

Early Terrestrial Animals, Evolution, and Uncertainty

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Abstract Early terrestrial ecosystems record a fascinating transition in the history of life. Animals and plants had previously lived only in the oceans, but, starting approximately 470 million years ago, began to colonize the previously barren continents. This paper provides an introduction to this period in life's history, first presenting background information, before focusing on one animal group, the arthropods. It gives examples of the organisms living in early terrestrial communities and then outlines a suite of adaptations necessary for survival in harsh terrestrial environments. Emphasis is placed on the role of uncertainty in science; this is an integral part of the scientific process, yet is often seized upon by god-of-the-gaps creationist arguments. We hope to illustrate the importance of both uncertainty and scientists' freedom to express doubt while a consensus is being built.

Keywords Terrestrialisation · Evolution · Arthropods · Palaeozoic ecosystems

Introduction

The impetus for this paper comes from a media report on the research of Garwood et al. (2009). The piece in question—in one of the more widely circulated but less universally respected newspapers of the UK—outlined the three-dimensional reconstruction of Carboniferous arachnids. Though the reporting was for the most part scientifically

accurate, the associated online comments section provided unfortunate contrast. The first entry was a typically trivial and superficial anti-evolutionist's jibe regarding these arachnids: "they look just like spiders do today. 300 million years and no change. [...] Kind of hard on the old evolution theory isn't it?" When the comment's author was asked to expand on his beliefs, the response was an entirely predictable: "Why do I have to come up with an alternative for your useless theory?"

This altercation encapsulates perfectly a common creationist mindset, one based on cursory (and often incorrect) observations coupled with complete ignorance (or at best patchy understanding) of the scientific context framing an argument. See, for example, the myriad arguments introduced in Part III of Scott (2009). It further relies upon a god-of-the-gaps argument, the belief that in the case of unanswered questions the proponent's personal worldview wins by default. No alternatives nor evidence supporting the proponent's perspective are required (Pennock 2007). The comment is flawed on a number of counts. Not least, the arachnid group in question, the trigonotarbids (Fig. 1), were indeed quite different from spiders in that they lacked the ability to spin silk (Shear 2000a) and possessed a segmented posterior body region (likely inherited from their last shared common ancestor with spiders; Dunlop 1997). Furthermore, as we shall see later in this article, a degree of morphological stasis over 300 million years is in no way antithetical to the theory of evolution. The comment is also unfortunate because the early terrestrial (land-based) animal communities in which this trigonotarbid lived provide us with resounding evidence for evolution. They also offer an excellent example of the unanswered questions and uncertainties inherent to—and a driving force in—scientific inquiry. It is these uncertainties that the arguments of antievolutionists seize upon. If they succeeded, this would stifle the colorful world of scientific discovery and reduce it

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Fig. 1 A computer model of the trigonotarbid arachnid *Eophrynus prestvicii* (Garwood et al. 2009) from the Late Carboniferous Coal Measures, UK. Reconstruction from a CT scan conducted at the Natural History Museum, London, UK. Fossil housed at Lapworth Museum of Geology, Birmingham, UK, 30 mm in length

to a Manichaen palette of unquestioning certainty and unknowable unknowns (the dualism of Nelson 1999).

With this in mind, we hope that this paper will not only introduce these fossil communities and outline their evolution, but also demonstrate that ambiguity in science is neither detrimental nor a weakness. Rather it is a vital part of our field, which stimulates debate and drives further research and discoveries.

The paper is split into sections—the next will introduce terrestrial life as a whole during this period in the Earth's history before we focus on one group of animals in particular, the arthropods. We will then introduce examples of early terrestrial fossils that run the gamut from entirely extinct groups to those that are largely unchanged compared to their modern relatives, living in ecosystems that closely resemble those today. We will finish by introducing some of the adaptations these animals have evolved for a life on land.

Terrestrial Palaeozoic Life

The Paleozoic Era lasts from the beginning of the Cambrian Period (542 million years ago; Gradstein et al. 2009), known for its famous explosion of marine animals, to the end of the Permian Period (251 million years ago); marked by the greatest mass extinction ever known (Sahney and Benton 2008). Prior to the Paleozoic, the only life on land was unicellular, a fact that—until recently—could only be inferred from indirect evidence (Rasmussen et al. 2009; Prave 2002). However, current research is revealing unexpectedly diverse terrestrial communities revealed in

one billion-year-old cellular fossils (Strother et al. 2011). It was during the Paleozoic Era that plants (first known from microfossils called cryptospores that appear in the mid-Ordovician, about 470 million years ago; Wellman and Gray 2000) and animals (known from Silurian fossils, at least 423 million years ago; Wilson and Anderson 2004) began to colonize the land. Land plants started as small, non-vascular mosses and liverworts (bryophytes; Edwards 2000), but by the Late Silurian, simple plants with axial organization and terminal sporangia (spore-bearing structures) were becoming common (e.g., *Cooksonia*; Kenrick and Crane 1997). During the Late Paleozoic—the Devonian (416–359 million years ago) and Carboniferous (359–299 million years ago) periods—the first widespread forest ecosystems became established (DiMichele et al. 2007). Although quite different from modern forests, by the Carboniferous, these were diverse (DiMichele 2001) and included early tree-like relatives of extant club mosses (lycopsids) and horsetails (*Calamites*), and a wide variety of ferns (Falcon-Lang and Miller 2007). These forests were home to a wide range of animals, which had first ventured on to land in the preceding 100 million years. One group of these were early ancestors of all terrestrial vertebrates, which had first ventured on to land during the Devonian (probably between 385 and 360 million years ago). Paleozoic fossils record this transition from fish to land-dwelling limbed organisms (tetrapods; Clack 2009) and also span the split between true amphibians and other vertebrates (mammals and reptiles/birds; Clack 2006; Coates et al. 2008). Many early tetrapods were still aquatic, and probably lived within rivers and other freshwater environments, with the possible occasional foray onto land (Benton 2005). Fully terrestrial species were common by the Carboniferous Period, however, and the earliest true reptiles had evolved by the end of the Paleozoic, in the form of small- to medium-sized insect eaters (Modesto et al. 2009).

The majority of animal diversity and abundance in Paleozoic terrestrial communities can be found in the arthropods (a group which has, in fact, been dominant in terms of animal species diversity for all of the past 520 million years; Edgecombe 2010). The phylum Arthropoda is a group of animals united by, amongst other traits: external and internal body segmentation with regional specialization (tagmosis, e.g., a thorax with legs and wings versus a limbless abdomen in the case of insects); an exoskeleton composed of articulated plates, hardened through calcification or sclerotization (protein cross-linking); body segments that primitively bear paired, articulated appendages; growth via molting (ecdysis); a pair of lateral faceted (compound) eyes that are innervated by the first of three segments that comprise the brain; and an open circulatory system featuring a dorsal heart with lateral valves (Grimaldi and Engel 2005). The unique features of arthropods indicate that they are a monophyletic

group (descendants of a common ancestor that possessed the diagnostic features of the group). Arthropoda (Fig. 2) includes the extinct trilobites, the insects, the myriapods (millipedes, centipedes, and relatives), the crustaceans (e.g., crabs, lobsters, shrimp), and the chelicerates (arachnids, such as spiders, scorpions and mites, and horseshoe crabs). Their abundance makes arthropods ecologically vital; for example, myriapods are important processors of leaf litter in forests, and termites consume large quantities of cellulose (Crawford 1992; Higashi et al. 1992). Without arthropods, the life and ecosystems of the Earth would be radically different. Their astounding diversity (constituting in excess of 75% of all described living species; Brusca and Brusca 2003) can help elucidate the patterns and processes of evolution. For example, the study of trilobites was central to the development of punctuated equilibrium as a model for evolutionary change (Eldredge and Gould 1972; Gould and Eldredge 1977), and the fruit fly *Drosophila* was the “model organism” used in much of the pioneering work on genetics in the early twentieth century as well as unraveling the genetics of development in the late twentieth century. It is for these reasons that the following discussion of terrestrial Paleozoic life and evolution will focus on the Arthropoda.

The Palaeozoic Fossil Record of Terrestrial Arthropods

The first terrestrial arthropods predated tetrapods by tens of millions of years (Shear and Selden 2001). Evidence of animal life on land before the first known arthropod body fossils can be found in the form of preserved traces that are likely to have been created by macroscopic organisms. Identifying the animal that made trackways or burrows is not always straightforward. For example, burrows assigned to the ichnogenus *Scoyenia* from Late Ordovician (ca 447 million years ago) rocks in Pennsylvania (Retallack and Feakes 1987) had been interpreted as having been made by millipedes (Retallack 2001), but this has been disputed based on how living millipedes burrow (Wilson 2006) and also because the sediments show evidence of a marine rather than terrestrial origin (Davies et al. 2010). The best candidates for trackways of Ordovician age that were made by an identifiable group of terrestrial arthropods occur in Late Ordovician rocks in Cumbria, UK, in ash and sandstones that were deposited subaerially (Johnson et al. 1994). A comparison with the locomotory traces of living “pin cushion” millipedes showed that the stepping gait of the Cumbrian Ordovician trackways is consistent with them having been made by an early millipede (Wilson 2006).

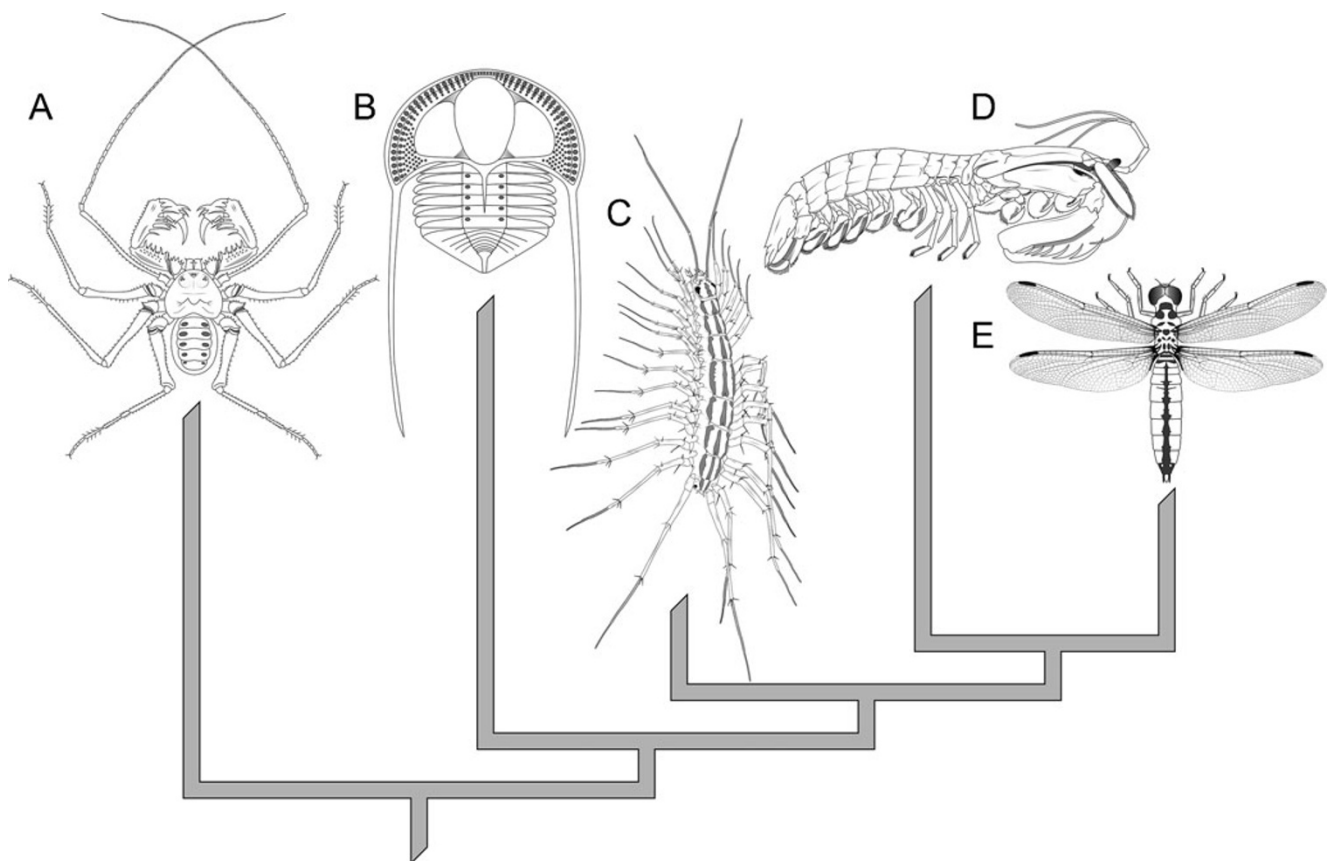


Fig. 2 Diagram showing the best-supported evolutionary relationships of the five arthropod groups: chelicerates (**a**) (here represented by an amblypygid arachnid), trilobites (**b**) (a member of the family

Trinucleidae), myriapods (**c**) (scutigermorph centipede *Scutigera coleoptrata*), crustaceans (**d**) (a stomatopod or mantis shrimp), and insects (**e**) (a dragonfly)

The first body fossil evidence of the animals responsible for such tracks dates from the Silurian Period (444–416 million years ago). Several millipedes have recently come to light from Stonehaven, UK (approximately 423 million years ago), including one species, *Pneumodesmus newmanii*, that provides the first evidence for air breathing in any form of animal (Wilson and Anderson 2004). This can be seen in spiracles (or, more biblically, stigmata)—openings into the tracheal (breathing) system which are a terrestrial feature by definition. Another of the Silurian millipedes has a paired structure on the anterior part of the trunk, in the usual segmental position and with a characteristic form of a gonopod, a modified pair of legs that male millipedes use to transfer sperm to the female's genital opening (Fig. 3; Wilson and Anderson 2004). The Silurian fossils thus provide direct evidence for a similar reproductive mode as their extant relatives.

The majority of fossils from around this time, however, are not discovered by simply splitting rocks in the field, but rather are found in acid macerate residues. These are “leftovers” from the acid digestion of rocks, to which the arthropod cuticle (exoskeleton), composed of chitin, is resistant. The earliest deposit from which this technique has recovered identifiable organisms is found in Ludford Lane, Shropshire, UK (approximately 417 million years ago) where both arachnids and centipedes are known (Jeram et al. 1990). A wider range of arthropods are recovered using this method from Middle Devonian (388 million years ago) rocks of Gilboa, New York. These include a number of different arachnids, including mites and pseudoscorpions (Shear et al. 1987; Norton et al. 1988; Schawaller et al. 1991; Selden et al. 1991), centipedes (Shear and Bonamo 1988), and possible fragments of insect exoskeleton (Shear et al. 1984).

Another famous Devonian (approximately 396 million years ago on the basis of radiometric dating, though spores suggest a slightly older age in the Early Devonian; Rice et al. 1995; Wellman et al. 2006) fossil locality is the Rhynie Chert, near Aberdeen, in Scotland. These translucent rocks were formed

in a hydrothermal hot spring setting in which silica-rich water inundated and silicified nearby vegetation, including a number of the animals—all arthropods—creating a near-perfect record of this early terrestrial ecosystem (Trewin et al. 2003). The incredibly well-preserved fossils are studied in slides made from the rock and often display the internal anatomy (e.g., book lungs, the respiratory organs of arachnids; Kamenz et al. 2008). Animals described to date include arachnids (Fayers et al. 2005), primitively flightless hexapods (springtails and a bristletail or silverfish), as well as true insects (Fayers and Trewin 2005; Engel and Grimaldi 2004), centipedes (Shear et al. 1998), and freshwater Crustacea, including extinct relatives of fairy shrimp and tadpole shrimp (Trewin and Fayers 2007). Another fossil locality from the Early Devonian is Germany's Alken-an-der-Mosel, from which a range of different arthropods, including several kinds of arachnids and relatives of millipedes called eoarthroleurids, were described by the Norwegian paleontologist Leif Størmer (1970; 1972; 1973; 1974; 1976), but few other deposits preserve anything more than isolated individuals. Despite the important anatomical, ecological, and temporal data provided by the Silurian and Devonian fossil deposits, the first widespread and well-preserved record of terrestrial ecosystems dates from approximately 20 million years later, in deposits of the Upper Carboniferous Period (Shear 2000b). During this period, a mountain-building event, the Variscan Orogeny, contributed to the assembly of the supercontinent Pangea (Cocks and Torsvik 2006). Despite glaciations at the poles, a wide zone carpeted with thick forests and vegetation spanned the tropics and even some higher latitudes (Cleal and Thomas 2005). These forests supported diverse ecosystems (Shear and Kukalová-Peck 1990). Many of them were in effect mires, wet environments in which organic matter accumulates (DiMichele 2001), and flooding was widespread (Falcon-Lang 2000; Plotnick et al. 2009). The resulting waterlogged boggy sediments create ideal conditions for the preservation of fossils within siderite (FeCO_3) nodules and also for the formation of coal (Curtis

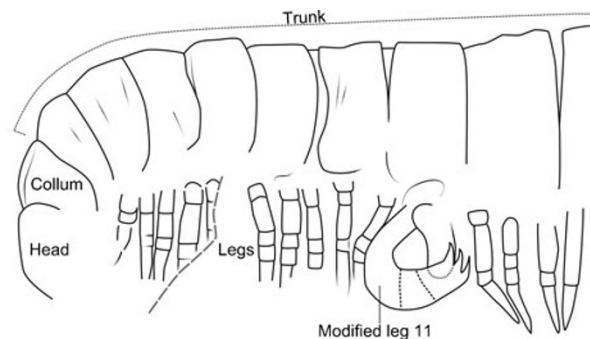


Fig. 3 Photograph and sketch of mid-Silurian millipede, *Cowiedesmus eroticopodus* (photograph courtesy of Yong Yi Zhen, Australian Museum). This, the front of the specimen, shows the head, collum (first segment behind the head, with no limbs), and then the start of the

body. Also visible is a modified leg, possibly associated with reproduction. Shown portion of fossil 12 mm in length. After Wilson and Anderson (2004)

and Coleman 1986). As a result, coal from this period is found throughout North America and Europe. In fact, the Carboniferous was responsible for fuelling the industrial revolution on both continents (Chandler Jr 1972; Hartwell 1967). Thus, a number of factors created ideal conditions for both the widespread preservation of fossils during the Carboniferous and the exploitation of these deposits by geologists more than 300 million years later. As a result, they provide one of the most important windows into early terrestrial ecosystems.

Evolutionary Relationships

Fossils from these early ecosystems record a number of arthropod groups at different grades of organization, which we will briefly compare here. Some are entirely extinct groups, such as the aforementioned arachnids, the trigonotarbids (Fig. 4a; Dunlop et al. 2008a). These are known from exceptionally well-preserved Rhynie Chert fossils and appear to have been amongst the most abundant arachnids in Carboniferous coal forests (Garwood and Dunlop 2011). The presence of two pairs of lungs on the same body segments as some extant forms provides a strong argument that they are most closely related to a group known as the tetrapulmonate arachnids, which includes the spiders, whip scorpions, whip spiders, and short-tailed whipscorpions (Dunlop 2010). Indeed, the fine structure of the book lungs from a Devonian trigonotarbid, examined using three-dimensional reconstruction techniques, is shared with living tetrapulmonates (Kamenz et al. 2008). The youngest fossil member of the group dates from 290 million years ago (Röbber et al. 2003). Thus, the trigonotarbids are an entirely extinct group, an evolutionary dead end, but one that shares a common ancestor with spiders and other arachnids with two pairs of lungs.

The earliest centipedes exhibit features that allow them to be classified in some of the major groups that have survived until today. The oldest of these, from the Late Silurian of the Welsh Borderlands in England, belong to a genus, *Crussolum*, that is better known from various body parts in the Early and Middle Devonian (as for many examples in this article, the Devonian fossils come from the Rhynie cherts in Scotland and Gilboa in New York State—Fig. 4b has an example; Anderson and Trewin 2003; Shear and Bonamo 1988). *Crussolum* is unambiguously a member of Scutigermorpha, a group that includes 100 living species that mostly live in the tropics and subtropics, but best known from the “house centipede,” *Scutigera coleoptrata*, an introduced species in many temperate parts of the world (Fig. 2c). *Crussolum* shares with the extant scutigermorphs such features as a pentagonal cross-section of the leg with each of the ridges that runs along the leg segments bearing a file of spines and thickened setae, but it lacks a few details that all of the living scutigermorphs share with each other. For example, though the fossils have the first pair of trunk legs modified into a functional part of the head (and housing the venom apparatus in all living centipedes), they do not have long “spine bristles” in fixed positions that are seen in all the living species. This mix of primitive and advanced characters in *Crussolum* is described using a convention called “stem groups”; *Crussolum* belongs to the stem group of Scutigermorpha. This means that the species is more closely related to Scutigermorpha than to any other living centipede group, but it branched earlier than the most recent common ancestor of all living scutigermorph species.

Amongst the earliest winged insects—and very common in the Carboniferous—were the Blattoptera, or “roachoids” (Fig. 4d). As the name suggests, these were similar to modern-day cockroaches. For example, they possessed

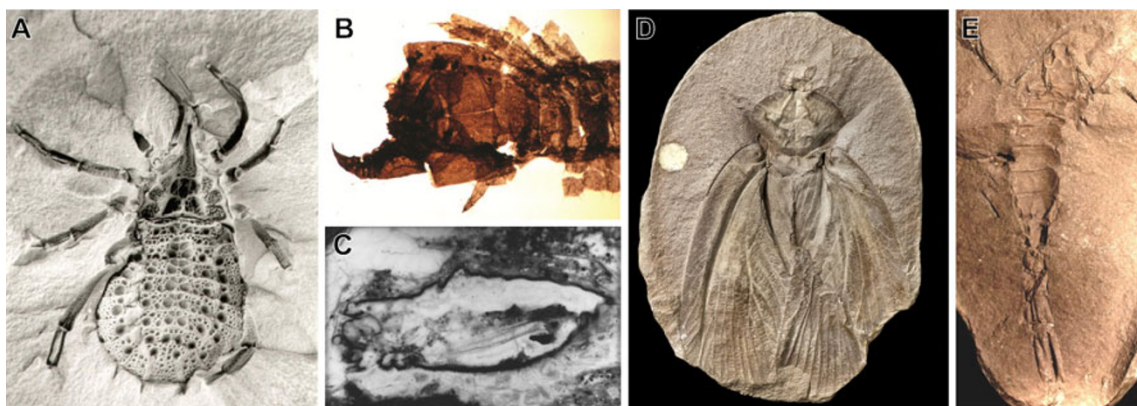


Fig. 4 **a** Fossil of trigonotarbid arachnid, *Eophrynus prestvicii*, from the Carboniferous of the UK (courtesy of Jason Dunlop). Fossil 30 mm in length. **b** The centipede *Devonobius delta* from the Devonian Gilboa deposit of New York State (Shear and Bonamo 1988). Shown portion of fossil 1.2 mm in length. **c** The Devonian

harvestman *Eophalangium sheari* from the Rhynie Chert (Dunlop et al. 2004). Fossil 6 mm in length. **d** Roachoid fossil *Archimylacris eggintoni* from the Carboniferous of the UK (Garwood and Sutton 2010). Fossil 41 mm in length. **e** Carboniferous scorpion *Comptoscorpius buthiformis* (Legg et al. 2011). Fossil 21 mm in length

hardened, protective forewings and a pronotum (a head shield originating at the first segment of the thorax), but unlike true cockroaches, they had a long needle-like ovipositor for laying eggs (Grimaldi and Engel 2005). The reason they are known as “roachoid” fossils is because—while they are superficially similar to cockroaches in appearance—they predate the split between the mantises and the cockroaches and termites (the termites are actually highly derived, eusocial cockroaches; Inward et al. 2007). As such, these weren’t an evolutionary dead end; collectively, “roachoids” represent a grade at the base of the evolutionary tree for Dictyoptera, the formal name for the mantises (and cockroaches+termites), making them another example of a stem group form. It is likely that some of the later Carboniferous fossils postdate the evolutionary divergence of the extant lineages of Dictyoptera, and they would accordingly belong to the stem groups of either the mantises or the cockroach/termite branch (Béthoux et al. 2009).

Scorpions are the earliest known arachnids and have a significant Paleozoic fossil record (Fig. 4e; Dunlop et al. 2008b). While debate remains regarding whether their earliest representatives were aquatic or terrestrial (Dunlop and Webster 1999; Kamenz et al. 2008), by the Carboniferous, there is little question the scorpions were land-dwelling (Jeram 1994a). Even by the Early Devonian, fragments of the book lungs of fossil scorpions indicate air breathing (Shear et al. 1996). All modern scorpions belong to a group known as the orthosterns, which possess spiracles within the plates on the scorpions’ underside rather than at their margin as seen in some of the oldest fossil species. The oldest members of this group are Carboniferous in age (Fig. 4e; Vogel and Durden 1966; Jeram 1994b; Legg et al. 2011), and the oldest known member of an extant family is at least 50 million years younger (Lourenço and Gall 2004). Thus, later Paleozoic scorpions probably fall in the stem group of modern families, but postdate the last common ancestor of the orthosternous scorpions. We can hence say that the origin of extant scorpions lies in the Carboniferous Period.

Perhaps some of the most impressive terrestrial Paleozoic fossils, however, are those of harvestmen (Fig. 4c): arachnids of the order Opiliones, which have a small fused body and often extremely long legs (Machado et al. 2007). The best fossils are once again those of the Rhynie cherts, which preserve the internal anatomy, including specimens that have the reproductive organs of either males or females (Dunlop et al. 2003). Their morphology suggests that they are essentially modern in form. The fact that the Devonian species was placed in one of the four major living groups of Opiliones (Dunlop et al. 2004) implies that harvestmen were amongst the earliest branching arachnids and corroborates recent molecular work suggesting a relatively early Paleozoic radiation in the group (Giribet et al. 2010).

Furthermore, the fact that they have remained morphologically largely unchanged for over 400 million years suggests that they exemplify evolutionary stasis. Why this is the case remains unclear, but this uncertainty regarding the cause of stasis in no way undermines evolution as a god-of-the-gaps proponent would suggest. Stasis within species is expected in a number of evolutionary models (Eldredge and Gould 1972; Sheldon 1996; Benton and Pearson 2001). Thus, in higher-level taxonomic groups with relatively low rates of speciation, we may expect elements of stasis (see discussion: Gould 2002, p. 936; Cavalier-Smith 2006, p. 999; and stasis in ecological assemblages: DiMichele et al. 2004). It is noteworthy, however, that stasis in taxonomic groups above the species level is the exception rather than the rule, as the above examples demonstrate. The fact that such stasis exists presents us with a compelling opportunity to explain its presence—it does not allow a non-naturalistic view to win by default.

Terrestrial Adaptations

Only nine of 58 extinct and extant animal phyla have terrestrial representatives (Labandeira and Beall 1990), largely because land presents a new and hostile environment for a marine organism (Selden and Jeram 1989; Selden and Edwards 1990). As a result, life on land requires a suite of adaptations. The presence of such changes to accommodate a new mode of life provides excellent evidence for evolution; they have a clear functional significance, and a number have evolved separately in different lineages (Raven 1985). To reiterate, the earliest known terrestrial animals were arthropods (Little 1983)—members of the Myriapoda (millipedes, centipedes, and their kin), Arachnida (spiders, scorpions, and relatives), and Hexapoda (insects and three smaller, primitively wingless groups). In this, the final section of the paper, we shall provide an overview of the adaptations present in terrestrial arthropod groups and then outline why their convergent evolution (independent origins in different lineages) has sometimes complicated efforts to assess arthropod relationships (Edgecombe 2010).

Water Loss

Of the problems associated with terrestrial life, perhaps the biggest is that of water retention (Hadley 1994). Water is a vital solvent for life, and minimizing water loss and ensuring its availability is vital for terrestrial organisms (Little 1983). A major part of the fight to avoid desiccation is the arthropods’ exoskeleton, the outermost layer of which (the epicuticle) is waxy and waterproof (Fig. 5a; Cody et al. 2011). This proofing is caused by

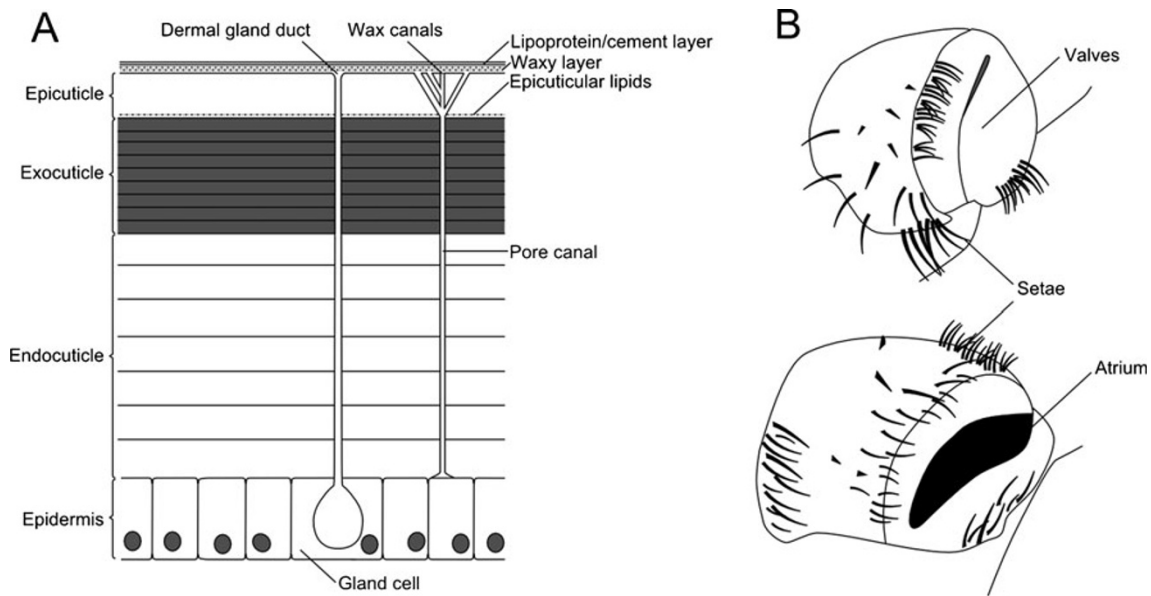


Fig. 5 a Structure of arthropod cuticle showing the four primary layers and fine structure of the surface. Also shown are vertical channels—dermal gland ducts extending from the epidermis and secreting an as yet unknown substance and pore/wax canals which

carry lipids from the epidermis to the epicuticle. After Hadley (1986). **b** Spiracles of a cockroach, shown closed (*top*) and open (*bottom*). After Bell and Adiyodi (1982)

lipids (hydrocarbons, in this case including paraffin-like molecules, wax esters, fatty acids, and ketones) both within the epicuticle and deposited on its surface (Hadley 1986). As well as waterproofing an organism, this very successfully prevents evaporation. As we shall see below, terrestrial arthropods employ a variety of independently derived respiratory systems. Despite these independent origins, all are internal, an arrangement which serves to lessen water loss (Brusca and Brusca 2003). Additionally, all possess spiracles (Fig. 5b)—the structures that provide the earliest evidence for fully terrestrial life in millipedes. Spiracles act as an opening through the cuticle into respiratory structures, and—despite independent origins—those of insects (Gullan and Cranston 2010), myriapods (Shear and Edgecombe 2010), and chelicerates (Levi 1967) have associated musculature to regulate gas entry and exit, and minimize water loss through the moist respiratory structures. This is even the case where the respiratory organs—introduced below—differ greatly, for example, between the book lungs of scorpions (Polis 1990) and the tracheal system of insects (Grimaldi and Engel 2005).

Another major source of water loss in organisms is excretion. When animals digest protein, excess nitrogen is produced and is usually liberated in the form of ammonia (NH_3), a toxic compound that requires rapid dilution or removal (Brusca and Brusca 2003). Dilution demands abundant water and is thus unsuitable for terrestrial organisms, for whom water is a precious resource. Thus, most terrestrial organisms convert ammonia into more complex yet less toxic compounds; in vertebrates, like us,

urea, but in arthropods uric acid is more common, which is often precipitated in solid form (Raven 1985). In arthropods, this waste is removed with the aid of two types of organs.

Nephridia are organs found on one or a few anterior body segments of all arthropod groups. The closest living relatives of arthropods, the velvet worms (Onychophora), have a pair of nephridia on most body segments, and they resemble those of many aquatic animals (Fig. 6a) in being composed of an excretory duct starting at the animal's exterior (opening to a pore at the inner base of each leg in velvet worms) and ending with a funnel-shaped, hair-lined opening into the body. The hairs direct fluid into the duct (Ruppert et al. 2003). As this moves through, the reabsorption and secretion of cells lining the duct modify the liquid, concentrating waste products (Ruppert and Smith 1988; Campiglia and Maddrell 1986; Bartolomaeus 1992). Waste is excreted to the exterior through the terminal opening, known as the nephridiopore. Nephridia of arthropods, in the form of coxal glands, antennal glands, maxillary glands, or labial kidneys (depending on where they are located), differ in being internally closed and the funnel is not ciliated. Nephridial organs are thought to have been present in the last common ancestor of all arthropods (known as a plesiomorphic trait).

Most terrestrial arthropods also possess or wholly replace nephridia with structures known as Malpighian tubules, which allow efficient waste removal. These are blind ducts which open at one end into the gut and remain unattached at the other end (Fig. 6b). They float and move around in arthropods' blood-filled body cavity (or hemo-coel) and absorb waste products. As the waste moves down

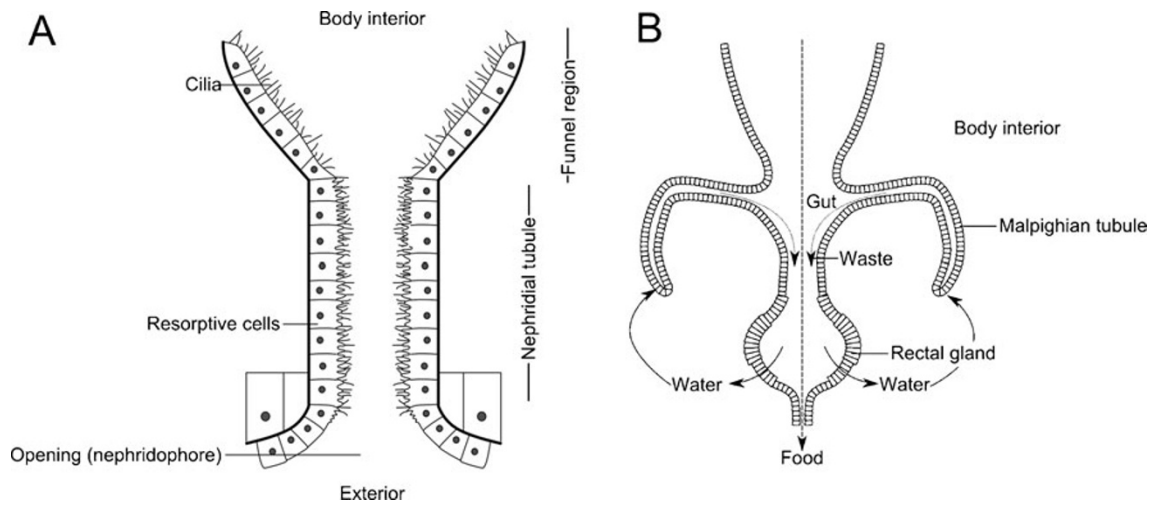


Fig. 6 **a** Example of a nephridium showing both cilia to direct fluid into the nephridial tube and resorptive cells that concentrate waste products. **b** Diagram showing Malpighian tubules, with arrows

showing the movement of waste and food, and the cycling of water in the system. Both based on diagrams in Barnes et al. (2001)

the tubule, water is reabsorbed, until crystals of uric acid are formed, and in the hindgut, further reabsorption occurs in a structure known as the rectal gland (Roberts 1986). The above description is based upon the Malpighian tubules of insects, and each individual can have hundreds of these (Brusca and Brusca 2003). However, very similar structures have been independently derived in both myriapods, which have just one or two depending on the group (Hopkin and Read 1992; Lewis 2007), and terrestrial chelicerates, which have several branching tubules (Barnes et al. 2001). Water loss can further be reduced through behavior—arthropods at risk of desiccation will often live in humid and moist environments to the extent that some extract moisture from the substrate (Crawford and Cloudsley-Thompson 1971). Many desert-dwelling species avoid periods of high temperatures by becoming inactive in burrows (Hadley 1974).

Gas Exchange

Another major issue with life on land is that of respiration, or gas exchange (Raven 1985). This cannot be done through

increasing the permeability of the exoskeleton, which would allow significant water loss. As we have seen, this is a significant consideration, and all but the smallest terrestrial arthropods have specialized gas exchange structures (Selden and Edwards 1990). These come in two flavors. The first—found in arachnids—are the book lungs: stacked, blood-filled lamellae extending into an air-filled cavity (Fig. 7a). This cavity (the atrium) opens to the outside through the spiracles (Scholtz and Kamenz 2006), and the thin lamellae provide a high surface area to allow gas exchange. The second type of respiratory structures, which probably evolved convergently in insects and myriapods (Grimaldi 2010), are known as tracheae (Fig. 7b). These are branching cuticle-lined tubules opening externally through the spiracles and terminating internally in the blood, or organ tissues (Barnes et al. 2001). This is an efficient system, allowing direct gas exchange with the internal organs and blood—so much so that a similar system has secondarily evolved from book lungs in some spiders (Schmitz and Perry 2001). Comparable structures called pseudotrachea are also found in woodlice, which are crustaceans of the order Isopoda (Edney 1968).

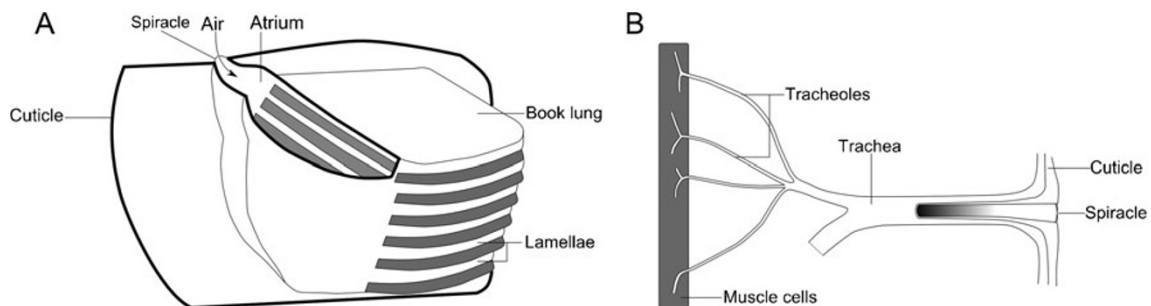


Fig. 7 **a** Simplified diagram showing an arachnid book lung. In reality, these have tens of lamellae. After Levi (1967). **b** The tracheal morphology of insects. After Brusca and Brusca (2003)

Reproduction

A less immediately apparent issue is that of reproduction—for arthropods in the marine realm, releasing eggs and sperm into the sea for external fertilization is a viable approach for reproduction (Selden and Jeram 1989). This is not as effective in the terrestrial realm, however, and internal fertilization is usually preferred. Associated with this is a wide range of complex sperm transfer techniques—for example, the use of packages of sperm known as spermatophores is common, protecting them (to an extent) from the harsh terrestrial environment. A bewilderingly vast array of sometimes complex courtship behaviors has developed in terrestrial arthropods (Choe and Crespi 1997). While there are myriad possible causes for this adaptation (Bastock 2007), in part this could be to ensure the successful transfer of spermatophores (for example, in the whip spiders, Fig. 2a; Weygoldt 2002). Direct sperm transfer in the form of copulation bypasses the risk of environmental damage in many more derived forms (Selden and Edwards 1990). Young are often helped with parental brooding during embryonic development or after birth (Labandeira and Beall 1990).

Locomotion and Senses

While life on land presents a plethora of other challenges, the last we will look at here stem from the physical differences between water and air. These can have a significant impact on an organism's morphology, given that water has greater buoyancy than air (Selden and Jeram 1989). To support themselves, terrestrial organisms require rigid skeletal elements, and the arthropods had a preexisting advantage in their presence of an exoskeleton (Raven 1985). Terrestrial arthropods also generally adopt a more stable hanging stance, standing on the underside of their limbs whose ends are at a low angle to the ground (a plantigrade tarsus; Størmer 1970; Fig. 8a). There are also a

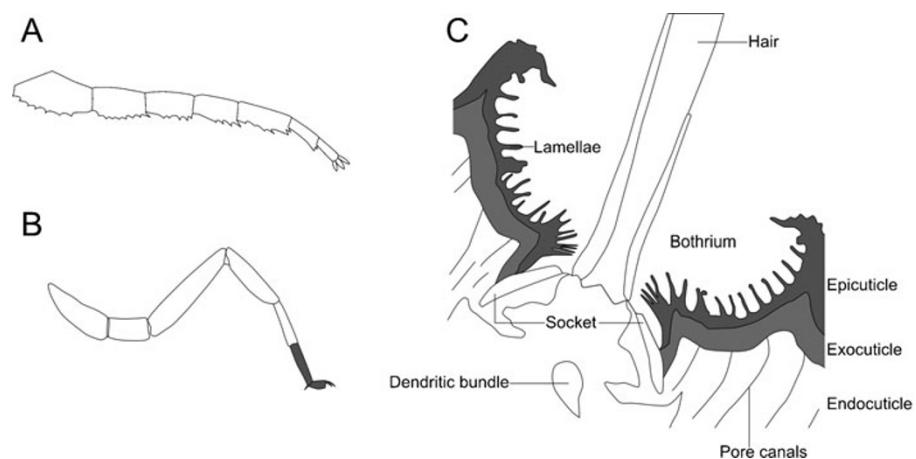
huge number of sensory adaptations to this new medium, for example, the trichobothria of scorpions (Fig. 8b)—long, thin hairs originating in a cup-shaped depression that can sense very slight air vibrations (Reissland and Görner 1985). This aids prey location and orientation relative to wind, but would not work in a fluid medium (Krapf 1986; Meßlinger 1987). Superficially similar trichobothria are also present in some myriapods (Haupt 1979); the distant relationship between these myriapods and arachnids indicates a convergent evolution of trichobothria.

As a result of this suite of adaptations—and a host of further physiological changes—arthropods are successful terrestrial organisms. So successful, in fact, that whether judged by number of species or individuals, they are thriving desert inhabitants (Edney 1967) and are vital members of these harshest terrestrial ecosystems (Whitford 2000).

Uncertainty

All of these evolutionary adaptations increase fitness in terrestrial environments, and as such, their parallel (convergent) evolution in multiple lineages under the same selective pressure is expected. However, they also effectively demonstrate a major cause of uncertainty amongst arthropod workers—the traditional basis for assessing evolutionary relationships is morphology (Darwin 1859; Skelton 1993). Thus, assessing whether structures are homologous (share a common origin) or homoplasious (the result of convergence) is vital to understanding a group's relationships (Edgecombe 2009). This is rarely clear-cut, however. To use examples we have seen already, insects and myriapods share tracheae and Malpighian tubules, and these features were traditionally ascribed to inheritance from common ancestry because insects and myriapods were considered sister taxa in a group known as the Atelocerata (Snodgrass 1938; Klass and Kristensen 2001; Bitsch and Bitsch 2004; see also discussion in Shultz

Fig. 8 **a** Example of a digitigrade stance based on the limbs of trilobites. After Størmer (1963). **b** A plantigrade stance based on the limbs of extant scorpions, the plantigrade segments of the limb termination in *gray*. After Størmer (1963). **c** Cross-section through a scorpion bothrium showing the sensory hair and socket in which it sits, three layers of the cuticle, and the pore canals. Also of note are the sensory dendritic bundle and lamellae. After Meßlinger (1987)



and Regier 2000 and Dohle 1998). They further share a suite of other characters, including single-branched appendages and a head comprising an antennal segment, a limbless (intercalary) segment, and then two segments bearing mouthparts. However, DNA analysis has never supported this grouping, with many different kinds of genetic data all agreeing instead that the insects share a common ancestor with the crustaceans (insects and crustaceans collectively forming a group called the Tetraconata; Jenner 2010). This is now largely accepted and has been corroborated by many features of the brain, eyes, and nervous system development that are unique to insects and crustaceans but not shared by myriapods (Edgecombe 2010). The evolutionary picture provided by the genes and nervous system suggests that tracheae and Malpighian tubules in insects and myriapods are an example of convergent evolution in two terrestrial lineages. However, the new consensus on an insect–crustacean relationship emerged from 20 years of research (including enormous technological and theoretical advances in molecular biology and new techniques of investigating anatomy) and through frank discussion of the opposing arguments.

This process of altering hypotheses on the basis of increased evidence is central to the science, yet such advances rely on uncertainty and debate. If god-of-the-gaps creationist opposition makes scientists reluctant to express their doubts on a subject—such as the issue of arthropod relationships outlined here—these advances would be slower-to-nonexistent. Due to the nature of evolution, ambiguity is ubiquitous; the outlined example of similarity as a result of either a common evolutionary origin or later convergence is just one of many sources of debate. It is for this reason that myriad unanswered questions regarding arthropod phylogeny remain, some at a fairly basic level. To present unanswered questions as a weakness, or pretend they undermine evidence, is disingenuous and incorrect. Rather, the possibility of new evidence, resulting in paradigm shifts and a greater understanding of the history of life, is one of the most exciting elements of science.

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