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Rustling in the Undergrowth: Animals in Early Terrestrial Ecosystems

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The study of animals in early terrestrial ecosystems as represented in the fossil record, long a neglected field, has undergone a striking renaissance in the past decade and a half. Spurred on at first by the recognition of unconventional kinds of fossil remains (Shear et al. 1984), we have now seen the exploration of informative new sites (Jeram et al. 1990; Shear et al. 1996), the development of new trace fossil evidence (e.g., Retallack and Feakes 1987; Banks and Colthart 1993; Trewin and McNamara 1995; Wright et al. 1995), attempts to integrate the animal evidence with that of plants (Scott 1991, 1992; Chaloner et al. 1991; Stephenson and Scott 1992; Edwards, Selden, et al. 1995), and frequent reviews of progress (Selden and Jeram 1989; Shear and Kukulová-Peck 1990; Shear 1990, 1992; Scott et al. 1992; Edwards and Selden 1993; Gray and Boucot 1994). Book-length treatments of the subject have also appeared [Little 1990; Behrensmeyer et al. 1992 (in part); Gordon and Olson 1995].

In this chapter, we propose to examine the presently available fossil evidence from two viewpoints: that of faunistics and that of trophic relationships, limiting our discussion to the Devonian and earlier. It is our hope that yet another review of this rapidly expanding field may usefully synthesize information old and new.

THE ECOLOGICAL SETTING

Earth's terrestrial environment in the mid Paleozoic must have presented a strikingly different picture from that with which we are familiar today. We now recognize that the greening of the landscape by early autotrophs was a protracted affair, which can be separated broadly into four or five overlapping phases (Gray 1985, 1993; Edwards and Selden 1993; see Kenrick and Crane 1997b, for a slightly different arrangement).

The first of these phases, which began in the Precambrian, consisted of microbial mats and occurs on bare mineral surfaces today. The second was a bryophytic phase, which began in the Ordovician and ended in the Early Devonian. This was overlapped by the third phase, which started in the Late Silurian. It consisted of small plants (rhyniophytoids) with axial organization and terminal sporangia, such as *Cooksonia*. The earliest good faunal evidence comes from this phase: the Ludford Lane biota. It is possible to imagine the Ludford Lane land animals (predatory centipeds and trigonotarbids) creeping through a salt-marsh rhyniophytoid sward and occasionally becoming commingled with the aquatic eurypterids, fish, and annelids during storms.

The fourth phase possibly began as early as in the Late Ludlow in Australia, or as early as the Gedinnian on the Laurentian continent, and represents the first major diversification of land plant life, such as zosterophylls, drepanophycales, and trimerophytes, and *Baragwanathia* in the southern hemisphere. All other early terrestrial faunas belong here (e.g., Gilboa, Alken-an-der-Mosel, and Rhynie), and the beginning of complex terrestrial ecosystems can be discerned. The decline of the fourth phase is difficult to determine. If the phase is recognized on plants alone, whether it includes the lycosid/sphenopsid/pteridosperm forests of the Late Paleozoic depends on whether such plant groups are included with their extinct progenitors or their modern descendants. It is possible that the advent of trees (i.e., *Archaeopteris*) in the Middle to Late Devonian contributed to the end of this phase and to the modernization that was to take place in the Late Paleozoic.

In ecological terms, we do not know how widespread herbivory was in the Late Paleozoic. Early terrestrial ecosystems were decomposer-based (see later), but just when modern herbivory became commonplace and signalled the start of phase five is unknown.

For 50 years after the discovery of the Rhynie Chert animals in the 1920s (Hirst 1923), until the description of the Alken-an-der-Mosel and Gilboa faunas in the 1970s (Størmer 1970, 1972, 1973, 1974, 1976; Shear et al. 1984), no new early terrestrial faunas were found. During the last 25 years, our knowledge of early terrestrial faunas increased enormously, as the Alken and Gilboa faunas were described in detail, and the Ludford Lane, Red Hill, South Mountain, and eastern Canada faunas came to light. Nevertheless, until quite recently, our understanding of early terrestrial animal life was based almost entirely on information from these few Lagerstätten.

It is satisfying that the faunal lists from these localities broadly match, so that a consensus view of early terrestrial animals is possible. In the last few years, some new localities in the Catskill delta area, the Welsh Borderland, and Canada have turned up, which may prove to be more informative in the future.

FAUNISTICS

This section will attempt to summarize the fossil evidence of early land animals from both a chronological and a systematic perspective. We will begin with an overview of the kinds of evidence available for the emergence and evolutionary development of land animals, then turn to a chronological, site-by-site survey of the fossil record.

Trace Fossils

Trackways and Traces

Prior to the appearance of more or less complete body fossils of animals (arthropods) in the Late Silurian (Jeram et al. 1990), trace fossil evidence and tiny fragments attributed to animals carry us back well into the Ordovician.

The Borrowdale Volcanics

Johnson et al. (1994) described a series of trackways attributed to the ichnogenera *Diplichnites* and *Diplopodichnus* from strata within the Caradocian Borrowdale Volcanic Group of northwestern England. They argued persuasively for the subaerial nature of the deposit bearing the trackways, but conservatively stopped short of attributing them to terrestrial animals. However, the trackways are consistent with ones made experimentally by modern millipeds (Diplopoda) and later-occurring trackways that seem definitively terrestrial (Trewin and McNamara 1995). The animals that made the Borrowdale trackways may have been capable of limited excursions on land, or indeed could have been terrestrial.

Potters Mills

Retallack and Feakes (1987) described meandering, subvertical burrows in an Upper Ordovician paleosol in Pennsylvania. These burrows have bilaterally symmetrical backfilling resembling that found in the burrows made through decaying wood by some living millipeds. However, it is presently impossible to say with any certainty whether these burrows were made by early millipeds (which do not appear as body fossils

until the Late Silurian), or even by arthropods. They remain a tantalizing bit of evidence of possible, very early colonization of the land by large animals.

Millerstown

Utilizing the technique of hydrofluoric acid maceration, Gray and Boucot (1994) recovered intriguing fragments of animals from the Lower Silurian (Llandovery) Tuscarora Formation, near Millerstown, Pennsylvania. Not formally trace fossils, they are treated here because at the present time it is impossible to attribute these fragments to specific taxa, even at the phylum level. They include pieces of bristles or setae which may be arthropodan (though they do not appear to be hollow, as are nearly all arthropod setae; annelid setae are not hollow), trachea-like tubes, and patches of cuticle with at least two kinds of spines. The evidence is strong that the Tuscarora Formation in Pennsylvania, at least the basal part examined by Gray and Boucot, was deposited as an alluvial fan. It is far from any contemporary paleoshoreline and lacks any marine fossils, including marine microfossils. Plant spores are abundant. The Tuscarora fragments suggest that some forms of freshwater or terrestrial animals were present by the Early Silurian; the trachea-like tubes are especially important, as they cannot be attributed to plants and have at least some of the attributes of the tracheae of air-breathing animals.

Newfoundland

Late Silurian trackways attributable to terrestrial or semiterrestrial arthropods are relatively abundant. Recently described examples include *Diplichnites* from Newfoundland, Canada (Wright et al. 1995). Wright and colleagues suspected the arthropleurid *Eoarthropleura* of being the maker of the Newfoundland trackway, a contention strengthened by the discovery of *Eoarthropleura* body fossils in the Lower Devonian of New Brunswick (Shear et al. 1996) and the Upper Silurian of Shropshire, England (Shear and Selden 1995). However, their argument was based on the anatomy of the leg tip of the much later (Carboniferous) *Arthropleura*, and recently

discovered material of the legs of *Eoarthropleura* show a strikingly different structure.

Western Australia

As many as eleven different species of arthropods (not all of them terrestrial) may have been responsible for a rich diversity of trackways and burrows in the Upper Silurian Tumblagooda Sandstone of Western Australia (Trewin and McNamara 1995). *Diplichnites* trackways range in width from 10 to 300 mm, some traceable for several meters across the exposures, crossing and recrossing similar trails. Other trails include drag marks between the footprints, as well as marks made by paddle-like limbs. Trewin and McNamara attributed the trackways to myriapods, eurypterids, scorpions, and euthycarcinoids; while some were made under water, a large number clearly represent animals walking on sediments exposed to air, and possibly on dry, wind-blown sand. These Australian trackways have a great deal in common with Lower Devonian ichnofossils from the Taylor Group of Antarctica (Bradshaw 1981; Gevers and Twomey 1982), and similar Devonian trackways are known from the Old Red Sandstone of Britain (e.g., Pollard and Walker 1984).

Tetrapod Trackways

Clack (1997) has reviewed the trackway evidence for terrestrial locomotion by Devonian tetrapods. She found the evidence, most of it from Famennian localities, to be ambiguous, and not clearly indicative in any one case of land-going behavior by any of the tetrapods now known from Devonian skeletal material. While some of the tracks, particularly those from the Genoa River Beds in New South Wales, Australia, undoubtedly represent those of tetrapods, there is no published independent support for the subaerial nature of the deposit; the animal that made them could have been swimming.

At the present time, most of the trackways that can be clearly attributed to tetrapods occur in regions that were, in the Devonian, far from the sites that have yielded skeletal material, and it is difficult to connect any of the known Devonian tetrapods to these trackways.

Coprolites

Yet another line of trace fossil evidence comes from coprolites. Upper Silurian and Lower Devonian coprolites attributable to microarthropods have been studied by Sherwood-Pike and Gray (1984) and Edwards, Selden, et al. (1995). The pellets described by Sherwood-Pike and Gray from the Silurian of Gotland, Sweden, contained fungal hyphae, attributed to the predominantly terrestrial Ascomycetes, while those studied by Edwards and her colleagues (1995) consisted of masses of spores of land plants. The coprolite evidence will be discussed in detail in a later section.

Injuries to Plants

Damage to plants, probably caused by arthropods, has been reviewed by Chaloner et al. (1991). Controversy still remains over the damage to Rhynie plants (Lower Devonian) first noted by Kidston and Lang (1921a) and reported in more detail by Kevan et al. (1975). Kidston and Lang initially attributed the lesions in Rhynie plants to damage from volcanic cinders or other purely physical agents, perhaps unaware of the presence of animal fossils in the deposit. However, in the light of data on the details of the kinds of damage caused by the attacks of insects and other animals on modern plants (Labandeira and Phillips 1996), the arguments of Kevan and his coauthors are quite convincing, although none of the known animals from Rhynie possess the right kind of feeding apparatus, nor are any of their modern analogues feeders on living plant material (Edwards and Selden 1993).

Banks and Colthart (1993) examined in detail damaged specimens of *Psilophyton* from the Lower Devonian (Emsian) of Gaspé, Québec, Canada. They found several types of wounding and wound reaction, suggesting attack by animals and subsequent response by the plants. Possible coprolites were also found, both within and outside of plant stems. Animal fossils have been reported from the same formation (Battery Point Formation), but none of

them are potential candidates for having caused the wounding (Labandeira et al. 1988; Shear et al. 1996). No further evidence of damage to plants by animals during the Devonian period has been found, but data on plant–animal interactions of this type from the Carboniferous onward are substantial (Chaloner et al. 1991; Scott 1992; Scott et al. 1992; Stephenson and Scott 1992) and growing (Labandeira and Phillips 1996).

Body Fossils

This evidence is organized chronologically and by fossil site. In subsequent sections, the major groups of animals will be treated in more detail as to their mode of life and ecological role.

Body fossils of Silurian and Devonian land animals occur in two preservational contexts: as organically preserved cuticle that can be extracted from the matrix using hydrofluoric acid (HF) maceration (Shear et al. 1984; Jeram 1994a; Braun 1997), and as impression fossils. Only lately has it been recognized that both types can occur together (Shear et al. 1996).

Silurian Period

The oldest reported fossil of a putatively terrestrial animal is that of the supposed milliped *Archidesmus loganensis* Peach, 1899, from the Llandovery of Scotland. However, both Rolfe (1980) and Almond (1985) have examined the specimen and are inclined to support the contention of Ritchie (1963) that it is probably a misinterpreted algal fossil. Almond (1985) noted myriapod-like arthropod fossils from the Wenlock Fish Beds of Lesmahagow, Scotland, but thought them best considered *incertae sedis*. From the Stonehaven Group of Scotland, other myriapod-like fossils have been recorded, including *Kampecaris obanensis* Peach, and a convincing, as yet unnamed, diplopod (Almond 1985; Shear 1998). Marshall (1991) has argued on the basis of spore evidence that the true age of the Stonehaven Group is Late Wenlock to Early Ludlow. From the setting, the terrestrial nature of these animals cannot be fully established. Most of these Silurian myriapod-like fos-

sils are typical impressions, but some also preserve cuticle (Rolfe 1980).

Ludford Lane. A basal Prídolí (c. 414 Ma) locality, Ludford Lane was well known for many years as an outcrop of the Ludlow Bone Bed, a concentration deposit containing vertebrate teeth and scales in a thin, rusty-weathering sandstone. The best-known outcrop of the Ludlow Bone Bed is at the junction of Whitcliffe Road (formerly known as Ludford Lane) and the main road to Leominster, just south of the bridge over the river Teme at Ludlow. Here, the Ludlow Bone Bed Member is a 0.21 m siltstone containing, in addition to the main basal bone-bed, a number of other thin bone-beds (see Bassett et al. 1982 for details).

Many years of eager collecting of the basal bone-bed, latterly using long chisels, had resulted in an overhang that threatened to collapse into the lane. The Nature Conservancy Council stepped in to remedy the situation and removed the overhanging rock before tidying up the site and preserving it. It was this removed material that was subjected to hydrofluoric acid treatment and that produced the Ludford Lane biota (Jeram et al. 1990).

The half-meter of material overlying the Bone Bed Member (the Platyschisma Shale Member) consists of storm-dominated silts with some minor concentration layers. Some of these lags consist of very fine, unoxidized mud, which is easily washed away. Hydrofluoric acid digestion of these sediments produced a diverse biota of marine (e.g., scolecodonts), brackish (e.g., eurypterids), and terrestrial components. It has been suggested that the storms washed components of a terrestrial ecosystem into the estuarine environment, where they were mixed with shallow marine fauna. The animals may have lived in a rhyniophytoid salt marsh. Sedimentology of the Platyschisma Shale Member reveals that the biota was deposited in lags within dominantly intertidal and storm-generated deposition. In some parts of the Platyschisma Shale, plant- and animal-rich blocks of finely (tidal?) laminated siltstone form breccias within channels, giving the impression of storm-induced erosion of a tidal salt marsh. Salt marshes are

more stable than bare muddy, sandy, or rocky littoral zones because of the ameliorating effect of the plants. Salinity, temperature, and water supply may fluctuate as much as on the bare shore, but at root, litter, and substrate level these fluctuations are lessened. Interestingly, salt marshes are providing a route for talitrid amphipods, crabs, and prosobranch and pulmonate gastropods to colonize the land at the present day, as well as for recolonization of the littoral by terrestrial insects and spiders (Little 1990).

The animal fossils consist of organically preserved cuticle and were recovered by HF maceration; only a single reasonably intact individual, a trigonotarbid, has been found (Dunlop 1996a). Fragments of eoarthropleurids (Shear and Selden 1995), scutigermorph centipeds (Shear et al. 1998), and scorpions have been identified. Numbers of other specimens cannot reliably be assigned to taxa but may include spiders and archaeognath insects.

Early Devonian Period

Rhynie. Perhaps the most famous (but comparatively little-studied) Devonian locale for early terrestrial animal fossils is the hot spring chert deposit at Rhynie, Scotland (Trewin 1994). Here, silica-saturated waters from a thermal spring flooded and silicified nearby vegetation, with dense growth of vascular plants, algae, and fungi.

Significant numbers of animals, all arthropods, were also preserved. The quality of preservation is unparalleled anywhere in the fossil record, with many of the animals three dimensionally embedded in the translucent chert and showing minute setae, cuticular microsculpture, and the impressions on the cuticle of individual epidermal cells. Although the technique has not been much used, some material may also be isolated from the matrix using HF.

The age of the chert has been set at Siegenian (Late Lochkovian–Early Pragian) by means of spores, while argon dating has produced a figure of 396 ± 8 mya, which spans from the Late Gedinnian through the entire Siegenian and Emsian to Early Eifelian (Trewin 1994); thus the oft-cited date of 404 mya is at the lower limit of

possibilities. In any case, the site can be considered to date from the middle to late Early Devonian.

The fauna includes hexapods [Collembola (Greenslade and Whalley 1986)], mites (Hirst 1923; Dubinin 1962), trigonotarbid arachnids (Hirst 1923; Shear et al. 1987) and a freshwater crustacean, as well as a possible eurypterid and an enigmatic pair of mandibles that may be insectan (Hirst 1923; unfortunately, this specimen seems to have been lost). In 1993, Andrew Jeram found part of the leg of a scutigermorph centiped in a sawn slab of Rhynie Chert, the first new animal to be discovered in the chert since 1923 (Shear et al. 1998). Current faunal studies by N. Trewin and L. Anderson (Aberdeen University) are also yielding new animals.

Alken-an-der-Mosel. The arthropod fauna of the Nellenköpfchen-Schichten of Alken-an-der-Mosel, Germany, was described by Størmer in a series of papers that culminated in a discussion of the paleoecology of the site (Størmer 1970–1976). Recently, Braun (1997) described some new material from the Alken site.

The Alken section comprises two horizons of plant-rich shales separated by about 20 m of sandstones and siltstones. During the Lower Emsian (upper Lower Devonian), there was an island bordered by tidal sand-flats with temporary lagoons. Marine- and brackish-water animals inhabited the lagoons, which were bordered by mangrove-type vegetation. Therefore, as at Ludford Lane, there is a commingling of terrestrial and aquatic organisms in the Lagerstätte.

Psilophytes were common, both terrestrial (and possibly partly submerged) and true aquatics. Størmer (1976) suggested that euryhaline bivalves were the permanent inhabitants of the lagoon. At flood times, marine animals were washed in. Some swimming animals probably wandered in and out of the lagoon: *Parahughmilleria*, *Jaekelopterus*, and other eurypterids, and the ostracoderm *Rhinopteraspis*. Xiphosurans, stylonuroid eurypterids, and scorpions were probably amphibious. Terrestrial animals recorded at Alken are trigonotarbids and the arthropleurid *Eoarthropleura*; the latter could have been amphibious (Størmer 1976).

Braun (1997) isolated trigonotarbid and spider cuticular remains from Emsian sediments of the Eifel region, and he also demonstrated that cuticle could be obtained from the Alken matrix.

Sites in Eastern Canada. Labandeira et al. (1988) macerated a single fragmentary specimen of an archaeognath insect, *Gaspea paleontognatha* Labandeira, Beall, and Hueber 1987, from a beach cobble probably derived from the Battery Point Formation. Jeram et al. (1990) argued that this specimen may not be a fossil, but a contemporary archaeognath that crawled into a crack in the rock. They pointed out that the three-dimensional preservation is unique, that there is no associated cuticle fauna, as generally found at other sites, that the specimen lacks the usual taphonomic signs (e.g., impressions of matrix granules), and that the morphological differences between *Gaspea* and living archaeognaths noted by the authors are not clear. Until more material is found, the true nature of *Gaspea* remains in doubt; as of 1999, nothing additional concerning this specimen has appeared in print.

Unquestionable terrestrial arthropod fossils were reported from Gaspé by Shear et al. (1996). Several specimens of a large, cylindrical milliped were found in the Battery Point Formation. They also briefly described a scorpion and an eoarthropleurid from the Campbellton Formation (Emsian) of New Brunswick, Canada. The scorpion specimen was notable because book lung tissue was preserved, the earliest evidence of air-breathing in scorpions. Extensive assemblages of vascular plants have been recorded from both the Campbellton and Battery Point Formations (Gensel 1982; Gensel and Andrews 1984; and see chapter 11).

Other Sites. Nearly contemporaneous with Rhynie are the milliped fossils briefly reported from the Early Gedinnian (Lochkovian) Lake Forfar by Trewin and Davidson (1996), and millipeds and kampecarids from elsewhere in Scotland (Almond 1985). Kampecarids and a variety of diplopod-like fossils appear sporadically in the Lower Devonian rocks of Britain; some of these represent new high-level taxa (Almond 1986; Shear 1998).

Middle and Late Devonian Period

Blenheim-Gilboa. The extensive exposures of Middle and Upper Devonian rocks found in New York State and Pennsylvania have yielded a great deal of evidence of the development of terrestrial animal life. The best-studied site at this time is mid-Givetian Blenheim-Gilboa of the Schoharie Valley of New York State (Shear et al. 1984), where a thick, plant-bearing lens of black shale was uncovered during excavations for a pumped storage power project. Before the reservoir was flooded, a large amount of matrix was collected by paleobotanists James Douglas Grierson and Patricia Bonamo.

The Gilboa (Brown Mountain) host rock is a dark gray shale that occurs as lenses within the thick Panther Mountain Formation. This formation forms part of the Catskill Clastic Wedge, a delta complex developed on the western side of a mountain chain, close to the equator, during the Devonian period.

Latest palynomorph data (Richardson et al. 1993) give an Eifelian/Givetian (382 Ma) age for the Lagerstätte, slightly older than suggested in previous literature. A tropical savannah climate with alternate wet and dry seasons has been postulated on paleogeographical and paleobotanical evidence (Shear et al. 1987). The stratigraphy associated with this deposit is complex (Woodrow 1985; Miller and Woodrow 1991), and it is difficult to place in relation to a constantly fluctuating paleoshoreline. However, *in situ* evidence suggests that the particular location of the Blenheim-Gilboa lens was probably an interdistributary pond on a prograding delta.

Subjecting this material to HF maceration to release plant fossils, Grierson and Bonamo discovered a complex fauna of terrestrial arthropods, including trigonotarbids (Shear et al. 1987), centipeds (Shear and Bonamo 1988), mites (Norton et al. 1988), spiders and amblypygids (Selden et al. 1991), scorpions, pseudoscorpions (Schawaller et al. 1991), arthropleurids, archaeognaths, and other as yet undetermined taxa.

The fossils consist of organically preserved cuticle, and while the level of preservation is not

as good as at Rhynie, it surpasses that at Ludlow Lane, and a larger number of more complete specimens have been recovered than have been found at other Middle and Lower Devonian cuticle-producing sites.

The main floral component of the Lagerstätte is the lycopsid *Leclercqia*, which apparently grew on stream banks and around ponds. This occurs in the rock in dense mats of stems interlocked by means of their hooklike, divided leaves. Other lycopods and shrubby progymnosperms are also found. Both *Leclercqia* and the animals in this Lagerstätte were perhaps transported to the site of deposition (allochthonous), possibly with the mats of drifted vegetation providing filters that trapped the animal debris during flood episodes (Shear et al. 1984). However, it is possible that the animals also lived among *Leclercqia* stems in life.

Other Catskill Sites. Other sites in the region have been explored and are yielding similar faunal elements, but much more remains to be done. Following up on the report by Kjellesvig-Waering (1986) of a scorpion from a shale quarry near Blenheim-Gilboa at South Mountain, Shear and Selden (1995) determined that instead of a scorpion, the cuticle fragments isolated using HF maceration by paleobotanist F. M. Hueber were from an eoarthropleurid. Subsequent exploration of this quarry has revealed one or more small lenses similar to the fossil-bearing rock at Blenheim-Gilboa, and maceration has produced more eoarthropleurid remains, trigonotarbids, spiders, mites, archaeognaths, and scorpions.

The age of the deposit was placed by Hueber and Banks (1979) at Early Frasnian, earliest Late Devonian, but recent examination of the spores by J. Beck (pers. comm., 1998) suggests a somewhat earlier late–latest Givetian to Early Frasnian. Thus, this site is clearly younger than Blenheim-Gilboa. While there are some similarities between this site and the *Leclercqia*-dominated Blenheim-Gilboa, the major floral elements yet described are psilophytes, liverworts, and archaeopterid trees (Hueber and Banks 1979). Lycopods, the dominant element at Blenheim-Gilboa, are apparently absent. The faunal differences noted may represent real

differences as opposed to sampling errors, since the flora is so strikingly different. The differences in flora may be due either to the ages of the two deposits, or to ecological differences.

From the upper Delaware Valley of New York State and Pennsylvania have come a few tantalizing specimens, including a flat-backed millipede resembling *Archidesmus*, and a trigonotarbid closely related to those found at the earlier Alken-an-der-Mosel site in Germany (Shear 2000). The authors were not successful in relocating the outcrops or any corresponding lithology during the field season of 1996, however, so the true provenance of these specimens remains in doubt. The exposures in the region range over much of Frasnian and Famennian time.

Red Hill, a latest Famennian site in central Pennsylvania, has produced material of the tetrapod *Hynerpeton bassetti* Daeschler, Shubin, Thompson, and Amaral 1994. Plant material, mostly derived from archaeopterid trees and *Protolepidodendron*, is unusually abundant and well preserved at this site; HF macerations yield mats of leaves and stems strongly reminiscent of the lower layers of modern forest litter. Brown in color and translucent, the fossilized litter is possibly secondarily oxidized, or perhaps was never reduced and carbonized to the extent of coeval deposits elsewhere. Terrestrial arthropod remains have also been discovered, including both large impression fossils and organically preserved cuticle. Elements found so far include trigonotarbids, scorpions, and fragments that cannot be assigned to known taxa.

Into the Carboniferous

A 23-million-year gap separates the modest Devonian terrestrial faunas from the extensive and complex ones of the Upper Carboniferous. At this time, there are no known Tournaisian records for terrestrial animals; but a single trigonotarbid specimen (*Pocononia whitei* Ewing 1930) has been collected from the Pocono Mountain Formation of Virginia, probably located near the Tournaisian/Visean boundary (Dunlop 1996b). A significant Visean site for terrestrial animals, including arachnids, myriapods, and a rich fauna of tetrapods is found at

East Kirkton, West Lothian, Scotland (Rolfe et al. 1994).

FAUNAL ELEMENTS

Chelicerata

Scorpionida

The earliest evidence of air-breathing in scorpions comes from the Emsian of New Brunswick, Canada (Shear et al. 1996). Among preserved scraps of scorpion cuticle is an abdominal plate with attached lung tissue. Mesoscorpions are a prominent element in the preserved cuticle faunas of the Silurian and Devonian, appearing at Ludford Lane, Gilboa, South Mountain, and Red Hill. It is difficult to establish terrestriality for scorpions without having certain body parts (lungs, leg-tips) present, but Jeram (in Shear et al. 1996) saw evidence for the terrestriality of all mesoscorpions. Contemporaneous aquatic Devonian scorpions are known from Alken (Brauckmann 1977), but the unique respiratory arrangements of *Waeringoscorpio* require reexamination; the supposed feathery gills of this scorpion are unlike the book gills of earlier, aquatic Silurian forms.

All extant scorpions are predatory (Polis 1990). The known morphology of fossil scorpions is consistent with these feeding habits. The size range of Devonian scorpions is not easy to establish. The New Brunswick Emsian scorpion may have been about 9.5 cm long (Shear et al. 1996), while the size of fragments found at Gilboa and South Mountain suggest animals less than 1 cm in length, although the maturity of any of these specimens cannot be assessed. Carboniferous terrestrial scorpions reached 30 cm (Jeram 1994b).

Trigonotarbida

Trigonotarbids are superficially spider-like arachnids lacking silk-spinning organs and with the abdomen enclosed in segmented armor. They range from Late Silurian to Early Permian (Dunlop 1996a). The single Silurian record is of *Eotarbus jerami* Dunlop 1996, from Ludford

Lane. Devonian records are scarce. Brauckmann (1994) reported two partial specimens from Emsian strata near Waxweiler, Germany, and found them similar to the ones previously recorded at the nearly contemporaneous Alken site (Størmer 1970), while Schultka (1991) assigned an Emsian trigonotarbid from the German Bensberger Shale to a Carboniferous genus, *Trigonotarbus*. The exquisitely preserved Rhynie trigonotarbids have been restudied by Dunlop, but the results have not yet been published (Dunlop, pers. comm. 1995). Shear et al. (1987) described three genera, containing seven species, from the cuticle fauna of Blenheim-Gilboa, although one of these is now known to be a spider (Selden et al. 1991). Trigonotarbid cuticle has been found at South Mountain, evidently not from any of the Blenheim-Gilboa species. As yet undescribed material, both from isolated cuticle and from a single complete impression fossil, is now known from the Late Famennian of Red Hill, Pennsylvania, and another new impression fossil is probably from the Upper Devonian of the Delaware Valley, New York. These are important because with *Pocononia* of the Early Carboniferous, they bridge the enormous time gap between the Middle Devonian and Late Carboniferous trigonotarbids.

Dunlop (1996c) attempted to untangle the classification and phylogeny of the trigonotarbids, an enterprise that is beyond the limited scope of this chapter.

Two ecomorphotypes of trigonotarbids can be recognized among the Devonian material. "Paleocharinids" are generally small (1–6 mm long), lightly sclerotized animals with remnant lateral eyes (a pleisomorphy) that probably were inhabitants of the litter. They are limited to the ?Silurian and Devonian. (The question mark is needed because the assignment of *Eotarbus jerami* to one or the other of these groups is uncertain.) "Aphantomartids" are larger, more heavily sclerotized animals without lateral eyes (apomorphic), postulated to be surface-dwellers or possibly arboreal; they range from ?Silurian to Permian. As far as can be determined, the functional morphology of the feeding apparatus of both types is that of a carnivore;

prey was probably chewed with the chelicerae and liquid remains sucked up (Dunlop 1994).

Araneae

A single species of Devonian spider, *Attercopus fimbriunguis* Shear, Selden, and Rolfe 1987 has been described from Blenheim-Gilboa (Shear, Palmer, et al. 1989; Selden et al. 1991; see the latter paper for discussion of other putative records of Devonian spiders). This is the oldest known fossil of this ecologically dominant arachnid order, and it appears to be a representative of a taxon forming the sister-group to all other spiders. However, undiagnostic scraps of cuticle from Ludford Lane (Upper Silurian) may be from spiders. Abundant new material of *Attercopus* has appeared in macerations from South Mountain, in somewhat younger (Frasnian?) rocks.

Attercopus possesses a well-developed spinning apparatus and was evidently capable of making silk constructs, although analogies with other primitive spiders make us suspect that it was a burrower and used silk only to line its burrow or possibly to construct simple trip-lines. All spiders so far studied are predatory and the anatomy of *Attercopus* does not differ significantly from living spiders in this respect.

Amblypygi

Echosis pulchibothrium Selden and Shear, 1991, known only from leg podomeres from Blenheim-Gilboa, may be an amblypygid (Selden et al. 1991) on the basis of the strongly ornamented trichobothrial base on the patella. However, the patella is differently shaped, lacking the adaptations found in living Amblypygi for reflexion of the leg, and the supposed tibiae have rows of large sockets bearing robust, striated, bifid spines unlike any known from modern amblypygids (but which do occur in liphistiomorph spiders!). It is possible that the material represents an undiagnosed order of arachnids, or of a very primitive amblypygid ancestor lacking the extreme flattening of the body found in Carboniferous–modern forms. This flattened habitus may have developed as an adaptation for hiding under loose tree bark, a habitat only

just available in the Middle Devonian. Chelicerae are unknown for *Ecchosis*, but all living amblypygids are predatory.

Pseudoscorpionida

The only known Devonian pseudoscorpion is *Dracochela deprehendor* Schawaller and Shear 1991 from Blenheim-Gilboa (Shear, Schawaller, and Bonamo 1989; Schawaller et al. 1991).

Pseudoscorpions are tiny predators living in soil, litter, or crevices in bark, or under stones (Weygoldt 1969). *Dracochela* is not very different from modern neobisoid pseudoscorpions and undoubtedly had a similar lifestyle.

Acari

The earliest mite fossils are specimens from the Rhynie Chert (Hirst 1923). Originally placed in but a single species, they may actually represent as many as four distinct families (Dubinin 1962) but require detailed reexamination (Norton et al. 1988). Two oribatid mites (Norton et al. 1988) and one alicorhagiid (Kethley et al. 1989) have been discovered at Blenheim-Gilboa. A few poorly preserved specimens of oribatids similar to one of the Gilboa oribatid families (Devonacaridae) have been recovered from the younger South Mountain site.

Oribatids are detritivores or fungivores in modern ecosystems; alicorhagiids are known to prey on nematodes. Mites are undoubtedly underrepresented in the record because of their low fossilization potential (Shear 1990). They play a major role in soil and litter communities today and doubtless did so in the past.

Atelocerata

Diplopoda

Milliped fossils may reach as far back as the Wenlock (Almond 1986; Marshall 1991), depending on the dating of the Stonehaven Group of Scotland, which contains myriapod-like fossils. If Marshall's proposed Wenlock-Ludlow boundary age for these strata is correct, or if Almond's Lesmahagow Fish Bed (Wenlock) specimens are in fact millipeds, these would be the oldest body

fossils of land-dwelling animals. With the exception of these specimens, *Archidesmus macnicoli* of the Scottish Gedinnian is the earliest milliped. In an unpublished thesis, Almond (1986) has comprehensively studied the few other Devonian milliped fossils and diagnosed a number of new taxa, some of which do not seem very close to modern millipeds and hint at an early diversity for this group.

Until very recently all records for Devonian millipeds were from Britain; Shear et al. (1996) have now described cylindrical millipeds from the Emsian of Canada. These specimens are very distinct from the British representatives and are similar to Carboniferous and modern analogues. Two specimens of flat-backed millipeds have recently turned up from the Upper Devonian of the Delaware Valley. Tesakov and Alekseev (1992) described possible milliped diplotergites from the Devonian of Kazakhstan, but this material is somewhat ambiguous. The absence of millipeds from any of the discovered cuticle faunas is curious, but it probably results from a preservational bias. The cuticle of millipeds is impregnated with calcium carbonate, which would readily disappear in the acid preservational environments with which cuticle faunas are associated. The organic fraction of the cuticle, thus weakened, would probably disintegrate.

With very few exceptions, all living millipeds are detritivores—a few rarely attack live plant material, and still fewer may scavenge carrion (Crawford 1992; Hopkin and Read 1992).

Chilopoda

Leg segments attributable to scutigermorph centipeds have been found at Ludford Lane (Silurian), Rhynie (Lower Devonian), and Blenheim-Gilboa (Middle Devonian). These distinctive podomeres are pentagonal in cross section and bear marginal setae and serrations (Shear et al. 1998). Shear and Bonamo (1988) diagnosed a new centiped order, Devonobiomorpha, on the basis of *Devonobius delta* Shear and Bonamo, 1988, from Blenheim-Gilboa. Both of these groups are heterotergous, an adaptation for fast running.

The scutigermorphs, with their extraordi-

narily long legs, were probably surface-running, rather than litter inhabitants, but the much smaller *Devonobius* (about 10 mm long) seems to have been cryptic. *Devonobius* bears well-developed poison claws with which to seize prey; today's scutigermorphs are also predators.

Arthropleuridea

Arthropleurids are an extinct class of atelocerates, ranging in the fossil record from Upper Silurian to Upper Carboniferous. Respiratory structures are not known for any arthropleurids, but it is widely assumed because of the preservational context and other anatomical features that they were at least partly terrestrial. Of the three orders (one as yet undescribed), two are known from the Silurian and Devonian (Shear 1998). Eoarthropleurids are a part of the Ludford Lane (Upper Silurian; Shear and Selden 1995) fauna, and they also occur at Alken and in New Brunswick (Lower Devonian; Størmer 1970; Shear et al. 1996) and South Mountain (Upper Devonian; Shear and Selden 1995). Ranging in size up to 15 cm long, they probably resembled large, flat-backed millipeds, but fully articulated specimens have never been found, so nothing is known of their heads or how many segments may have been in the trunk. Later Carboniferous forms were detritivores (Rolfe and Ingham 1967).

An unnamed order of arthropleurids is prominent in the Blenheim-Gilboa and South Mountain faunas. These animals were probably less than 5 mm long, with but 9 or 10 trunk segments. The structure of the head is very similar to that of millipeds, except that eyes and antennae seem to be lacking, and suggests detritivory as a feeding habit (Shear 1998; Wilson and Shear, in press). At Blenheim-Gilboa, this animal is one of the most abundant, and thus it was probably a significant portion of the prey available to the trigonotar-bids, spiders, and centipeds.

Hexapoda

Parainsecta are represented in Devonian faunas by Collembola (springtails) from Rhynie. Greenslade and Whalley (1986) and Greenslade (1988) claimed that *Rhyniella praecursor* Hirst, 1923,

belongs to the living family Isotomidae, and that other species of springtails remain to be described from the chert, including neanurids.

Collembola are entognathous detritivores/fungivores that occur in modern soils in enormous numbers. A few species are also found in aquatic to semiaquatic situations, feeding on algal mats; this may have been the original habitat and may have carried them onto land very early (Shear and Kukalová-Peck 1990).

The evidence for Devonian insects is equivocal. We have already alluded to the problems with the supposed earliest insect fossil, *Gaspea paleoentognatha*; more material must be discovered and the original specimen described in detail before it can be accepted as genuine. Meanwhile, pieces of cuticle closely resembling that of modern archaeognaths have been found at a number of cuticle-bearing sites. The cuticle is thick, often poorly preserved, and bears short, arched rows of oblong sockets for the insertion of scales. There is a single scrap of this distinctive cuticle from Ludford Lane, large sheets have appeared in macerations from Blenheim-Gilboa, and a few pieces from South Mountain still have the scales in place. In addition, a series of antenna-like fragments and compound eye scaffolding from Blenheim-Gilboa may signal the presence of insects; particularly intriguing are ?antennomeres with unevenly bifurcate setae, known from living thysanurans.

Several unusual fossils from South Mountain are very similar to the cibarial or frontal pumping apparatus that occurs on the heads of modern insects with sucking mouthparts. This is particularly intriguing, given recent evidence of suctorial damage to Lower Devonian plants (Banks and Colthart 1993).

Thus, while the evidence is suggestive, unquestionable fossils of insects have yet to be found in Devonian rocks; the earliest known insect at this time is *Delitzschala bitterfeldensis* Brauckmann and Schneider, 1996, from the lower Namurian A of Germany. This becomes the first known Lower Carboniferous insect fossil courtesy of a redefinition of the Lower Carboniferous to include the lower part of the Namurian A.

Living archaeognaths are microherbivores (subsisting on algal and fungal crusts and films) or detritivores.

Chordata

Vertebrata, Tetrapoda

All evidence of Devonian tetrapods is limited to the Late Frasnian and Famennian. No less than eight genera of tetrapods have been named, coming from localities in Greenland, Scotland, Pennsylvania, Australia, Russia, and Latvia (Ahlberg and Milner 1994; Daeschler and Shubin 1995). The ecological setting of most sites seems clearly to be deltaic or lacustrine, though there are indications of a shallow marine environment for *Tulerpeton* (Clack 1997).

Vertebrates were comparative late-comers to land, and the evidence suggests that they retained a strong connection to the aquatic habitat throughout the Late Devonian. An approximately 23-million-year gap in the record during the Early Carboniferous makes it very difficult to relate these early tetrapods to later forms (Carroll 1992).

The evidence tells us that by the time of their first appearance in the fossil record in the Frasnian and Famennian, tetrapods had already achieved considerable diversity and worldwide distribution, so their actual origin must be placed at some time earlier in the Devonian. The earliest record of limb bones (Ahlberg 1991) is from the Frasnian of Scat Craig, Scotland, of *Elginerpeton pancheni* Ahlberg 1995. *Obruchevichthyes*, from Latvia and Russia, is of a similar age (Ahlberg and Milner 1994). Famennian tetrapods, in additional genera, come from Australia, Greenland, and North America (Daeschler and Shubin 1995). The phylogenetic relationships of these genera and the abundant and diverse tetrapods of the upper Early Carboniferous are not well understood (Thomson 1991; Carroll 1992; Ahlberg and Milner 1994).

The ecological setting and habits of the early tetrapods have been the subject of some controversy. Bendix-Almgreen et al. (1990) pointed to evidence suggesting that *Acanthostega* of

Greenland lived in active channels in fluvial-dominated environments. Work by Clack and her colleagues (summarized by Zimmer 1995) has shown that the forelimbs of *Acanthostega* may have been paddle-like, and that the animal retained internal gills. They suggest that *Acanthostega* inhabited weed-choked river channels, where it lay in wait for prey. It is not clear whether this form was primarily or secondarily aquatic, but it probably spent little, if any, time on land.

The exact sedimentary context from which the large number of *Ichthyostega* specimens comes has not been established (Clack 1997) and the animal has been reconstructed by Jarvik (1996) as much more of a terrestrial creature, albeit with a fishlike tail supported by fin rays. Clack (1997), on the other hand, pointed to a number of anatomical details that suggest a primarily aquatic lifestyle. In particular, she argued for massive, powerful forequarters, much smaller, paddle-like hind limbs, and a relatively rigid, barrel-shaped body, leading her to postulate a seal-like lifestyle. The large, sharp, recurved teeth of *Ichthyostega* would have served well for catching and holding fish.

Conversely, the teeth of other early tetrapods, such as *Elginerpeton* and *Acanthostega*, are relatively small and closely set. The flattened skulls of all three genera, with eye sockets located dorsally, suggest a shallow-water habitus and the taking of prey from on or near the surface. It is possible that *Acanthostega*, at least, fed on insects or other land dwellers that fell into streams.

Thus, the early tetrapods of the Devonian seem to have been carnivores based in aquatic environments, playing only a limited role, if any, in the terrestrial food chain.

TROPHIC RELATIONSHIPS

Co-occurrences of Animals with Plants

Early terrestrial plant and animal fossils often occur commingled at the same localities. However, there are many sites that have yielded only plants, not animals, since plants are generally more abundant as fossils. The co-occurrence of

plant and animal fossils is mainly the result of paleobotanists finding the animal fossils in passing, while looking for plants (this is certainly true of Rhynie and Gilboa), and later searches for animal fossils rely on finding good plant fossils, which indicate that animals may also be present.

Nevertheless, there seems little doubt that plants and animals were associated ecologically in early terrestrial ecosystems. What is the nature of the relationship? Presumably, plants occupied the producer trophic level on which the remainder of the ecosystem is based. In this section, we examine the evidence for direct interaction between plants and animals in early terrestrial ecosystems.

Animal–Plant Interactions

Animal–plant interactions in modern ecosystems can be classified into feeding, shelter, transport, reproduction, and coevolution (Scott et al. 1992); examples of all of these have been found in the fossil record, but evidence only of feeding and coincidental spore dispersal in the Siluro-Devonian.

Feeding by animals on plants includes not only direct herbivory but also digestion of dead plant material and its decomposing microflora by detritivores. Fossil evidence for animals feeding on plants comes from four sources: (1) plant morphology (anatomy and pathology), (2) animal morphology, (3) direct associations between animals and plants, and (4) coprolites.

Evidence from Plant Morphology and Pathology

Indirect paleobotanical evidence for plant–animal interaction in early terrestrial ecosystems comes from plant morphology—in the form of adaptations for defense from animal attack, and pathological reactions to attack—in the form of healed wounds. Both are presumably related to herbivory.

Defensive Adaptations.

Spines and Enations. Many early terrestrial plants bore spines, which suggests they may have been defensive adaptations against herbivory. However, other reasons for the spines have been proposed. Kevan et al. (1975) suggested that the

short, upward-pointing, scalelike enations of early vascular plants facilitated upward (but not downward) climbing of plant axes by arthropods; this would favor spore-eaters, which might then jump or glide off the sporangium after feeding, thus aiding dispersal.

Outgrowths from the axis in early vascular plants would undoubtedly increase surface area for photosynthesis, and possibly some of the outgrowths contained chlorophyll, although this is difficult to prove given the state of preservation (Lyon and Edwards 1991). Dense, silvery hairs, on the other hand, are used by plants in exposed areas today to prevent excess transpiration (e.g., hairy alpenes and cacti). Another reason suggested for axial lateral branches is to enable support and separation of axes in dense stands, or for a scrambling habit.

Nevertheless, some of the spines on early terrestrial plants look like sharp, defensive spines, and some occur on sporangia (Fanning, Edwards, and Richardson 1991), although a nutritional role has been postulated by these authors in addition to the possible defensive one. Finally, spines on spores, which commonly have bent or bifid tips, may not be defensive but could have attached to the bodies of animals for dispersal (Kevan et al. 1975).

The main problem with a defensive role for spines on the axes of early terrestrial plants is that they are too large to have been an effective deterrent against the animals that are known to have occurred with the plant fossils. While smaller animals could conceivably have been overlooked in the rock matrix, one would expect larger animals to be preserved. (On the other hand, processing rock in acid without looking at the surfaces could result in larger animals being disintegrated into unrecognisable pieces. For this reason, it is always advisable to search rock surfaces carefully before maceration.)

Evidence for Chemical Defenses. Darkly pigmented residues within spinous cellular hairs on aerial axes of the zosterophyll *Trichopherophyton* from the Rhynie Chert were considered by Lyon and Edwards (1991) as possible evidence for the formation and/or storage of substances that were toxic or distasteful to herbivores. These

authors argued, however, that this suggestion was not in accord with the lack of evidence for herbivore fossils in this Lagerstätte.

Spore Coats. Silurian spores are simpler, with no, fewer, or less complex spines and other ornament, than those of the Devonian and later. An increase in complexity continued throughout the Devonian so that a great many palynospecies are recognizable by the end of the period (see Kevan et al. 1975: pl. 55). These authors postulated that such a radiation must be adaptive, since energy is involved in the formation of ornament. Reasons for spore ornament include increased dispersal resulting from increased buoyancy in air or water or attachment to a dispersal vector. Since dispersal is a primary function of spores, such function is clearly useful. However, complex ornament would also help deter spore-eating organisms, for which the spore coat is nutritively valueless in comparison with the internal protoplasm. The thick spore coat of sporopollenin would also deter palynophagy (spore feeding) in addition to preventing water loss. Kevan et al. (1975: Appendix) discussed these and other adaptations of spore coats in great detail.

It is difficult to be sure how much coat thickness and ornament are directed against adverse physical, animal, or pathogen attack and how much toward dispersal mechanisms, including animal dispersal externally or in guts. Nor do we know how much coat thickness and ornament are related to the intrinsic needs of the spores (e.g., resistance to desiccation and increased buoyancy). There may also be constraints on spore structure that are essentially nonadaptive.

Wounds in Fossil Plants. Wounds in *Psilophyton* from the Emsian (394–387 Ma) of Canada were described by Banks (1981), Banks and Colthart (1993), and Trant and Gensel (1985). Banks and Colthart (1993) described wounds apparently produced by chewing and piercing in *Psilophyton* and an unnamed trimerophyte from Gaspé. The surface (presumed chewing) wounds on *Psilophyton* axes are generally small (<3 mm in diameter) and elliptical. They apparently occurred on erect axes 1 to 3 feet above ground level, and there is evidence, in the form

of cell proliferation, for wound repair. Hence, Banks and Colthart (1993) concluded that the wounds were formed while the plants were alive. Piercing wounds were identified by their cone-like form, the apex extending into the axis.

Lesions with a distinct tissue reaction were recognized in Rhynie plant axes by Kidston and Lang (1921a). These lesions (figured also by Kevan et al. 1975) commonly consist of dark areas extending from the epidermis into the cells in a wedgelike form, in most cases not reaching the vascular tissue, and outward to form a blister-like shape. Clear cells surrounding the wound apparently show an elongate growth reaction. The dark material (“opaque organic matter” of Kevan et al. 1975) is presumably some sort of healing exudate. Kevan et al. (1975) distinguished three types of lesions, which differ in the regularity of the wound and the amount of opaque organic matter.

Kidston and Lang (1921a,b) speculated that prolonged exposure to siliceous water or water vapor from the hot springs may have been the cause of these lesions. Kevan et al. (1975), citing Tasch’s (1957) study, which concluded that the Rhynie plants did not grow in “soil saturated with hot silicic waters” (Tasch 1957:17), suggested the alternative possibility: that the injuries could be attributed to sap-feeding animals. They pointed out that the juicy phloem-equivalent tissue of *Aglaophyton* was close to the surface of the plant. Labandeira and Phillips (1996) noted that wound reactions, such as cell proliferation, a dark exudate around the damaged area, and stylet insertion paths (some to vascular tissue) point to deliberate piercing by animals with sucking mouthparts rather than accidental injury. These have not been demonstrated in Rhynie plants.

It seems to us that there are a number of ways in which lesions could have been produced in early land plants. Chemical irritation, as originally suggested by Kidston and Lang (1921a,b), may well have been present in the hot-spring environment, but its effect probably would not have been to produce deep, thin lesions more suggestive of stylet wounds. Physical wounding can be caused accidentally, not just for the pur-

pose of extracting nutriment from the plants. Again, hot water is unlikely to have produced the type of wounding seen; wind-blown sand grains are a possibility, but perhaps improbable too. As previously mentioned, some of the early vascular plants were spinose, and the spines may well have been able to puncture adjacent axes. It is conceivable that spinose stems gave their bearer an advantage over naked stems, which were thus vulnerable to wounding.

Deliberate wounding by animals in the form of chewing was suggested by Banks and Colthart (1993); this seems a less sophisticated method of feeding than sap sucking, since presumably only the cell contents could be digested, not the cellulose walls. However, it may well have been more efficient than sap sucking, since many cells would be attacked simultaneously; unless the sap sucker penetrated vascular tissue and tapped a continuous supply of fluid, the stylet would be able to puncture only one cell at a time. But the question arises whether just taking the occasional nip from a plant stem would be a very rewarding way of feeding. Perhaps the plants were deliberately wounded to allow sap to escape, which could then be lapped up.

Though not conclusive, the evidence for sap sucking in the Rhynie Chert and Gaspé plants is more than suggestive. Cell fluids are more easily digestible than cell walls, so sap feeding could have evolved easily, and there is the possibility of pre-adaptation to fluid sucking as a feeding method in aquatic precursors.

Evidence from Animal Morphology. A general survey of the animals found in early terrestrial ecosystems was given earlier in this chapter; here, we concentrate on the evidence from animal morphology for plant–animal interactions.

Animals, particularly arthropods, exhibit a wide variety of methods of feeding on plants, including biting, sawing, cutting, chewing, rasping, mining, boring, mopping exudate, swallowing whole, and piercing and sucking juices. Some of these are particular to certain plant organs (e.g., boring wood and seeds, leaf mining, and swallowing whole seeds, pollen grains, and spores). Animal mouthparts can be a good

clue to their mode of feeding—the lepidopteran “tongue,” for example. However, piercing and sucking mouthparts occur in parasites of both plants and animals, and chewing mouthparts may be considered generalized. So, morphology alone is often not good enough, and comparison with modern relatives of the systematic group to which the animal belongs is normally necessary to determine the probable method of feeding.

Arachnids Largely Predatory. Earlier in this chapter, the feeding methods of the various arachnid groups known from early terrestrial Lagerstätten were briefly discussed. All modern arachnids are predators with the exception of some mite groups (see later). Reports exist of spiderlings ingesting pollen grains (possibly by accident) and of nectar feeding by some adult spiders (Taylor and Foster 1994).

The oldest known mites (Acari) occur in the Rhynie Chert. Hirst (1923) thought the specimens were conspecific; he named them *Protacarus crani*, and he placed them, with some doubt, in the modern family Eupodidae. Dubinin (1962) considered they represented five species belonging to four families: *Protacarus crani* (Pachygnathidae), *Protospeleorchestes pseudoprotacarus* (Nanorchestidae), *Pseudoprotacarus scoticus* (Alicorhagiidae), and *Paraprotacarus hirsti* and *Palaeotydeus devonicus* (Tydeidae). John Kethley (Field Museum of Natural History, Chicago) restudied the specimens and questioned the alicorhagiid affinity of *Pseudoprotacarus scoticus* because of its pretarsal morphology (Kethley et al. 1989). He considered all to belong to the family Pachygnathidae (pers. comm. in Norton et al. 1988) with the exception of the nanorchestid (a family that is nevertheless included in the superfamily Pachygnathoida).

Little is known about the food preferences of living pachygnathoid mites, but Krantz and Lindquist (1979) reasoned that pachygnathoids probably feed by sucking fluid from algal cells; they pointed to the sharply pointed mouthparts of these mites, thought by Trägårdh (1909) to be a piercing organ, and work by Schuster and Schuster (1977), who observed nanorchestids feeding on algal mats and refusing animal food.

Feeding Methods of Collembola and Archaeognatha. Devonian Collembola are known only from the Rhynie Chert (Greenslade and Whalley 1986). In his comprehensive review of the biology of Collembola, Christiansen (1964) noted that very little is known about the food preferences of collembolans with piercing and sucking mouthparts, but suggested that fungal juices might form their diet. What information is recorded about other Collembola is patchy and not always reliable. For example, some will eat almost anything when in captivity but are highly selective in the wild. Among the foods listed by Christiansen (1964) are fungal hyphae, bacteria, decaying plant and animal material, frass, algae, and spores. Some forms will eat living plant roots and seedlings and undecayed leaves, while others are carnivores preying on smaller animals (Protura, rotifers, tardigrades, and other Collembola).

Archaeognathans, known from Gilboa, South Mountain and perhaps Ludford Lane, have milling mouthparts that are used to scrape algae and lichens from rocks (Ferguson 1990).

Kraus and Kraus (1994) gave a brief review of food preferences of Tracheata, in which they concluded that a food niche common to all the main tracheate taxa was piercing/sucking. For example, Symphyla feed on plant rootlets, other soft tissues of plants, and small arthropods. Pauropoda and Protura apparently suck the juices of fungal hyphae. Some members of Zygentoma, Pterygota, and Collembola also feed in this way. These authors pointed out that relatively few, unrelated, tracheate groups have developed new (i.e., apomorphic) feeding mechanisms, and that these correlated with a body size increase, as in many Pterygota.

Chilopoda Predatory. Modern centipedes are generally unspecialized predators. While the Devonian Devonobiomorpha have no modern representatives, their morphology points to them as undoubted predators. Scutigermorpha are among the earliest known land animals, found in the Silurian at Ludford Lane, and the Devonian of Rhynie and Blenheim-Gilboa (Shear et al. 1998). Modern scutigermorphs are fast-running predators; *Scutigera coleoptrata* is a common house centiped in the Mediter-

ranean region and has been introduced into houses widely throughout warm parts of the world, where it can be seen chasing insects attracted to lights at night.

Diplopoda and Arthropleurida Detritus Feeders. Millipeds are principally detritivores, although some use gut flora to digest living plant tissue. In modern millipeds, the density of teeth on the gnathal lobes determines the size of food particles ingested; smaller species have smaller teeth, and the smaller the particles, the greater the proportion of food assimilated (Köhler et al. 1991).

Millipeds gain nutriment not only directly from the detrital material but also by digesting saprotrophic microorganisms present on the detritus, which may proliferate during the passage of food through the gut. They eat a variety of foods but when provided with choice show a clear preference for partly decayed leaves from particular species (Kheirallah 1979; Pearce 1989).

Coprophagy is common among litter feeders, and autocoprophagy is essential for the milliped *Apheloria montana* (McBrayer 1973). It may be that this species has to continually reinfect its gut with appropriate microbes. Enzymes are excreted by salivary and midgut epithelial glands and pass through the peritrophic membrane to digest the food. One function of the peritrophic membrane, which occurs in a variety of arthropods and annelids in addition to millipeds, is to protect the gut epithelium from abrasion by coarse detritus. Martin and Kirkham (1989) have shown how the membrane wraps around individual gut items and may also be involved in the digestive process. Broken-down peritrophic membrane passes out with the feces, and the membrane is renewed at ecdysis in arthropods. In Diplopoda, anal glands secrete a glue-like substance that binds fecal particles together (Schlüter 1982, 1983).

Arthropleurids appear to have had mouthparts similar to millipeds, and a Carboniferous *Arthropleura* specimen found with gut contents (Rolfe and Ingham 1967) showed it ate plant detritus. We presume that the Devonian eoarthropleurids were detritivores, too.

Direct Associations of Plants and Animals.

Trigonotarbid in Sporangia. A good example of

a direct association between plants and animals in an early terrestrial ecosystem is the trigonotarbid found within axes and dehisced sporangia in the Rhynie Chert (Kevan et al. 1975: pl. 56; Rolfe 1985: pl. 1, fig. 1). Kevan et al. (1975) reported the suggestion of W. D. I. Rolfe, who brought these specimens to their attention, that the trigonotarbid could have gotten there actively, for feeding or to avoid adverse physical conditions (e.g., temperature, humidity, wind-speed), or passively by postmortem transport. Kevan et al. (1975) rejected the latter on the basis of the autochthonous/parautochthonous nature of the deposit, and preferred the idea of trigonotarbid entering the plant cavities actively, possibly to feed on spores.

Since trigonotarbid are almost certain to have been carnivores, it is more likely that they sought shelter there, perhaps for molting (Rolfe 1980). Indeed, Rolfe (1980) reported that none of about 15 dehisced sporangia still in growth position examined by Dianne Edwards showed any trigonotarbid remains, and the geopetal infill of the trigonotarbid carcass and the plant axis shown in Kevan et al. (1975: pl. 56, fig. 1) indicated that the sporangium containing the trigonotarbid was not in life position.

Many occurrences of trigonotarbid in the Rhynie Chert can be shown to be of molted animals (Rolfe 1980); one interesting example shows a trigonotarbid leg inside a trigonotarbid abdomen within a plant axis (Kevan et al. 1975: pl. 56, fig. 1). This lends support to the idea that trigonotarbid used dead plant axes and empty sporangia as refugia for molting rather than for palynophagy. We note here that Bonamo and Richardson examined the contents of more than 150 *Leclercqia* sporangia but found no animal remains (reported in Shear et al. 1987).

Coprolites. Coprolites bearing plant remains provide direct evidence of plant-animal interaction in early terrestrial ecosystems. However, this evidence needs careful evaluation. Coprolites are proving to be not uncommon in macerates of early terrestrial sediments, although they are not always recognised as such, especially if their constituents are poorly aggregated, but also if they are composed of spores that are all of the same type, in which case they show a

superficial resemblance to sporangia (Edwards, Selden, et al. 1995). The main occurrences of coprolites in Siluro-Devonian sediments are reviewed here. By Carboniferous times, coprolites had become relatively common (Scott and Taylor 1983).

Silurian. Possible coprolites containing fungal hyphae were described from the Late Silurian (Ludlow) Burgsvik Sandstone of Gotland, Sweden, by Sherwood-Pike and Gray (1985). The possible coprolites are subcylindrical, 62 to 260 mm long and 18 to 40 mm in diameter, and consist of hyphae in an amorphous groundmass. These authors discussed the possible producers of the fecal-like masses, and fungivorous arthropods seemed to be the most likely candidates. Nevertheless, they conceded that the hyphae may have been later invaders of the coprolites, a view echoed by Scott et al. (1992).

Judging from the photographs and drawings in their paper (Sherwood-Pike and Gray 1985: fig. 2G, fig. 5F,G), the hyphae appear to be continuous, and not broken into segments as might be expected if the producer was feeding on the contents. However, the walls of the hyphae in the supposed coprolites appear to be more irregular than those of the hyphae found loose in the macerates.

Sherwood-Pike and Gray (1985:9) discussed and dismissed the possibility of modern contamination as the source of the fungi in their samples; in contrast, Selden (1981: fig. 23m) illustrated fungi etched from Silurian limestones of the Baltic region, which he concluded were modern fungi growing on the surface of weathered rock before etching. Devonian fungi are well known from the Rhynie Chert (Taylor, Remy, et al. 1995) and Gaspé (Banks and Colthart 1993).

If the hyphal aggregates described by Sherwood-Pike and Gray (1985) are indeed coprolites, then they represent an early example of presumably terrestrial coprolites, but not necessarily, in our opinion, of fungivory.

Devonian of Gaspé. Banks and Colthart (1993) described possible coprolites or regurgitates among material of *Psilophyton* and other trimerophytes from the Lower Devonian (Emsian) of Gaspé, Canada. A larger mass (3.0 × 1.5 mm) consisted of an unstructured mix of collenchyma and

xylem tissues, while smaller pellets of amorphous material occurred within stems. The authors concluded that these two types of coprolite must have had different producers: The larger type seems to have resulted from indiscriminate chewing of a variety of tissues, while the smaller pellets seem to have been produced by animals munching their way along the inner cortex of the plant stems. It seems to us that the larger coprolite could have been produced by an animal eating living or dead plant tissue—that is, a herbivore or a detritivore.

Spore-bearing Coprolites from the Welsh Borderland Silurian and Devonian. Edwards, Selden, et al. (1995) described coprolites stuffed with numerous types of spores from a number of Silurian and Devonian sites in the Welsh Borderland. Because they contain spores, the coprolites were initially thought to be sporangia, but their regular shape, lack of a sporangial wall, and the presence of more than one spore type (up to nine in some specimens) and other debris ruled out this possibility.

Eighty-five coprolites range from 0.95×0.74 mm to 3.3×1.27 mm in size. Some are regularly cigar-shaped while others are truncated at one end. Consistency in shape, and the production of fecal pellets of a similar size and shape by some modern millipeds, suggested that the truncated examples are complete. Less regular shapes were interpreted as coprolites on their composition. Spore-dominated examples have smooth contours except where impregnated by pyrite. In contrast, those with cuticle, unidentifiable plant debris, and sporadic spores are less regular, with voids separated by draped debris.

Ninety-five percent of the coprolites contain spores, which occur in varying proportions with cuticle, tubes, and unidentified plant material. At least 25 different spore types were distinguished. Nonspore constituents include a featureless film, quite distinct from macerated cuticle, possibly solidified mucilage; featureless sheets interpreted as cuticle; occasional examples of sterome and tracheids; and possible nematophyte tubes.

Edwards, Selden, et al. (1995) discussed whether the coprolites were derived from terrestrial or aquatic animals, and whether they

were feeding on living or dead plant tissue. The coprolites had clearly drifted into a fluvial overbank flood deposit. Some evidence favored aquatic producers—for example, the presence of cuticles of possible aquatic animals in the same sedimentary sequence: eurypterids, scorpions, and kampecarid myriapods occur there, although evidence suggests that some or all of these animals may have been terrestrial or amphibious in the Devonian. There is evidence for a land origin for the coprolites in the presence of predominantly land-derived debris, with the same preservational characteristics as in the productive samples, and the lack of identifiable remains of unequivocal aquatic organisms in the coprolites.

Extant herbivores exploit gut fungi and bacteria to degrade cellulose, but even with their assistance the nutrient value of living vegetative tissues would have been low; thus palynophagy is an attractive possibility. Because sporopollenin-impregnated spore walls would be largely impermeable to enzymes, a spore-eating animal would have to crack the spores to digest them; the evidence suggested that the few damaged spores seen in the coprolites were broken as a result of post-depositional phenomena, not deliberate cracking. Another possibility is that herbivores fed on peripheral exospore layers or locular fluids, or on sporangial contents before sporopollenin deposition occurred. Immature sporangia would have provided an energy-rich nutrient source of presumably relatively high nitrogen content.

Edwards, Selden, et al. (1995) concluded that the coprolites indicated an animal that was ingesting spores and spore masses, but there is no evidence of the spore contents having been digested. Since the coprolites consisted entirely of organic matter, and no sedimentary particles, the producer was unlikely to have been a soil or sediment feeder. Litter feeders eat a variety of foods, and studies of fecal contents of detritivorous invertebrates showed that a variety of matter passes through the gut, including spores, which remain undigested. The paucity of recognizable plant matter other than spores in the coprolites is consistent with their production by a detritivore. Digestible matter in litter is quickly

broken down, in contrast to indigestible spores; many litter arthropods ingest their own feces or those of other detritivores, in which case a great deal of breakdown would already have occurred; indeed such a habit would tend to concentrate resistant items like spores in feces. A significant proportion of nutrition in detritivores is derived from the digestion of saprotrophic fungi and bacteria, so it is possible that the animal was selectively ingesting spores on which microorganisms were consuming the exospore—for example, the remains of extra-spore material such as demonstrated for *Cooksonia* sporangia.

Overrepresentation of spore-containing coprolites might reflect the lack of recognition of non-spore-bearing coprolites. Feeding experiments with millipeds show that fecal pellets dominated by plants are less regular and so, in fossils, could be overlooked or discarded as very poorly preserved fragments of plant axes. The available evidence suggests that the coprolites were produced by detritivores that fed on litter rather than a mixture of litter and sediment, and that ingested spores and spore masses, which were abundant in the debris. Digestive processes, coprophagy, and selective feeding were given as possible explanations for the high concentration of spores seen in the coprolites.

An impression of the size of the producer was deduced from the size of the coprolites and knowledge of the sizes of modern animals, so most collembolans, mites, nematodes (too small), and earthworms (too large) were excluded from consideration. The coprolites predate the earliest fossils, and the presumed origin, of terrestrial isopods and gastropods. Enchytraeid oligochaetes are common components of the soil fauna at the present day, but their casts would not resemble the coprolites. This leaves millipeds (or other myriapods) and possibly large collembolans, both of which are known as fossils in Devonian terrestrial biotas. Kampecarid myriapods occur in the same beds as the coprolites, but little is known of their biology. It is most likely that the animals producing the coprolites were terrestrial detritivores feeding on litter and were possibly arthropods similar to modern millipeds.

Undescribed Coprolites from the Devonian of Rhynie. Undescribed coprolites from the Rhynie Chert were brought to the authors' attention by Hass and coworkers. These are recognizable as coprolites from their shape and because identifiable contents are mainly fragmentary. They contain very few spores, and of the other identifiable contents, some dense material may be sporangium wall. Possible chitinous (i.e., arthropod) cuticles may also be present. In some preparations fungal hyphae appear to pass through the coprolites. The presence of possible arthropod cuticles would suggest a detritivore, since predatory arachnids would suck fluid out of prey and leave no cuticle-bearing coprolites. However, the rejectamenta of arachnids that chew their prey could possibly resemble coprolites.

TROPHIC RELATIONSHIPS IN EARLY LAND ECOSYSTEMS

Little Evidence for Herbivory

We have shown that most of the terrestrial animals found as fossils in early terrestrial biotas belong to primarily carnivorous groups. Some mites and collembolans could be microherbivores (fungivores or sap suckers) or decomposers; some of the myriapod taxa were probably detritivores. There is no evidence of animals that eat living, growing plant material.

The preponderance of carnivores in the Rhynie Chert was discussed by Kevan et al. (1975), who suggested three possible explanations: (1) small, soft-bodied prey animals were not preserved; (2) some of the arthropods were facultative herbivores; or (3) some of the predators were amphibious and returned to the water to feed.

Rolfe (1980) saw no problem with the lack of herbivores; he advanced the hypothesis that herbivores followed plants onto land and were succeeded by carnivores—a trophic-level succession with time. However, Rolfe (1985) rightly emphasized that the greatest proportion of primary production in the terrestrial ecosystem

passes through the decomposer chain at the present day.

Shear et al. (1987:9) mentioned the “striking predominance of predatory arthropods” in both the Rhyne and Gilboa faunas, and they gave as potential reasons the small sample, the differential preservation of arthropod cuticles, and the possibility of soft-bodied herbivores. Selden and Edwards (1989) mentioned two possible reasons for the lack of herbivores in early terrestrial ecosystems: poor preservation/recovery of herbivores because of their probable small size, and the greater importance of the decomposer food chain.

In a review of early terrestrial ecosystems, Shear (1991) pointed out that the fossil record should be taken at face value (particularly since new localities preserving early faunas showed similar suites of arthropods). Siluro-Devonian ecosystems may have been based on detritivores and microherbivores, herbivory evolving only much later (Carboniferous?) when animals had developed gut microfloras to aid in the breakdown of lignin, other recalcitrant materials, and toxins, a view echoed by Edwards and Selden (1993).

A New Definition of Herbivory

Biologists are as guilty as laymen in relating more to large, conspicuous bushes, trees, birds, and mammals than to the unseen microbes and microarthropods with which terrestrial ecosystems teem. Price (1988) termed this “Noah’s Ark Ecology.” In his review of ecosystem development over time, Price (1988) pointed out the importance of the substrate, be it marine mud or terrestrial soil, and of the availability of nutrients in decaying organic matter. Other authors, such as Seastedt and Crossley (1984), have emphasized that, even at the present day, cycling of nutrients through the decomposer niche has a greater impact, in most cases, than herbivory in terrestrial ecosystems.

For reasons that will become clear in the discussion to come, we wish to propose a much narrower definition of herbivory than has been current in the literature. While herbivores have traditionally been considered to be animals

feeding on any plant parts, we believe that at least three subgroups can be recognized, and we will limit our concept of herbivory to only one of them.

Herbivore processing of plant material is inefficient. An examination of the feces of any animal that feeds primarily on live plant material (aside from spores, seeds, or fruits) often reveals identifiable fragments of the plants eaten. Large numbers of other organisms have adapted to exploit these feces, which speaks volumes about the nutrient value still remaining.

The absence of endogenous cellulases and lignases, for example, from nearly all herbivorous animals strongly suggests that herbivory could not have been a primary adaptation of animals. Instead, plant-eating animals adopt various strategies that suggest that herbivory is a much later adaptation, developed through the acquisition by animals of mutualistic microbes that do most of the digestion for them. We will examine the reasons for thinking this is so.

Plants as Food

This section relies heavily on the information from the book edited by Abrahamson (1989).

Allelochemicals

Allelochemicals are substances produced by plants that offer some degree of protection against herbivores (Fraenkel 1959; Rosenthal and Janzen 1979). These are known as secondary compounds, because they have no role in the primary metabolic pathways of plants. The presence of such chemicals is nearly universal in vascular plants, with some being so poisonous that they are virtually immune to herbivory. Since plants have no excretory systems, these often-toxic chemicals must be sequestered. The longer a plant part is in existence, the more toxic it becomes as molecules of these compounds accumulate.

Nor is toxicity the only effect. Allelochemicals can inhibit feeding, act as repellents, reduce digestibility, and even mimic animal hormones, speeding up or slowing down developmental changes (Weis and Berenbaum 1989; Lindroth 1989).

Ephemeral parts of plants, such as flowers, are therefore not likely to accumulate large amounts of these substances, nor are seeds or spores. Fruits, which are designed to be eaten, very rarely contain appreciable amounts of toxins.

Strategies available to herbivores to circumvent allelochemical defenses include avoidance, detoxification by endogenous enzymes (Brattsten 1979), detoxification by gut microorganisms (Lindroth 1988), and sequestering. At least a few insects have co-opted plant toxins for their own defense (Duffey 1980).

Low Nutrient Content

Animals require not only calories, but specific nutrients, such as certain amino acids and minerals. Thus, the value of their food depends not just on the available calorific content, but on the amounts of micronutrients and protein available. Seeds, fruits, pollen, and spores may not only have a very dense calorific content but also be high in proteins and contain little indigestible material.

Leaves and shoots of plants, on the other hand, are not particularly nutritious. Much of the carbohydrate biomass is fundamentally indigestible by animals, consisting of such recalcitrant molecules as cellulose, hemicellulose, and lignin. While high in calorific value, these substances cannot be broken down by the endogenous enzyme systems of animals.

The protein content of plant foliage is very low, as measured by percent nitrogen. A number of studies have demonstrated that nitrogen content is an important regulator of insect feeding; nitrogen-poor food must be consumed in much greater quantities (Weis and Berenbaum 1989). Amino acid balance is also highly significant, and particular plants may be deficient in amino acids required by herbivores.

All parts of plants may be low in micronutrients; the best example is sodium, which is found in very low concentrations in plant tissues. Vertebrate herbivores may have to seek out other sources to overcome sodium deficiencies, hence the well-known phenomenon of the salt lick. The analogous process in some insects is "puddling," in which Lepidoptera, in particular,

gather at animal feces, urine, or carrion to lap up sodium-rich fluids (Arms et al. 1974).

Furthermore, the quality of plant food changes drastically over time, perhaps by as much as an order of magnitude, so animal digestive systems must be prepared to adapt to such changes (Scriber and Slansky 1981).

Problems for Sap Suckers

Feeders on plant juices not only face most of the problems just outlined but in addition may incur problems of water balance. In particular, xylem sap is so low in nitrogen content that insects feeding on it must process up to 1,000 times their body weight in sap each day (Horsfield 1978). Both xylem and phloem sap are available only if the requisite tissues can be reached, and the channel must be kept open.

Our Concept of Herbivory

First, we consider as herbivores only those animals that feed on the living tissues of plants; animals that process dead or decayed plant material are detritivores. Their food is nutritionally very different from living plant material because it has already been attacked by fungi and bacteria, which render it more digestible and also enhance the nutrient content by converting some of the carbohydrate to protein.

We also consider as special cases animals that feed primarily on seeds, spores, and pollen. These plant parts, while living, are nutritionally very different from the vegetative parts of the plant; in particular, they may be high in calorific value and contain abundant lipids and protein. While seeds may be heavily defended by recalcitrant shells and coats, they usually contain little indigestible material and the rewards for cracking the defenses are high. Spore and pollen coats are largely indigestible and must be cracked physically or chemically to be digested.

The discussion will be more illuminating if we focus instead on the use of the vegetative parts of plants as food, because this draws into consideration all the problems of plants as food briefly surveyed here. *Thus, for us, true herbivores are animals that routinely feed on leaves, shoots, and roots.*

Where feeders on plant fluids fit in the scheme (or how feeders on plant fluids are defined) depends on the case; while avoiding the problem of indigestibility, most sap or cell content feeders are confronted by the same difficulties of nutritional deficit and allelochemicals.

Fundamental Adaptations of Herbivores

Because of the low nutrient content of their food, herbivores have only a limited number of options. One is to consume enormous quantities of low-quality foods and to extract from it what they can; this is a common strategy among lepidopteran larvae and orthopterans. The gut becomes extremely large to handle the mass of food, and conversion values are low. This strategy is probably not available to larger herbivores, such as mammals.

A second strategy, adopted by nearly all vertebrate herbivores and many arthropods, is to form mutualistic relationships with microorganisms that live in the gut and process the food. The host herbivore then either digests the mutualists or lives on their by-products. The coadaptations of the participants can become extremely detailed, such that the herbivore host regulates conditions in its gut to enhance the growth of the mutualists, which in turn may tune their life histories to changes in the host, signalled by hormonal changes.

Microorganisms play a vital role in digestion in litter-feeding invertebrates; for example, it is unlikely that arthropods can digest cellulose without the aid of gut microflora (Swift et al. 1979). In millipeds, there is no evidence that the gut microorganisms exist in a symbiotic relationship, as they do in termites (Hopkin and Read 1992), but the flora does include soil and intestinal bacteria, actinomycetes, and fungi (Szabo et al. 1992, and references therein). Indeed, the digestive efficiency of millipeds is reduced if microorganisms are excluded from the diet, and the microorganisms proliferate within the warm, moist conditions of the gut (Anderson and Ineson 1983; Tajovsky 1992). Desert spirostrepsid millipeds bask in the sun to increase body temperature and thus aid digestion (Crawford et al. 1987), an activity that ren-

ders the animals susceptible to water loss and predation. The microorganisms themselves form an important part of the diet of millipeds, as shown by the experiments of Bignell (1989, reported in Hopkin and Read 1992). The passage time of gut contents for three milliped species was measured as 2 to 5 hours during constant feeding, and 11 to 12 hours without food (Brüggel 1992). Assimilation efficiency has been measured in many ways by a number of authors (Brüggel 1992: table 3), and Hopkin and Read (1992) advocated caution when assessing figures based on subtraction of weight of feces from weight of food ingested, because of changes in moisture content and gut passage times. It is likely that a maximum efficiency of 30 percent is typical for millipeds.

The milliped example may illustrate how the mutualistic strategy evolved. For soil detritivores, the soil itself has been described as a vast, external rumen. Not only is new plant matter that hits the ground eaten, but fecal pellets are ingested and reingested as long as they have any nutritional content; they are worked on by the gut flora of the detritivores as well as by free-living soil bacteria and fungi. Indeed, there may be no clear line of demarcation between the two.

When detritivores ingest soil, plant remains, and microorganisms, the biochemical activity of the microorganisms continues in the gut, and some forms will colonize the gut cavity and adapt to life there. This, in turn, would lead to adaptations on the part of the host to retain and "culture" them. With a highly adapted gut flora, animals could attack fresher and fresher plant material, perhaps eventually shifting to parts of live plants.

This is, of course, but one hypothetical path to herbivory. Others must lead through the route of sap sucker and seed or spore eating.

CONCLUSIONS

The fossil animal evidence shows a preponderance of carnivores, the presence of some detritivores, and the absence of herbivores. Hence it

points strongly toward a food chain based in detritivory. This is common in soils today, and note, too, that modern herbivory involves gut floras that evolved presumably from detritivorous ancestors.

This suggests that either we are sampling a soil ecosystem, or that the food chain, even for surface dwellers, was detritivore based. Although Devonian evidence is scarce, no definitively herbivorous terrestrial animals have been found, even aside from the major cuticle-bearing *Lagerstätten* (Shear et al. 1996). If the latter is true, then trophic relationships in early terrestrial ecosystems were radically different from those in today's herbivore-dominated world.

Plant evidence presents a somewhat different

picture. There is evidence (previously summarized) for damage to plants, and it is reasonable to hypothesize that at least some of this damage was caused by animals in attempts to feed on living plants. The perpetrators of the damage are entirely unknown, but the pattern suggests feeding on plant fluids, either by piercing vascular tissue or by damaging the plants and lapping up any fluids that leaked out. Conclusive evidence for animals (insects) eating the vegetative parts of plants does not appear until the Late Carboniferous (Labandeira and Phillips 1996), and we can infer from anatomy that herbivorous vertebrates appeared even later, near the Carboniferous–Permian boundary.

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