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Arthropod Terrestriality

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INTRODUCTION

Since the late Paleozoic, insects and arachnids have diversified in the terrestrial world so spectacularly that they have become unquestionably the most diverse group of organisms to ever inhabit the planet. In fact, this 300 million year interval may appropriately be referred to as the *age of arthropods*. What is the origin and history of terrestrial arthropods? How is arthropod diversity maintained on land? In this rhetorical context we will discuss (1) the degree to which terrestriality is found in arthropods, (2) the physiological barriers to terrestrialization that arthropod clades confronted, (3) the historical record of arthropod diversity on land based on paleobiological, comparative physiological and zoogeographical evidence, and (4) some tentative answers to the "why" of terrestrial arthropod success. We are providing a geochronologic scope to terrestriality that includes not only the early history of terrestrial arthropods, but also the subsequent expansion of arthropods into major terrestrial habitats.

The term "terrestrial" has been used in various contexts to refer to land but may or may not include freshwater. Therefore, clarifications of the term must be made. From the Latin, "terrestrial" both denotes and connotes land, and it is in this more restrictive sense that we are using the term. Freshwater ecosystems are excluded here, although those land-based habitats that are frequently moist (e.g., humus, leaf litter, cloud forest canopies, carrion, dung) are included. Since the boundary between freshwater and land ecosystems is occasionally arbitrary, we will use the term "nonmarine" for the former. Consequently, we consider a "terrestrial organism" to be one that is obligately adapted to land; facultative behavioral adaptation of marine arthropods to a land-based existence is technically excluded (see Powers and Bliss, 1983, for a refinement of this concept). When both groups are discussed, we will refer to the first group as terrestrial and the last group as semiterrestrial. True terrestriality requires an obligate physiological commitment to life on land.

FREQUENCY OF TERRESTRIALITY AMONG ANIMALS
AND ARTHROPODS IN PARTICULAR·

Only nine of 58 extinct and extant animal phyla have terrestrial representatives (Blackwelder and Garoian, 1986). The two phyla that are prominently terrestrial — Arthropoda and Chordata — can be compared in various ways. Both arthropods and chordates first occur during the · Early to Middle Cambrian, but fully terrestrial members do not enter the fossil record until the Siluro-Devonian and Late Devonian, respectively (see also Shear, this volume; Campbell and Bell, 1977; Jarvik, 1980, fig. 140). Evidence indicates that all terrestrial chordates are traceable ultimately to a single monophyletic vertebrate lineage, whereas among arthropods there have been at least six invasions of land when evaluated at the ordinal or higher taxonomic level: arachnids; scorpions; tracheates (myriapods + hexapods; also known as uniramians in part: see Emerson and Schram, this volume); and amphipod, isopod and decapod crustaceans. At the species level, the frequency of terrestrialization increases severalfold (see Little, 1983). The two dominant arthropod groups, hexapods and arachnids, are conspicuous and dominant because of high diversities, abundance and biomass; by contrast vertebrates achieve subdominance by virtue of their relatively large size. Extant arthropod diversity is 20.5 times that of extant chordates and this figure can be expected to increase dramatically as new species are inventoried from taxonomically poorly-documented regions (Erwin, 1982; Wilson, 1988).

Hexapods (of which 99.5 percent are insects) are the most diverse of arthropods, with 876,200 described and known species, followed by arachnids with 63,000 species, and myriapods with 21,160 species (Parker, 1982; Labandeira, 1990). Only a small fraction of the 39,000 species of crustaceans are nonmarine. Collectively these groups occupy every major terrestrial environment, including hot, dry deserts, polar and high-altitude environments and the hyporheic zone of river aquifer deposits (Cloudsley-Thompson, 1988). They consume virtually every nutritionally-rewarding resource conceivable, including wax, wood and wrack.

PHYSIOLOGICAL BARRIERS TO A TERRESTRIAL EXISTENCE

Although the fossil record and comparative biochemistry of extant organisms indicate that life originated in the ocean (Spaargaren, 1978), the greatest species-level diversity now occurs on land. This transition from a marine to a terrestrial existence has involved adaptations to several major physiological barriers. These barriers center on fundamental, physical properties that distinguish a liquid medium (water) from a gaseous medium (air). (Much of the following discussion in this section is extracted from Little, 1983, and, to a lesser degree, Selden and Edwards, 1989.)

Osmoregulation.— Osmotic regulation is essential for the proper balance and sequestering of electrolytes needed for processes such as muscle contraction, waste elimination and molting. Marine arthropods achieve internal salt balance by diffusion from the ambient medium and from food; in terrestrial arthropods it is obtainable only from food.

All animals possess particular internal osmotic concentrations which are either greater, equal to, or less than that of their external environment. An organism that regulates its internal osmotic concentration is an osmoregulator. Osmoregulation may take the form of hyperregulation or hyporegulation, depending on the osmotic concentration of the external medium. An organism that lacks such a regulatory mechanism is an osmoconformer and maintains an internal concentration approximately equal to that of its environment.

In general marine arthropods are osmoconformers. Small, nonmarine arthropods such as some isopods (pillbugs, woodlice, sowbugs) and amphipods (beach fleas, waterlice, landhoppers) have internal osmotic concentrations that are correspondingly more dilute; they also have a significant *range* of osmotic concentration values as a group. Thus small freshwater arthropods are capable of only weakly osmoregulating, if at all. This presence of low and variable osmotic concentrations among most nonmarine (especially terrestrial) arthropods occurs since high surface-to-body ratios incur an excessive metabolic expense. By contrast larger freshwater arthropods, such as many decapods (crabs, crayfish) retain high osmotic concentrations and are efficient osmoregulators. These larger freshwater arthropods with lower surface-to-body ratios have an internal ionic balance that is more stable and have a greater metabolic capability for osmoregulation.

Arachnids (spiders and relatives), various myriapodan groups (centipedes, millipedes and relatives), and hexapods (entognaths and insects) possess elevated osmotic pressures. This, in conjunction with the relative small size of members in plesiomorphic clades within all three groups, has led researchers to infer that they have invaded land by the direct route. Particularly in primitive hexapods, the *combined* presence of efficient osmoregulation and a high tolerance to widely fluctuating levels of external osmotic concentrations, suggests a marine rather than a freshwater ancestry.

Respiration.— The maximum amount of oxygen per unit of volume is 30 times greater in air than in water. Also, water is 50 times more viscous than air — a feature that, though it is near ideal for supporting tissue, drastically impedes the movement of oxygen and organism alike. These two features place a premium on the oxygen-extracting capabilities of marine arthropods that possess a special type of appendicular-based metachronal ventilation and expansive surfaces of gill lamellae for increased oxygen uptake. In comparison to the lamellar gills of aquatic arthropods, terrestrial arthropods possess four major types of respiratory organs: book-lungs (scorpions, some arachnids, scutigeromorph chilopods), branchial lungs (some anomuran

crustaceans), pseudotracheae (isopod crustaceans), and tracheae (other arachnids, myriapods, hexapods) either with (pterygote hexapods) or without spiracular valves. While gills and lungs are ventrally paired organs that supply the entire organism with oxygen, they are limited in number and must be associated with respiratory pigments in the blood that transport oxygen to areas of metabolic activity. Tracheates possess a fundamentally different design that is imposed by the gaseous context of oxygen availability; and consists of an extensive system of branching tubes and tubules that originate at surface spiracles and ramify into tissues at the cellular level. The complexity of this tracheal system obviates the need for respiratory pigment, although many secondarily aquatic insects have acquired respiratory pigments in their hemolymph in lieu of tracheae.

The metabolic consequence of oxygen acquisition is carbon dioxide elimination. The solubulity of carbon dioxide is 25 times greater in water than in air — a relationship inverse to that for oxygen. Thus carbon dioxide is eliminated easily in water by passive diffusion or other means, but with difficulty in air. Various mechanisms for accommodating carbon dioxide in terrestrial organisms have been documented, including exoskeletal calcitization, carbonate buffering systems in the hemolymph, and a high tolerance to respiratory acidosis.

Water Balance.— Although acquisition of water is essential for the maintenance of intracellular electrolytic balance and tissue well-being in particular, not even all aquatic arthropods can readily obtain water. For those that osmoregulate, osmotic gradients frequently do not favor entry of water into a marine organism, thus necessitating active methods of water uptake. The situation is far more serious for terrestrial arthropods, where the low thermal capacity of air and the often depressed water vapor pressure conspire against both water acquisition and prevention of water loss. Structural modifications inhibiting water loss in terrestrial arthropods include epicuticular waterproofing by hydrophobic lipids (especially waxes), presence of spiracular closure mechanisms, production of nitrogenous waste as insoluble uric acid rather than soluble ammonia or urea, and increase in absolute body size to minimize surface-to-volume relationships. Numerous behaviors for preventing dessication exist, such as occupation of fossorial and cryptozoic habitats, nocturnality, and coprophagy. (See Edney, 1977, for further details.)

Nitrogenous Waste Excretion.— An often-stated but gross generalization is that nitrogenous waste in the form of soluble (but highly toxic) ammonia characterizes aquatic animals whereas minimally soluble and unsoluble (but nontoxic) urea and uric acid characterizes terrestrial animals (Little, 1983). Insects most closely conform to the ammonia/urea/uric acid sequence suggested for a marine to terrestrial series; subadult aquatic forms excrete ammonia and their terrestrial adult counterparts generally excrete uric acid. Chelicerates are unique in excreting nitrogen waste predominantly as uric acid. However, certain terrestrial isopods excrete ammmonia but accumulate urea and

uric acid in their body; myriapods excrete both ammonia and uric acid. Thus the mode of nitrogenous waste excretion appears linked to both ecologic and phylogenetic factors, with no consistent pattern emerging.

Thermoregulation.— The thermal capacity of water is 3000 times greater than air. Thus, thermal fluctuations are significantly ameliorated in the aquatic realm, whereas on land there are dramatic spatial and temporal differences in air temperature, particularly poleward of the tropics. Both the thermally buffered nature of water and its three-dimensional aspect are features that allow for considerable avoidance of thermal stress among marine arthropods. By contrast, thermal stress is a major feature of terrestrial life.

The two most basic physiological mechanisms promoting thermoregulation in terrestrial arthropods are cuticle waterproofing, which insures airproofing as well (see Plotnik, this volume), and spiracular closure mechanisms (Cloudsley-Thompson, 1988). Terrestrial arthropods frequently avoid thermal stress by behavioral means, such as changing their orientation to the sun, and stilting their body proper above a hot, stagnant, soil/air boundary layer. It has long been known that butterflies possess the physiological ability to facultatively thermoregulate by positioning their vascularized wing surfaces for maximum interception of radiant solar heat during early morning hours (Vielmetter, 1958); in fact, Kingsolver and Koehl (1985) suggested that wings may have evolved as a means of reducing thermal stress. A similar avoidance of hypothermia occurs during a rapid increase in thoracic temperature that is achieved by rapid contraction of flight muscle for heat generation in bees (Heinreich, 1975). Recently, examples of evaporative cooling have been documented in sawfly larvae that exude watery fluids from their anus (Seymour, 1974), and in bumblebees that regurgitate crop-stored nectar on their mouthparts during periods of heat stress (Heinreich, 1980a,b). Finally, one effect of complete metamorphosis in insects was confinement of the resting (subadult) stage to the climatically inclement part of the year and emergence of the reproductive (adult) stage during the thermally less-stressed part of the year (Hinton, 1948). Our current work on the origin of holometaboly indicates that thermal stress may be one of the primary factors favoring the continuation of this macroevolutionary phenomenon.

Sense Organs.— The sensory structures of terrestrial arthropods have been studied more intensively than those of aquatic arthropods, and certain patterns can be identified tentatively. Apparently, aquatic arthropods prefer chemical means to search for food in contrast with terrestrial members, which exhibit a tendency for using visual means (Bliss, 1968). This is particularly true for predaceous species, although it may not be applicable to herbivorous species, in which gustatory activity is induced by plant odor (Bernays and Barbehenn, 1987). Hearing is better developed in terrestrial arthropods, where high-frequency vibrations are often differentiated, unlike the low-frequency vibrations typifying hearing in aquatic arthropods.

Of the various specialized sensory structures occurring on the surface of the arthropod exoskeleton, one type, the trichobothrium, is associated with a terrestrial existence (McIver, 1975). Trichobothria are sensitive to air currents and have originated polyphyletically in many terrestrial arthropods (see Slifer and Sekhon, 1970).

Reproduction and General Behavior.— Marine arthropods liberate eggs and sperm into ambient seawater for external fertilization and subsequent planktonic larval development, often with a general lack of parental brooding or care. Fertilization in terrestrial arthropods is internal, with young kept in a favorable environment that is often followed by parental brooding during embryonic development or after birth. There are two basic types of internal fertilization: *indirect* by transferral of a sperm-containing spermatophore from the male to the female, or *direct* sperm transfer by copulation. The former method is ubiquitous among small arthropods inhabiting cryptic environments whereas larger arthropods occurring in exposed habitats overwhelmingly have direct sperm transfer (Ghilarov, 1960), although there is no consistent phylogenetic pattern. Terrestrial arthropods also engage in complex courtship displays, which achieve an acme in the intricate intraspecific behaviors of subsocial and social insects and arachnids (Wilson, 1975).

Food Procurement.— Terrestrial arthropods principally use extraoral digestion of items that may or may not be physically torn apart. These items are either acted upon enzymatically in a preoral chamber or, in derived forms, are injected with lytic enzymes resulting in liquifaction of the contents followed by sucking of food contents by suctorial mouthparts with a pharyngeal pump. The presence of an occlusible preoral cavity anterior of the pharynx was suggested by Størmer (1976) as a prerequisite for land life. A preoral chamber maintains the liquid environment necessary for the transport and activity of enzymes on captured food, whereas such a structure would be functionless in an aquatic environment because of enzyme dilution. By the Early Devonian terrestrial arthropods possessed a preoral chamber (Størmer, 1977).

HISTORICAL RECORD OF TERRESTRIAL ARTHROPODS

One of the most exciting fields in current paleobiology is the study of the historical record of terrestrial ecosystems. These studies include not only the gradual greening of the land and emergence of early terrestrial lineages, but also study of the earliest nonforested and forested ecosystems (Beerbower 1985; DiMichele et al., 1985) and the concurrent interactive rise to prominence of the two most critical and dominant groups that provide structure to terrestrial life: vascular plants and arthropods. It is in this context that we abstract the history of terrestriality, highlighting those macroevolutionary events that have had a major impact on structure of land ecosystems.

The historical record of terrestriality is based on three fundamental types of evidence, in order of importance: the fossil record, comparative physiology (discussed in previous section) and biogeography. Although the fossil record of terrestrial animals has been stated by some as inferior to that of marine organisms, it is also qualitatively different. While containing more stratigraphically barren intervals than the marine record, the terrestrial record contains a probably greater proportion of *Lagerstätten* deposits with excellent anatomical preservation than the marine record. Such *Lagerstätten* are notable since fossil arthropods are found in taphonomic contexts as different as three dimensional silicifications, lacustrine shale compressions, siderite concretions, and amber and brea deposits. For hexapods there are about 100 such known deposits (Labandeira, 1990). When assessed in its entirety, the terrestrial arthropod record is comparable to the marine arthropod record. Although there are fewer stratigraphic occurrences, when terrestrial fossils do occur, few marine fossils can match the preservational quality of, for example, an intact amber arthropod replete with genitalial microstructure for comparison to recent species (Larsson, 1978). When the vertebrate and arthropod records are compared, there is an overwhelmingly greater number of complete arthropod fossils than vertebrate fossils — a reflection of the smaller size, greater abundance, and probable greater likelihood of preservation in lacustrine sediments (Carpenter and Burnham, 1985). It should be noted that for the fossil insect record, approximately 50 percent of all extant families have fossil occurrences (Sepkoski and Hulver, 1985) — a figure that is respectable when compared to the fossil records of other animal groups.

TRAJECTORIES ONTO LAND

Evidence from comparative studies of the physiology of various related and unrelated terrestrial arthropods (Powers and Bliss, 1983; Little, 1983, 1989; Spicer et al., 1987) can, in some instances, provide evidence for inferring the trajectories that arthropods have used in becoming terrestrial. In other instances, the evidence is confusing due to an interplay of other factors, including the effects that scale (size) and microenvironment have had on physiology. In addition, use of zoogeographic distributions to infer ancestral environment of particular lineages has been important for amphipod and decapod crustaceans, which apparently are relatively recent additions to the terrestrial scene.

From a consideration of evidence based principally on comparative physiology of extant clades of terrestrial arthropods, it appears that five major trajectories were used in the arthropod colonization of land. These are (1) *freshwater* including lotic and lentic water bodies, (2) *littoral-marginal marine* environments, such as estuaries, saltmarshes and mangrove swamps, (3) *littoral-flotsam*, including sea-derived driftwood and wrack, and land-derived leaf litter and humus, (4) *littoral-interstitial*, mainly sand, but possibly other substrates, and (5) the *marine transporter* route, where there is the landward

transportation of seawater by branchial reservoirs that bathe book-gills for the active uptake of oxygen by decapods. The first four routes produced truly terrestrial arthropods; the last has resulted in only semiterrestrial representatives. (See Figure 1 for a diagrammatic explanation.)

Freshwater Route.— The freshwater route to terrestrial and semiterrestrial habitats was taken by various decapod crustaceans, namely astacurans (crayfish); potamoid, pseudothelphusoid and parathelphusoid brachyurans (crabs); grapsid brachyurans (shore crabs); and scorpions. Although astacurans exhibit tendencies toward terrestriality, they can only be considered as semiterrestrial. Many are fossorial and are capable of walking on land, but ultimately require water to moisten gill lamellae for oxygen uptake. Scorpions, because of their relatively large size, high osmotic pressure, and occurrence in
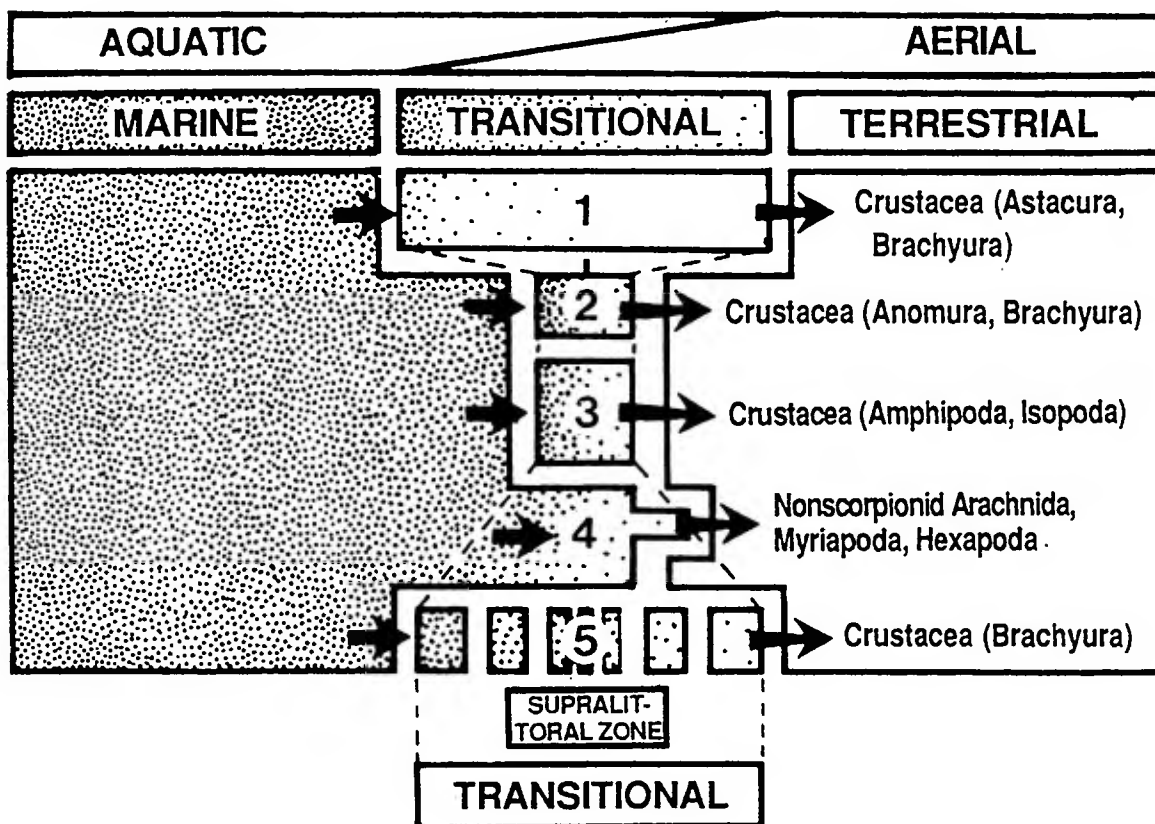

FIGURE 1— The five trajectories that marine arthropods have used in their colonization of land. 1: freshwater route, 2: littoral-margin marine route, 3: littoral-flotsam route, 4: littoral-interstitial route, and 5: marine transporter route. See text for details.

probable nonmarine deposits of Late Silurian age, are also presumed to have become terrestrial through the freshwater route (see Selden and Jeram, 1989).

Littoral-Marginal Marine Route.— Marginally marine environments along the shoreline have been a route to terrestriality taken by coenobitid anomurans (coconut crabs), gecarcinid brachyurans (land crabs), and possibly grapsid brachyurans. As with the freshwater route, only arthropods that are of large size and are osmoregulators have been favored. Coconut crabs are among the most terrestrial of all decapods since they will drown if submerged for any length of time (Gross, 1955). Gecarcinids lack the well-vascularized and highly folded epithelial lining of branchial chambers found in coenobitids, but do occur in coconut plantations, mangrove swamps, forests and grassy glades far inland of tropical and subtropical shores. Mangrove-inhabiting grapsid brachyurans are arboreal insectivores and are the least terrestrial of these three groups.

Littoral-Flotsam Route.— The route onshore via littoral flotsam has been inferred for talitrid amphipods (Spicer et al., 1987; Wildish, 1988) and oniscoid isopods (Edney, 1968; Cloudsley-Thompson, 1988). Within the Amphipoda, only members of the family Talitridae (landhoppers) have become terrestrial, occupying cryptic, surface-litter and occasionally above-ground habitats in mesic forests, grasslands and fern thickets of the pantropics and Southern Hemisphere (Friend and Richardson, 1986). Talitrid distribution is apparently restricted to areas of high rainfall, although the availability of chloride ion has been suggested as a limiting factor (Bousfield, 1968). Semiterrestrial, supralittoral amphipods are considerably more compact and robust than their marine relatives, and have lost appendicular features unsuited to a high-energy habitat. Because of the close phylogenetic relationship of supralittoral and terrestrial talitrids, Wildish (1988) deduced five plausible routes for land colonization directly from the marine realm. All but one of the routes involved a transitional phase of occupation of driftwood, wrack or macroalgal detritus along supralittoral environments. Comparative physiological evidence (Morritt, 1988; Little, 1989) supports this interpretation.

Oniscoid isopods (pillbugs, woodlice) are the most terrestrial group of crustaceans, coexisting with insects in mesic habitats such as leaf litter, subcortical bark, soil, fossorial and even in various xeric habitats (Edney, 1968). The Oniscoidea comprises six largely detritivorous families which can be arranged in a series of increasing terrestriality (Warburg, 1968), and there are indications that the invasion of land occurred several times along the direct marine route (Vandel, 1965). The invasion apparently involved exploitation of dead supralitoral vegetation (Paris and Sikora, 1965).

Unlike amphipods, oniscoid isopods are dorsoventrally compressed and in terrestrial species there is a tendency toward size reduction, ability to enroll, increased elaboration of surface cuticular

ornamentation such as spines and tubercles, and the development of pseudotracheae in pleopods that were used as organs of gas-exchange and as swimming appendages in marine ancestors (Cloudsley-Thompson, 1988). Terrestrial isopods have a unique respiratory system whereby lunglike structures, the pseudotracheae, originated by the modification of the lateral pleopod margins (Hoese, 1982; see Unwin, 1932, for microstructural details). These nonocclusible pseudotracheae, the absence of a waterproofed cuticle, and processing of nitrogenous waste as ammonia indicates that isopods experience significant water loss, unlike the hexapods which co-occur in the same habitats. For supralittoral and mesic terrestrial isopods, there is some evidence that behavorial mechanisms such as enrollment, communal sharing of burrow networks and crepuscularity, rather than physiological mechanisms, are used to retard water loss (Powers and Bliss, 1983). Little is known about possible physiologically-based water conservation mechanisms of xeric isopods.

The Littoral-Interstitial Route.— The overwhelming bulk of terrestrial arthropod species — arachnids (minus scorpions), myriapods and hexapods — are inferred to have arrived on land directly as marine microarthropods living in interstitial sand (Ghilarov, 1959). Extant nonscorpionid arachnids have high osmotic concentrations (Little, 1983) and are relatively small in size. Interestingly, palpigrades often occur interstitially among sand grains, possibly indicating a direct marine route (Selden and Jeram, 1989), although phylogenetic arguments suggest that this nearshore marine ecology is secondarily derived. Because of the diversity of respiratory organs among extant arachnids (Levi, 1967), it has been suggested that arachnids entered the terrestrial realm in several phases. While evidence indicates that scorpions became terrestrial through a freshwater phase, it is not clear that other arachnid groups entered independently and at different times. The occurrences of tube tracheae appear to be polyphyletic derivations from ancestors having the plesiomorphic condition of book-lungs. The iterative evolution of tracheae leaves open the question of the frequency of arachnid terrestrialization. It is most likely that a single, nonscorponid arachnid lineage became terrestrial some time before the Devonian, although for now polyphyly cannot be excluded.

Tracheates (Myriapoda + Hexapoda) invaded land through a direct marine route of interstitial sand as suggested by their relatively high osmotic concentrations, relatively small size, and intolerance to low humidities in primitive forms (Ghilarov, 1956, 1959; Little, 1983). A debate, based on paleontological and comparative structural evidence remains as to whether a freshwater or a terrestrial subadult stage is primitive for the Tracheata (Hinton, 1977; Messner, 1988; Wootton, 1988). Although myriapods generally lack some of the more pronounced modifications for terrestrial existence when compared to hexapods, such as occlusible spiracles (Curry, 1974) and waterproofed cuticle (Cloudsley-Thompson, 1968), particular species have been shown to exhibit some surprising features. Polydesmid and spirobolid millipedes are able to close spiracles by a combination of appression of coxae and

diplosegmental overlap (Steward and Woodring, 1973). Crawford (1972) demonstrated that the behavior of coiling can reduce water loss at elevated temperatures in a spirostreptid millipede whereas Cloudsey-Thompson (1950) documented that, although an epicuticular wax layer is absent, an exocuticular lipoid layer in some taxa effectively reduces permeability in a strongylosomid millipede.

Plesiomorphic hexapods also demonstrate susceptibility to low humidity levels, a feature that is documented in intertidal collembolans (Joosse, 1983), archaeognathans (Smith, 1970) and thysanurans (Lindsay, 1940). Pterygote hexapods are the paragon of terrestriality and have escaped the humid, cryptozoic microclimates of more plesiomorphic tracheates. They have done this principally by means of (1) increasing respiratory efficiency by the evolution of a ramifying tracheal system with sphincter valves, (2) temperature control achieved with size increase and body compartmentalization, countercurrent retes, behavioral regulation and a complete cuticular wax layer, and (3) nitrogen excretion by elimination of waste mostly as uric acid.

The Marine Transporter Route.— The previous four trajectories of marine arthropods onto land have produced truly terrestrial arthropods, although semiterrestrial species also exist for each route. A different approach is used by some decapod crustaceans that migrate on land by having respiratory organs that essentially function as book-gills located inside branchial chambers laden with reservoirs of seawater or freshwater. These decapods are semiterrestrial since air can not be taken up directly by structurally unsupported gill lamellae. Air diffuses into water within the branchial cavity, which in turn is taken up by functionally aquatic gill lamellae. Essentially the terrestrial habit is accomplished by transportation of a relevant part of the marine environment landward, rather than physiological adjustment to *in situ* terrestrial conditions. Ocypodids (ghost crabs) are the most important members of this group.

A BRIEF HISTORY OF ARTHROPOD TERRESTRIALITY

Terrestrial arthropods have acquired seven fundamental structural and behavioral improvements that have affected dramatically their role in terrestrial ecosystems. These are (1) the acquisition of a respiratory system physiologically unconnected to free water (i.e., book-lungs, tracheae, pseudotracheae), (2) a waterproofed exocuticle, (3) wings, (4) metamorphosis, (5) phytophily, (6) silk, and (7) subsociality or eusociality (cf. Hinton, 1977; Durden, 1984b; Carpenter and Burnham, 1985; Niklas, 1986). The first six features were acquired before the end of the Carboniferous. Termite eusociality may be as old (based on the presence of a Carboniferous sister-group to Isoptera), while wasp and bee eusociality is apparently a Cretaceous event. The timing of various subsocial arachnid lineages is unknown. Phytophily refers to the initial intimate dependence of arthropods on particular vascular plant food resources, and the subsequent establishment of coevolutionary

insect/vascular plant interactions such as leaf-mining, or nectar-feeding and associated pollination. This latter phenomenon, anthophily, has only been dated substantively to the Late Cretaceous, coincident with the emergence of angiosperm plants (Crepet and Friis, 1987) although it was undoubtedly associated with cycadeoid pollination during the Early Mesozoic (Crepet, 1972, 1974) and may have even an earlier legacy (Malyshev, 1968).

The history of diversifiction and dominance of terrestrial arthropods is intimately tied to the history of vascular land plants (Crepet, 1972; Smart and Hughes, 1973). Some even have suggested that during the succession of floras in the course of evolution there has been a similar turnover in land arthropods, particularly in those that are obligately linked with specific plants (Niklas et al., 1985; Tahvanainen and Niemalä, 1987, fig. 3). However, the picture is far more complex, as we discuss later. Zwölfer (1978) offers a two-cycled model explaining the evolutionary mechanism of positive feedback between plant diversification and phytophagous insect diversification and phytophagous insect diversification and carnivorous insect diversification (Figure 2). It centers on a given intrinsic increase in plant diversity that triggers the diversification of phytophagous insects by increasing the total pool of regulatory mechanisms that mediate attack by insects and responding defenses by plants. This increase in insect diversity in turn triggers diversification of predatory arthropods in the same way.

One outcome of this ecological pump is an increase in the number of arthropod species over time as the flora expands its anatomic, taxonomic and ecological diversity. Such a view is consistent with the *expanding resources hypothesis* of Whittaker (1977). In contrast, the *ecological saturation hypothesis* of Raup (1972), May (1981) and Gould (1981) maintains that the total number of ecosystem roles or "niches" are saturated at an early time. Although "players" enter and exit, the total number of positions remain constant. These contending concepts (Strong et al., 1984) can be tested with the terrestrial arthropod fossil record, keeping in mind that the measures by which a "role" is defined may include a taxonomic unit, a food-resource guild, ecological communities, or even a particular habitat type.

A cautionary note must now be made. Use of uniformitarian approaches that employ analogs to reconstruct ancient terrestrial systems, particularly those of the Paleozoic, is extremely problematic. The frequent uncritical application of taxonomic and ecologically-based uniformitarianism suggests, for example, that Paleozoic taxa, often differentiable from modern taxa at the ordinal level, are biologically comparable to selected modern taxa for purposes of analysis. Outcomes based on a Paleozoic arthropod and its presumed modern analog can lead into epistemological blind alleys wherein any modern analog can be retrieved for purposes of making a statement on a particular adaptation. A similar case can be made for inferring the trophic structure of Paleozoic communities based on putatively similar modern communities. Avoidance of considerations such as the structural or ecological
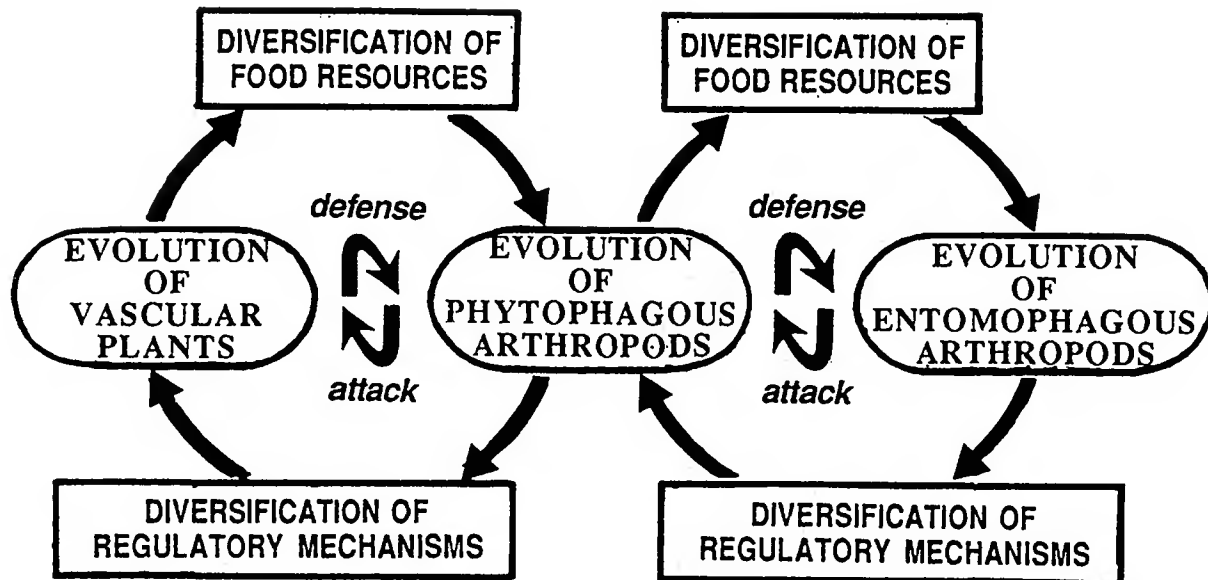
FIGURE *2*— Summary of relationships between food resources, regulatory
mechanisms and the three principal actors in terrestrial ecosystems
(vascular plants, phytophagous arthropods and entomophagous
arthropods) (from Zwölfer 1978).

uniqueness of Paleozoic arthropods or whether ancient communities are in
fact organized in the same way as "appropriate" modern communities
results in reconstructions from fossil data that are self-fulfilling
prophecies. Essentially, a strict analogical approach tends to assume
that evolution has not occurred among the players, when it is really the
evolution in these ancient systems that interests us. Many aspects of
ancient (particularly Paleozoic) communities are *not* analogous to any
modern community. Accordingly, more deductive, general principles of
how organisms and ecosystems interact and function should be favored
over alternatives such as taxonomic and ecological uniformitarianism.

Late Ordovician to Early Silurian.— The earliest evidence for
nonmarine ecosystems are Upper Ordovician plant fragments that include
spore tetrads which presumably originated from liverwort-like plants,
trilete spores referred to mosslike plants, and various enigmatic,
astomate sheets of cells of uncertain affinity (Gensel and Andrews,
1984; Gray, 1985a). These assignments have been questioned by some
(Chaloner, 1985; Selden and Edwards, 1989) and their affinities remain
in taxonomic limbo. Younger Silurian deposits contain helical tubular
elements of uncertain affinity (Lang, 1937; Gensel and Andrews, 1984)
and convincing fungal spores and hyphae (Sherwood-Pike and Gray, 1985)

probably of an ascomycetous grade. The only indications of terrestrial animals during this interval are undescribed microarthropod fragments attributed to a nonmarine provenance (Gray, 1985b), and burrows in Upper Ordovician paleosols interpreted as the feeding traces of a bilaterally-symmetrical animal, perhaps a millipede (Retallack and Feakes, 1987). However, the size-frequency distributions of the burrow diameters has been challenged on statistical grounds (Kopaska-Merkel, 1988), and the trace fossils need to be corroborated by body fossils of an appropriate culprit (Beerbower, 1985).

Late Silurian to Devonian.— The fossil record of the earliest occurrences of terrestrial arthropods during the Late Silurian to Devonian are summarized by Shear (this volume) and presented in Figure 3. This interval was characterized by the initial greening of the landscape and the simultaneous invasion of arthropods. As the first terrestrial ecosystems developed, a number of plant-arthropod interactions were established. (The reader is referred to Kevan et al., 1975, for additional details on plant-arthropod relationships.) Scorpions and arachnids were terrestrial during the Late Silurian to Devonian. We disagree with Rolfe's (1980) and Selden and Jeram's (1989) interpretation that the lack of apparent spiracles in pre-Carboniferous scorpions indicates that they were not terrestrial. Spiracles have low preservation potential and often occur intersegmentally on arthrodial membranes in a number of arachnid orders, or on a concealed portion of the sternite, as in Mississippian (Jeram, 1990) and Triassic (Beall, pers. obs.) scorpions. Arachnids that established a terrestrial existence during the Late Silurian to Devonian are trigonotarbids (Hirst, 1923; Størmer, 1969; Shear et al., 1987), spiders (Shear et al., 1989a, Figure. 4b), pseudoscorpions (Shear et al., 1989b), and at least four families of mites (Hirst, 1923; Dubinin, 1962; Norton et al., 1988). The recent discovery of a true spider (Araneida) spinneret from the Late Devonian Gilboa site (Shear et al., 1989a) marks not only the earliest record of spiders, but also the earliest suggestion of silk production and use. However, although virtually identical structurally to the median spinnerets of liphistiomorph spiders, the absence of tartepores in the Devonian spinneret calls into question whether silk-production was present. A tartepore represents a "scar" where a former, abandoned silk-producing gland perforated the cuticle for supplying liquified silk to the seta-like spigot. Since the Devonian spinneret does not possess tartepores and thus lacks evidence for the shifting of spigots during ontogeny, silk-production may have been absent. An alternative explanation for the Devonian fossil is that it was an exaptation that became co-opted into a silk-producing apparatus in later lineages.

Tracheates enter the terrestrial record at almost the same time as chelicerates. Myriapods that existed by the Devonian include the taxonomically enigmatic kampecarids (Rolfe, 1980; Almond, 1985), millipedes (Almond, 1985), centipedes (Shear and Bonamo, 1988) and arthropleurids (Størmer, 1976; Shear, 1986). The terrestriality of

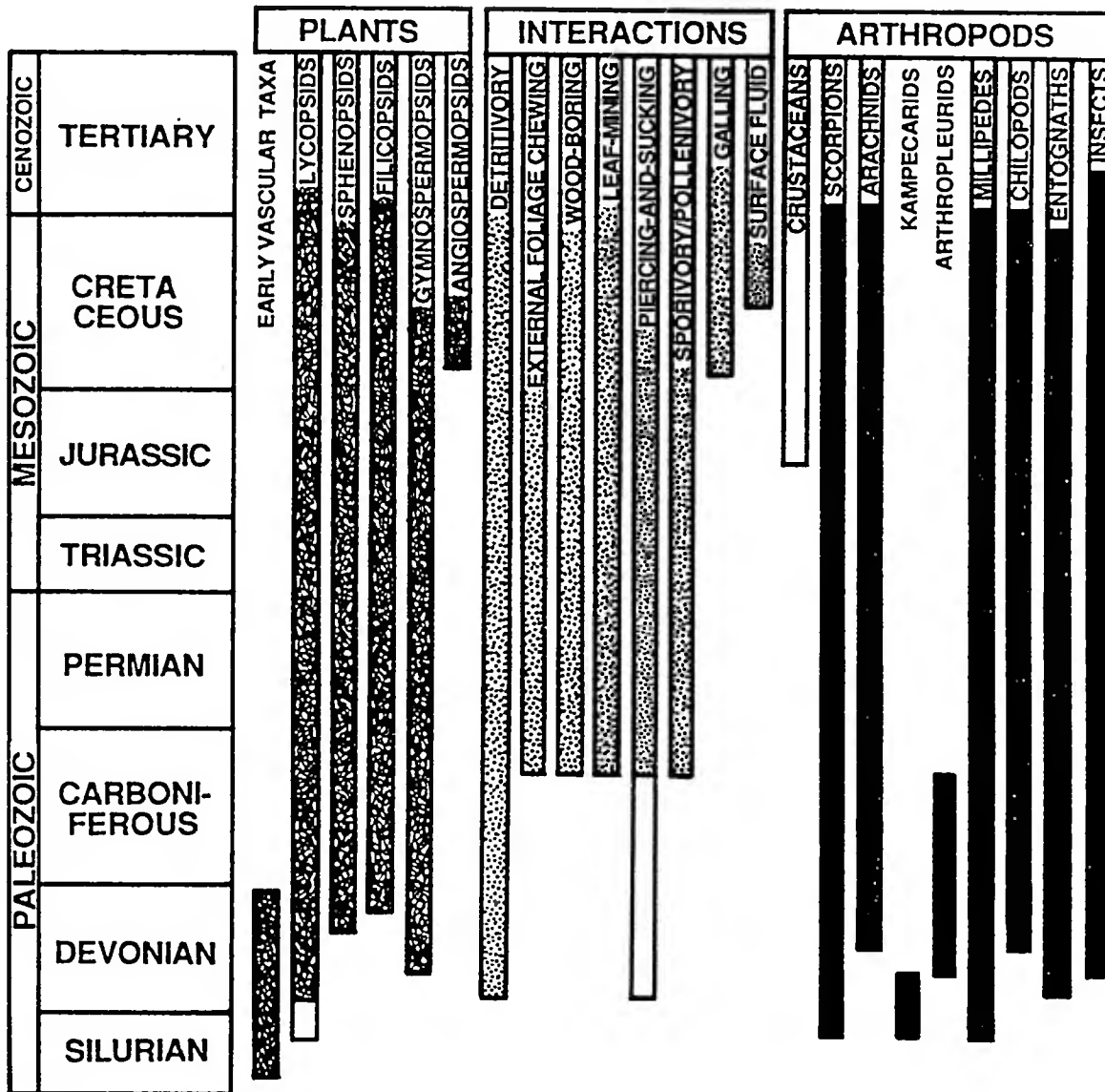FIGURE 3— Geochronology of major vascular plant taxa, arthropod/ vascular plant interactions and major arthropod taxa in terrestrial ecosystems.

kampecarids and earlier millipedes has been questioned (Almond, 1985), although the sedimentary contexts of these occurrences are nonmarine. The earliest hexapod fossils are Early Devonian collembolans (Hirst and Maulik, 1926; Greenslade and Whalley, 1986) and an Early Devonian

archaeognathan (Labandeira et al., 1988a-c, Figure 4a). An archaeognathan is also known from the Middle Devonian (Shear et al., 1984).

Carboniferous.— The only well-documented Early Carboniferous (=Mississippian) tracheates are myriapods. A tally of ordinal diversity of myriapods from the Devonian and Mississippian suggests a greater diversity than among hexapods. Whether this relative diversity is a real pattern or due to a major preservational bias is uncertain. However, it is certain that by the Early Pennsylvanian the pattern reverses permanently and insectan ordinal diversity explodes after the origin of wings. During the earliest Late Carboniferous (=Pennsylvanian) thirteen orders of paurometabolous insects (characterized by the absence of a vermiform, soft-bodied larval stage and a pupal stage) suddenly appear. Since no known Early Carboniferous pterygote (winged) insect is known (see Nelson and Tidwell, 1987, for a possible exception) it is unclear whether wings evolved relatively early during the Devonian and were taphonomically excluded, or whether they evolved rapidly immediately preceding the Late Carboniferous. In terms of general feeding groups during the Mississippian, circumstantial evidence indicates the presence of detritivores and herbivores among hexapods and most myriapods, and carnivores among centipedes and arachnids.

The available fossil evidence indicates that the Carboniferous is the time interval when insects became dominant on land, occupying most of the ecological roles that they now occupy and with a taxonomic diversity unparalleled for any terrestrial animal group. By the early Late Carboniferous (probably earlier) insects had organs of dispersal (wings) which allow them to occupy three-dimensional habitats and by the end of the period they were able to partition through holometamorphosis developmental stages into immature trophic-dominated phases (larvae), an intercalary resting phase (pupa), and a reproductive adult phase (imago). The origins of the modern insect fauna, now dominated by beetles and weevils (Coleoptera), true flies (Diptera), moths and butterflies (Lepidoptera) and sawflies, wasps, ants and bees (Hymenoptera), can be traced to common ancestors and extinct related groups occurring during the Late Carboniferous. Support for this includes sister-group relationships between plesiomorphic holometamorphic forms and their closest paurometabolous clades (Hennig, 1981), the direct evidence of a Late Carboniferous caterpillar-like larva belonging to the common ancestor of the Mecoptera (scorpionflies) and Hymenoptera (Kukalová-Peck, 1988), and indirect evidence of larval feeding strategies attributable to leaf-mining and wood-boring holometabolous insects (Beall and Labandeira, submitted; Labandeira, pers. obs., Figure 5a-d,h).

It has been assumed that Carboniferous food-resource guilds were primarily, if not exclusively, detritivorous, and that herbivory (in the broadest sense of consumption of live plant tissue) was either nonexistent or was minimally important (Smart and Hughes, 1973; Cox, 1974; Swain, 1978; Strong et al., 1984; Southwood, 1984). However,

considerable evidence from compression- and coal-ball floras of Late
Pennsylvanian times indicates that most of the major food resource
guilds were already present. They included highly stereotyped external
foliage-feeding (Van Amerom and Boersma, 1971; Beall and Labandeira,
submitted, Figure 5i), wood-boring (Cichan and Taylor, 1982; Labandeira,
pers. obs.; Figure 5c), sporivory (Labandeira, pers. obs. Figure 5g),
piercing-and-sucking (Sharov, 1973), and stem- and leaf-mining (Müller,
1982; Rothwell and Scott, 1983; Beall and Labandeira, submitted, Figure
5a,b,d,h), as well as ubiquitous detritivory (Scott and Taylor, 1983;
Labandeira pers. obs., Figure 5e,f). So far, no evidence exists for
leaf-galling or nectarivory, although some Late Carboniferous seed ferns
do exhibit small, capitate structures on leaf-surfaces similar to
secretory glands on angiosperms (Taylor and Millay, 1979).

Apparently, Carboniferous arthropods not only invaded most of the
food-resource guilds that vascular plants offer, but also began to
partition different tissue types within some of these guilds.
Structural evidence of insect mouthparts indicates that shallow and deep
piercing-and-sucking of live tissue was common among palaeodictyo-
pteroids (Carpenter, 1971; Sharov, 1973; Müller, 1977; Kukalová-Peck,
1987) and that short to long orthopteroid ovipositors with sawtooth
valves were used for lancing live plant tissue for oviposition
(Carpenter, 1971; Jarzembowski, 1987). Recent documentation of
arthropod damage on many tissue types from root, stem, leaf and
sporangial organs from the five dominant plant groups in Carboniferous
swamp forests (lycopsids, shenopsids, filicopsids, and seed ferns and
cordaitean gymnosperms) indicates a histologically-based partitioning of
food resources similar to the modern angiosperm-dominated insect fauna.
Tissues as diverse as leaf-cushion parenchyma, secondary xylem (wood),

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FIGURE 4— Recent important discoveries of fossil arthropods. A: the
earliest known insect, the bristletail *Gaspea palaeoectognathae*
Labandeira, Beall and Hueber, 1988, from the Lower Devonian of
Québec. Scale bar is 0.1mm. B: the earliest known spider, as
represented by a spinnneret from the Middle Devonian of New York
(Shear et al., 1989). Scale bar is 0.1mm. C: a silverfish-like
monuran, *Lepidodasypus sharovi* Durden 1978, from the Lower Permian of
Kansas. Scale bar is 1mm. D: a meganeurid dragonfly, probably
Meganeura monyi Brongniart, from the Lower Permian of Kansas (Durden,
1988). Scale bar is 1cm. E: the earliest known moth, *Archaeolepis*
mane Whalley, 1985, from the Lower Jurassic of Dorset, England.
Scale bar is 1mm. F: one of the earliest known weevils, *Probelus*
curvispinus Arnoldi, 1977, from the Upper Jurassic of the Soviet
Union. Scale bar is 1mm. G: evidence of Lepidopteran (?Nepticulidae)
leaf-mining damage on a corystospermacean seed fern from the Upper
Jurassic of Queensland, Australia. Scale bar is 1mm. H: the earliest
known flea, *Tarwinia australis* Jell and Duncan, 1986, from the Lower
Cretaceous of Victoria, Australia. Scale bar is 1mm. I: the earliest
known bee, *Trigona prisca* Michener and Grimaldi, 1988a,b, from Upper
Cretaceous New Jersey amber. Scale bar 1mm.
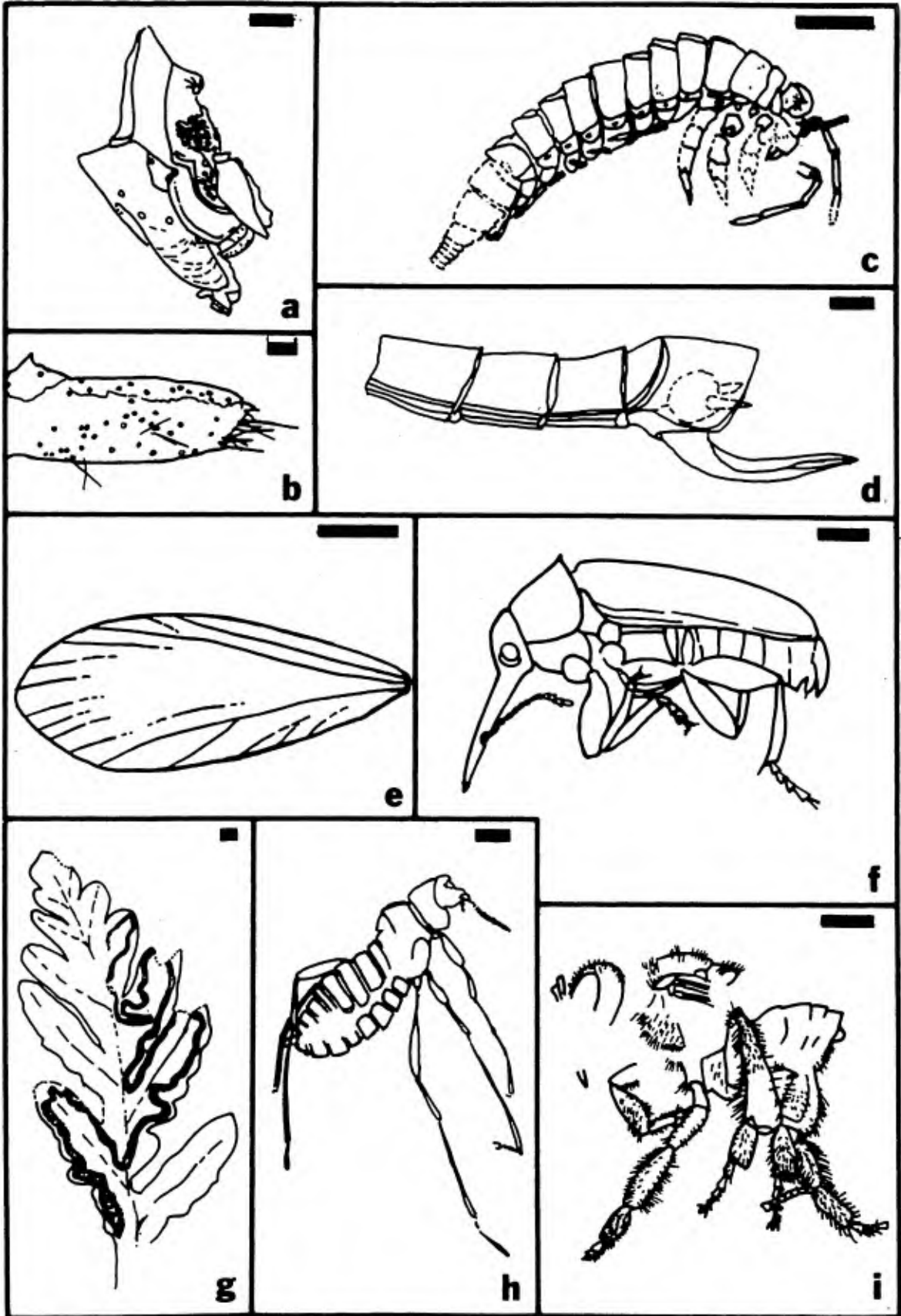
pith and interstelar ground tissue, foliar vascular tissue and
sporangial megaspores were being consumed (Labandeira, pers. obs.,
Figure 5). These data should force a major revision of the current
paradigm of coal swamp insects as trophically primitive forebearers
compared to their successors in gymnosperm- and angiosperm-dominated
Mesozoic floras. Maceration of arthropod cuticles from coals and
associated shales (Scott, 1977; Bartram et al., 1987) containing
stereotyped arthropod-plant interactions will aid in placing taxonomic
constraints on identifying the culprits of various types of plant tissue
damage.

In addition to data supporting occupation of a broad array of
dietary-partitioned food resource guilds, there is good evidence for
carnivory and probable insect predation. Carpenter (1971) has described
mantis-like protorthopterans with spine-bearing prothoracic legs and
Brauckmann and Zessin (1989) have figured meganisopteran dragonflies
with raptorial mandibles and legs. Arachnids experienced a rise in
diversity with at least seven orders entering the fossil record, in
addition to holdovers from the Devonian and Mississippian, including
spiracle-bearing terrestrial scorpions (Vogel and Durden, 1966). Modern
arachnids are both ambush and pursuit predators and evidence exists for
the presence of camouflage in Late Carboniferous phlangiotarbids

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FIGURE 5— A sample of vascular plant/arthropod interactions in swamp
    environments from the Upper Carboniferous (Westphalian D Stage) of
    the Illinois Basin. A: Two U-shaped regions of damage on the distal
    margin of a pinnule of *Cyclopteris*, a seed fern (Gymnospermopsida of
    Figure 3). This damage is probably a leaf-mine. Compression nodule
    from Mazon Creek (FMNH, PP11665). Scale bar is 5mm. B: Mined out area
    of vascular tissue, with fecal pellets in the basal attachment area
    of a *Neuropteris* pinnule, a seed fern. Coal ball section parallel to
    plane of pinnule lamina (UIUC, 38043-Lbot). Scale bar is 1mm. C:
    Wood-borings with packed fecal pellets in *Amyelon*, a cordaitean
    gymnosperm. Radial section through a stem in a coal ball (UIUC,
    32277-18A-Abot). Scale bar is 1mm. D: Large ellipsoidal coprolites
    (3mm X 1mm) in a stem of the filicopsid *Psaronius*, indicating a mined
    area between ground tissue (top) and sclerenchyma (central diagonal
    band). Inner root mantle at bottom. Oblique section of stem and root
    mantle in a coal ball (UIUC, 38048-Dtop). Scale bar is 1mm. E: Large
    elliptical coprolite bearing various plant tissue fragments. Section
    from a coal ball (UIUC, 38055-Cbot). Scale bar is 1mm. F: Fecal
    pellet clusters in lacunae between adaxial secondary xylem and
    abaxial outer cortical tissues of *Sphenophyllum*, a sphenopsid.
    Transverse section of stem in a coal ball (UIUC, 38044-Bbot). Scale
    bar is 0.1mm. H: Mined region with fecal pellets in *Lepidophloios*
    leaf cushion. Longitudinal section through stem in a coal ball; stem
    to left and distal lamina of cushion to right (UIUC, 38055-Ctop).
    Scale bar is 1mm. I: Cuspate excisions of *Neuropteris* lamina margin,
    indicating external foliage feeding. Compression nodule from Mazon
    Creek (FMNH, PP11665). Scale bar is 1cm.
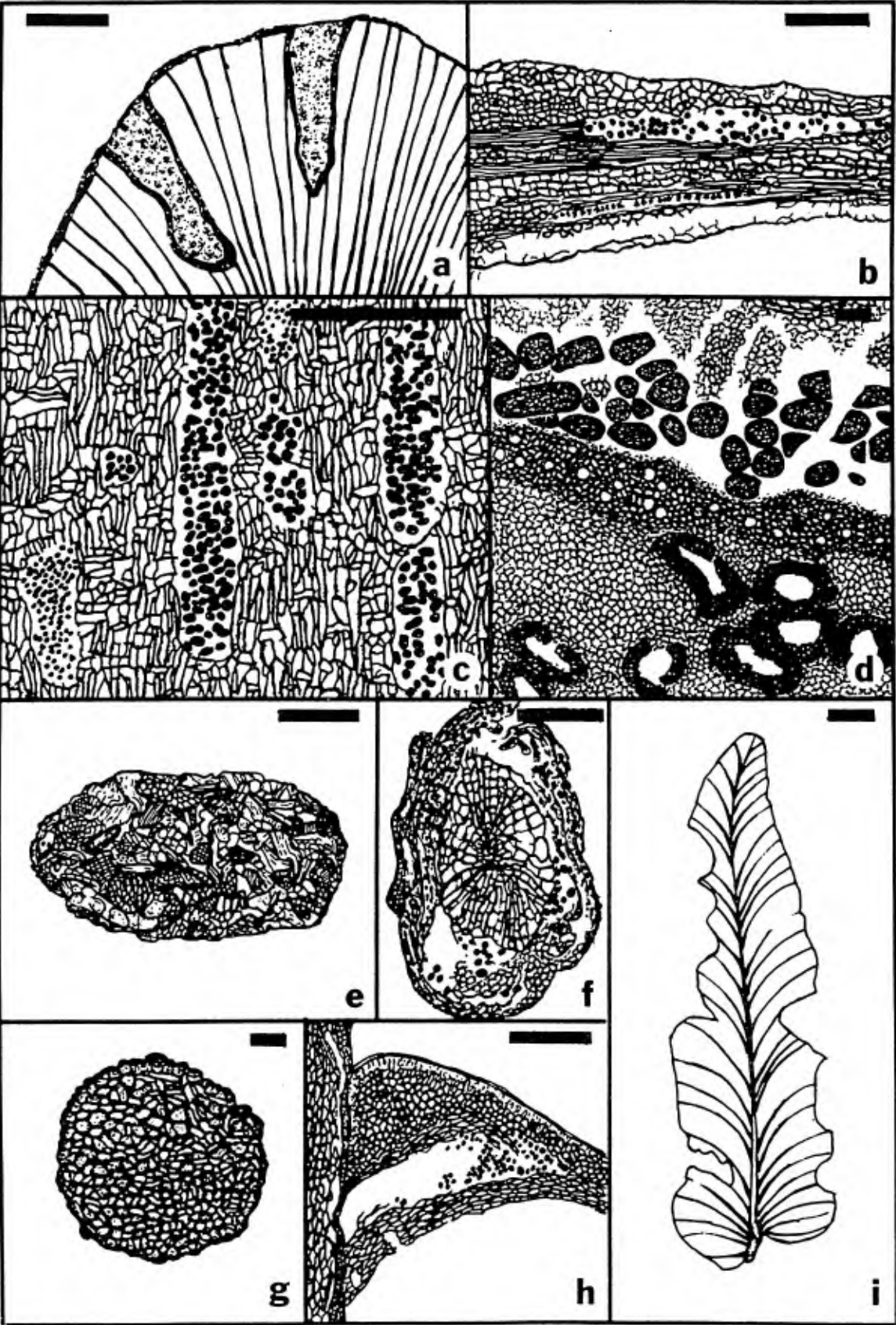
representing a form of crypsis either for sequestering prey or as predator avoidance among arborescent lycopsids in both coal and clastic swamps (Beall, 1984). Other terrestrial or semiterrestrial arthropods that have been suggested to use camouflage include horseshoe crabs (Fisher, 1979) and cockroaches (Pruvost, 1919; but see Jarzembowski, 1987). Grasshopper-like insects (Protorthoptera) with large forewing eyespots have been documented by Carpenter (1971), representing presumably an example of disruptive mimicry.

The third major terrestrial group, crustaceans, are still aquatic during the Late Paleozoic, although recent studies of shrimplike malacostracans from nearshore Lower Carboniferous deposits indicate an early radiation of malacostracans into brackish, marginal marine to near-freshwater habitats (Cater et al., 1989; Briggs and Clarkson, 1989). Landward from these brackish-water habitats were aquatic nymphs of a few insect groups occurring in freshwater. These nymphs had terrestrial adult stages (Wootton, 1988) and were probably filter-feeding or substrate-scraping detritivores, based on studies of recent representatives of the same clades.

Evidence for complete metamorphosis (=holometaboly) in Late Carboniferous insects originates from the presence of small wood-boring galleries in gymnospermous cordaitean wood and U-shaped leaf-mine tunnels in seed fern pinnules that are assigned to leaf-mines (Labandeira, pers. obs.; Beall and Labandeira, submitted) and were probably constructed by small larvae. Moreover, the presence of a compression fossil of a caterpillar from Mazon Creek (Figure 4c) (Kukalová-Peck, 1988) suggests the modest beginning of an herbivorous or pollenivorous lineage related to scorpionflies (Mecoptera) and sawflies (plesiomorphic Hymenoptera). These and other data indicate that metamorphosis originated in dominantly equitable habitats rather than seasonal habitats (contrary to much current thought) and that some of the earliest known larvae were small, but not outside the modern size range. These data suggest a macroevolutionary pattern wherein the earliest members of particular lineages are small, followed by an increase in size variance in subsequent representatives (Stanley, 1973). Although there are numerous explanations for the advantage of holometaboly, recent experimental evidence indicates that holometabolic development is more efficient than nonholometabolous development because of elimination of the burden of cuticle production during subadult feeding stages (Bernays, 1986). Moreover, varying morphologies of different life stages permit exploitation of previously unutilized resources (Beall and Labandeira, in prep.).

Like the origin of metamorphosis, the origin of wings is a subject of current debate, and represents some of the most innovative paleobiological research on terrestrial arthropods. Kukalová-Peck (1978, 1983) elaborated the leg exite theory of wing origin, presenting evidence against the previosly dominant paranotal theory. The leg exite theory suggests that modern insectan wings are serially homologous to laterally-positioned, segmented leg exites on the thorax. The basal

articulatory sclerites for movable wings were accordingly supplied evolutionarily by an articular band of small sclerites through the incorporation of the epicoxal region into the dorsolateral thoracic wall. This pleural origin of wings (Kukalová-Peck, 1978, 1983) contrasts with the paranotal theory, which stipulates that wings evolved as initial dorsolateral, tergal outgrowths for gliding, followed by development of articulatory sclerites for flapping flight (Crampton, 1916; Sharov, 1966; Wootton, 1976). In a major contribution using an experimental approach, Kingsolver and Koehl (1985) concluded that "wings" could have been used initially as thermoregulatory devices in small insects and subsequently became exaptations for aerodynamically-sound flight organs in those lineages with upscaled body sizes and concomitant large wing sizes. Thus an isometric increase in body size during evolution produced a qualitative shift in function from thermoregulation. The issue of wing origins remains contentious (Kukalová-Peck, 1987; Kingsolver and Koehl, 1989).

The terrestrial arthropod fauna during the Early to Middle Pennsylvanian experienced a significant extinction event at the Westphalian D/Stephanian boundary (Beall, 1986), coincident with the demise of several major members of the Westphalian swamp forests, notably lycopsids (DiMichele et al., 1985). This extinction appears to be due to a drying trend that is the precursor to more extreme conditions during the Permian. The presence of this event would appear not to support the Carboniferous faunal continuum hypothesis of Schram (1979), which was based principally on analyses of nonterrestrial invertebrates, and was extended to nonmarine biotas by Rolfe et al. (1982), among others.

Permian.— Permian arthropods, particularly insects, are sufficiently different taxonomically from those of the Carboniferous, that they can be viewed as transitional to modern (i.e., Mesozoic and Cenozoic) arthropods. However, the absence of Permian arachnids precludes excessive inference. As a whole, Permian insects are relatively small, often setose and coriaceous forms that apparently occurred in seasonal climates (Durden, 1984b), when compared to much larger, mesic-adapted insects of pantropical, Euramerican swamp forests during the Carboniferous. Thus, Permian insect faunas represent the expansion of major holometabolous groups, including alderflies (Neuroptera), snakeflies (Raphioidea), antlions and lacewings (Planipennia), beetles and weevils, scorpionflies, caddisflies (Trichoptera), and the extinct glosselytrodeans. Carboniferous holdovers include primitively flightless monurans (Figure 4c), a few giant dragonflies (Figure 4d),various mandibulate-chewing protorthopterans, and mostly various piercing-and-sucking palaeodictyopteroids, which occur in decreased abundance as they were being replaced by the emerging, plant-sucking Homoptera (cicadas, treehoppers, whiteflies and scale insects). Large ovipositor-bearing cockroaches of Carboniferous aspect were rare (Carpenter, 1971; Durden, 1984a) and became replaced by modern eggcase-laying froms by the Early Mesozoic. Because of this singular

combination of Carboniferous and modern orders of hexapods, the Permian Period had a relatively high ordinal diversity of about 25 orders, compared to the 34 orders of today.

Direct evidence for plant-insect interactions is sparser for the Permian than for the Carboniferous, perhaps because of the demise of coal-swamp forests, but probably because of fewer Permian deposits. Plumstead (1963) and Srivastava (1987) have documented external foliage feeding resembling that of a caterpillar- or grasshopper-like insects on *Glossopteris* leaves. The extinct family Lophioneuridae, probably related to thrips (Thysanoptera) is presumed to have mouthparts for punching-and-sucking spore or pollen contents (Rohdendorf and Rasnitsyn, 1980).

Several orders of insects whose fossil records extend to the early Late Carboniferous became extinct sometime during the Late Permian (Sekposki and Hulver, 1985). Explanations for this extinction range from inclusion of terrestrial arthropods in the overall catastrophic extinction that befell marine life at the end of the Permian (Raup, 1979; Sepkoski, 1986), to preferential vertebrate predation on Paleozoic-aspect forms that lacked holometaboly, to reduced ability to cope with increasing seasonality and desiccation (Beall, in prep). The absence of holometaboly, and hence the ability of insects to enter enclosed and cryptic habitats that were safe from vertebrate predation, resulted in the successful survival of more-derived holometabolous forms and those nonhomometabolic forms with aquatic nymphs (Downes, 1987). Whatever the cause, the Early Mesozoic insect fauna was demonstrably modern in taxonomic aspect at the ordinal level, and by the Late Jurassic many modern families had appeared.

Triassic to Early Cretaceous.— During the early and middle Mesozoic, prior to the emergence of angiosperms, the terrestrial arthropod fauna, particularly insects, became modern in taxonomic aspect, and established morphologies that were later co-opted by angiosperms, resulting in a subsequent spectacular radiation insects. Throughout the early to middle Mesozoic there was a radiation of three of the four major holometabolous orders — Coleoptera, Hymenoptera and Diptera (Ponomarenko, 1969; Rasnitsyn, 1969; Rohdendorf, 1974; Kalugina and Kovalev, 1985), and the modest beginnings of the fourth, the Lepidoptera, during the Jurassic (Rasnitsyn, 1983; Whalley, 1985, Figure 4e). Advanced lepidopterans (higher moths, butterflies) appear to be a Cretaceous phenomenon (Skalski, 1979; Whalley, 1986). Also, there were modest radiations of nonholometabolous groups, particularly mayflies (Edmunds, 1972), dragonflies (Pritykina, 1981) and grasshoppers and relatives (Zeuner, 1939; Sharov, 1971; Zessin, 1987). As for arachnids, the presence of orb-weaving spiders during the Early Cretaceous indicates the presence of behaviors associated with the use of silk for ensnarement (Selden, 1989). Evidence for the earliest case of terrestrial arthropod eusociality comes from the oldest known termite, from the Early Cretaceous (Lacasa-Ruiz and Martínez-Delclós, 1986).

Much of what we know of this time originates from several highly diverse *Lagerstätten* from the Soviet Union (Rohdendorf et al., 1961; Rohdendorf, 1968; Rohdendorf and Rasnitsyn, 1980; Ponomarenko, 1988).

Insight into the interactions between major vascular plant groups and modern-aspect insects come from both insect damage on plants as well as feeding specializations indicated by external insect structure. Wood-boring galleries from the bark and heartwood of araucariaceous gymnosperms from Germany (Linck, 1949) and Arizona (Walker, 1938) provide evidence for the existence of taxa with behaviors similar to modern metallic wood-boring beetles, powder post beetles and bark engraver beetles (Crowson 1981). Also from Upper Triasic deposits are highly stereotyped chew marks on cycadophyte pinnules (Geyer and Kelber, 1987) and leaf-mines on voltziacean conifers (Rozefelds and Sobbe, 1987). From a Middle Jurassic (taxodiaceous?) conifer in China, wood-borings ascribed to beetles have been documented (Zhiyan and Bole, 1989). Finally, the occurrence of lepidopteran leaf-mines, possibly made by a nepticulid moth, on a corystosperm seed fern of the Upper Jurassic/Lower Cretaceous boundary (Rozefelds, 1988; Figure 4g) calls into question current dogma about the obligate coevolution of lepidopterans and their angiosperm hosts (e.g., Strong et al., 1984).

Recently, it has been recognized that pollination mechanisms preceded the arrival of angiospermous plants and that cycadeoids, and possibly gnetaleans and seed ferns were insect pollinated. Delevoryas (1968) and Crepet (1974) have presented evidence for the presence of the "mess-and-soil" pollination syndrome (Faegri and van der Pijl, 1981) in Jurassic cycadeoids, whose ovulate strobilar axes were chewed by insects, apparently beetles (Crowson, 1981; Gottsberger, 1988). Researchers have documented Late Jurassic and Early Cretaceous weevils with long anteroventrally-directed rostra (Arnoldi, 1977; Whalley and Jarzembowski, 1985; Figure 4f) capable of probing and consuming indurated plant tissues, and other beetles with procumbent, scythe-shaped mandibles whose modern descendents are cycad-associated (Crowson 1981). Moreover, it is noteworthy that some extant cycads — relatives of Mesozoic cycadeoids — are pollinated by a relatively primitive weevil (Norstog, 1987) whose lineage extended into the Jurassic (Muñiz and Barrera, 1969; Hamilton, 1978; Sanborne, 1981), suggesting the appearance of the "mess-and-soil" pollination syndrome before angiosperms. The presence of flies with fleshy, sponging proboscides and wasps with "squeezing-and-lapping" mouthparts during this interval (Labandeira, 1990) indicates that insects with more efficient pollination capabilities were available to plants with exposed pollen organs (Crepet, 1972; Labandeira, 1990). (Sporivory is documented in coal swamp forests [Figure 5g] and has been considered as a precursor to pollenivory [Malyshev, 1968].)

The occurrence of several groups of blood-sucking insects, particularly mosquitoes, horseflies and related Diptera, during the Jurassic and Cretaceous is well-documented (Rohdendorf, 1974; Kalugina and Kovalev, 1985). Virtually all members of these groups currently are

parasitic on warm-blooded vertebrates (birds and mammals), and it has
been suggested that they may have fed originally on warm blooded
dinosaurs, or early birds and mammals, or both (Remm, 1976; Grogan and
Szadziewski, 1988). However, Downes (1971) concluded, based on a clear
structural differentiation of blood-feeding lineages in Lower Jurassic
deposits, that this food resource guild originated during the Triassic,
when therapsids were the dominant vertebrate elements. Other members of
the blood-feeding food resource guild includes fleas, traceable only to
the Early Cretaceous (Jell and Duncan, 1986; Figure 4h), but which may
have originated considerably earlier, during the Early Mesozoic or Late
Paleozoic (Hennig, 1981), based on a sister group relationship with
either the Mecoptera (Kristensen, 1981) or the Diptera (Boudreaux,
1987). Sucking lice, which lack a respectable fossil record, may have
been present as early as the Late Cretaceous (Waage, 1979) based on
their high level of host monospecificity on eutherian mammals (Kim,
1988). An Early Cretaceous insect, *Saurophthirus*, was inferred to have
been ectoparasitic based on the presence of several specializations
(Ponomarenko, 1976). This unique form has been allied with
scorpionflies (Rasnitsyn, 1988) and with fleas (Dmitriev and Zherikin,
1988), although it probably warrants separate ordinal status.

Late Cretaceous to Cenozoic.— The last major pulse in land arthropod
diversification is associated with the origin of flowering plants during
the last two-thirds of the Cretaceous. After this evolutionary burst,
there was taxonomic stabilization at the familial level during the
Tertiary, although there was significant biogeographical reshuffling
because of the change from climatically equitable latitudinal gradients
during the Late Cretaceous (Labandeira, 1989) to the general climatic
deterioration during the Cenozoic (Dorf, 1969). The taxonomic
continuity of arthropods during this interval is evidenced by the high
number of arthropod taxa in various Cretaceous and Tertiary ambers that
are assigned to extant families and even extant genera (see Larsson,
1978; Keilbach, 1982).

The relatively recent upsurge in documentation of various Cretaceous
ambers (McAlpine and Martin, 1969; Zherikin and Sukacheva, 1973; Schlee
and Glockner, 1978; Keilbach, 1982) has resulted in a much more complete
picture of the diversity of Cretaceous insects that co-occurred with
emerging angiosperms. Enough is known of the potential pollinators
available to angiosperm plants that a sequence of the stages by which
angiosperms became dependent on insects for their reproductive success
can be inferred (Crepet and Friis, 1987; Willemstein, 1987). It is
highly likely that the earliest, generalized angiosperms sequestered
such "mess-and-soil" pollinators as beetles (Crepet, 1972; Willemstein,
1987) and pollenivorous sawflies (Krassilov and Rasnitsyn, 1982) that
were already consuming pollen of cycadeoids, conifers and perhaps other
Mesozoic seed plants. These pollinators were succeeded by more mobile
and faithful pollinators such as mandibulate micropterygid moths (Thien
et al., 1985) or various nectarivorous brachyceran flies or
pollinivorous/nectarivorous aculeate wasps with fleshy, prolonged

mouthparts used for surface fluid feeding (Gottsberger, 1988). The
recent discovery of a *highly derived* melponine bee about 80 m.y. old
(Michener and Grimaldi, 1988a,b; Figure 4i) probably extends the
diversification of bees to the Early Cretaceous. Michener and Grimaldi
suggest that the elaborate structural modifications for capturing and
storing the pollen and nectar that is important for honey production in
a specialized eusocial caste system may have evolved during the rise of
angiosperms or even before. Eventually, during latest Cretaceous times,
bilaterally-symmetrical and deep, tubular flowers originated — flowers
which currently attract advanced, faithful pollinators, particularly
apoid bees, advanced lepidopterans (butterflies; large, nocturnal moths,
etc.) and several families of flies with long, fleshy proboscides
(Crepet and Friis, 1987; Willemstein, 1987). By the Early Eocene, an
inventory of floral types revealed the presence of the four modern
pollination syndromes (Crepet, 1979a,b), although certain minor
refinements had not evolved by that time.

Although insect pollinators were attracted to plants, other
herbivorous insects were repulsed by various plant defenses, including
secondary compounds, leaf trichomes, thickened cuticles and production
of intracellular crystals (Edwards and Wratten, 1980). Examples are the
various taxonomically disparate groups of plant-galling insects that
attack all organs of plants: their record commences during the Late
Cretaceous and expands during the Tertiary (Mamaev, 1975; Larew, 1986).
Similarly, although lepidopteran leaf-mines have been documented on
early Late Cretaceous angiosperms (Kozlov, 1988), the number of
documented instances of leaf-mining increases dramatically during the
Tertiary. An "arms escalation" between host plants and plant predators
(Ehrlich and Raven, 1964) has been a major explanation for rapid
diversification of angiosperms and angiosperm-dependent insects during
and since the Late Cretaceous. Only recently have tests of this
hypothesis been performed. In an elegant study of representatives of
sister-groups within several examined clades, Mitter et al. (1988) have
shown that taxonomic diversification is strongly associated with those
sister-groups that have adopted herbivory, and diversification is not
associated with the corresponding sister-group that adopted
nonherbivorous diets. This conclusion is consistent with many
monospecific and obligate associations between herbivorous insects and
their plant hosts (Jermy, 1984). A case in point is a 48 million year
association among a species of galling aphid and its hosts, a moss and
the sumac genus *Rhus* (Moran, 1989).

Isopod, amphipod and decapod crustaceans are the most recently
terrestrialized of arthropod groups, and are evidently still undergoing
significant modification for life on land. The earliest terrestrial
isopods (Oniscoidea) are Eocene (Cloudsley-Thompson, 1988), whereas
terrestrial amphipods (Talitroidea) lack a fossil record (Schram, 1986).
However, because of a well-documented vicariant distribution of
amphipods on almost all Gondwanan land masses, an early or middle
Mesozoic origin has been suggested by Schram (1986). Bousfield (1984)
however favored multiple invasions, specifically a symplidactylate group

emerging onto mangrove swamps during the Cretaceous angiosperm radiation, and a cuspidactylate group invading land via driftwood and wrack during the early Tertiary (see Wildish, 1988). The terrestrial decapod record begins during the mid-Tertiary, although Edwards et al. (1970) proposed an origin tied to an earlier diversification of broadleaved angiosperm forests adjacent to marine settings. It would be of interest to determine whether the marine stocks from which terrestrial decapods originated were groups participating in the Mesozoic Marine Revolution of Vermeij (1987).

A Case Study.— A general overview of one aspect of hexapod success is provided by a recent analysis of hexapod mouthparts by Labandeira (1990). Recent hexapod mouthparts are classified into 34 fundamental structural types, based on an analysis of 1365 extant hexapod species representing all orders and 70 percent of the families. These basic types have an associated dietary spectrum: a few consume eclectic diets but most have relatively constrained diets. From a distribution of these mouthpart types in the fossil record (all but three have significant records based on direct fossil evidence), the evolution of mouthpart form as well as the development of food resource guilds can be tracked through time in terrestrial and freshwater ecosystems. A major conclusion of this study is the disjunction between taxonomic diversity and structural diversity, as reflected in the geochronologic distribution of mouthpart classes. With the emergence of the modern (Mesozoic and Cenozoic) insect fauna, taxonomic diversity rises modestly until the appearance of angiosperms; however, about 85 percent of the mouthpart classes were established during the Early and Middle Mesozoic, if not earlier. (In the following discussion, bracketed numbers refer to mouthpart classes in Figure 6).

Mandibulate mouthparts appear the earliest [1,2,?4], and surprisingly so does a stylate, piercing-and-sucking type without an ensheathing haustellum [22]. By the Late Carboniferous piercing-and-sucking types with haustellate stylets [24] were probably the dominant mouthpart class; presumably members of this class fed on phloem and other plant tissues bearing concealed fluids. This mouthpart class reappeared during the Permian. There also was a diversity of mandibulate mouthpart classes [3,4,6-8] during the Late Paleozoic that undoubtedly were associated with consumption of a wide range of plant tissues (Figure 5). Subadult nymphs (naiads) entered freshwater ecosystems during the Late Paleozoic by becoming filter feeders or other aquatic detritivores [10]-

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FIGURE *6—* Summary of the geochronologic distribution of Recent hexapod mouthpart classes and their associated diets. Bar codes: black - fossil occurrences, grey - inferred presence based on cladistic relationships, hatchure - indirect fossil evidence (e.g., trace-fossils). Adapted from Labandeira (1990).

DT DT Om Om Om In DT N/I HI DA DA DA He | In In N/I Ne Om
1 2 3 4 5 6 7 8 9 10 11 12 13 | 14 15 16 | 17 18

MANDIBULATE | MANDIBULO-CANALICULATE | LABELLATE

Age (m.y.a.) Era Period

		CENO	TERTIARY
100		MESOZOIC	CRETA-CEOUS
200			JURASSIC
			TRIASSIC
300		PALEOZOIC	PERMIAN
			CARBONI-FEROUS
400			DEVONIAN

1 ENTOGNATHATE
2 MONOCONDYLATE
3 ADULT ECTOGNATHATE
4 LARVAL ECTOGNATHATE
5 MAXILLOLABIATE
6 RAPTORIAL ECTOGNATHATE
7 MORTAR-AND-PESTLE
8 ROSTRATE
9 RHYNCHOPHORATE
10 PECTINATE
11 MOUTHBRUSH
12 MANDIBULOBRUSTIATE
13 SERICTERATE
14 FOSSATE COMPLEX
15 TUBULOMANDIBULATE
16 MOUTHHOOK
17 HAUSTORIATE
18 LABELLATE

Ne Ne Ne Fu Fu Om Bl He I/N I/N Bl Bl Bl Bl Pf Ap
19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34

SIPHONATE | GLOSSATE | STYLATE-HAUSTELLATE | STYLATE-HAUSTELLATE | REDUCED

Age (m.y.a.) Era Period

		CENO	TERTIARY
100		MESOZOIC	CRETA-CEOUS
200			JURASSIC
			TRIASSIC
300		PALEOZOIC	PERMIAN
			CARBONI-FEROUS
400			DEVONIAN

19 SIPHONATE
20 SIPHONOMANDIBULATE
21 GLOSSATE
22 ENTOGNATHOUS-STYLATE
23 ECTOGNATHOUS-STYLATE
24 SEGMENTED BEAK
25 BUCCAL CONE
26 MOUTHCONE
27 MONOSTYLATE DISTYLATE
28 DISTYLATE TETRASTYLATE
29 HEXASTYLATE
30 TRISTYLATE
31 TUBULOSTYLATE
32 SIPHONOSTYLATE
33 REDUCED TROPHIC
34 NONTROPHIC

OR 34 MOUTHPART CLASSES ABOVE

TD	Detritivory (Terrestrial)	He	Herbivory (mostly folivory)
TA	Detritivory (Aquatic)	HI	Herbivory (indurated foods)
In	Insectivory	Fu	Fungivory
N/I	Necrovory/Insectivory	Bl	Blood-feeding
I/N	Insectivory/Nectarivory	Om	Omnivory
Ne	Nectarivory (with or without pollenivory)	Pf	Parasitic, fluids (not blood)
		Ap	Aphagy

-a trend that continued into the Middle Mesozoic as holometabolous
larvae entered freshwater as well [11,12]. Other holometabolous larvae
contributed three terrestrial mouthpart classes during the Permian and
Early Mesozoic — these were dominately insectivorous, modified
mandibulate forms that sucked liquids through mandible-associated tubes
or canals [14-16].

Structurally diverse and highly modified mouthpart classes with
prolonged, often fleshy distal surfaces for sponging, lapping and
siphoning exposed fluids [17-21] originated with one exception [19]
during the Middle Mesozoic, most of which subsequently became co-opted
during the Late Mesozoic as angiosperm pollinators. The larvae of many
of these taxa were members of a mandibulate, silk-secreting mouthpart
class [13] that are frequently obligately dependent on consumption of
vascular plant foliage. Also during the Middle Mesozoic there was the
origin of certain clades in typically plant-feeding stylate-haustellate
mouthpart classes [24,26] as well as newly evolved stylate-haustellate
mouthpart classes [27-29] that were predatory on other terrestrial
arthropods. Some of these mouthpart classes [24,28,29] as well as new
mouthpart classes that emerged during the Late Mesozoic to Paleogene
[25,30-32] became obligate blood-feeders on warm-blooded vertebrates.
During the Mesozoic there were several invasions by small beetles
bearing multiply-convergent, stylate, piercing-and-sucking mouthparts
[23] into a fungal food resource guild. Contemporaneously there was the
development of a snout-borne, mandibulate mouthpart class [9] modified
for the comminution of indurated foodstuffs such as grain, seeds and
wood. Finally, from the Late Paleozoic to the Recent, many insect
groups lost most mouthpart elements during their larval phases due to
endoparasitism, or communal feeding by other castes in eusocial clades
[33], or simply became nonfeeding during their adult phase [34].

Summary.— Although there are suggestions indicating the existence of
terrestrial communities before the Late Silurian, current evidence
supports the invasion by three major arthropod groups (arachnids,
myriapods and hexapods) into lowland terrestrial habitats during the
Late Silurian to Early Devonian. By the Late Carboniferous, various
combinations of myriapods, winged insects and arachnids became the
dominant detritivore, herbivore and carnivore elements in panequatorial
coal- and clastic swamps. Collectively, terrestrial arthropods had the
advantage of an efficient gaseous exchange system, a relatively
impermeable integument, silk, wings, and by the end of the period,
obligate plant dependency and complete metamorphosis. By the Late
Carboniferous, arthropods comprised most of the major food resource
guilds and were partitioning diets according to tissue types within each
guild.

Following major climatic and floral changes during the latest Carboniferous, there was a taxonomic shift in both insects and arachnids. One-fourth of the arachnid orders became extinct at this time, including all of the dominant groups. Similarly, large-sized, paurometabolous Carboniferous groups were replaced by modern holometabolous groups, many of which were structurally convergent, during the more seasonal Permian. This differential survival of most of the Permian holometabolous groups and only a few Carboniferous paurometabolous groups gave a modern facies to the worldwide fauna during the Early Mesozoic.

The Early and Middle Mesozoic was characterized by a radiation of the four dominant orders of insects (Coleoptera, Diptera, Hymenoptera and eventually the Lepidoptera) and moderate rebounds of a few Carboniferous holdovers, notably the Orthoptera. There is strong evidence during this interval for the first appearance of vascular plant/insect pollination, predation on (warm-blooded?) vertebrates for blood as food, and later orb-weaving by spiders for capture of prey. Although major vascular plant-insect interactions typical of the Paleozoic continued during the Early and Middle Mesozoic, there was a qualitative increase in the diversity of interactions with the arrival of angiosperms and establishment of initially facultative and later obligate pollination, leaf-mining, and stem- and leaf-galling. These interactions originated by both de novo coevolution and by lateral transfer from existing nonangiospermous hosts. By the Paleogene several lineages of angiosperms had developed advanced entomophilous flowers highly coevolved with their faithful pollinators, the dominant holometabolous insects. Contemporaneous with the expansion of terrestrial insects and arachnids onto flowering plants was the multiple invasions of various clades from two crustacean groups — amphipods and decapods. Isopods may have become terrestrialized earlier.

CONCLUSIONS

No other phylum of animals has colonized the land as successfully as arthropods. By any measure of dominance — species diversity, biomass, trophic integration into ecosystems — arthropods contribute fundamentally to land ecosystem structure, together with terrestrial vascular plants and, to a lesser degree, vertebrates. At least six major invasions of land habitats through five marine-to-land routes have been mounted by arthropods, all which have succeeded. At least two of these are continuing today. Although only a small sample of marine phyla made it onto land, it is among terrestrial arthropods where about two-thirds of all extant species-level diversity resides. Thus there is something unique to land arthropods (insects and arachnids) that favors rapid diversification.

Five general features contributing to arthropod success on land are those limited predominately to tracheates and arachnids. Possibly most important is (1) a waterproofed exoskeleton that limits absolute size,

based on the decreasing propensity for internal body support as volume-to-body surface ratios decrease with increasing size. This restriction to small size, combined with (2) respiratory systems that can penetrate and ramify oxygen-demanding tissues (the unique solution of tracheates and some arachnids) or transport of oxygen from book lungs through hemolymph pigments to oxygen demanding tissues (the "vertebrate style" of most arachnids), are two salient aspects of arthropod terrestriality that contribute to a small, compact, efficiently-breathing organism. Two other features important for terrestriality are (3) behavioral modification of activity level as a response to changing external conditions, and (4) presence of relatively rapid generation times in most forms, which allows for dispersal into new environments and rapid rates of colonization. Finally, (5) since the basic arthropod body plan involves a metameric construction with segmented appendages (see Emerson and Schram, this volume), there is much raw materal with which evolution can act on. In this context hexapod mouthparts are instructive. Although the number of co-optations between and among the five major mouthpart appendage-bearing segments of the head is numerous, the theoretical number of possible combinations is nearly infinite. It is because of numerous intersegmental and intrasegmental modification of mouthpart regions and appendages that hexapods have entered every major food resource guild during the last 400 million years. Thus hexapods consume any nutritionally rewarding substance because they can sequester food by chewing, piercing-and-sucking, filter-feeding, sponging, rasping, siphoning, lapping-and-squeezing, sweeping or scraping, boring, and other numerous ways. Contemporaneous modifications of metameric arachnids probably evolved in response to their predominant insectan prey.

Specific features found in more derived clades that contribute to arthropod success are the monophyletic features of wings and metamorphosis, and the polyphyletic developments of silk, sociality, and phytophily. Most, if not all of the above features involve relationships between insects and vascular plants, and between insects and their predators (especially arachnids). These niche-specific features have contributed to insect and arachnid diversity as vascular plant diversity increases.

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