytes. *Cooksonia* only grew to a few centimeters, so was moss-like in stature. The term "marsh" (often used in descriptions of these wetlands) is functionally problematic in its application to *Cooksonia*-dominated wetlands. Marshlands generally are considered to be dominated by deeply rooted herbaceous vegetation (e.g., Keddy, 2000), decimeters to meters in height (Mitsch and Gosselink, 2000; Keddy, 2000). Pre–Late Devonian plants were mostly less than a meter in height and were not deeply rooted (Fig. 1).

Some research has inferred that simple rhyniophytoid plants, like *Cooksonia,* inhabited salt marshes (Jeram et al., 1990; Shear et al., 1989). Modern salt marshes are a special wetland type inhabited by a low diversity of plants adapted to salt stress caused by brackish to marine tidal inundation or sea spray. Late Silurian plants were simple plants lacking morphological features common in modern salt marsh plants, such as deeply buried rhizomes, salt-excluding roots (e.g., pneumatophores), and bark or leaves that might contain salt glands, and do not appear to have any obvious adaptations to varying soil salinities. As a consequence, it is likely that early rhyniophytes grew under freshwater conditions.

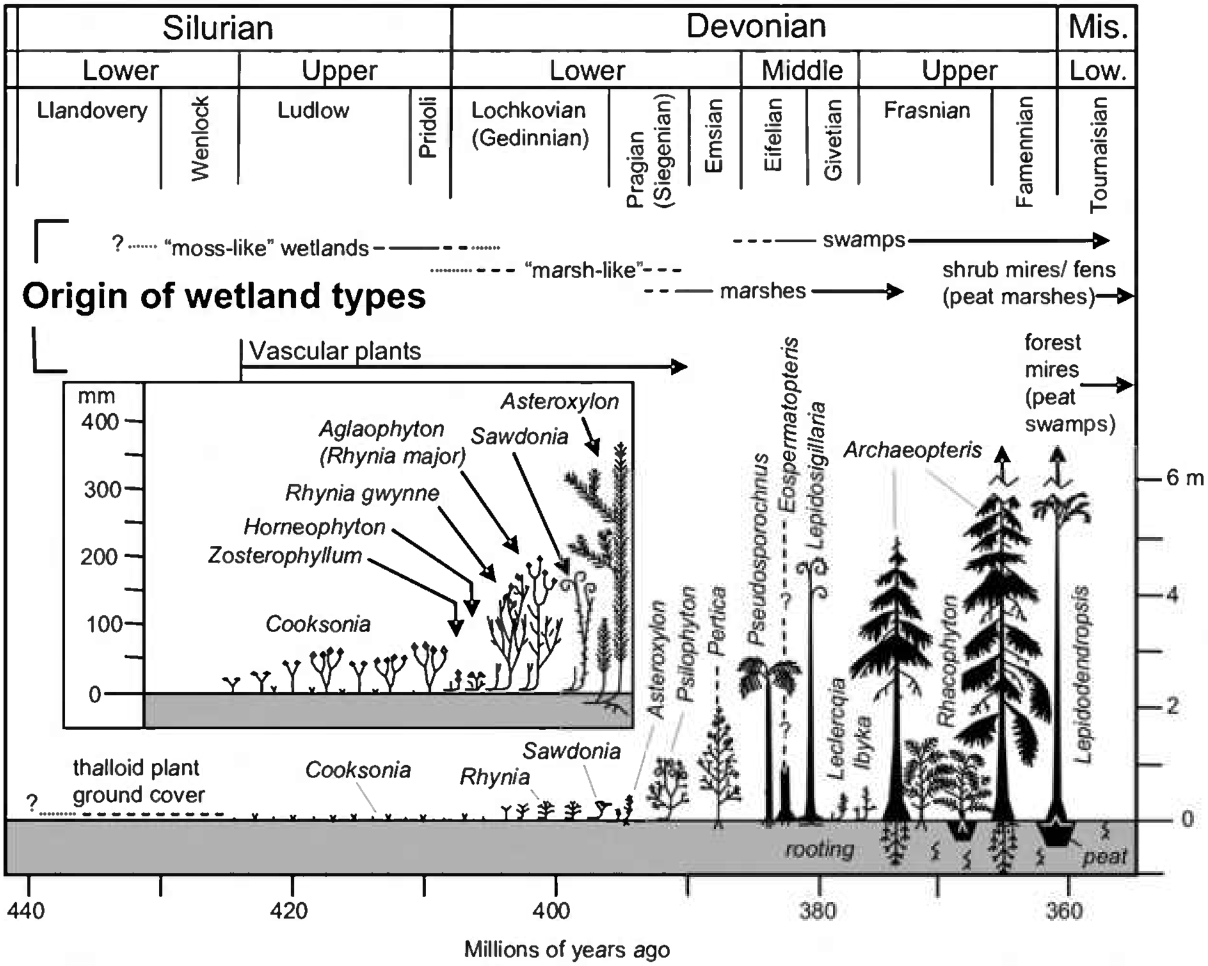

Figure 1. Evolution of wetland types in the Silurian and Devonian. The heights of major floral components are shown as is the inferred depth of rooting. Heights of plants from various sources. Estimates of root depth from Algeo et al. (1995).

LATE SILURIAN–EARLY DEVONIAN

Arthropod Terrestrialization in Wetlands

Arthropods are the oldest terrestrial animals. Putative paleosols and terrestrial arthropod trace fossils are inferred for strata as old as the Ordovician (Retallack and Feakes, 1987; Retallack, 2000; Shear and Selden, 2001), but the oldest undisputed terrestrial land animal, *Pneumodesmus*, is a millipede from the Middle Silurian of Scotland (Wilson and Anderson, 2004). Upper Silurian terrestrial arthropods include trigonotarbids (spider-like arachnids), kampecarids (millipede-like arthropods) and fragments of possible centipedes (Jeram et al. 1990; Rolfe, 1990). Silurian arthropod terrestrialization was linked closely to vascular plant evolution in wetlands (Rolfe, 1980; Jeram et al., 1990). In fact, the transition from an aqueous to a terrestrial habit may have been aided by low-structured vegetation that created humid microclimates near the soil surface (Rolfe, 1985). Most Late Silurian and Early Devonian arthropods are found associated with freshwater marsh-like vegetation in both autochthonous and allochthonous deposits, providing the earliest evidence of habitat function in wetlands. The oldest possible insect is the fragmentary remains of *Rhyniognatha*, from the Lower Devonian (Pragian) Rhynie Chert (Engel and Grimaldi, 2004). The slightly younger and more complete remains of a bristletail from the Emsian (Lower Devonian) of Quebec, Canada, was inferred by Labandeira et al., (1988) to indicate hexapod origins in wet, marsh-like habitats. Similar deposits from the Emsian of Canada have produced millipedes, arthropleurids, and terrestrial scorpions (Shear et al., 1996). The Alken-an-der-Mosel fauna (Emsian), which includes trigonotarbids, arthropleurids, and the oldest non-scorpion arachnid (Størmer, 1976), is preserved along with lycopsids and rhyniophytes (wetland plants) (Jeram et al., 1990; Shear and Selden, 2001). The Middle Devonian (Givettian) Gilboa fauna includes eurypterids and terrestrial arthropods, including arachnids, centipedes, a possible insect, and the oldest spider, and is in association with herbaceous lycopsids and progymnosperms (Shear et al., 1984; Selden et al., 1991).

The spread of kampecarid arthropods (myriapods) is an example of the possible paleoecological significance of wetlands in arthropod evolution. Kampecarids were millipede-like arthropods that were restricted to freshwater aquatic or near-aquatic habitats in which they fed on plant detritus (Almond, 1985). In the Silurian, plant detritus would have been restricted in and around moss-like to marsh-like wetlands. Modern millipedes prefer moist litter horizons and dead wood as habitats, and they are critical agents for nutrient cycling in tropical wetlands and wetland forests as litter-horizon detritivores. The radiation of kampecarids and true diplopods (millipedes) into the earliest wetland communities undoubtedly contributed to increased nutrient cycling, which increased soil quality and contributed to increasingly complex food webs as the terrestrial floral and faunal radiations progressed.

DEVONIAN

The Spread of Wetlands

Most of the Early to Middle Devonian terrestrial fossil record is confined to subtropical-to-tropical wetland habitats, with plants restricted to monotypic stands in freshwater, near-channel, deposits (Edwards, 1980; Beerbower, 1985; Edwards and Fanning, 1985; DiMichele and Hook, 1992). Hence, these assemblages mostly would be classified as paludal or riverine wetlands. Late Silurian rhyniophytes were joined by several new clades in the Early Devonian, including zosterophylls (Gedinnian) and trimerophytes (Siegenian) (Kenrick and Crane, 1997; Bateman et al., 1998), all low-stature (centimeters in height) vegetational types (Fig. 1). Lycopsids also are found in the Early Devonian (Siegenian), and may represent an additional new clade if a Silurian age for *Baragwanathia* is discounted. *Baragwanathia*, a primitive lycopsid from Australia, originally was assigned a Late Silurian (Ludlovian) age (Lang and Cookson, 1935; Garratt et al., 1984), but this determination is controversial. *Baragwanathia* actually may be of Early Devonian age (Edwards et al., 1979).

All Early Devonian vascular plants were small and homosporous, which means that their gametophytes required water-mediated fertilization (Remy, 1982). Likewise, the small rhizoids of these rhyniophytes, trimerophytes, and zosterophylls indicate habitats characterized by nearly continuous moisture (DiMichele and Hook, 1992; Hotton et al., 2001)—in other words, moss-like to at most marsh-like wetlands, but still smaller in height than the flora that typically inhabits extant marshes (Fig. 1).

Geothermal Wetlands

By far the most famous early terrestrial biota is from the Rhynie Chert (Siegenian) of Scotland. Chert in this wetland deposit preserves the three-dimensional remains of fungi, algae, small non-vascular polysporangiophytes, a lycophyte, small vascular plants, arachnids (mites, trigonotarbids), an insect, and freshwater crustaceans (Remy and Remy, 1980; Rolfe, 1980; Trewin, 1996; Rice et al., 2002). Rhyniophytes have been interpreted as "swamp" (e.g., Knoll, 1985), "marsh" (Trewin and Rice, 1992), and "bog" plants (Rice et al., 1995), although the terms have been applied somewhat indiscriminately. Although the term "swamp" is sometimes used informally to describe any type of wetland, formal use in several classification systems requires arborescent vegetation, which were lacking at Rhynie. "Marsh-like" rather than "marsh" might be more appropriate because of the small stature of herbaceous vegetation preserved. The term "bog" is even more problematic because bogs are peat-accumulating wetlands. Although silicified organic laminae have been called "peat mats" at Rhynie (Knoll, 1985), these are not thick (millimeters thick) and much thicker peats would be more typical of the modern peat-forming wetlands classified as bogs.

Recently, the cherts were shown to have been deposited in a fluvio-lacustrine setting within, or on the margin of, a hydrothermal basin (Trewin and Rice, 1992; Trewin, 1994, 1996;

Rice et al., 1995, 2002). In situ plant assemblages accumulated in ambient waters of interfluves and overflow pools between hydrothermal ponds and geysers. Hence, at least some part of the Rhynie Chert biota represents inland geothermal wetlands as defined in the Ramsar classification (Fig. 2).

The association of freshwater crustaceans with the Rhynie biome is interesting because crustaceans are one of the most common groups of modern wetland-inhabiting arthropods. The Rhynie crustaceans (*Lepidocaris, Castracollis*) are branchiopods, similar to modern tadpole shrimp (*Triops*) and fairy shrimp (*Artemia*) (Anderson and Trewin, 2003; Fayers and Trewin, 2004). Extant branchiopods are common in wet meadows (vernal ponds) where they are important parts of detritivore-based food webs. Extant wet meadows are ephemeral wetlands dominated by herbaceous grasses and shrubs (Keddy, 2000; Mitsch and Gosselink, 2000). Crustaceans can thrive in ephemeral wetlands because of the lack of fish, which also seems to have been the case in the Rhynie ecosystem. Today, wet meadows (considered by some as a subset of marshes) are dominated by angiosperms (grasses and sedges). In the middle Paleozoic, rhyniophytes may have occupied similar niches, although rhyniophytes were likely less drought resistant than the flora of wet meadows today, and the relationship between their life history pattern and seasonal drought is not understood.

The Oldest Marshes

By the Middle Devonian (Eifelian), several plant groups had evolved shrub or bush morphology (Fig. 1). The lycophyte *Asteroxylon mackiei* (Emsian-Givetian) from the Rhynie Chert may have grown to heights of 50 cm (Gensel and Andrews, 1984; Gensel, 1992). *Pertica quadrifaria,* a trimerophyte from the Trout Valley of Maine (United States), grew to at least a meter in height (Kasper and Andrews, 1972; Allen and Gastaldo, this volume) if not taller. As such, wetlands comprised of these emergent plants formed the earliest marshes (inland shrub-dominated wetlands sensu Ramsar classification). Middle Devonian wetlands began to exhibit floral partitioning (Allen and Gastaldo, this volume), possibly in response to salinity, water chemistry, nutrients, or sedimentation and flooding (duration and periodicity of inundation). This partitioning undoubtedly involved feedback loops with stands of vegetation also influencing flooding and sedimentation as seen in modern freshwater marshes and wet meadows. In the riparian and lake-margin settings in which much of the Middle Devonian flora is found, wet meadows were likely common, as increasing stature, rooting, and floral partitioning allowed for some plants to adapt to seasonal inundation or exposure.

Sphenopsid-like plants are another important shrubby clade that emerged in the Late Devonian. Included among these plants are the Iridopterids (Stein et al., 1984). Calamitalean sphenopsids of the Carboniferous appear to have been adept particularly at colonizing disturbed environments, such as riparian wetlands susceptible to flooding and sedimentation (Scott, 1978; DiMichele and Phillips, 1985; Gastaldo, 1987; Pfefferkorn et al., 2001). In modern coastal, lacustrine, and riverine marsh settings, some emergent, reed-like plants are simplified (reduced) as an adaptation for living in these disturbance-prone areas. Reed-like

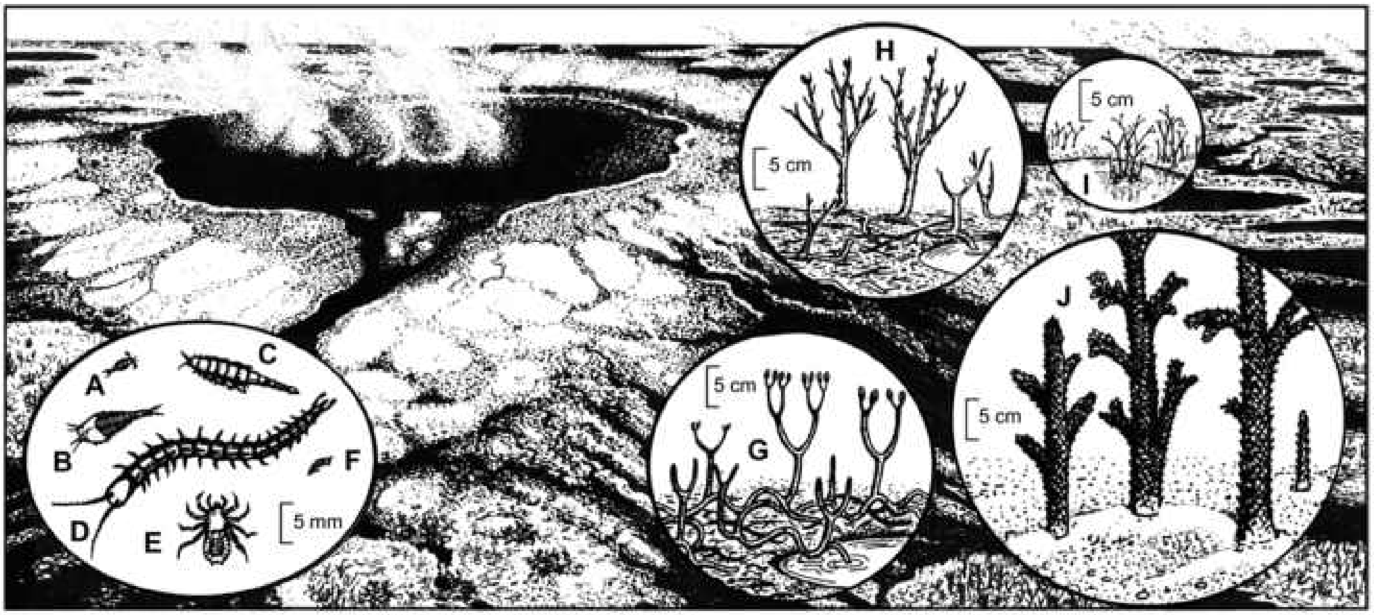

Figure 2. Illustration of the Rhynie geothermal wetlands. Arthropods include the crustaceans (A) *Lepidocaris* and (B) *Castracollis*, (C) a euthycarcinoid, (D) the partial remains of centipede, (E) the trigonotarbid *Palaeocharinus*; and (F) the partial remains of a springtail. Flora include (G) *Aglaophyton,* (H) *Rhynia,* (I) *Horneophyton*, and (J) *Asteroxylon.* All floral members drawn to same scale. Illustrations based on data and reconstructions from the University of Aberdeen, Scotland (www.abdn.ac.uk/rhynie/).

morphologies limit damage from storms and flooding through reduction of surface area, and clonal growth allows reestablishment of aerial shoots if the emergent parts of the plants should be broken (Keddy, 2000) or buried (Gastaldo, 1992). Sphenopsid reed-like morphologies in disturbance-prone Carboniferous environments created a framework similar to that presently created by reeds and rushes. Thick stands of reeds in modern marshes serve important functions in terms of sedimentation control, water filtering, flood control, and habitat, all of which are likely to have originated in Devonian marshes.

The Oldest Swamps

During the Middle to Late Devonian, lycopsids and progymnosperms attained tree-like stature, which led to the evolution of the first true forested wetlands, by definition, swamps (Fig. 1). Lycopsids were the first land plants to develop shallow substrate-penetrating roots (Remy and Remy, 1980), which advanced the process of soil development. Other clades evolved root systems later in the Devonian (Driese and Mora, 2001), altering pedogenic processes. Root systems were essential to the development of an arborescent growth habit because of the centralized growth form of most trees. Arborescence continued the pattern of increasing vegetational zonation, with the development of tiered canopies, including both trees and understory shrubs (Scott, 1980). Zonation contributed directly to the differentiation of swamps and marshes and the development of new niche space (Scheckler, 1986a; Cressler, this volume), and thereby biodiversity.

What may be the oldest swamps (forested wetlands) were reported by Driese et al. (1997) from the Middle Devonian of New York. Large stumps and shallow-penetrating roots, attributable to cf. *Eospermatopteris*, are preserved in a gray-green, gleyed, pyritic mudstone, interpreted as a waterlogged paleosol. Bartholomew and Brett (2003) have redescribed similar in situ stumps of *Eospermatopteris* (possibly a cladoxylalean) from the famous Gilboa locality in New York, from which the genus was described originally (Goldring, 1924). Although the habit of this plant is uncertain, stumps of approximately one meter in diameter have been reported, suggesting large trees adapted to wetland (swamp) conditions.

The progymnosperm *Archaeopteris* sp. is considered the oldest typically woody, tall tree (Figs. 1, 3), growing to heights of 18 m and occupying poorly drained flood plains and coastal areas (Beck, 1962, 1964; Retallack, 1985; Scheckler, 1986; Meyer-Berthaud et al., 1999). As such, they formed true gallery forests in floodplain environments constituting riverine or paludal forested wetlands, riparian forest-wetlands, or swamps (when defined as forested wetlands on mineral substrates). Arborescent progymnosperms had flattened branch systems and leaves, providing for a canopy and the potential for a shaded understory, which, in the Late Devonian, was dominated by the scrambling fern-like plant *Rhacophyton* (Fig. 3). In combination, this plant association would have increased litter input to the swamp floor (DiMichele and Hook, 1992; Algeo et al., 1995; Algeo and Scheckler, 1998), providing increased nutrients to surrounding wetland, fluvial, and upland ecosystems. The result of litterfall detritus in extant wetlands is the formation of a complex detritus-based food web that supports a great diversity of aquatic invertebrates, fish, and amphibians, often with greater biodiversity than in adjacent uplands because of the "edge effects" of ecotones (Bacon, 1997; Keddy, 2000; Mitsch and Gosselink, 2000). Such a food web was likely in place by the Middle Devonian.

The development of deep, extensive roots in Frasnian progymnosperms resulted in increased substrate stabilization (Figs. 1, 3) and a change in the rate at which paleosols formed and sediment was discharged (Algeo and Scheckler, 1998; Algeo et al., 2001). Devonian substrate stabilization also decreased sediment fluxes and reduced catastrophic flooding in wetland habitats (Schumm, 1968; Beerbower et al., 1992). This latter consequence

Figure 3. Devonian lacustrine wetland dominated by the pre-fern *Rhacophyton* and the progymnosperm *Archaeopteris*, whose roots stabilize the banks of the oxbow lake.

is an important function of modern wetlands, where flooding is prevented through the "breaking" action supplied by thick stands of plants against floodwater velocity, as well as through floodwater storage (Mitsch and Gosselink, 2000; Keddy, 2000). It also could lead to reduced runoff and increased precipitation, leading to significant changes in the global hydrological cycle (Algeo and Scheckler, 1998; Algeo et al., 2001).

Roots are central in the process of denitrification, which is important in global nitrogen cycling (e.g., Keddy, 2000). This critical function presumably originated in mid-Devonian marshes but increased with the evolution and spread of true swamps, and the development of upland forests leading to a dramatic increase in vegetative primary productivity. These expansions across the landscape would have increased carbon consumption and atmospheric carbon dioxide (pCO_2) drawdown. In combination with increased nutrient flux and bottom water anoxia and organic carbon fluxes, these perturbations could have led to global cooling, Devonian glaciation, as well as the end-Devonian mass extinction (Berner, 1993, 1997; Algeo et al., 1995; Algeo and Scheckler, 1998).

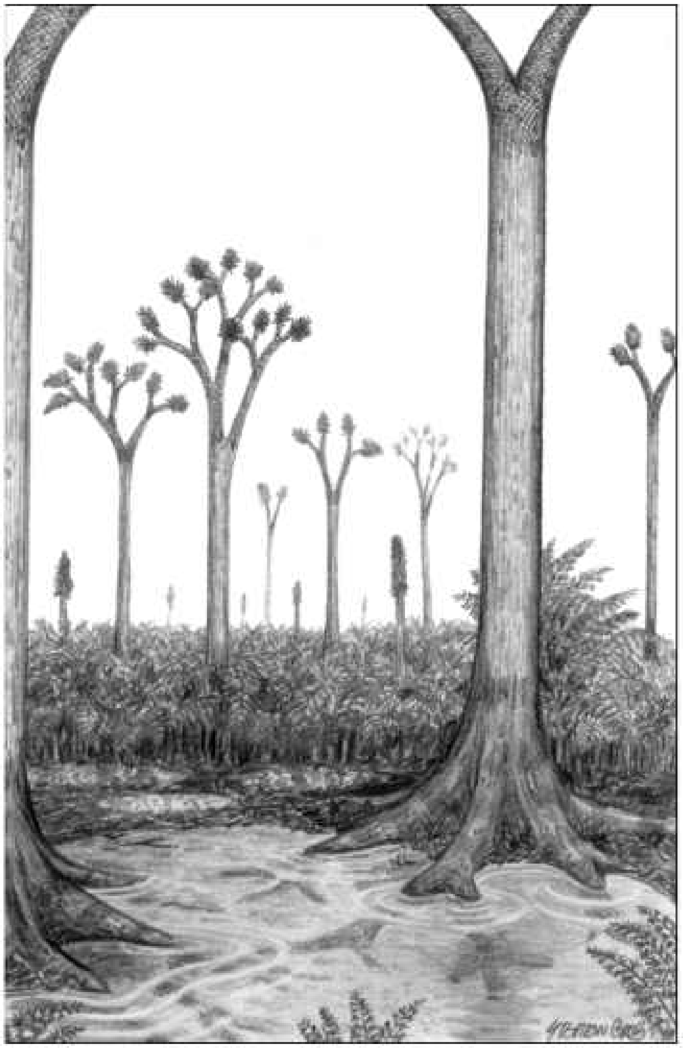

Figure 4. Devonian mires were dominated by the pre-fern *Rhacophyton,* but arborescent lycopods with stigmarian roots became increasingly common.

The Oldest Mires

Late Devonian coals record the evolution of the first peat-accumulating wetlands, indicating when plants had evolved the production and shedding of prolific amounts of biomass, which allowed peat to accumulate under specific chemical conditions. There is a distinction made between modern peat and non-peat-forming wetlands in most discussions (Mitsch and Gosselink, 2000; Keddy, 2000), and many authors differentiate between swamps and mires (bogs, fens; e.g., Gore, 1983). Peats are composed of at least 50% organic (mostly plant) material and accumulate where organic production outpaces decomposition, generally in wet, low-oxygen substrates. Often, the presence of an impervious aquiclude underlying the peat mire allows for the stilting of the water table, promoting litter accumulation (Gastaldo and Staub, 1999). Peat substrates present plants with considerably different challenges than mineral substrates. Most importantly, many peats are relatively nutrient deficient because organic matter chelates mineral nutrients. Stability for rooting also differs from mineral substrates. Finally, pore waters in peat, in some cases, have a lower pH than what most plants experience on other types of substrates (DiMichele et al., 1987; Cross and Phillips, 1990; Gastaldo and Staub, 1999). Peat accumulation in the Devonian resulted in new types of wetlands and new wetland functions associated with mires.

Some of the earliest coals are interpreted as sapropelic "boghead" coals, which form from the accumulation of algae in brackish to freshwater restricted environments (Thiessen, 1925; Sanders, 1968), although most result from the accumulation of terrestrial detritus. Several Late Devonian (Frasnian) coals of eastern North America are dominated by the herbaceous scrambling fern *Rhacophyton* (Scheckler, 1986a; Cross and Phillips, 1990). These sites would be classified as shrub-dominated peat wetlands or "fens" (Fig. 1; Gore, 1983; Keddy, 2000; Mitsch and Gosselink, 2000). Because *Rhacophyton* grew in both mineral and peat substrates, it likely was preadapted to oligotrophic conditions, which allowed this marsh plant to become one of the initial mire creators/occupiers.

Forested mires also appear in the Late Devonian and are composed of lycopsids (Figs. 1, 4). Late Devonian coals of China are dominated by the arborescent lycopsids *Lepidodendropsis, Lepidosigillaria,* and *Cyclostigma* (Xingxue and Xiuyhan, 1996). Arborescent lycopsids originated in non-peat-accumulating Devonian swamps and later expanded their range into peatlands, where they became dominant. It has been inferred that as peatlands expanded, these ecosystems became refugia for relict plants (like the lycopsids), as increasing morphological innovation allowed other clades to expand outside of wetland habitats

(Knoll, 1985; DiMichele et al., 1987). The stigmarian root systems of lycopods (Fig. 4) permitted growth in wet, oxygen-poor, soft-sediment substrates (Rothwell, 1984; DiMichele and Phillips, 1985; Phillips et al., 1985) and allowed lycopods to become the dominant vegetation of the Carboniferous peatlands.

Late Devonian forested mires may represent the earliest bogs, depending on the use of the term. Bogs generally are differentiated from fens by the accumulation of thicker peat composed of vegetation that is at least partly arborescent. In this respect, Late Devonian forest mires could be termed bogs. Devonian forest mires, however, were not ombrotrophic or dominated by mosses, characteristics implied in some uses of "bog" (Mitsch and Gosselink, 2000; Keddy, 2000). In terms of their ecological functions, these Devonian fens and forest mires mark the initiation of a new carbon sink, contributing to changes in the global carbon cycle and remaining important to this day. Also, the high water-storage capacity of peats means that mires can significantly influence local and regional hydrology (Mitsch and Gosselink, 2000; Keddy, 2000), which likely began in the Devonian but would have greater impact with the spread of mires in the Carboniferous.

Tetrapod Evolution and Wetlands

Tetrapods made landfall in the Late Devonian (Milner et al., 1986; Clack, 2002) from lungfish and lobe-finned fish ancestors. In fact, low-oxygen conditions caused by decaying plant matter in freshwater wetlands and wetland-fringing lakes may have spurred the evolution of tetrapod lungs (Randall et al., 1981; Carroll, 1988; Clack, 2002). Extant lungfish, such as the Australian *Neoceratodos forsteri* and African *Protopterus,* inhabit freshwater rivers, ponds, and marshes. They survive in ephemeral wetlands by burrowing into and estivating within wet substrates, surviving for many months until seasonal rains reflood their habitat (Speight and Blackith, 1983).

Acanthostega is one of the earliest aquatic tetrapods. Its multidigit appendages were preadapted for use on land, having first evolved in water (Gould, 1991; Clack, 1997; Clack and Coates 1995; Coates and Clack 1995). In the fluvial environments in which *Acanthostega* is preserved, it has been hypothesized that digitation was useful in strong currents for grasping onto rocks and water plants (Clack, 1997). Terrestrial mobility may have originated as a preadaptation in these earliest tetrapods that developed in association with maneuvering through vegetation in fluvial (riparian) wetlands dominated by dense stands of *Rhacophyton* in Late Devonian riverine marshes (Fig. 5).

Amphibians are common in many modern riverine/riparian wetlands (Mitsch and Gosselink, 2000) and many extant species require this habitat for part of their life cycle. Modern amphibian distribution is influenced by predation and the stability, light intensity, and temperature of their habitats (Skelly et al., 1999, 2002). Broad wetlands, with distinct microhabitats of overstory, midstory, and shrub, provide different types of food and cover where amphibians generally are abundant (Rudolph and Dickson, 1990). By the Late Devonian, tiering and canopy zonation in marshes, swamps, fens, and forest mires was well established, and created the types of food and cover in which tetrapods could thrive, adding another layer to both freshwater aquatic and terrestrial food webs.

MISSISSIPPIAN

Tetrapod and Wetland Diversification

Tetrapods continued to evolve and diversify into the Carboniferous as exemplified by one of the most famous Lower Carboniferous sites in East Kirkton, England. The fossil-bearing limestone preserves a wide variety of vertebrates, including chondrichthyan and acanthodian fish, lungfish, temnospondyls, anthracosaurs, and a reptiliomorph (reptile-like) animal (Milner and Sequeira, 1994). At one time, the reptiliomorph nicknamed "Lizzie" was interpreted as the oldest amniote (reptile; Smithson, 1989). More recent studies, however, have suggested that it was only a close relative of amniotes (Smithson et al., 1994), and possibly even a stem-tetrapod or an early amphibian, rather than a true amniote (Laurin and Reisz, 1999).

The East Kirkton tetrapod assemblage occurs in an alkaline, freshwater lake rimmed with marshes formed from reed-like calamites and a pteridosperm with *Sphenopteris* foliage (Milner et al., 1986). Volcanogenic rocks preserve several different plant assemblages within hydrothermal hot-spring deposits (Rolfe et al., 1990; Brown et al., 1994; Scott and Rex, 1987; Galtier and Scott, 1994; Scott et al., 1994). The vertical juxtaposition of these assemblages indicates that East Kirkton initially was a

Figure 5. *Acanthostega* maneuvers through stands of the pre-fern *Rhacophyton* and roots of the arborescent progymnosperm *Archaeopteris* in a flooded Devonian riparian marsh.

lake surrounded by drier, pteridosperm-dominated woodlands; these subsequently were altered to wetter substrates in which lycopod-dominated swamps are preserved (Scott et al., 1994). Many Carboniferous tetrapod assemblages accumulated in similar open-water bodies fringed by marshes or forest swamps, and in swamp-filled pools (oxbows, billabongs) (Milner et al., 1986; Hook and Baird, 1986; Garcia et al., this volume).

Tuffs containing fusain at East Kirkton may indicate that volcanic activity ignited wildfires (Brown et al., 1994), which in turn may have driven the vertebrates from this landscape into the lakes where they perished (Scott et al., 1994). Fires are important elements in the ecology of most modern wetlands and influence floral content and community succession in extant wetlands (Keddy, 2000). This probably has been the case since the Late Devonian (Scott, 1989).

Possible Mangal Wetland Origins

The Mississippian provides the first evidence for the expansion of any clade into nearshore and marginal marine sites, those under possible saline influence. Inasmuch as the term "mangrove" often is applied to woody taxa, the term mangal—any salt-tolerant plant—would be applied to these assemblages. Gastaldo (1986) interpreted the stigmarian-rooted lycopsids reported by Pfefferkorn (1972) in the Battleship Wash Formation, Arizona, as representing the first mangal taxon. Gastaldo et al. (this volume) also demonstrate that some Mississippian back-barrier marshes were inhabited by herbaceous, cormose lycopsids. Most arborescent lycopsids are interpreted to have been intolerant of salt water (DiMichele and Phillips, 1985), although smaller, cormose forms, such as *Chaloneria*, have been interpreted as living in coastal marsh-like habitats (DiMichele et al., 1979), as well as fresh-water marshes and peat-forest swamps (Pigg, 1992). It is not a simple proposition to identify morphological features that would support a brackish-habitat interpretation for Paleozoic plants because not all of these adaptations (for example stilt roots) are solely an adaptation to saline tolerance. Transgression (onlap) could result in burial of freshwater, near-coast taxa in marine sediments, confounding interpretations of mangal habit based on sedimentological evidence. In addition, many extant freshwater wetland plants and mangals live on freshwater lenses in the soil, adjacent to brackish or marine waters. Few plants can tolerate the precipitation of salts in marine-water influenced soils. Therefore, interpretation of mangal habit is, in part, a matter of recognizing that the plants did not live directly within fully marine salinities but could tolerate the incursion of salt water, or recognizing physiological features that allow an interpretation of salinity tolerance.

Spreading Mires and Lowland Swamps

Within the coastal plains and continental interiors, extensive swamps and thick peat mires first occur in the Late Mississippian throughout Eurasia including Canada, western Europe, Ukraine, Belarus, Russia, and China (Wagner et al., 1983; Scotese, 2001; Rygel et al., this volume). These are dominated by arborescent lycopsids that range throughout the late Early Carboniferous up to near the Mississippian-Pennsylvanian boundary, where they first are joined by typical Pennsylvanian lycopsid taxa. The lycopsids *Lepidophloios* and *Paralycopodites* remain a component of these mires into the Pennsylvanian, while new species of the lepidodendrid complex replace typical Early Carboniferous forms. A few floristic elements of the Early Mississippian (Visean) persist into the Namurian mires in the Silesian basin, mostly within the sphenopsids (*Archaeocalamites* and *Mesocalamites*) and fern/pteridosperms (Purkynová, 1977; Havlena, 1961). Although much of the global Mississippian is recorded in carbonate ramp deposits, it is these lycopsid-dominant swamps and mires that set the stage for the extensive accumulation of peatlands in the Pennsylvanian.

PENNSYLVANIAN

The Heyday of Tropical Mires

Pennsylvanian (Upper Carboniferous) coals are known from basins in the eastern and central United States, eastern Canada, England, eastern and western Europe as well as parts of China and East Asia (Walker, 2000; Scotese, 2001; Thomas, 2002). These areas straddled the Pennsylvanian equator (Fig. 6), with some coals representing the most widespread tropical mire systems in earth history (Greb et al., 2003).

Much is known about the ecology of Pennsylvanian wetland plants and plant communities, a consequence, in part, of exposures made possible by the mining of economically important coals. The ecologies of the dominant plant groups have been reviewed by DiMichele and Phillips (1994), but recent data from the Early Pennsylvanian (Langsettian) may indicate that the partitioning of ecospace within mires occurred through the Pennsylvanian (Gastaldo et al., 2004). In brief, giant lycopsid trees were restricted mostly to wet, periodically flooded substrates. These trees dominated Early and Middle Pennsylvanian forest mires. Lycopsids were spore producers, although some had seed-like "aquacarps," adapted for aquatic fertilization and dispersal in forested wetlands (Phillips and DiMichele, 1992). They were supported by bark, rather than wood, and had highly specialized rooting systems (*Stigmaria*) that facilitated growth in low-oxygen, soft substrates. There was a variety of lycopsid tree genera with specializations to different levels of disturbance and substrate exposure (Fig. 7A–7E).

Other spore-producing groups coexisted with the lycopsids in these mires. Marattialean tree ferns of the genus *Psaronius* were cheaply constructed plants (Baker and DiMichele, 1997); tree habit was made possible by a thick mantle of adventitious roots (Figs. 7A, 7C, 7F). The calamiteans were another group, closely related to modern scouring rushes and horsetails of the genus *Equisetum*. Extant *Equisetum* is a small, widespread, non-woody plant that grows in moist places and poor soil. Calamiteans appear to have inhabited the same environments (Fig. 7A), although some calamiteans grew to heights in excess of 5 m and, hence, would have served functions more similar to small trees than shrubs (Fig. 7D). The calamiteans were the only major Late Carboniferous tree group to exhibit clonal growth. Aerial stems developed from subterranean rhizomes in most species, a growth form that permitted them to exploit habitats with high rates of sediment aggradation (Fig. 7F) in which the stems could be buried repeatedly by flood-borne siliciclastics and continue to regenerate (Gastaldo, 1992).

Two seed-producing tree groups also were common in peat-substrate mires, the cordaites (Fig. 7F) and the medullosan pteridosperms (Figs. 7C, E). Cordaites were woody trees and shrubs closely related to extant conifers. In the middle Westphalian, cordaitean gymnosperms became abundant in some parts of mire landscapes (Fig. 7F), apparently reflecting areas with periodic extended substrate exposure or disturbance (Phillips et al., 1985). Cordaites were also common components of late Paleozoic Angaran (Asian) wetlands (Oshurkova, 1996). Some forms have been reconstructed as mangroves (Cridland 1964; Raymond and Phillips, 1983), although evidence of stilt-like roots is lacking in preserved *Cordaites* tree trunks (Johnson, 1999). It also has been suggested that they could tolerate brackish conditions (Wartmann, 1969). There is, however, substantial reason to doubt a mangrove interpretation, given that the plants appear to prefer rotted peat, possibly subject to exposure, and that they occur in a complex flora associated with an array of other plants that do not appear to be specifically adapted to salt-water tolerance (Phillips et al., 1985; Raymond et al., 2001).

Medullosan pteridosperms were small trees largely confined to nutrient-enriched substrates. They produced large fronds on which were borne some of the largest seeds known among Carboniferous tropical plants (Gastaldo and Matten, 1978). Medullosans were free standing and formed thickets or tangles of plants that leaned on each other for support (Wnuk and Pfefferkorn, 1984). In addition to these tree forms, representatives within the pteridosperms, ferns, sphenopsids, and lycopsids also displayed ground cover and liana (vine) growth strategies (Fig. 7B–7D, 7F). A liana growth strategy is important in modern tropical wetlands because it allows plants to compete for light amongst tall trees. These forms were systematically diverse and occasionally abundant in the community (Hamer and Rothwell, 1988; DiMichele and Phillips, 1996a; DiMichele and Phillips, 2002).

Non-Peat-Forming Swamps

Non-peat-forming swamps, sometimes referred to as "clastic swamps" (e.g., Gastaldo, 1987; Mapes and Gastaldo, 1986; Gastaldo et al., 1995) also were widespread in Pennsylvanian coal basins. These habitats supported a vegetation much like that of forest mires, although there were many species-level differences and the environments were dominated by different plants. Swamp habitats often were enriched in lycopsids but included pteridosperms as major components (Wnuk and Pfefferkorn, 1984; Scott, 1978; Collinson and Scott, 1987; Gastaldo, 1987). In the late Middle Pennsylvanian, marattialean tree ferns began to increase in abundance in all parts of the wetland landscapes, although the increase in fern abundance can be detected in clastic substrate habitats (marshes and swamps) before it appears in mire habitats (Pfefferkorn and Thomson, 1982). A major extinction at the end of the Middle Pennsylvanian (Westphalian) resulted in a significant reorganization of wetland ecology (Phillips et al., 1974; DiMichele and Phillips, 1996b). Following the extinction, Euramerican Late Pennsylvanian (Stephanian) mire and riparian swamps became more similar in overall patterns of dominance and diversity. *Psaronius* tree ferns were dominant, medullosan pteridosperms were subdominant, and *Sigillaria* (Fig. 7D), a tree lycopsid that may have preferred periodic substrate dryness, was locally common.

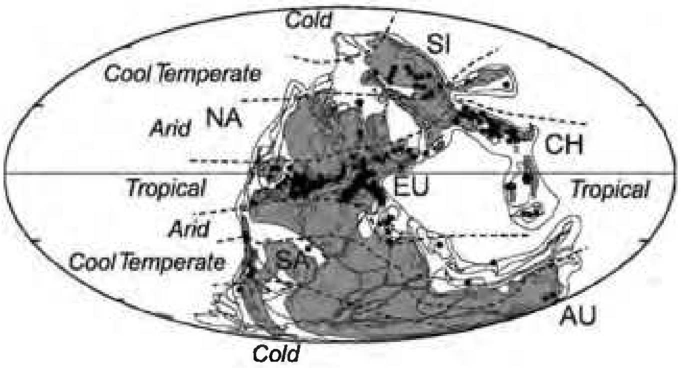

Figure 6. Upper Carboniferous paleogeography and climates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001). AU = Australia, CH = China, EU = Europe, NA = North America, SA = South America, SI = Siberia.

The Development of Wetland Successions

Many modern peatlands exhibit a temporal succession of wetland types in response to changing hydrology and nutrients (Gore, 1983; Moore, 1989; Mitsch and Gosselink, 2000; Keddy, 2000). The earliest definitive successions in ancient wetlands are from the Pennsylvanian. Studies of English Pennsylvanian coals by Smith (1957, 1962) noted that many exhibit vertical changes in spore content, which were inferred to represent changes or successions in plant (and wetland) types. Coals also exhibit vertical changes in ash yield, sulfur content, palynology, and petrography, which result from temporal succession of different wetland types (Cecil et al., 1985; Esterle and Ferm, 1986; Eble and Grady, 1990; Greb et al., 1999a, 2002). Successional patterns also have been inferred from coal balls (Raymond, 1988; Pryor, 1993; Greb et al., 1999b).

Many Euramerican coals began in topographic lows as marshes or swamps (Figs. 7A) and then became mires as conditions allowed for the uninterrupted accumulation of biomass. In some cases, successions occurred between different mire types. Thin peats, rooted seat earths (poorly developed soils—e.g., incep-

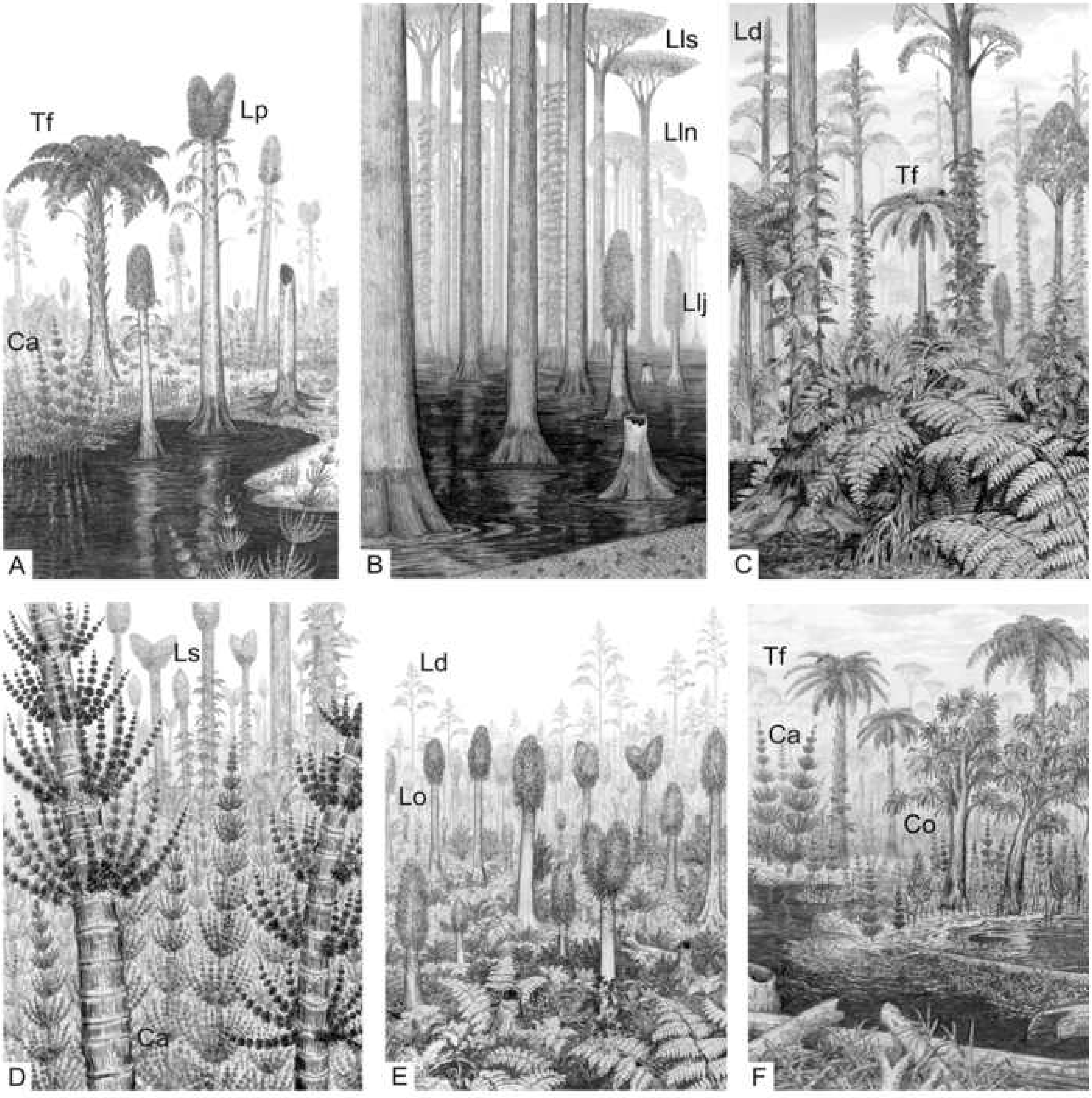

Figure 7. Pennsylvanian wetlands were diverse and included (A) pioneering topogenous riverine and paludal mires and swamps, (B) flooded swamps and topogenous forest mires, (C) paludal swamps, (D) riverine/riparian-margin marshes and swamps, and (E) ombrogenous mires. Disturbance-prone mires (F) along wetland margins were dominated by disturbance-tolerant flora. Swamps and forest mires were dominated by lycopods including *Paralycopodites* (Lp), *Lepidophloios* (Lls), *Lepidodendron* (Lln), *Sigillaria* (Ls), and *Omphalophloios* (Lo). Juvenile *Lepidodendron* (Llj). Lycopod reconstructions based on DiMichele and Phillips (1985, 1994). Other arborescent flora included tree ferns (Tf), sphenopsids such as *Calamites* (Ca, which ranged from herbaceous to arborescent), and the gymnospermous tree *Cordaites* (Co). Sphenopsids also occurred as vines (lianas). Ground cover was dominated by ferns and sphenopsids.

tisols or entisols), and in situ tree stumps within mineral substrates form in a wide variety of swamp and marsh settings (e.g., Teichmüller, 1990); thick peats can accumulate in fens and forested mires. Extant planar peatlands, also called topogenous mires or low-lying moors, generally occur at or just below the ground-water table and tend to fill in the topography (Gore, 1983; Moore, 1989). Ombrogenous mires, or raised mires in which peat doming may occur, build up above the topography in everwet climates (Gore, 1983; Clymo, 1987; Moore, 1989). Successions from topogenous to ombrogenous mires have been inferred for numerous Euramerican Pennsylvanian coals on the basis of palynological analyses (Cecil et al., 1985; Esterle and Ferm, 1986; Eble and Grady, 1990; Greb et al., 1999a, 1999b). Because modern ombrogenous mires build up above surrounding river levels, they are low-nutrient habitats without standing water cover and are dominated by stunted vegetation in the domed areas (Gore, 1983; Moore, 1989). In the Pennsylvanian, similar conditions are inferred for ombrogenous mires, which appear to have been dominated by stunted lycopsids *(Omphalophloios)* and ferns (Fig. 7E; Esterle and Ferm, 1986; Eble and Grady, 1990; Greb et al., 1999a, 1999b).

Figure 8. Giant arthropods in Pennsylvanian wetlands included the millipede *Arthropleura* and giant mayflies (lower right) here shown in a lycopod swamp.

Giant Arthropods in Wetlands

The record of Carboniferous arthropods is very good, partly because of the many Carboniferous concretion locations that are fossiliferous, including the famous Mazon Creek area of the Illinois Basin and Montceau-les-Mines, France (Darrah, 1969; Gastaldo, 1977; Nitecki, 1979; Baird et al., 1986). Much of the primary plant productivity in Late Carboniferous wetlands continued to reach animal food webs through arthropod detritivores, although a relatively complete trophic web of detritivores, herbivores, and carnivores had developed (DiMichele and Hook, 1992; Labandeira and Eble, 2006). *Arthropleura* was a giant millipede-like arthropod (Fig. 8) that consumed the inside of rotting lycopod trunks on swamp and forest-mire floors (Rolfe, 1980; Hahn et al., 1986; Scott et al., 1992). At 1.8 m in length, *Arthropleura* is the largest terrestrial arthropod of all time (Rolfe, 1985). Their large size suggests that arthropleurids filled a niche that had yet to be shared with tetrapods (DiMichele and Hook, 1992), or that tetrapods were not yet large enough to pose a threat. Millipedes are still important wetland detritivores but are much smaller than *Arthropleura*. Cockroaches are another common extant detritivore and were particularly abundant in Carboniferous wetlands (Durden, 1969; Scott et al., 1992; Easterday, 2003), reaching 8 cm in length.

In addition to their importance as litter-dwelling wetland detritivores, some Carboniferous arthropods also evolved flight (Kukalova-Peck, 1978, 1983: Scott et al., 1992; Labandeira and Eble, 2006). One explanation for the origin of flight is that wings evolved from gills in aquatic stages, and flight evolved through surface-skimming, a process used by extant, wetland-inhabiting stone flies (Plecoptera) and subadult mayflies (Ephemeroptera; Marden and Kramer, 1994). Giant mayflies with wingspans of more than 40 cm are known from Late Carboniferous wetland facies (Fig. 8; Kukalova-Peck, 1983). The most commonly depicted flying insect in Carboniferous illustrations is *Meganeura*, a dragonfly-like hexapod, which had a wingspan of more than 60 cm. The precursors of extant dragonflies, the Protodonata, also evolved in the Carboniferous, and some had wingspans of more than 60 cm (Carpenter, 1960). Extant dragonflies are common predators of wetlands. Because most dragonflies have aquatic nymphs, they require wet habitats for part of their life cycle. In fact, the evolution of metamorphosis in insects appears to have occurred in wetland or wetland-fringing ecosystems (Kukalova-Peck, 1983; Truman and Riddiford, 1999).

Insect flight also may have contributed to the rise of insect herbivory, as flying insects could exploit new food resources (DiMichele and Hook, 1992). Some Carboniferous insects (e.g., megasecopterans and paleodictyopterans) developed mouth parts for sucking and piercing. Evidence for this strategy is found in permineralized swamp-and-mire plants (Scott et al., 1992; Labandeira and Phillips, 1996; Labandeira and Eble, 2006). In fact, most major insect herbivore functional feeding groups on land were established by the late Paleozoic and are preserved in wetland and wetland-fringing estuarine and lacustrine sediments (Labandeira and Eble, 2006). Insect herbivory brought the wetland food web closer to modern trophic systems.

Amniote Evolution and Wetlands

The oldest undisputed amniote, the "protorothyridid" *Hylonomus* from the Middle Pennsylvanian of Joggins, Nova Scotia (Dawson, 1854; Carroll, 1964; DiMichele and Hook, 1992; Calder, et al., 1997; Calder et al., this volume), appears to be a very early member of the lineage that led to diapsids. Although reptiles do not require aqueous conditions for breeding, as do amphibians, many do require wetlands for food and cover (Fig. 9; Clark, 1979). At present, reptile abundance is influenced by the availability of horizontal and vertical habitat (Jones, 1986), as may have been the case in the Carboniferous. In the layered canopies of Pennsylvanian peatlands and forest swamps, there was abundant habitat availability for food and cover. At Joggins, reptiles were found within fossil hollowed lycopsid tree stumps; Dawson (1854) originally thought that the animals had fallen into the stumps and been trapped. More recent investigations interpreted the stumps as possible dens in which the reptiles died during wildfires (Calder et al., 1997; Falcon-Lang, 1999). This interpretation is plausible, given that modern wetlands are susceptible to seasonal wildfires, especially crown fires (Scott, 2001).

PERMIAN

High-Latitude Peatlands in Gondwana

Although Permian coals are sometimes considered part of the first great coal-forming period (Permo-Carboniferous), most, with the exception of some coals from the Permian of China (Xingxue and Xiuyhan, 1996), are geographically and floristically separate from their Carboniferous precursors. Pennsylvanian coals represent mostly tropical to subtropical mires that were widespread in Euramerican basins. By the Early Permian, North American coals were restricted to the northern Appalachian Basin, and these mires represented a holdover of Pennsylvanian floras into the Permian. Tropical coals became restricted to several Asian plates (Scotese, 2001). The most widespread peatlands flourished in the cool-temperate climates of the southern Gondwana supercontinent (Fig. 10). These included the first evidence of peats accumulating under permafrost conditions, similar to modern palsa mires (Krull, 1999). Some of these high-latitude Gondwana mires were the first extensive, nontropical mires in earth history and data suggest that there was latitudinal plant zonation (toward both poles), analogous to the modern latitudinal gradients in Northern Hemisphere wetlands (Retallack, 1980; Archangelski, 1986; Cuneo, 1996; Xingxue and Xiuyhan, 1996).

Figure 9. *Hylonomus*, one of the first reptiles, takes shelter in a hollow lycopod trunk during a Pennsylvanian swamp fire in what is now Nova Scotia.

The majority of coal resources in present-day Australia, India, South Africa, and Antarctica are of Permo-Triassic age (Archangelsky, 1986; Walker, 2000; Thomas, 2002). The floral composition of Gondwana coals is distinctly different from the Carboniferous coals of the Northern Hemisphere. Whereas Carboniferous mires were dominated by lycopods and tree ferns, Permian Gondwana mires were dominated by gymnosperms (Archangelski, 1986; Falcon, 1989; Cross and Phillips, 1990; Shearer et al., 1995). In the Early Permian, *Gangamopteris* was dominant. By the Middle Permian, *Glossopteris* was dominant. Many species are interpreted to have had both herbaceous and arborescent growth strategies (Falcon, 1989; Taylor and Taylor, 1990; White, 1990; Stewart and Rothwell, 1993; Shearer et al., 1995). Arborescent *Glossopteris* taxa were tall, with *Dadoxylon-Araucarioxylon*-type gymnospermous wood and *Vertebraria*-type roots (Fig. 11, Gould and Delevoryas, 1977; Stewart and Rothwell, 1993). The arrangement of secondary xylem and the presence of large air chambers in the roots indicate that these trees were adapted to standing water or waterlogged soils in swamp and forest mire settings (Gould, 1975; Retallack and Dilcher, 1981; White, 1990). The similarities between *Glossopteris* taxa on different Southern Hemisphere continents, and the recognition that *Glossopteris*-rich, coal-bearing strata accumulated under different climatic conditions from those of today, were some of the original data used to support the theory of continental drift.

Glossopteris mires also were composed of abundant horsetails, ferns, herbaceous lycopsids, and bryophytes (Neuburg, 1958; Archangelski, 1986; White, 1990) in a wide array of wetland types, including algal ponds, reed fens dominated by the sphenopsid *Phyllotheca*, wet forest mires, and dry swamp forests (Diessel, 1982). The association of bryophytes with high-latitude mires continues to this day in the world's most widespread peatlands, the *Sphagnum*-dominated peats of West Siberia (Botch and Masing, 1983) and the Hudson Bay Lowlands (Zoltai and Pollett, 1983). Another wetland association that began in the Permian was that with large semiaquatic vertebrates. Today alligators, crocodiles, and gavials play a similar ecological role. In

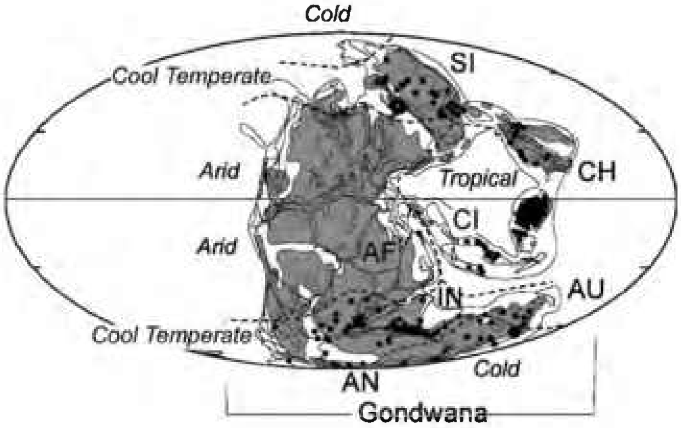

Figure 10. Permian paleogeography and paleoclimates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001). AF = Africa, AN = Antarctica, AU = Australia, CH = China, CI = Cimmeria, IN = India, SI = Siberia

the Permian, (and Late Carboniferous) large, semi-aquatic labyrinthodont temnospondyls were found in these roles. The 1.8-m long *Eryops* is one of the most common and widespread early Permian labyrinthodonts (Carroll, 1988). Later in the Permian, the rhinesuchids evolved from the eryptoid labyrinthodonts. Rhinesuchids had elongated skulls with eyes on top of their skull similar to extant crocodilians (Fig. 11).

Climatic Changes and Shrinking Wetlands

At the same time that the northern and southern continents were amalgamating to Pangaea, the late Paleozoic ice age was ending, with the last vestiges of Southern Hemisphere ice disappearing in the earliest Permian (Frakes et al., 1992). The termination of ice-age climates, and the sea-level periodicity associated with them, led to an overall climatic warming, which resulted in drying and a dramatic decrease in the scale and extent of wetlands when compared with the Carboniferous. Under these new conditions, some of the previously dominant spore-producing plants were restricted to narrow riparian corridors and lakeside settings (DiMichele and Chaney, this volume). The exception to this pattern occurs on the Chinese microcontinents, which remained climatically wet owing to their proximity to oceanic moisture sources. This region maintained wetland floras similar to those of the Middle Pennsylvanian (lycopsids, cordaites, tree ferns); such floras persisted into the Late Permian (Xingxue and Xiuyhan, 1996; Rees et al., 2002).

Changing climates and flora resulted in distinct global floristic zones (Ziegler, 1990; DiMichele and Hook, 1992; Rees et al., 2002). Today, latitudinal climate distribution results in zonation of different types of wetlands (e.g., extensive *Sphagnum* bogs at high latitudes, marshes in the temperate zone, and mangrove swamps in the Neotropics). Middle to Late Permian coals of the Southern Hemisphere are dominated by wood and leaves of the pteridosperm *Glossopteris* (Fig. 11), whereas coeval peats in Siberia are composed of biomass from ruflorian and voynovskyalean cordaites (e.g., Meyen, 1982; Taylor and Taylor, 1990). Ziegler (1990) discusses latitudinal zonation of Permian biomes. Regional Permian drying resulted in the diversification of seed plants, with the evolution and diversification of ginkgophytes, cycads, peltasperms, and filicalean ferns.

Figure 11. During the Permian, forest mires spread across Gondwanaland with gymnosperms replacing lycopods as the dominate wetland trees. The mire is dominated by *Glossopteris* trees and a ground cover of ferns and horsetails. *Rhinesuchus* (in the water) watches a dicynodont on shore. *Glossopteris* tree reconstruction after Gould and Delevoryas (1977).

Just as the loss of wetland habitats perturb modern ecosystems, the loss of Permian wetlands had profound influences on terrestrial ecosystems at the close of the Paleozoic. In the Karoo Basin of South Africa, where the most complete terrestrial record occurs across the P-Tr boundary, there is a basinward shift from riparian wetlands to dry uplands through the Permian. This shift is accompanied by a decrease in abundance and ultimate extinction of the *Dicynodon* (a therapsid) assemblage (Smith, 1995), which was replaced by the Early Triassic *Lystrosaurus* assemblage (Rubidge, 1995) soon thereafter. Dicynodonts (Fig. 11) were the most conspicuous terrestrial animals of the Late Permian, and among the first herbivorous vertebrates. They may have used their tusks for digging and slicing horsetail stems and buried rhizomes (Rayner, 1992). Some, like *Lystrosaurus*, were semiaquatic and inhabited lowland riparian wetlands (Carroll, 1988).

The evolution of vertebrate herbivory opened up a new niche to be exploited in wetland food webs. Modern wetlands support a wide variety of large grazing and browsing mammals including buffalo *(Syncerus caffer)* and hippopotamuses *(Hippopotamus amphibius)* in Africa, moose *(Alces alces)* in North America, water buffalo *(Bubalus bubalis)* in Asia, and the manatee (*Trichecus* sp.) in the Neotropics (Bacon, 1997). In extant wetlands, large herbivores modify and reshape wetlands. Their trails become corridors for other animals and may even modify flow paths. Herbivory can lead to increasing diversity of habitat and thereby species, modification of nutrient cycles, as well as expanding resilience and resistance of flora to disturbance (Naiman and Rogers, 1997; Mitsch and Gosselink, 2000).

Effects of the End-Permian Extinction on Wetlands

Reduction in wetland area in the modern world has been shown to decrease biodiversity because so many animals rely on wetlands for at least part of their life cycle (Mitsch and Gosselink, 2000: Bacon, 1997; Keddy, 2000); the reduction of wetland area in the Permian may have caused similar perturbations throughout Gondwana, leading into the end-Permian extinction event. Aside from loss of habitat, food, and nutrients, reductions in wetland area would also have reduced critical hydrological functions provided by wetlands. Decreasing flood storage capacity would have led to increased variability in continental and coastal hydrology, and possibly increased susceptibility of ecotonal areas to flash flooding.

The end-Permian mass extinction caused almost total collapse of the remaining wetland ecosystems (Retallack 1995; Visscher et al., 1996; MacLeod et al., 2000; Rees et al., 2000). This is indicated by the dieback of arborescent vegetation and the high-diversity *Glossopteris* flora (Visscher et al., 1996), as well as the global absence of coal beds in the Early Triassic (Retallack 1995; Retallack and Krull, this volume*)*. In the northern continents, many pteridospermous taxa and most of the arborescent lycopsids that had dominated the vast peatlands of the Carboniferous went extinct (Phillips et al., 1985; DiMichele and Hook, 1992; Stewart and Rothwell, 1993).

TRIASSIC

Wetland Recovery

Postextinction wetland habitat recovery occurred first with the short-term occupation of low-lying areas, by lycopsid isoetalean swamp forests and marshes, presumably from refugia. Isoetaleans were preadapted to oligotrophic conditions, so may have had an advantage in the post-catastrophic environments of the Early Triassic (Looy et al., 1999, 2001). Extant *Isoetes* (quillworts) are terrestrial to submerged aquatic plants with slender, quill-like leaves. Air chambers in the leaves of extant and fossil *Isoetites* support an aquatic ancestry (Taylor and Hickey, 1992). In some modern wetland investigations, submergent and floating vegetation characterizes shallow water or aquatic (e.g., Keddy, 2000) wetlands. Although emergent pteridophytes had been common in wetlands along lake and river margins in the Paleozoic, adaptation to a submerged habit in Triassic *Isoetes* would have allowed for the expansion of wetlands further into the riverine, littoral, and palustrine aquatic realms. Not only did isoetelean lycophytes diversify into freshwater aquatic wetlands, but some genera may also have been salt tolerant. *Pleuromeia* and *Cyclostrobus* have both been interpreted as salt-marsh plants because of their occurrence in coastal lagoon facies (Retallack, 1997).

As the postextinction recovery continued, lycopsid-dominated wetland assemblages were replaced by gymnosperm-dominated assemblages, divided broadly into the *Dicroidium* (pteridosperm) flora of southern Pangaea and the *Sciatophyllum* flora of northern Pangaea (Retallack, 1995; Looy et al., 1999, 2001). By the Middle Triassic, peatlands once again became part of the global ecosystem witnessed by the presence of thin coals in Northern Hemisphere rift basins and more extensive and thick coals in Antarctica (Fig. 12; Visscher et al., 1996; Looy et al., 1999; Retallack, 1995; Walker, 2000; Scotese, 2001; Thomas, 2002). The widespread coals in Antarctica continued the trend of high-latitude peat mires begun in the Permian. In Antarctica, mires were dominated by gymnosperms assigned to the Peltaspermales *(Dicroidium)*, cycadophytes, and ferns (Taylor and Taylor, 1990), whereas tree ferns and rhizomatous ferns, conifers, cycadeoids, gnetaleans, and pentoxylaleans became more common in the Late Triassic and persisted into the Cretaceous (Pigg et al., 1993; Retallack et al., 1996). There is growing evidence that many plant lineages that characterize later Triassic and Jurassic landscapes, including wetlands, originated in the Permian, and thus survived the Permo-Triassic extinction. These include peltasperms (Kerp, 1988), some cycads (DiMichele et al., 2001), and corystosperms (Kerp et al., 2004). As a consequence, the Permo-Triassic event or events that led to massive marine extinctions may have affected terrestrial landscapes mainly by causing ecological restructuring more than mass extinction—this in spite of an apparent global absence of mire habitats in the early Triassic.

Seasonal and Riparian Wetlands

Parts of the famous Petrified Forest of the Chinle Formation in the southwestern United States are examples of the reestablished forest swamps (non-peat-forming wetlands) during wetter Triassic intervals (e.g., Demko et al., 1998; Creber and Ash, 2004). The Chinle represents a paludal complex of streams, lakes, and swamps (Stewart et al., 1972; Blakey and Gubitosa, 1983;

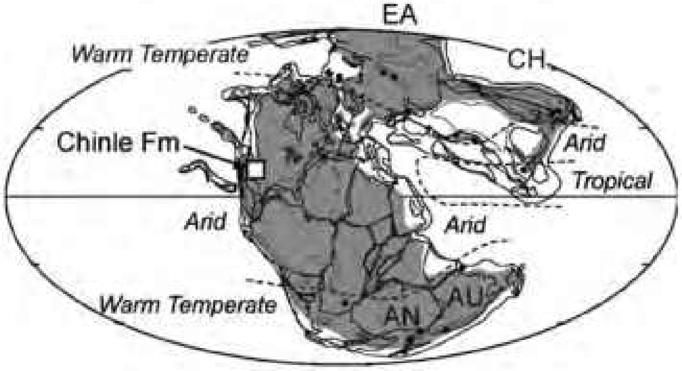

Figure 12. Triassic paleogeography and paleoclimates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001). AN = Antarctica, AU = Australia, CH = China, EA = Eurasia.

Long and Padian, 1986). The famous petrified logs are assigned mostly to *Araucarioxylon*-wood, although several new taxa have been recognized (Creber and Ash, 2004). These trees are interpreted as conifers that grew to heights of 56 m with diameters of 3 m (Ash, 2003). The lineages originated in the Southern Hemisphere (Stockey, 1982; Stewart and Rothwell, 1993) and spread northward into riparian settings, including forested wetlands. Common neocalamites, ferns, and lycopsids grew in emergent freshwater marshes within the Chinle paludal complex (Fig. 13), whereas horsetails, cycadeoids, cycads, and ferns occupied floodplains (Demko et al., 1998). Some *Equisetites* were arborescent, similar to their Carboniferous ancestors (Fig. 7D).

Increasing evidence of seasonality in the Chinle complex (Fiorillo et al., 2000; Therrien and Fastovsky, 2000) suggests that wetlands may have been more similar to seasonal riparian marshes and wet meadows than to more continuously wet marshes or bogs. Remains of carnivorous archosaurs, phytosaurs, metoposaurs, and small dinosaurs (such as *Coelophysis*, Fig. 13) are known from the Petrified Forest National Park (Stewart et al., 1972; Long and Padian, 1986; Therrien and Fastovsky, 2000). Dicynodonts, such as *Placerias*, also are found (Fig. 13) and play a role similar to that of large wetland herbivores in Permian wetlands. In modern semiarid to arid areas, riparian wetlands are critical to maintaining vertebrate biodiversity (National Research Council, 1995; Bacon, 1997), and likely were similarly important in ancient semiarid and arid environments (Ashley and Liutkus, 2002).

Phytosaurs and Crocodile Ancestors in Wetlands

Crocodiles, alligators, and gavials are common in modern wetlands especially in estuarine wetlands, coastal marshes, and mangrove swamps. In some wetlands, crocodilians are keystone species and play a crucial role in faunal and floral maintenance as biological “wetland engineers.” In the Everglades, for example, the paths and dens of alligators (gator holes) maintain waterways that would otherwise fill with sediment, and may be the only pools remaining in dry seasons. Thus, the alligators’ behavior provides crucial habitats for a wide variety of wetland species (Craighead, 1968; Jones et al., 1994). The relationship between crocodylomorphs (crocodile-like and other reptiles) and wetlands began in the mid-Triassic, during the adaptive radiation of archosaurs. In the Triassic, the crocodylomorphs replaced labyrinthodonts as the dominant large, semiaquatic wetland predators. Several archosaur groups with crocodile-like ankles (crurotarsi) evolved in the Triassic, and two taxa are convergent with modern crocodiles in habitat and morphology—the Phytosauria and Suchia. Phytosaurs (Parasuchia) look like modern gavials but had nostrils on top of their heads near their eyes, rather than at the end of the snout (Fig. 13). Phytosaurs were common in the fluvial and riparian marsh and forest wetlands of the Triassic in Virginia and

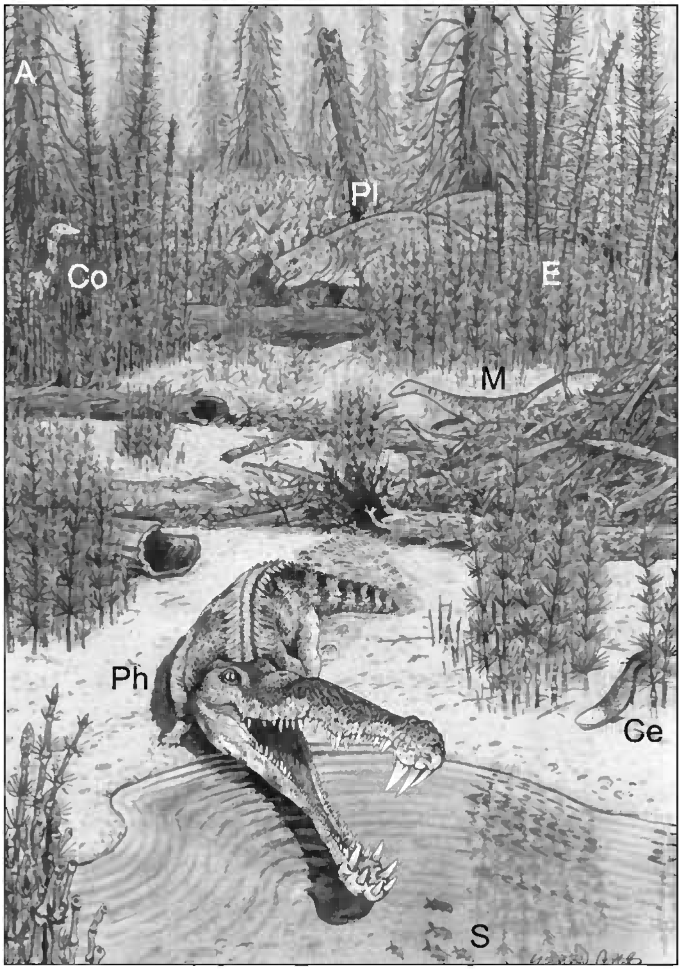

Figure 13. A phytosaur (Ph) maneuvers through a riverine marsh in the Triassic of the southwestern United States. Some of the *Equisetites* (E) horsetails were arborescent. The riparian wetland is also home to the small fish *Semionotus* (S), the large dipnoan *Ceratodus* (Ce), the protosaur *Malerisaurus* (M), large, herding *Placerias* (Pl) dicynodonts, and the small theropod dinosaur *Coelophysis* (Co). The floodplain consists of horsetails and ferns bordered by a riparian forest of giant *Araucarioxylon* (A) conifers.

the southwestern United States but were extinct by the end of the Triassic (Chatterjee, 1986; Long and Padian, 1986).

Suchians, the group that includes the Crocodylomorpha and is ancestral to extant crocodilians, originated as small, terrestrial, bipedal reptiles in the Triassic. The evolution of an aquatic habit by eusuchian crocodylomorphs in the Jurassic allowed these semiaquatic archosaurs to replace the phytosaurs. By the Cretaceous, giant crocodile-like eusuchians, such as the 12 m long *Deinosuchus*, were inhabiting estuarine wetlands along the southern coast of North America (Schwimmer, 2002). Also by the Cretaceous, Crocodylia (modern crocodile group) had evolved (Schwimmer, 2002) and represented the only surviving archosaurs (Carroll, 1988).

TRIASSIC-JURASSIC

Frogs, Salamanders, and Turtles in Wetlands

Among the most common animals in extant tropical and temperate wetlands are frogs, salamanders, and turtles. Although the association of amphibians and reptiles with wetlands began in the Paleozoic, extant classes did not evolve until the Mesozoic. The possible ancestor of frogs, *Triadobatrachus*, is reported from the Early Triassic and provides a link between earlier labyrinthodonts and frogs (Carroll, 1988). *Chunerpeton,* the oldest salamander, is known from Triassic lacustrine deposits of Mongolia (Gao and Shuban, 2003). Likewise, *Proganochelys* (=*Triassochelys*), the oldest freshwater turtle, is known from paludal marsh deposits of Germany, Southeast Asia, and North America (Gaffney, 1990). Members of each of these groups are dependent on wetlands for part of their life cycle and serve as important links in the trophic web (Weller, 1994; Mitsch and Gosselink, 2000). For example, tadpoles eat small plants and invertebrates and in turn, are eaten by fish. Later in life, adult frogs eat insects. Similar trophic links between these taxa likely were established by the Jurassic.

JURASSIC

Global Perturbations and Expanding Wetlands

The end-Triassic mass extinction is coincident with greenhouse warming, resulting in global perturbations in the carbon cycle and a near-total species-level turnover of megaflora (McElwain et al., 1999). Throughout the Jurassic, global warming and increased precipitation caused a gradual shift in wetland habitats from narrow riparian, lake-fringing swamps and marshes to more extensive conifer-dominated swamps and mires in the Cretaceous (Cross and Phillips, 1990). Southern Hemisphere swamps and forest mires were dominated by podocarpaceous and araucarian conifers, and Northern Hemisphere swamps and forest mires were dominated by taxodiaceous conifers (Wing and Sues, 1992; Askin and Spicer, 1995). Elements of this zonation remain to this day. An extinct conifer family, the Cheirolepidiaceae, were common in the Tropics, particularly in coastal wetland settings.

Krasilov (1975) interpreted a series of typical Jurassic wetland floral zonations in northern Eurasia. *Ptilophyllum* bennettites are interpreted to have occupied mangrove-like wetlands, while marshes were characterized by monospecific stands of large *Equisetites*. Bogs (forest mires) along lake margins and in riparian settings had a canopy formed from taxodiaceous conifers (*Elatides)* and arborescent ferns *(Dictyophyllum*, *Todites)*, with an understory composed of ferns and *Ptilophyllum* bennettites. Cycadeoids were the dominant flora of the Middle Jurassic coals of Mexico (Person and Delevoryas, 1982; Cross and Phillips, 1990). Ferns (e.g., *Coniopteris*), with lesser contribution from conifers and ginkophytes, dominated Middle to Late Jurassic mires of western North America (Silverman and Harris, 1967; Miller, 1987). Jurassic coals of China were dominated by tree ferns, dwarf coniferophytes, and secondary cycads (Miao et al., 1989). These examples highlight the increasing variability of floral associations in Jurassic wetlands. By the Late Jurassic, coals also were accumulating in several basins in the former Soviet Union, Mongolia, south China, and Iran (Fig. 14; Scotese, 2001; Walker, 2000; Scotese, 2001; Thomas, 2002).

Wetland Preservation of Early Mammals

Much of our understanding of the early diversification of mammals comes from material collected in a brown coal from the Guimarota coal mine, central Portugal. The mine was worked from 1973 to 1982 exclusively for paleontological purposes (Gloy, 2000; Martin, 2000), providing a detailed insight into the changing seres within the mire. The largest biomass contribution to the Guimarota paleomire was from *Araucariaceae* (conifers) and horsetails *(Equisetites)* with lower biomass contribution from pteridophytes *(Deltoidospora, Dicksoniaceae)*, cycads, and ginkgophytes (Van Erve and Mohr, 1988). Entombed within the Guimarota peat are ostracods, gastropods, freshwater and brackish molluscs, hybodont sharks, amphibians, small reptiles (turtles, crocodiles, lizards), the giant crocodile *Machimosaurus*, small dinosaurs, and mammals. The exceptional mammalian biota consists of Multituburculata, Docodonta, and Holotheria (Martin, 2000). In many modern wetlands, small mammals (especially rodents) are the dominant terrestrial and semiaquatic herbivores (Speight and Blackith, 1983). Although the Guimarota mammals show that small mammals were occupying wetland habitats, expansion into semiaquatic lifestyles may not have occurred until the Tertiary.

JURASSIC-CRETACEOUS

Mangals in Wetlands

Coastal mangals of coniferous affinity are interpreted from Wealden strata across the Late Jurassic–Early Cretaceous of the Northern Hemisphere. This group, informally known as the frenelopsids, are woody trees assigned to the Cheirolepidiaceae that produced *Classopollis*-type pollen (Axsmith et al., 2004).

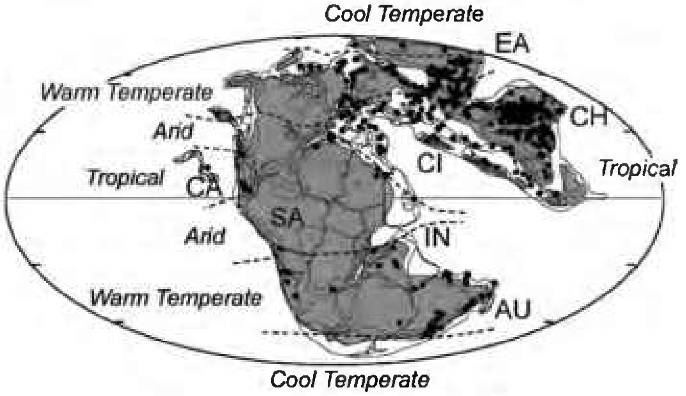

Figure 14. Jurassic paleogeography and paleoclimates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001). AU = Australia, CA = Central America, CH = China, CI = Cimmeria, EA = Eurasia, IN = India, SA = South America.

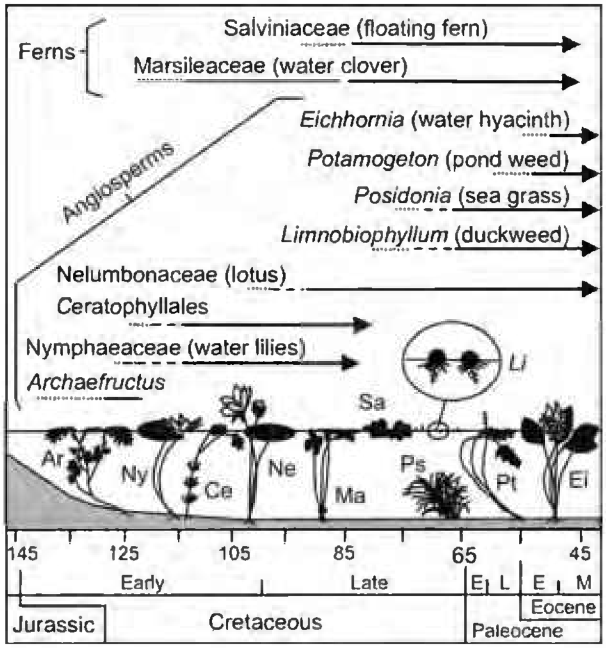

Figure 15. Radiation of aquatic plants and thereby aquatic wetlands in the Cretaceous and early Tertiary periods. Dates and image for *Archaefructus* from Sun et al. (2002); Ceratophyllales from Dilcher et al. (1996); *Eichhornia* from Patil and Singh (1978); *Limnobiophyllum* from Kvaček (1995); Marsileaceae from Lupia (2000); Nelumbonaceae from Dilcher (2000); Nymphaeaceae from Friis et al. (2001); *Potamogeton* from Berry (1937), Bremer (2000), Collinson (2002); ancestral Salviniaceae from Hall (1975); *Posidonia* and *Thalassocharis* (not shown) seagrasses are inferred to have Cretaceous origins in Brasier (1975) and Kuo and den Hartog (2000).

Pseudofrenelopsis and related taxa are common components of Early Cretaceous deposits of Africa, England, eastern Europe, and North America, and sedimentological criteria were used by Upchurch and Doyle (1981) to place these trees within a low-diversity, tidally influenced coastal regime. This is similar to the Upper Jurassic Purbeck beds where an in situ forest is preserved within a thin, carbonaceous marl paleosol (a well-drained, immature rendzina) of an intertidal and supratidal sequence (Francis, 1983, 1986). Associated with the Purbeck conifers are a few cycadophyte stems. Although these trees exhibit no evidence of buttressing or mangrove habit, they are encased in an algal stromatolitic limestone that formed in response to a change in base level of saline marine waters. Physiognomic characters of the frenelopsids including shoot morphology, the presence of thick cuticles, reduced leaves, sunken stomata, and succulent appearance, are morphological adaptations to water stress in saline or dry environments (Upchurch and Doyle, 1981; Gomez et al., 2001). Aside from stratigraphic and physiognomic indicators, several isotopic studies of Cretaceous European fossil plant assemblages using isotopic $^{12}C/^{13}C$ analysis indicate that *Frenelopsis* in marginal marine facies has elevated ^{13}C relative to other genera in more distal facies, suggestive of stress and possibly saline influences in salt-water marshes (Nguyen Tu et al., 2002).

JURASSIC-CRETACEOUS

Aquatic Ferns in Wetlands

Marsileaceae and Salviniaceae are heterosporous aquatic ferns whose origins can be traced to the Late Jurassic-Early Cretaceous (Yamada and Kato, 2002) and mid-Cretaceous, respectively (Hall, 1975; Skog and Dilcher, 1992; Pryer, 1999). Extant *Marsilea* are rooted shallow-water ferns, while the Salviniaceae consist of free-floating aquatic ferns. Free-floating habits extended the diversity of vascular macrophytes in wetlands, a trend that would be duplicated by unrelated angiosperms later in the Cretaceous and in the Tertiary (Fig. 15). Extant *Salvinia* have the ability to grow quickly and can form thick mats that limit sunlight and open water for other wetland plants and aquatic fauna (Julien et al., 2002). By the mid-Cretaceous, water ferns like *Hausmannia* were influencing lacustrine aquatic wetlands, acting as pond colonizers in mires (Spicer, 2002). In extant wetlands, the accumulation of aquatic plant mats and detritus, as well as sediment trapping from rooted aquatic plants, is an important part of pond-filling successions.

CRETACEOUS

Aquatic Angiosperms in Wetlands

Today, with notable exceptions, wetlands are dominated by angiosperms. The timing of origin of this group is subject to considerable debate, but the oldest undisputed fossil angiosperms are from the Early Cretaceous (Hickey and Doyle, 1997; Sun et al., 1998, 2002; Sun and Dilcher, 2002). Angiosperm origins are hotly debated (Scott et al., 1960; Crane, 1993; Crane et al., 1995), with some authors inferring evolution in upland areas (e.g., Stebbins 1974, 1976) while others have suggested origination in coastal lowlands (e.g., Retallack and Dilcher, 1981). Regardless of their origin, some of the oldest angiosperms were aquatic plants (Sun et al., 1998). *Archaeofructus,* the oldest known possible angiosperm, is interpreted as a submerged aquatic plant (Sun et al., 2002). Aquatic angiosperms (Fig. 15) developed a series of biochemical, morphological, and physiological specializations that allowed them to diversify into shallow aquatic wetlands (littoral, limnetic). By the Early to mid-Cretaceous, several freshwater families with rooted, floating leaf habits are recorded. These include water lilies (Nymphaeaceae, Cabombaceae), lotus (Nelumbonaceae), plants with affinities to hornworts (Ceratophyllaceae) (Dilcher, 2000; Dilcher et al., 1996; Friis et al., 2001), and possible water milfoils (Halogragaceae) (Hernández-Castillo and Cervallos-Ferriz, 1999). By the Late Cretaceous, the radiation of aquatic angiosperms also included a free-floating habit, with *Lymnobiophyllum* providing a possible ancestral link between duckweeds (Lemnaceae) and the aroids (Araceae) (Stockey et al., 1997). The diversification of aquatic angiosperms and ferns with floating leaves and free-floating morphologies would have provided new habitats and trophic links for fish, amphibians, and aquatic invertebrates in freshwater lacustrine and riverine wetlands, as well as in shallow, open-water wetlands. Likewise, the diversification of various aquatic plant morphologies would have set the stage for increased partitioning of flooded wetlands and hydroseres, more similar to those found in extant limnic and paludal wetlands.

CRETACEOUS

The Return of Extensive Peatlands

The Cretaceous represents the second episode of global coal formation. Extensive Cretaceous coals in western North America, China, the former Soviet Union, Central America, northwestern South America, and New Zealand (Saward, 1992; Walker, 2000; Scotese, 2001; Thomas, 2002) indicate that mires (fens, bogs, forest swamps) once again became widespread (Fig. 16). Northern Hemisphere peatlands continued to be dominated by conifers (*Abietites, Athrotacites, Moriconea, Podozamites, Protophyllocladus, Sequoia, Metasequoia*) with an understory of ferns, *Equisetites,* and less commonly, cycadophytes (Parker, 1975; Knoll, 1985; LaPasha and Miller, 1985; Spicer and Parrish, 1986; Miller, 1987; Cross and Phillips, 1990; Pelzer, et al., 1992; Saward, 1992; Spicer et al., 1992; Shearer et al., 1995; Hickey and Doyle, 1997; Spicer, 2002). In some raised mire successions, ferns and mosses were important (Hickey and Doyle, 1997). In the Southern Hemisphere, the palynology of coals from New Zealand and Australia indicates that podocarps and ferns dominated forest mires (Moore et al., this volume). These trends demonstrate an evolutionary stability and/or longevity in mire settings (as compared with floral changes in upland environments), a pattern of conservatism that has occurred several times in the geologic past and may be explained by incumbency. In essence, there is an ecological asymmetry between swamp environments and terra firma environments (DiMichele et al., 1987); plants adapted to the flooded, often low-nutrient conditions of swamps display physiological specializations that reduce their competitive abilities in terra firma settings. In contrast, the stringent physical conditions of permanently to periodically flooded environments exclude plants from terra firma environments. This results in sharp differences in species richness between these broad environmental categories within any given climatic zone (DiMichele et al., 2001). Hence, although angiosperms dominated many terrestrial ecosystems by the end of the Cretaceous (Lidgard and Crane, 1988; Wing and Boucher, 1998; Graham, 1999), and palms and at least 20 broad-leaved angiosperm taxa, including genera that contain common extant wetland plants such as *Platanus* (sycamore), are preserved in Cretaceous coal-bearing strata (Parker and Balsley, 1977; Tidwell, 1975; Balsey and Parker, 1983; Cross and Phillips, 1990), angiosperms remained only minor components in peat-accumulating wetlands (Pelzer et al., 1992; Saward, 1992; Hickey and Doyle, 1997; Wing and Boucher, 1998; Nguyen Tu et al., 2002). The exception occurs in the Southern Hemisphere, where the coniferous flora began to be replaced by *Nothofagus* (southern beech) in Antarctica and then Australia toward the end of the Cretaceous (Muller, 1984; Saward, 1992; Hill and Dettman, 1996).

Dinosaurs in Paludal Wetlands

Many reptiles inhabited—or traversed—and perished in Mesozoic wetlands. By the early Jurassic, herbivorous dinosaurs had replaced synapsids in terrestrial wetlands. The most famous dinosaurs associated with Cretaceous wetlands are the Bernissart *Iguanodons* from the Luronne coal seam, collected in Belgium in 1878 (Fig. 17). These ornithopods are historically famous for

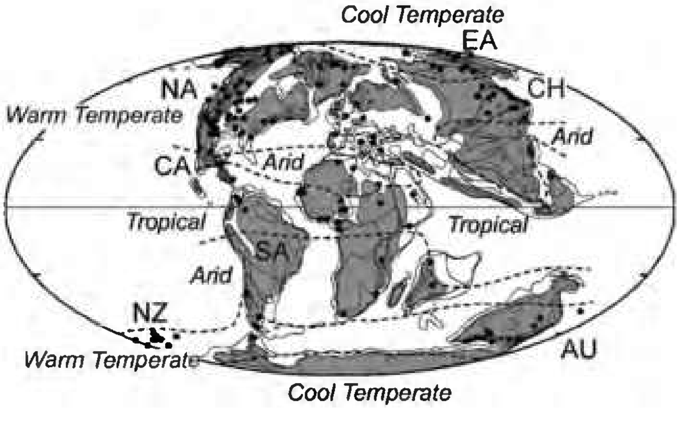

Figure 16. Cretaceous paleogeography and paleoclimates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001). AU = Australia, CA = Central America, CH = China, EA = Eurasia, NA = North America, NZ = New Zealand, SA = South America.

(1) being the first complete dinosaur skeletons recovered, (2) providing the first evidence that dinosaurs traveled in groups, and (3) proving that some dinosaurs were bipedal (Norman, 1980; Forster, 1997). Although such bones are not preserved commonly in peat, the unusual groundwater chemistries of wetlands can enhance preservation. In North America, the recovery of a putative fossilized four-chambered heart of the ornithischian dinosaur *Thescelosaurus* may owe its preservation to burial in a riparian forest habitat (Fisher et al., 2000).

In many cases, trackways provide evidence of vertebrates in wetlands. Thousands of dinosaur footprints have been found in the roof strata of Cretaceous coal mines (Peterson, 1924; Balsey and Parker, 1983; Parker and Rowley, 1989). Likewise, trackways from the Wessex Formation, Isle of Wight, England, were preserved in coastal floodplain, riparian wetlands. Twenty-two dinosaur species are known from the Isle of Wight, including *Iguanodon* and the fish-eating theropod *Baronyx* (Martill and Naish, 2001). Some beds represent catenas formed in seasonal wetlands, similar to modern tropical and subtropical river systems such as the Pantanal of the Amazon Basin, Brazil (Wright, et al. 2000).

Angiosperm Mangroves

Mangroves are a large group of unrelated, salt-tolerant trees and associated non-woody taxa including ferns (mangals). Although earlier plants have been interpreted as occupying possible mangal habitats, unequivocal salt-tolerant mangroves related to extant species appeared after the angiosperms in the Cretaceous (Muller, 1984; Aaron et al., 1999; Hogarth, 1999; Gee, 2001). *Nypa* palms (Arecaceae) evolved during the Cretaceous and rapidly spread into many wetland and wetland-fringing environments of the Neotropics (Singh, 1999). The Late Cretaceous to Paleocene marks the zenith of systematic diversity in the genus, with only *N. fructicans* constituting monotypic stands of the palm presently. Associated with *N. fructicans* in tidally influenced coastal zones is the mangrove fern *Acrostichum*, which is first reported from the Late Cretaceous (Bonde, 2002), and spread into the Eocene (Collinson, 2002).

Another Cretaceous mangal is *Weichselia reticulata* (Shinaq and Bandel, 1998). This tree fern is found in the Late Cretaceous of Bahariya, North Africa, with bivalves, gastropods, sharks, fish, turtles, crocodyliforms, and at least five genera of dinosaurs. The dinosaur *Paralititan stromeri* is one of the largest herbivores, whereas *Spinosaurus* and *Charcharodontosaurus* are two of the largest carnivores, of all time (Smith et al., 2001; Lacovera et al., 2002). All appear to have lived in or around this Cretaceous coastal swamp.

Modern mangrove swamps serve many important ecological functions, including nutrient cycling, and are net exporters of organic material into adjacent estuaries. They are important habitats for fluvial, estuarine, and coastal ecosystems (Bacon, 1997; Mitsch and Gosselink, 2000). These links lead to high productivity and biodiversity, a possible reason for the diversity and size of the gigantic dinosaurs at the Bahariya site (Smith et al., 2001). Modern mangrove swamps also play an important function in sedimentation and storm surge baffling along tropical coastlines. These functions probably existed in earlier inferred mangal habitats, but the adaptation of extant taxa in the Cretaceous allows for more actualistic comparisons of mangrove functions in the Late Cretaceous through Tertiary, based on the functions of extant genera.

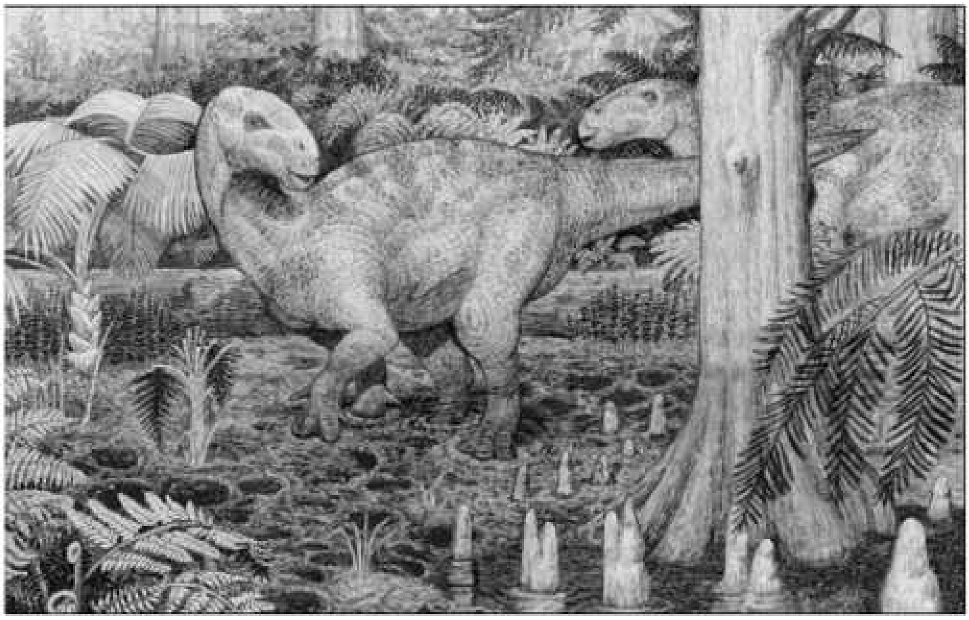

Figure 17. Dinosaurs in a Euramerican Cretaceous mire. *Iguanodon* herd passes through conifer-dominated forest mire. Ground cover consists of abundant ferns, Equisetites, and less common palms.

CRETACEOUS–TERTIARY

Marine Angiosperms: Sea Grasses

Phylogenetic analyses of extant sea grasses suggests that marine angiosperms have evolved in at least three separate lineages (Les et al., 1997). Sea grasses have a relatively poor fossil record, but *Posidonia* (Potamogetonaceae) is known from the Cretaceous (Kuo and den Hartog, 2000) and phylogenetic analyses support a Late Cretaceous origin (Bremer, 2000). Macrofossils of the sea grass genera *Thalasssodendron, Cymodocea* (Potamogetonaceae), and *Thalassia* (Hydrocaritaceae) are known from the middle Eocene of Florida (Lumber et al., 1984). Sea grasses are halophytes, and their evolution involved physical reduction in floral and leaf structures and xylem tissue, changes in reproductive strategies, and a physiological change to bicarbonate utilization in photosynthesis (Brasier, 1975; Stevenson, 1988; Kuo and den Hartog, 2000). Extant sea grasses are completely aquatic, with habitats extending to more than 6 m depth (which is the present limit of wetlands by the Ramsar classification). Hence, the evolution of submerged sea grasses extended the range of wetlands in coastal marine and subtidal estuarine environments, providing new habitats and resources for invertebrates and vertebrates. Sea grasses are particularly important because they dominate some of the most productive habitats on Earth (Stevenson, 1988; Bacon, 1997), and their presence changes local hydrodynamics, thus enhancing sedimentation of fines out of the water column. In fact, there is a recognized facultative successional sequence between mangrove swamps, sea grass meadows, and coral reefs, which may have its origins in the Late Cretaceous with the first appearance of sea grasses and mangroves (Brasier, 1975; McCoy and Heck, 1976). Such a succession and integrated trophic web explain the shared pan-Tethyan distribution of sea grasses with coral reef fish, decapod crustaceans, molluscs (McCoy and Heck, 1976), foraminifera (Brasier, 1975), and even manatees (Domning et al., 1982).

Carnivorous Plants in Wetlands

Low-nutrient fens and bogs support some of the rarest and most diverse plant communities in modern mires, including carnivorous plants (National Research Council, 1995; Bacon, 1997). Modern species of carnivorous plants, including bladderworts *(Utricularia)*, sundews *(Drosera)*, and butterworts *(Pinguicula)*, grow in acidic fens, bogs, and swamps. This relationship may indicate that plant carnivory arose in angiosperms as an adaptation to acidic, low-nutrient conditions of mire habitats. Carnivory arose not just once, but separately in 18 genera among six different plant orders (Juniper et al., 1989; DeGreef, 1997). Seeds of *Paleoadrovanda splendus*, which are similar in appearance to those of the extant carnivorous genus *Aldrovanda* (Droseraceae), a free-floating aquatic plant, are known from the Late Cretaceous (Knobloch and Mai, 1984; DeGreef, 1997). *Aldrovandra* is recognized in the Oligocene (Collinson et al., 1993) and spores of *Utricularia* (Lentibulariaceae) have been identified from the Miocene (Muller, 1984). The fossil history of other carnivorous plants is less certain. In general, their small stature and delicate nature, in combination with alteration due to early and late diagenesis within organic-rich substrates, result in a poor fossil record.

Amber in Wetlands

Most of the world's amber deposits are found in Cretaceous and Tertiary lignites, although amber often is reworked into other sedimentary deposits. Cretaceous ambers are known from England, Alaska, and New Jersey in the United States, Canada, Burma, and the Middle East. More well known are the Tertiary deposits from the Baltic, Dominican Republic, and Mexico (Poinar, 1992; Grimaldi et al., 2002). The New Jersey Cretaceous ambers preserve the most diverse assemblage of plants and animals, including 25 orders comprising 125 families and more than 250 species. New Jersey ambers formed in coastal swamps dominated by the conifer *Pityoxylon* (Pinaceae similar to *Pinus*, *Picea*, or *Larix*). These ambers contain the oldest fossil mushroom, ant, potter wasp, and bee, as well as the only Cretaceous flower preserved in amber (Grimaldi et al., 2000).

Tertiary Baltic amber was produced by *Agathis*-like (Kauri pine) araucariacean trees in conifer-dominated swamps and moist lowland forests. These ambers preserve a diverse assemblage including amphipods, isopods, centipedes, millipedes, dragonflies, roaches, beetles, and the oldest praying mantids (Poinar, 1992). Common wetland forms, including aquatic larvae and nymphs of caddis flies, mayflies, and waterbugs, provide evidence for standing water in some parts of the araucarian swamps (Larsson, 1978).

Blood Suckers in Wetlands

Many people associate black flies (Diptera) and mosquitoes (Culicidae) with wetlands. Although insects have been associated with wetlands since at least the Devonian (e.g., Rolfe, 1980), the oldest undisputed black flies and mosquitoes date from Late Cretaceous amber (Poinar 1992; Grimaldi et al., 2000, 2002). Modern mosquitoes are important transmitters of diseases such as malaria, yellow fever, dengue fever, and encephalitis. The association of these diseases with tropical wetlands is ingrained in our society. In fact, the translation of the word malaria (*mal aria*) means bad air, derived from the disease's association with fetid marshes. When wetland mosquitoes (and other insects) began to transmit diseases is uncertain (Martins-Neto, 2003), although Statz (1994) speculated that Oligocene mosquitoes spread diseases. Insect-borne diseases may have influenced the evolution of our own species, as indicated by the relationship between malaria and sickle cell disease. Although famous as pests and disease vectors, mosquito and black fly larvae are important parts of many wetland food webs (Bacon, 1997).

Effects of the K-T Extinction on Wetlands

The K-T extinction of the dinosaurs and a wide array of vertebrates and invertebrates led to extensive ecological restructuring in wetlands. At the same time, some of the fauna that survived were obligate wetland inhabitants, such as crocodiles, turtles, and frogs, suggesting that wetlands served as a faunal refugium during the K-T event. Wetlands tend to be inhabited by conservative taxa adapted to some aspect of limiting conditions, so wetland fauna may be preadapted to survival of mass extinctions.

The extinction is also associated with global floristic changes (Vajda et al., 2001), although these were mostly concentrated in the Northern Hemisphere, dominantly, North America (Askin, 1988; Johnson et al., 1989; Wolbach et al., 1990; Wing and Sues, 1992; Nichols and Pillmore, 2000). In some parts of western North America, the iridium anomaly occurs within coal beds, which provide a unique glimpse of successive responses to global catastrophe. In these areas, the ejecta cloud from the inferred bolide impact deposited a thin layer of glassy debris in the mires that eventually was altered to kaolinite (Nichols and Pillmore, 2000). This was followed by an increase in ferns, the “fern spike” found at many locations worldwide. The increase in ferns is associated with the elimination of much of the pre-existing swamp flora (especially deciduous dicots), and is interpreted to represent post-catastrophic colonization by pioneering taxa (Tschudy et al., 1984 Askin, 1988; Nichols and Pillmore, 2000). The most significant influences were on the angiosperms; the least were on conifers, ferns, pteridophytes, and mosses (Nichols and Fleming, 1990), the common wetland inhabitants. Likewise, in New Zealand, Vajda et al. (2001) interpreted recolonization of a waterlogged, K-T acidic substrate by a succession of moss and ground ferns, and then tree ferns. These plants would have been preadapted to post-catastrophic acidic environments through adaptations gained in pre-catastrophe mire habitats.

TERTIARY

Thick Peats and Peatland Successions

The Tertiary represents the third major interval during which widespread peat accumulation occurred. Tertiary coals are known from many basins worldwide (Scotese, 2001; Fig. 18), although the greatest resources are in western North America, northwestern and western South America, Germany, and Southeast Asia (Walker, 2000; Thomas, 2002). Tertiary coal beds can be as much as 90 m thick, whereas the thickest modern ombrotrophic mires are generally less than 20 m thick (the peat representing accumulation over the last ~7000 years). In fact, ombrotrophic mires may be limited in their potential thickness by numerous conditions including microbial respiration within the underlying peat (Moore, 1995). Hence, the great thickness of some Tertiary coals suggests that they cannot represent the accumulation of a single peat mire, but rather the accumulation of multiple, stacked mires (Shearer et al., 1994; Moore, 1995).

Even single coal beds may represent a wide variety of mire types. Palynological evidence indicates that Paleogene mire floras initially were dominated by gymnosperms with increasing importance of angiosperms through time (Nichols, 1995). This continued a trend that started in the Late Cretaceous when mires were dominated by conifers (Wing and Boucher, 1998; Graham, 1999). As angiosperms became increasingly important quantitatively, the resultant coals varied significantly in organic facies and in quality (Nichols, 1995), because of the increasing diversity of specialized mire types that could contribute to a single peat and ultimately coal bed. Eocene coals of the U.S. Gulf Coast accumulated from successions of freshwater herbaceous communities enriched in ferns, to freshwater Juglandaceous mire forests codominated with palms and *Nyssa* (tupelo), and, depending upon the sequence stratigraphic relationship of the coal to overlying marine sediments, even to mangrove swamps (Fig. 19A; Raymond et al., 1997). Miocene lignites from central Europe exhibit complex successions of wetlands including limnic to littoral aquatic wetlands with *Potamogeton* (pond weed), reed thickets in freshwater marshes, *Taxodium-Nyssa* forest mires, mixed herbaceous angiosperm fens, palm-dominated fens and forest mires, *Myrica* (bayberry) bogs or fens, riparian emergent wetlands with thickets of *Alnus* and *Cornus* (dogwood), mixed conifer (*Marcoduria*, *Sequoia*) forest mires, and oligotrophic low-diversity conifer bogs or raised mires (Fig. 19B; Teichmüller, 1958, 1962, 1982; Lancucka-Srodoniowa, 1966; Knobloch, 1970; Schneider, 1992, 1995; Mosbrugger et al., 1994). These examples illustrate the increasing diversity of angiosperms in Tertiary wetlands, as well as resultant wetland partitioning, when compared with those of the Cretaceous and Carboniferous.

Likewise, Tertiary plate tectonics exerted a profound effect on the distribution and biogeography of wetland floras (especially in the Southern Hemisphere), as the Gondwanan continents separated, and in some cases collided with northern continents (Christophel, 1989; Wing and Sues, 1992; Askin and Spicer, 1995; Burnham and Graham, 1999; Graham, 1999).

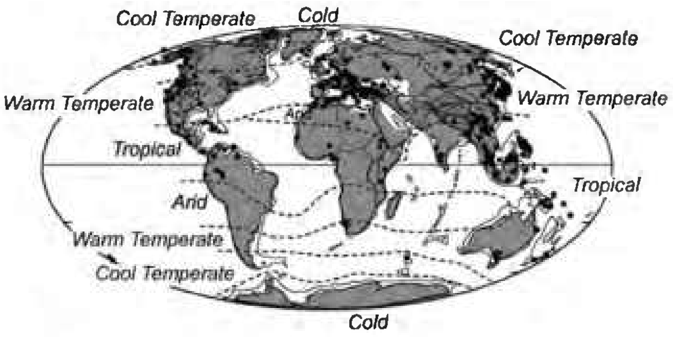

Figure 18. Tertiary (Miocene) paleogeography and paleoclimates showing locations of coal (black dots) and thereby known paleomires (modified from Scotese, 2001).

Cypress Swamps and Mires

Taxodiaceous conifers had dominated Cretaceous Northern Hemisphere wetlands (Stewart and Rothwell, 1993; Shearer et al., 1995), but *Taxodium* sp. (bald and pond cypress) did not become dominant in swamps and forest mires until the early Tertiary (Wing, 1987; Schneider, 1992, 1995; Kvaček, 1998; Collinson, 2000). By the Eocene, angiosperm-dominated wetlands had become more common in temperate riparian and lacustrine-margin settings (Graham, 1999), but taxodiaceous swamps persisted at high latitudes above the Arctic Circle during the Eocene thermal maximum (Francis, 1991; Basinger et al., 1994; Greenwood and Basinger, 1995; Williams et al., 2003a, 2003b). Taxodiaceous swamps on Axel Heiberg Island in the Canadian High Arctic consist of in situ assemblages of mummified tree stumps and forest-floor leaf-litter mats buried at different times over century to millennial time intervals. The picture that emerges in these swamps is one of a vegetational mosaic wherein taxodiaceous conifers *(Metasequoia and Glyptostrobus)* are laterally or stratigraphically adjacent to mixed coniferous forests and angiosperm/fern bogs, with the taxodiaceous swamp phase accounting for peat accumulation. Hence, taxodiaceous swamps were more extensive than at present, with geographic restriction to their present latitudinal distribution occurring during the Paleogene and Neogene. At least by the Oligocene, these wetlands occupied coastal settings of central Europe (Gastaldo et al., 1998), a distribution that continued into the Miocene (Kovar-Eder et al., 2001); along the Atlantic and Gulf coasts of North America, taxodiaceous swamps became well established in the Neogene (Rich et al., 2002). Both peat-accumulating and minerogenic swamps persisted into the Miocene. Taxodiaceous and other coniferous taxa, however, continued to contribute the bulk of biomass to north temperate peat mires, with little contribution from woody angiosperm taxa (Mosbrugger et al., 1994). In the late Cenozoic, access to continuous habitats across latitudinal gradients controlled the distribution of taxodiaceous conifers. *Taxodium* remained in eastern North America because there were continuous habitats it could occupy during late Cenozoic climate changes; *Metasequoia* went extinct in western North America because similar habitats were not present (Potts and Behrensmeyer, 1998).

Tropical Palm Swamps

Angiosperms show marked increase in Tertiary wetlands. Palms (monocots) are found in Tertiary coals from North America, Europe, Asia, and New Zealand (Packnall, 1989; Raymond

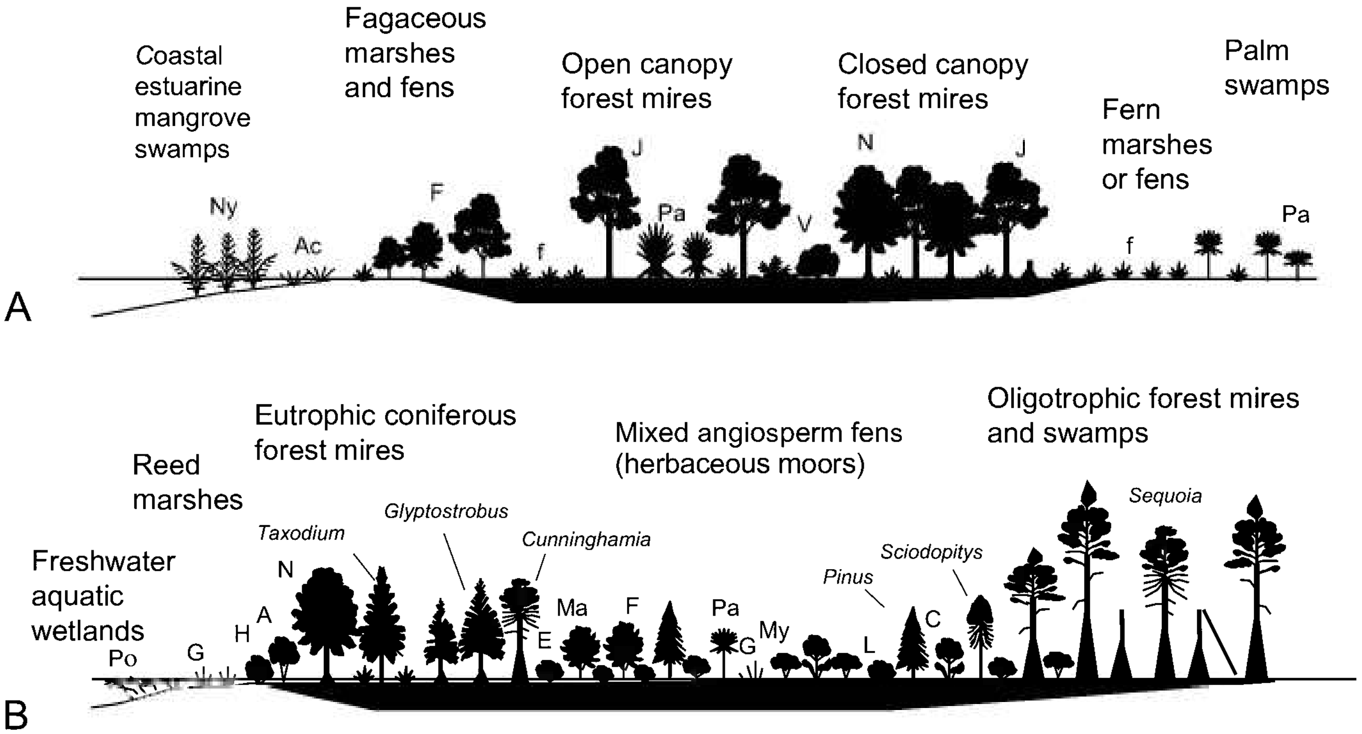

Figure 19. Diversification of wetland flora in Tertiary wetlands. (A) Wetlands interpreted from Eocene Gulf Coast coals (after data from Westgate and Gee, 1990, and Raymond et al., 1995). (B) Wetlands interpreted for Miocene brown coals in Europe (based on data from Teichmuller, 1962, 1982, and Schneider, 1992, 1995). Coniferous trees are labeled. Angiosperms include A = Alnus (alder), C = Cyrilliceae, E = Ericaceae, F = Fagaceae, G = Glumiflorae (reeds), H = Hamamelidaceae (sweet gum), J = Juglandaceae, L = Lauraceae, Ma = Magnoliaceae, My = Myrica (myrtles and bayberry), N = *Nyssa* (Tupelo), Pa = Palm, Po = *Potamogeton* (pond weed), and V = *Viburnum*. Ac = *Acrostichum* (mangrove fern).

et al., 1997; Lenz and Riegel, 2001). Today palms occupy a wide range of habitats including wetlands, but most wetland palms occupy non-peat-producing swamps rather than mires. In the Tertiary, on the other hand, palms inhabited swamps and mires. *Nypa* mangrove palms dominated coastal swamps of the Eocene Gulf Coast of North America, often in close association with tropical woody angiosperms, lycopsids, and ferns, similar to extant genera in coastal mangrove, back-mangrove swamps, and freshwater swamps (Fig. 19A; Fredriksen, 1985; Westgate and Gee, 1990). These estuarine mangrove palm swamps are associated with a diverse fauna including invertebrates, sharks and rays, bony fish, amphibians, turtles, alligators, the giant aquatic snake *Pteroshenus,* and a wide array of mammals including the four-toed horse *Epihippus*, the odd-toed ungulate *Amynodon* (which may have been semiaquatic), and sirenians (Westgate and Gee, 1990).

Although currently confined to a pantropical belt (Uhl and Dransfield, 1987; Myers, 1990), palms extended into midlatitude wetlands during the Eocene global warming event (Uhl and Dransfield, 1987). Palm distribution since the Eocene has been influenced by plate movements and climate changes (Burnham and Graham, 1999). The principal genera in extant palm wetlands are *Mauritia*, *Raphia*, and *Metroxylon* (Myers, 1990). The oldest *Mauritia* fossils are from the Paleocene and this genus became widespread throughout the Tertiary of South America (Muller, 1984; Junk, 1983; Uhl and Dransfield, 1987; Maraven, 1998). Extant *Mauritia flexurosa* has pneumatophores to cope with inundation in the swamps it inhabits, such as the várzea of the Amazon River in South America. Downriver in the Amazon, pure stands of *Raphia* and *Manicaria* palms are adapted to twice-a-day tidal inundation. *Manicaria* is known from the early Eocene London Clay (Collinson and Hooker, 1987). Further shoreward, mangrove palms dominate the river mouth and coastal estuaries (Junk, 1983; Brinson, 1990). Another palm adaptation can be seen in *Calamus* sp., the rattan palm, spores of which are found from the Paleocene (Muller, 1984). Extant rattan palms are climbing vines and are common in many tropical wetlands. These examples illustrate the wide range of wetland habitats to which palms have adapted and the specialization that typified the radiation of angiosperms in the Tertiary, resulting in a diverse array of wetland types and structural complexity within subcommunities of wetlands.

The Spread of Freshwater Broad-Leaved Wetlands

Aside from Palmae, there is a well-documented latitudinal expansion of angiosperms throughout the Tertiary (see summaries in Wing and Sues, 1992; Potts and Behrensmeyer, 1992; Askin and Spicer, 1995; Wing and Boucher, 1998; Graham, 1999). Although the spread of angiosperms into wetland habitats lagged behind the spread of sister taxa outside of wetlands, partitioning of wetland habitats increased as angiosperms became increasingly specialized, as shown in the examples in Figure 19A and 19B. Higher-latitude wetlands show more floral turnover than tropical and lower latitude wetlands, some elements of which remained from the early Tertiary. In the Southern Hemisphere, one of the most important arborescent angiosperms was *Nothofagus* (southern beech), which originated in Late Cretaceous high latitudes of South America or Antarctica (Muller, 1984; Hill and Dettman, 1996) and dispersed into Tertiary coal-forming mires of Australia and New Zealand (Barlow and Hyland, 1988; Christophel, 1989; Kershaw et al., 1991). Miocene and Oligocene peats of Australia and New Zealand accumulated as coastal and estuarine mires often dominated by *Nothofagus* with Myrtaceae, palms, podocarps, and ferns (Pocknall, 1985; Kershaw et al., 1991; Shearer et al., 1995). Some of these peats may reflect successions from podocarp- and fern-dominated floras to raised bogs with *Nothofagus* (Sluiter et al., 1995).

Among common northern-latitude arborescent genera, *Nyssa* (tupelo, black gum), *Alnus* (alder), *Platanus* (sycamore), *Populus* (poplar), and *Salix* (willow) became increasingly common in Tertiary temperate freshwater wetlands (Berger, 1998; Gastaldo et al., 1998; Kvaček, 1998; Graham, 1999), with many similarities to assemblages in extant North American Gulf Coast swamps (Mosbrugger and Utescher, 1997). Some Eocene forest mires in Germany were dominated by Fagaceae (oak and chestnut) and Betulaceae (beech), (Lenz and Riegel, 2001). Late Eocene to Oligocene Baltic amber swamps included common *Fagus* (chestnut) and *Quercus* (oak) (Poinar, 1992; Stewart and Rothwell, 1993). Following late Miocene cooling, taxonomically diverse broadleaved forests (including *Acer*, Fagaceae, and Juglandaceae) spread into northern-latitude wetlands (Askin and Spicer, 1995; Agar and White, 1997).

Wetland species in these angiosperm groups developed a wide array of adaptations to wet substrates. Tupelo and black gum have pneumatophores and buttressed bases, similar to bald cypress (Mitsch and Gosselink, 2000), an example of parallel evolution in different lineages of plants under the same physical conditions. Willows (*Salix* spp.) and cottonwoods (*Populus deltoides*) have adventitious roots, which permit recovery from periodic flooding. Some modern willow and cottonwood species have seeds that can germinate while submerged (Kozlowski, 1997). Willows also have large lenticels—structures that allow for gas exchange, an advantage in low-oxygen wetland habitats (Mitsch and Gosselink, 2000). These adaptations, and others, resulted in a wide variety of freshwater swamp types (e.g., red maple swamps, bottomland hardwood swamps) that were distinct in terms of dominant tree taxa, climate, frequency of flooding, and flood duration among other factors.

Mangrove and Mangal Wetlands

Mangroves increased in diversity throughout the Cenozoic, with *Rhizophora* (red mangrove) the most common extant genus replacing *Nypa* sp. during the early Tertiary (Plaziat, 1995; Aaron et al., 1999; Graham, 1999). Some of the most recognizable modern genera evolved prior to the Miocene (Fig. 20). All modern mangrove genera, except one, evolved before the close of the eastern Tethys Ocean in the late Miocene, with continental drift and changing climate altering species distributions (Plaziat, 1995; Aaron et al., 1999).

Modern mangroves exhibit a wide variety of adaptations to salinity stress, some being modifications of wetland root types that had previously evolved in other wetland flora in response to inundation and oxygen stress. *Rhizophora* has prop and drop roots, *Bruguiera* has knee roots, and *Avicennia* has pneumatophores (Fig. 20). In mangroves, cell membranes in these root systems exclude salt ions. Some modern mangrove species exhibit new adaptations to salt tolerance among wetland flora, such as salt-secreting glands and the ability to concentrate and then shed salt in bark and old leaves (Kozlowski, 1997; Hogarth, 1999). Viviparity is another important adaptation to salt tolerance in some mangroves (Koslowski, 1997; Hogarth, 1999; Mitsch and Gosselink, 2000). *Rhizophora* propagules germinate on the plant and then fall into the water, where they float until reaching water of appropriate salinity; the propagules then tilt on end and take root. At what point each of these adaptations evolved is uncertain, although fossil evidence of viviparity is known from the early to mid Eocene London Clay (Collinson, et al., 1993; Collinson, 2000).

The biogeographic distribution of mangroves throughout the Cenozoic parallels global climate changes up until the Eocene thermal maximum, with a range contraction of this wetland to its present pantropical distribution thereafter. The timing of mangal expansion toward the polar regions may have differed in the hemispheres; *Nypa* mangrove communities became established in New Zealand (Crouch and Visscher, 2003) and Tasmania (Pole, 1996) prior to the thermal maximum, whereas mangroves related to the genus *Bruguiera* and *Ceriops* are known first from the Eocene London Clay in southern England closer in time to the event (Chandler, 1951; Collinson, 1983). Most localities are identified on the basis of fruits, seeds, and pollen of mangrove taxa. In fact, the preservation and recognition of in situ coastal mangrove paleoswamps is undoubtedly biased because they occupy very narrow coastal habitats, tend to be non-peat producing, and are subject to erosion during sea-level rise (e.g., Liu and Gastaldo, 1992). Marsh-to-swamp transitions may be the result of less than a 30 cm change in elevation (e.g., Gastaldo et al., 1987) and mangrove-to-swamp transitions are similar (e.g., Gastaldo and Huc, 1992).

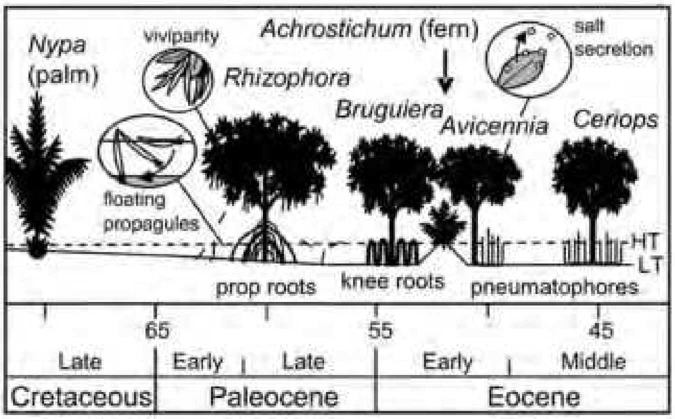

Figure 20. Earliest occurrence of extant mangrove taxon based on data compiled in Aaron et al. (1999). Various adaptations to saline wetland conditions are shown for modern species of genera shown.

The onset and zenith of the thermal maximum allowed for the expansion of mangals to higher latitudes but also may have perturbed the tropical wetlands closer to the equator. Rull (1999) documents a stepped and gradual change in the marsh and back-mangrove swamps of the Maracaibo Basin in Venezuela, where Paleocene taxa are interpreted to be of pantropical distribution, whereas Eocene assemblages are more restricted to the Neotropics. Thereafter, there is near-complete replacement of these Middle Eocene forms with typical Oligocene–Recent mangrove taxa, including *Rhizophora,* a trend reported globally (Muller, 1980; Rull, 1998).

Faunal Traps in Wetlands

Tertiary lignites and associated strata contain diverse flora and fauna. Some of the most famous Eocene vertebrates come from German lignites. The Geissel peat was a faunal trap with many fossils found in so-called sinkholes within the accumulation, as well as in lacustrine and fluvial facies. The most common vertebrates are crocodiles, tortoises, and mammals. At least 14 different orders of mammals are recorded as well as fish, amphibians, snakes, lizards, and birds (Franzen et al., 1993). Some component of the famous Messel deposits is also likely related to Eocene wetland inhabitants. Plant fossils in the Messel lake deposit include swamp cypress (Taxodiaceae), water lilies (Nymphaeaceae), sedges (Cyperaceae), club mosses, and ferns (Schaal and Ziegler, 1992), all common Eocene wetland taxa.

In Thailand, claystone interbeds in late Eocene lignites have yielded gastropods, pelecypods, turtles, a crocodile, and an early primate, *Siamopithecus* (Udomkan et al., 2003). A diverse fauna including primates is also known from lignites in Hungary. In fact, Kordos and Begun (2002) suggest that great apes in these wetlands may have migrated to Africa following Miocene climate changes. Some hominoid primates continued to occupy wetlands in the Oligocene of Africa. At the famous Fayum deposits of Egypt, *Aegyptopithecus* and *Propliopithecus* occur with a wide variety of mammals including anthracotheres, arsinöitheres, proboscideans, basilosaurs, and sirenians; reptiles including turtles, crocodiles, and the giant snake *Gigantophis;* and avifauna including storks and herons. The famous vertebrate fauna is associated with coastal mangrove and back-mangrove swamps (Bown et al., 1982), as well as with freshwater marshes and swamps interpreted as similar to modern Ugandan swamps (Olson and Rasmussen, 1986).

Some of the vertebrates associated with these sites have been interpreted as obligate wetland inhabitants similar to modern semiaquatic *Hippopotamus*, including the Eocene perissodactyls *Amynodon* and *Metamynodon* (Wall, 1998), the Eocene pantodont *Coryphodon* (Ashley and Liutkus, 2002), the Eocene–Oligocene ungulate *Moeritherium* (Carroll, 1988; Bown et al., 1982), and the Eocene–Pliocene artiodactyl ungulates of the Anthracotheriidae (Carroll, 1988; Berger, 1998; Kron and Manning, 1998). The latter are a link to true hippopotamuses, which evolved in the Miocene (Carroll, 1988). Likewise, several large proboscideans also may have been adapted to middle Tertiary wetland habitats. The Miocene elephants *Ambelodon* and *Platybelodon* both had broad shovel tusks, commonly interpreted as an adaptation for feeding on aquatic vegetation in marshes and submerged wetlands, although this assumption may be an oversimplification (Janis et al., 1998). All of these large, herbivorous mammals may have relied on wetlands for habitat and food and, in turn, had the potential to exert dramatic influence on the wetlands they inhabited.

Aquatic Mammal Evolution in Wetlands

During the Eocene, some terrestrial mammals evolved morphologic changes that allowed them to become permanent occupants of aquatic environments. This transition from terra firma to a fully aquatic environment occurred within (or at least through) wetlands. The Archaeocetes (ancient whales) had elongate mouths and probably had ecological roles similar to crocodiles in coastal, riverine, and lacustrine habitats (including wetlands) (Thewissen et al., 2001). The small whale *Kutchicetus minimus* was found in Eocene lignites from India and is interpreted to have inhabited backswamp environments (Bajpai and Thewissen, 2002). Likewise, sirenians (manatees, dugongs) are known from Miocene amber-bearing marls of Puerto Rico (Iturralde-Vinent and Hartstein, 1998) and the Oligocene Fayum deposits (Bown et al., 1982). Extant sirenians inhabit estuaries, streams, and coastal areas associated with aquatic and mangrove wetlands, where their primary diet is sea grass (Domning et al., 1982). Since the Eocene, they have played a unique role as large aquatic herbivores. Eocene and Miocene sirenians were mostly restricted to coastal riverine and estuarine aquatic wetlands (Domning, 1982). Evolution through the Tertiary appears to have been driven by the spread of sea grasses and the evolution of new aquatic macrophytes (Domning et al., 1982; Savage et al. 1994).

Birds in Wetlands

Although birds evolved in the Jurassic, transitional shorebirds are not recognized until the Late Cretaceous (e.g., Yang et al., 1994). The adaptive radiation of modern waterfowl lineages did not begin until after the K-T extinction, during the Tertiary radiation of birds (Feduccia, 1995, 1999). This radiation was concurrent with the spread of angiosperm-dominant wetlands and mangrove wetlands, all habitats that are used by birds for food, shelter, and breeding. The spread of aquatic wetlands was likely of particular importance to the diversification of waterfowl, since aquatic plants are a major part of waterfowl diets. Approximately one-third of extant North American bird species use wetlands as habitat and breeding grounds (Kroodsma, 1979; Mitsch and Gosselink, 2000; Stewart, 1996; Keddy, 2000).

The Presbyornithidae were a group of long-legged wading birds that may have originated in the latest Cretaceous and continued into the Tertiary. *Presbyornis* had the body of a flamingo and the head of a duck (Fig. 21; Feduccia, 1999). Mass death accumulations of *Presbyornis* associated with the Eocene Green River shales indicate that these early waterfowl lived in large colonies, similar to modern wetland-inhabiting flamingoes (Olson and Feduccia, 1980). True flamingoes evolved in the Eocene (Feduccia, 1996). A possible charadriiform shorebird has been identified from Eocene subtropical swamp sediments in China (Hou and Ericson, 2002). Long-legged wading birds, such as herons and storks (Ciconiidae), have a limited fossil record but can be traced back to the late Eocene or Miocene (Feduccia, 1996; Miller et al., 1998).

Ducks (Anatidae), the largest group of modern waterfowl and common inhabitants of wetlands around the world, are known from the Oligocene from several places around the world (Olson and Feduccia, 1980). Interestingly, seeds similar to those of modern duckweed (*Lemna* sp.), an aquatic plant favored by many extant duck species, also are known from the Oligocene to the recent (Mai, 1985). Modern duck genera became dominant

Figure 21. *Presbyornis,* a wading bird, that lived in Cretaceous–Tertiary marshes, looks for food in an Eocene lacustrine marsh. *Typha* dominates the lake margin. Marsh inhabitants in the Eocene Green River Formation included the alligator *Procaimanoidea*, the turtle *Baptemys*, the alligator gar *Lepisosteus*, and the famous *Knightia* fish. Sycamores and palms occupy fringing forests.

elements in freshwater marshes by the Pliocene (Carroll, 1988; Feduccia, 1996, 1999). The adaptation of these various bird groups to wetlands introduced a new avian component to wetland trophic systems. Recent studies have shown that increases in waterfowl will cause increases in benthic detritus, macrophytes, and fish in inland lakes (Mitsch and Gosselink, 2000). It is likely that the diversification of birds into wetland habitats in the Cretaceous and into the Tertiary caused similar changes through time.

Freshwater Grass, Reed, Rush, and Sedge Marshes

Modern freshwater marshes are dominated by a mosaic of diverse emergent herbaceous taxa, with some of the most common temperate members belonging to the grasses (Poaceae) such as *Phragmites* (reed grass), reeds (Typhaceae) such as *Typha* (cattails), rushes (Juncaceae) like *Juncus* sp., and sedges (Cyperaceae) such as *Scirpus* (bullrush), *Carex* sp. and *Cyperus* sp. The Cyperaceae alone includes more than 3500 species of grass-like herbs (Plunkett et al., 1995), many of which are common in wetlands. Some species of sedges, such as *Cyperus papyrus* (papyrus reeds), are highly productive wetland plants (Weller, 1994; Mitsch and Gosselink, 2000). Unfortunately, because these monocotyledons have no woody tissue, their preservation potential is limited to fruits and seeds (van der Burgh and Zetter, 1998).

Many extant wetland monocots are thought to have readapted to an emergent marsh habitat after the mid-Tertiary radiation of grasses, but some freshwater monocot wetland taxa may extend back to the Cretaceous. *Typha* (Fig. 21) and partially synonymous *Cyperacites* are reported from the Late Cretaceous (Tidwell, 1975; Muller, 1984; Mai, 1985; Bremer, 2000) but are not common floristic components until the Paleogene (MacGinitie, 1969; Machin, 1971; Muller, 1984; Collinson and Hooker, 1987; Collinson, 2002). Both have aerenchyma in their root tissues, commonly found in plants from mostly wet substrates. Seeds similar to those of the modern rush, *Juncus* sp., are reported from the upper Eocene/lower Oligocene (Collinson, 1983; Collinson et al., 1993) and from the Miocene of Europe (Mai, 1985). Most extant members of the family are freshwater species. Sedges (Cyperaceae) occupy diverse habitats today and are known from Eocene pollen and seed remains (Muller, 1984; Collinson and Hooker, 1987; Cross and Phillips, 1990; Bremer, 2000; Collinson, 2000). Wetland sedges, such as fossil *Phragmites* (Thomasson, 1986), a common constituent of European "reedswamps" and *Scirpus* (Van der Burgh and Zetter, 1998), are known from the latest Oligocene, and sedges were occupying peat mires in Australia by the late Oligocene or early Miocene (Blackburn and Sluiter, 1994), although much of the diversification of the Cyperaceae appears to be post-Miocene (Potts and Behrensmeyer, 1992).

An important aspect of the spread of grass, reed, and rush marshes during the drying climates at the end of the Tertiary is that these wetlands would have been the only sources of water and moist habitat in the vast grasslands that dominated many continental interiors, similar to vernal ponds and prairie potholes today. The diversification of the Anatidae (ducks) beginning in the Miocene and into the Pliocene is coincident with the spread of rushes, sedges, and grasses into freshwater marshes. This parallel expansion perhaps cemented the important wetland-habitat association that exists to this day.

Analyses of extant sedges in freshwater marshes indicate that they use a C_4 pathway for photosynthesis, in which CO_2 is fixed into a four-carbon molecule (Jones, 1988; Keeley, 1998; Ehleringer and Monson, 1993). Most plants use the C_3 pathway (CO_2 fixed into a three-carbon molecule). Molecular phylogenies and fossil evidence suggest that the C_4 pathway has arisen in different families at different times, but the initial appearance of this physiology appears to have been post-Cretaceous (Ehleringer and Monson, 1993; Kellogg, 2001) and in aquatic plants (Sage, 2001). The C_4 pathway has a physiological advantage when atmospheric conditions consist of low CO_2 pressures accompanied by warm, dry climates. Although this would not seem to be an advantage to wetland plants, plants using the C_4 pathway have increased nitrogen efficiency, which is a definite advantage in low-nutrient substrates such as those of oligotrophic wetlands (Jones, 1988; Ehleringer and Monson, 1993).

Salt-water Grass, Rush, and Sedge Marshes

Salt marshes are among the most productive ecosystems on Earth, and are common along tidally influenced coastlines except in the Tropics, where mangroves dominate most coastal wetlands. Although numerous Paleozoic and early Mesozoic wetland deposits have been interpreted as possible salt marshes, the inference is often based on the juxtaposition of overlying transgressive marine deposits, rather than on morphological features of the fossil flora or paleosols. That said, modern salt marshes are dominated by grasses, particularly cordgrass (*Spartina* sp.), rushes (*Juncus* sp.), and sedges (*Carex* sp.), such that the evolution of these wetland habitats postdates the evolution of angiosperms.

The oldest of the extant salt-marsh families is the Juncaceae (rushes), which appears at least by the middle Eocene, similar to the Cyperaceae (sedges) (Graham, 1999; Bremer, 2000). As mentioned previously, most extant members of both families are freshwater species. Thus, it is likely that the evolution of rushes and sedges with salt tolerance postdates the evolution of the families as a whole. Again, analyses of the photosynthetic pathways of saline marsh plants provide insight into the evolution of salt tolerance in emergent marsh monocots in lieu of fossil evidence. In many coastal and inland saline wetlands, C_4 plants replace C_3 plants as salinity increases (Ehleringer and Monson, 1993). The C_4 pathway has better water-use efficiency than the C_3 pathway (Jones, 1988; Keeley, 1998). Although water-use efficiency may not be important in freshwater marshes (except for vernal pools and prairie potholes), it is critical in saline environments (Ehleringer and Monson, 1993). The C_4 pathway appears to have evolved multiple times in monocots since the Cretaceous, but the earliest definite C_4 macrofossils are from the Miocene (Kellogg, 2001). Extant C_4-pathway saline grasses (Poaceae), such as salt grass (*Distichlis* sp.) and cordgrass (*Spartina* sp.), do not have an extensive fossil record and may postdate the Miocene. It is unlikely that there was significant competition from preexisting flora in the niche now occupied by halophytes such as *Spartina.* This is important to consider in terms of paleoecology, because it may indicate that many of the functions provided by extant saltwater marshes (both coastal marine and inland) were nonexistent (or at least diminished) earlier.

TERTIARY-QUATERNARY

Sphagnum-Mire Complexes

The development of cold climate in the Pliocene led to pine dominance of northern conifer forests and to development of lowland tundra, forest tundra, and permafrost (Agar and White, 1997). Two of the world's largest modern wetlands are the high-latitude mire complexes of the West Siberian and Hudson Bay lowlands. Northern-latitude mires are dominated by the peat moss, *Sphagnum* sp., and co-inhabited by a wide variety of plants, including conifers such as black spruce (*Picea mariana*) and tamarack (*Larix laricina*), woody angiosperms such as birch (*Betula*), and groundcover monocotyledons and dicotyledons such as heaths, sedges, and pitcher plants (Botch and Masing, 1983; Zoltai and Pollett, 1983).

Precursors of *Sphagnum*, the Protosphagnales, are reported from the Permian of Russia (Neiburg, 1958), and spores of *Sphagnum* are recorded from Jurassic coals of China (Miao et al., 1989), Cretaceous coals of Alaska (Hickey and Doyle, 1997), and Tertiary coals of North America and Europe (Steere, 1946; Cross and Phillips, 1990). The point at which *Sphagnum* began to dominate oligotrophic mires is uncertain, although it appears to postdate the late Neogene. Obviously, the extent of current *Sphagnum*-dominated wetlands is related to the last Pleistocene glacial retreat. In fact, there is a repetitive expansion and contraction of the northern-latitude coniferous forests (and associated wetlands) with each ice advance and retreat (Agar and White, 1997). In some cases, these wetlands acted as refugia for both flora and fauna during interglacial periods (Speight and Blackith, 1983). Access to continuous habitat across latitudinal gradients was a strong selective criterion in sorting which elements of the wetland flora and fauna survived late Cenozoic climate changes (Potts and Behrensmeyer, 1998).

Sphagnum almost certainly was preadapted to oligotrophic habitats, with the development of extensive aerenchymatous tissues allowing it to grow in low-oxygen environments. This anatomical feature is related to the plant's ability to leak oxygen through its roots to create a local aerobic environment. Its compact growth habit, overlapping leaves, and rolled branch leaves enhance water retention (Mitsch and Gosselink, 2000). Modern *Sphagnum* has the ability to acidify its surroundings, which may aid in retarding bacterial decomposition, allowing peat to accumulate even in an environment of low primary productivity (Mitsch and Gosselink, 2000). Additionally, acidity helps alter mineral substrates on which the peat mosses accumulate, creating and maintaining a clay-rich, impermeable layer that further promotes waterlogging and peat accumulation.

Giant Wetland Mammals

High rates of biomass production and recycling in wetlands support trophic tiers of abundant animals, albeit each of relatively low species diversity. The abundance of food resources in this setting permitted extraordinarily large animals to inhabit these environments. In fact, the largest rodent of all time was a wetland inhabitant. *Phoberomys pattersoni* was more than ten times larger then the largest living rodent, the capybara, and inhabited late Miocene freshwater paludal marshes of Venezuela. *Phoberomys* was semiaquatic or foraged in water on wetland grasses, as do extant capybaras (Sánchez-Villagra et al., 2003).

Beavers belong to the family Castoridae, which appears to have originated in North America during the Oligocene (Kurten and Anderson, 1980; Carroll, 1988). Beavers are not only wetland inhabitants, but also creators of wetland habitat, so-called natural wetland engineers (Jones et al., 1994). Wetlands and ponds created by beavers (Fig. 22) are important habitats for amphibians, mammals, and birds (Keddy, 2000). The oldest beaver, *Dipoides*, is known from the late Neogene (Pliocene) of Eurasia and North America. Fossil beaver dams in the Plio-

Figure 22. Mastodons along the shore of a Pleistocene beaver pond in a boreal fen. The pond is also home to turtles, ducks, and other birds. Aquatic plants include water lilies (lower left) and *Potamogeton* sp. (pond weed) (lower right). Sedges (*Carex* sp.) and mosses are common. The fen is bordered by a black spruce (*Picea mariana*) swamp, with tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), and a few deciduous trees and shrubs such as oak (*Quercus* sp.) and willow (*Salix* sp.).

cene indicate that dam construction was an early part of this animal's behavior (Tedford and Harington, 2003). During the Pleistocene, the giant beaver *(Castoroides ohioensis)* reached lengths of 2.5 m in North America. Remains of ice age giant beavers have been preserved in numerous Eurasian Pleistocene peats and pond-paludal wetland deposits (Kurten and Anderson, 1980; Hansen, 1996).

Many skeletons of ice age mammals, including mammoths, mastodons, ground sloths, and wooly rhinoceroses, have been excavated from fluvial, paludal, and peat permafrost in the northern high latitudes. Some of these finds have included soft-part preservation of hair, skin, and internal organs (e.g., Lister and Bahn, 1994). Numerous mastodons (Fig. 22) also have been found trapped in peat and wetland-fringing pond deposits of eastern North America (Eiseley, 1945; Miller and Nester, this volume). Indeed, the first mastodons to be described were found at Big Bone Lick, Kentucky, along with mammoths, bison, and other mammalian taxa. The Big Bone fauna is interpreted as having accumulated in a "bog" fed by a salt-and-mineral spring (e.g., Jillson, 1968), although a lacustrine marsh (non-peat producing) may be a more appropriate term. These wetland bones were used by Cuvier in the late 1700s and early 1800s to argue for the idea of extinction (Rudwick, 1997; Semonin, 2000).

QUATERNARY

Wetland Archeology

Wetlands have had a profound effect on human civilization and, of course, humans have dramatically influenced wetlands; unfortunately, in modern times the influence mostly has been detrimental. Wetlands were historically used as sources for construction materials, fuels, fishing materials (traps, poisons, dyes), iron, textiles, dyes for cloth, tannin for leather preservation, compost, sugar, vinegar, honey, fermented drinks, medicines, contraceptives, aphrodisiacs, waxes, incense, glues, and as a food resource, through fishing, hunting, and aquaculture (Bacon, 1997).

Shaped stone tools found with the bones of straight-tusked elephants and other mammals in wetland clays of Torralba and Ambrona, Spain, may represent early hominid butchery or scavenging sites on the margins of wetlands (Klein, 1987: Nicholas, 1998). By the late Pleistocene, a hunting-and-gathering lifestyle was firmly established among humans, and several archaeological sites in Europe indicate that wetlands were an important resource base (Nicholas, 1998). Among the European sites are the oldest known hunting spears, found with butchered remains of horses, from a coal mine in Schöningen, Germany (Dennell, 1997; Thieme, 1997). Preservation of the 400,000-year-old spears was aided by tannic acids from the overlying peat.

At Monte Verde, Chile, the oldest human occupation site in the Americas is situated beneath a water-saturated reed-and-shrub bog that covered the site with a layer of peat, isolating the material from oxygen and deterioration. Mastodon bones and meat, wooden lances, planks and stakes, knotted reeds, and animal hides have been recovered from the site, as well as blood hemoglobin from a tool (Tuross and Dillehay, 1995). Not only was the preservation of this site reliant upon wetland chemistry, but it also appears that bogs and freshwater and salt-water marshes provided construction material and food for the Monte Verde culture (Dillehay, 1989). Likewise, in North America, lacustrine aquatic wetlands preserved mastodon intestines filled with sand and gravel, indicating that prehistoric humans filled these organs as "clastic anchors" to keep the bodies on the bottoms of peaty, anoxic ponds for winter meat storage (Fisher, 1995).

The development of modern civilizations around the Fertile Crescent of the Tigris and Euphrates Rivers, as well as the Nile Valley, resulted from their location along rivers with fertile flood plains, marshes, and riparian wetlands. Aside from food and water available within these ecosystems, wetland plants provided the Egyptians with papyrus *(Cyperus papyrus)*. The word "paper" is derived from papyrus, and Egyptians began to use this marsh plant to make paper by 2000 B.C. Many of the classic writings of ancient Egypt, Greece, and Rome were inscribed on the smashed stem piths of these plants. At the same time that paper was being made from wetland plants in Egypt, man-made wetlands were being created to grow rice in lowland deltas and flood plains in Southeast Asia.

One of the most interesting wetland-associated anthropological finds is the "bog bodies" of northern Europe (Glob, 1965; Menon, 1997) and Florida (Doran et al., 1986). These remains date back to 8000 B.C. and are famous because they are mummified with excellent soft-tissue preservation. Additionally, they provide information about social behavior as indicated by a wide range of burial mechanisms, including ritual burial, accidental death, and murder (executions, sacrifices). Possibly the most unusual example of soft-tissue preservation is the Middle Archaic (8000-year-old) brain tissues and DNA recovered from human remains in a pond peat from Windover, Florida (Doran et al., 1986). At Windover, Native Americans buried their dead underwater on the bottom of a pond. Over time, lacustrine peat covered the bodies, promoting exceptional preservation.

Human Impacts on Wetlands

Our civilization's expansion has come at the expense of wetland habitats. More than 70% of the world's population inhabits coastal areas, and increased population growth in the past several hundred years has resulted in a loss of as much as 50% percent of the world's wetlands (Keddy, 2000). This loss has resulted in the deterioration of many wetland functions, such as contributions to wildlife habitat, biodiversity, natural water quality improvement, natural flood mitigation through water storage, as well as shore and bank stabilization (Mitsch and Gosselink, 2000; Keddy, 2000). Bacon (1997) noted that because of their variability, geographic distribution, and biological richness, wetlands contain a significant amount of the world's biodiversity, and thereby a large pool of genetic resources. Loss of wetland habitats may endanger the future genetic resources of plants and animals. The fossil record is our best source of baseline data from which to assess the long-term impacts of environmental perturbations on global ecology and biodiversity. Through better understanding of the fossil record and the evolution of wetland types, wetland functions, and wetland interactions with other ecosystems, we can better understand and possibly mitigate detrimental influences on wetlands and associated ecosystems.

SUMMARY

Modern wetlands are a diverse array of habitats with equally diverse floral and faunal associations, controlled by a host of interacting factors. Most of the functions recognized in extant wetlands originated in the Paleozoic. At some times in the past, certain functions have played a far more significant role than they do today, for example, in natural carbon sequestration or the natural alteration of the world's biogeochemical and hydrological cycles.

The oldest wetlands were similar in stature to moss-lichen communities but were non-peat-accumulating. Floral adaptations and evolution led to the first marshes, swamps, fens, and, eventually, forested mires in the Devonian. The diversification of wetland habitats profoundly influenced the terrestrialization of plants, invertebrates, and vertebrates, as well as sediment stabilization and global biogeochemical cycles. By the Carboniferous, wetlands dominated by trees and other plants were widespread and included the largest tropical mires in earth history. The spread of mires from the late Devonian to the Carboniferous increased the importance of wetlands as global carbon sinks. Within these environments, the flora and fauna greatly diversified through time. Most of the Paleozoic terrestrial fossil record comes from these Carboniferous environments. During the Permian, floral adaptations to cooler climates allowed for the development of the first high-latitude mires, latitudinal zonation of wetland floras, and a switch from mires dominated by lower vascular plants to those dominated by gymnosperms. Large, semiaquatic herbivores and carnivores also made their first appearances in Permo-Carboniferous wetlands. Changes in climate and tectonics at the close of the Paleozoic resulted in dramatic upheavals within wetland habitats, leading to major disruptions of many wetland ecosystems. Decrease in wetland area at the end of the Permian likely was accompanied by a significant decrease in wetland functions.

Recovery in the Mesozoic was slow, with the reconstitution of wetlands ultimately by a different "framework" vegetation than that of similar habitats in the late Paleozoic. During the Mesozoic, continental movements resulted in the physical separation of Northern and Southern Hemisphere landmasses, with resultant evolution of distinct wetland floras in these areas, particularly visible among newly evolved conifer groups; some of these differences persist to this day. In the latter part of the Mesozoic, angiosperm evolution led to dramatic floristic changes in almost all terrestrial environments including wetland habitats. Additionally, angiosperm diversification resulted in novel morphologies that permitted the exploitation of habitats on the margins of existing wetlands. Angiosperm expansion allowed for the development of extensive fresh and saline floating and submerged communities, as well as tidal-estuarine salt marsh and mangrove-forest wetlands fringing today's coastal zones. These wetlands are among the most productive ecosystems on the planet and are tied intricately to food webs in surrounding communities. The evolution of extant wetland groups, such as frogs, salamanders, turtles, and crocodiles occurred during the mid-Mesozoic; genera from these groups would be among the few terrestrial vertebrate survivors of the K-T extinction, illustrating the value of wetlands as refugia. Mid- to late Mesozoic wetlands were also important faunal traps for early mammals and dinosaurs, including some of the largest herbivores and carnivores in earth history. Amber from Mesozoic and Tertiary wetlands provides unique insight into the radiation of insects that accompanied the radiation of angiosperms.

The Cenozoic radiation of angiosperms allowed for abundant floral partitioning and the development of a wide array of specialized subcommunities within wetland ecosystems. This radiation was coeval with the radiations of mammals and birds, both of which developed specialized niches within wetland ecosystems. The development of modern grass- and herb-dominant marshes accompanied mid-Cenozoic cooling and likely was a dramatic influence on extant waterfowl-marsh associations. By the late Cenozoic, most modern biomes had formed including extensive high-latitude *Sphagnum*-dominated mire systems, the most extensive wetlands in the world today. The late Cenozoic has also witnessed the expansion of our own species along the margins of wetlands, with early civilization utilizing a wide array of wetland flora and fauna for food and materials. The expansion of civilization resulted in the infilling and draining of global wetlands. Only recently have the repercussions of wetland loss been realized, with increasing attempts to restore and protect these vital parts of our global ecosystem. As public awareness of the importance of wetlands continues to grow, we will need to understand better how these systems respond to perturbations, how they recover from major environmental disruptions, and how wetland biotas interact with those of surrounding environments. The fossil record is our best source of information on these concerns, and it will become increasingly important as the details of ancient wetlands and the vagaries of their dynamics are investigated and clarified.

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