Water-to-Land Transitions

16

Jason A. Dunlop, Gerhard Scholtz and Paul A. Selden

Contents

16.1 Introduction 417
16.1.1 The Significance of the Sister Group 418

16.2 Secrets of Success 418
16.2.1 Brave New Worlds? 419

16.3 What is 'Terrestrial'? 419

16.4 A Time Framework for the Transition 420
16.4.1 Trackways 420
16.4.2 Body Fossils 423
16.4.3 Molecular Clocks 426

16.5 Challenges and Solutions 427
16.5.1 Body Size 428
16.5.2 Locomotion 429
16.5.3 Osmoregulation 429
16.5.4 Reproduction and Development 430
16.5.5 Gas Exchange 432

16.6 Concluding Remarks 435

References 436

16.1 Introduction

Arthropods are, by a considerable margin, the most species-rich group of animals alive today and have long been a major component of the Earth's biodiversity. Exact counts of the total number of species are not easy to come by, but Zhang (2011) offered a recent summary. Together the ca. 1,023,559 described living species of hexapods, 11,885 myriapods and 110,615 arachnids—most of which live on land—massively outnumber the ca. 66,914 recorded crustaceans, 1,322 sea spiders and the four species of horseshoe crab. Put bluntly, in terms of raw species numbers the primarily terrestrial lineages (Hexapoda, Myriapoda, Arachnida) outnumber the primarily aquatic ones ('Crustacea', Pycnogonida, Xiphosura) by a factor of almost seventeen to one. In fairness, there is a degree of bias in these figures. Some arachnids, such as water mites, are secondarily aquatic, but by the same token, some crustaceans such as woodlice and a number of crab species are also to a greater or lesser extent terrestrial. Despite the common opinion that terrestrial arthropods are easier to collect than (deep) marine ones, which may influence the total number of described taxa, new species of terrestrial insects, arachnids and myriapods are still being regularly described, particularly from the tropics. Aquatic arthropods seem unlikely to approach the

J. A. Dunlop (✉)
Museum für Naturkunde, Leibniz Institute
for Research on Evolution and Biodiversity
at the Humboldt University Berlin, Invalidenstr.
43, 10115 Berlin, Germany
e-mail: jason.dunlop@mfn-berlin.de

G. Scholtz
Humboldt-Universität zu Berlin, Institut für
Biologie, Vergleichende Zoologie, Philippstr. 13,
10115 Berlin, Germany
e-mail: gerhard.scholtz@rz.hu-berlin.de

P. A. Selden
Paleontological Institute, University of Kansas,
1475 Jayhawk Boulevard, Lawrence, Kansas 66045,
USA
e-mail: selden@ku.edu

A. Minelli et al. (eds.), *Arthropod Biology and Evolution*,
DOI: 10.1007/978-3-642-36160-9_16, © Springer-Verlag Berlin Heidelberg 2013

diversity levels seen in megadiverse insect orders such as beetles, butterflies, true flies, or the bees, wasps and ants. This begs the questions *how*, *when*, *why* and *how often* did arthropods become successful in the terrestrial environment. We should also consider whether they came onto land via salt or fresh water.

16.1.1 The Significance of the Sister Group

Phylogeny has a crucial impact on evolutionary scenarios. If the sister group of a given terrestrial arthropod taxon also lives on land, we can infer that the last common ancestor of both groups was already terrestrial too. For instance, the traditional view of a close, or even a sister-group, relationship between hexapods and myriapods (the Antennata, Atelocerata or Tracheata concept) implied that the shift onto land took place in the common stem lineage of Antennata (see Kraus and Kraus 1994). This in turn biased the search for, and interpretation of, fossils as putative stem-lineage representatives of Antennata, further influencing hypotheses about the water–land transition within this group (see Haas et al. 2003; Kühl and Rust 2009). Today, the prevailing view is that Hexapoda is deeply nested within Crustacea (e.g. Regier et al. 2010; Rehm et al. 2011), although the hexapod sister group among the crustacean subgroups remains ambiguous (Glenner et al. 2006; von Reumont and Burmester 2010; von Reumont et al. 2012). Depending on the analysis, Remipedia, Branchiopoda or Malacostraca emerge as the closest relatives of the hexapods. This leads to the next problem. In contrast to remipedes and malacostracans, recent branchiopods are—with a few evidently derived exceptions—freshwater animals (e.g. fairy shrimps, tadpole shrimps, water fleas). If their sister-group relationship to hexapods were to be corroborated by further data, then we have to consider that the water-to-land transition in the hexapod lineage began in a freshwater habitat. This scenario might change if fossil branchiopods are included, since these animals were most likely marine (Olesen 2009).

Where monophyletic taxa are exclusively terrestrial, it is plausible to assume that the last common ancestor of the clade was terrestrial too. Nevertheless, given the frequent water-to-land transitions among arthropods—and animals in general—one has to ask whether parsimony considerations alone are enough to make a clear case for a single-terrestrialisation event, even in monophyletic groups. The case becomes stronger if structural apomorphies are also present as adaptations to a terrestrial life style; the book lungs of arachnids being a good example here (Scholtz and Kamenz 2006). This may seem trivial, but for the major terrestrial lineages of arthropods, there are surprisingly few unambiguous examples of anatomical terrestrial adaptations defining monophyletic groups. For instance, the tracheae of myriapods are so diverse in their position and structure that their homology has been seriously doubted (Ripper 1931; Dohle 1988; Hilken 1997). The same might apply to hexapod tracheae, and functionally similar tracheal tubes have also evolved more than once in the arachnids; at least twice just within the spiders where they can occur as tube or sieve tracheae (cf. Levi 1967) whose origins may be independent.

16.2 Secrets of Success

It seems self-evident from modern phylogenies (e.g. Regier et al. 2010) that land-living clades evolved independently within the overall arthropod tree. On the face of it, there must have been at least seven separate terrestrialisation events, enacted by: hexapods, myriapods, arachnids and at least four groups of crustaceans, namely isopods, amphipods, ostracods and decapods. Some authors have inferred multiple events within the arachnids too, but see Scholtz and Kamenz (2006) for counterarguments. Recall as well that among the arthropods' closest relatives (see Chap. 2), both Onychophora (velvet worms) and Tardigrada (water bears) are also now wholly or partially terrestrial. What these groups all share in common is a body plan with legs. While terms such as 'preadaptation' have fallen out of favour, it is fair to say that the arthropod ground pattern—which presumably originated in the early Palaeozoic seas (see Chap. 15)—possessed much which would later prove very useful in animals attempting to make the transition onto land. In addition to their jointed legs, which required only minimal modifications for locomotion on land, arthropods possess a tough external cuticle over the whole body which could later be waterproofed with a waxy epicuticle layer. In most of these cases, the respiratory organs are essentially invaginations of the body wall with thin cuticle.

16.2.1 Brave New Worlds?

We can only speculate about the evolutionary pressures that drove arthropods to exploit terrestrial ecosystems. Avoidance of predators would be one possibility. Horseshoe crabs were present by at least the early Ordovician (Van Roy et al. 2010), and it is conceivable that their modern mating behaviour—emerging onto shorelines to lay their eggs—is a relict of a distant time when the land was a safe and predator-free environment. In general, it is hard to envisage a terrestrial community of animals existing without at least some degree of plant cover and/or soil habitat. When this first became available remains a topic of debate, but there are microfossils of tough, desiccation-resistant spores as far back as the mid-Cambrian (Strother et al. 2004). Whether these indicate land plants is controversial (cf. Kenrick et al. 2012). By the mid-Ordovician, there are dispersed spores, often called cryptospores, consistent with belonging to terrestrial plants (Strother et al. 1996), and these presumably evolved into the small, branching *Cooksonia* type of vegetation recorded as body fossils by the mid-Silurian. Once plants became established as primary producers, there was clearly an opportunity for herbivores—or more likely at first the decomposers and detritivores—to exploit this new niche. Predators would then be able to follow too. The sclerotised head limbs of arthropods may also have played a role here, being easily modified into a variety of mouthpart structures suitable for different feeding ecologies.

Although the focus here is on crown-group arthropods, we should not forget that soft-bodied organisms, from protozoans to tardigrades to various platyhelminth, nematode and oligochaete worms, may also have played a role in the earliest soil habitats (see also comments in Pisani et al. 2004). The chance of such animals being preserved as fossils is unfortunately very small. There is a Devonian plant-associated nematode (Poinar et al. 2008), and creatures like this would have been a potential food source for at least the smaller early terrestrial arthropods.

16.3 What is ‘Terrestrial’?

Before discussing the timing and mechanisms of terrestrialisation further, we need to be clear about what we mean by a terrestrial animal. At what point does an arthropod become fully terrestrial? A water/land dichotomy is too simplistic, since a whole range of intermediate habitats can be envisaged. Examples would include regularly inundated algal strandlines on beaches. These are a typical feeding habitat today for sandhoppers (Amphipoda: Talitridae). Another would be the wet interstitial spaces between soil or sand particles. Marine interstitial environments play host to certain collembolans (Thibaud 2007), halacarid and occasionally oribatid mites (Bartsch 1989; Bayartogtokh and Chatterjee 2010) and to the rare palpigrade arachnids (Condé 1965). We must caution against assuming that such modern arthropods are ‘primitive’, or relicts of the first semi-terrestrial fauna. Today, we may be looking at secondary colonisations of beaches or river banks. For example some water mites (Acari: Hydrachnida) effectively live in a water/land transition zone, but phylogenies do not recover them as a particularly basal mite clade.

The marine interstitial route onto land has been widely suggested for early arthropods (Little 1990) and would have allowed a gradual accumulation of terrestrial adaptations.

However, in some cases, a transition from fresh water to terrestrial habitats is more likely (De Deckker 1983; Diesel et al. 2000). The typical micro- and meiofauna of a sandy beach today were summarised by Armonies and Reise (2000), who recorded tiny arthropods such as copepods, ostracods and mites, as well as the arthropod relatives, the tardigrades. Microarthropods living in soil and/or sand can effectively remain in an aquatic habitat by living in water films around the sediment particles; see, for example, Villani et al. (1999) for a review of the implications of edaphic habitats for terrestrialisation. As we will argue for crustaceans in particular, there are gradations of increasingly terrestrial habitats and lifestyles and corresponding gradations of anatomical adaptations. As is often the case in biology, the boundaries of what can be defined as terrestrial are not very sharp and we prefer to leave it somewhat fuzzy. Is a crab terrestrial when it lives completely on land and only larval spawning and development take place in seawater? This means the crab feeds on leaf litter, breathes air, excretes purine, mates in the forests and carries the eggs on land for a certain phase of development. If we define terrestrial arthropods by their life history, then reproduction and development (see also Cannicci et al. 2011) are among the strongest limiting factors hindering transitions onto land. For the purposes of this chapter, we consider an arthropod to be fully terrestrial if it does not need to return to water in order to complete its life cycle.

16.4 A Time Framework for the Transition

For a broad perspective on the origins of animal biodiversity on land—and the associated key events in Earth history—see Benton (2010). We cannot say for certain which arthropod group(s) first placed their feet on the shore, or exactly when they achieved it. But we can make inferences by combining direct evidence, in the form of body fossils, with indirect evidence drawn from trace fossils and molecular clock data. Arthropod terrestrialisation has been reviewed in its wider context by Størmer (1976), Rolfe (1985), Selden and Edwards (1989), Shear and Kukalová-Peck (1990), Shear (1991), Selden (2001, 2012), Shear and Selden (2001), Garwood and Edgecombe (2011) and Kenrick et al. (2012). We refer to these studies for further details and additional literature.

As outlined in Fig. 16.1, from the Cambrian–Ordovician boundary onwards (ca. 488 Ma), there are strong hints that arthropods of some description were able to walk, if only briefly, across terrestrial sediments. By the Silurian (ca. 416–443 Ma), myriapods and arachnids were unequivocally living on land and hexapods appear soon afterwards in the early Devonian (ca. 398–416 Ma). Today's land-living crustaceans do not appear to have been part of this early radiation. The oldest fossils implicit of terrestrial crustacean clades are Mesozoic. It is nevertheless important to remember that the early terrestrial fossil record of arthropods remains fragmentary. Much of our present knowledge is based on only a handful of 'windows' of opportunity. Key localities include the Silurian of Ludford Lane in England (Jeram et al. 1990), the Early Devonian Rhynie and Windyfield cherts of Scotland (reviewed in Anderson and Trewin 2003) and Alken an der Mosel and some adjacent sites in Germany (e.g. Størmer 1976), as well as the Middle Devonian of Gilboa in the USA (Shear et al. 1984, 1987). The more important discoveries are outlined below, and new fossils from even older localities would undoubtedly change the overall picture.

16.4.1 Trackways

Trace fossils (ichnofossils) cover a broad spectrum of fossilised animal activity, including faeces, burrows and nests, as well as locomotion traces from individual footprints through to fully developed trackways left by animals walking over the substrate. A review of the ichnological

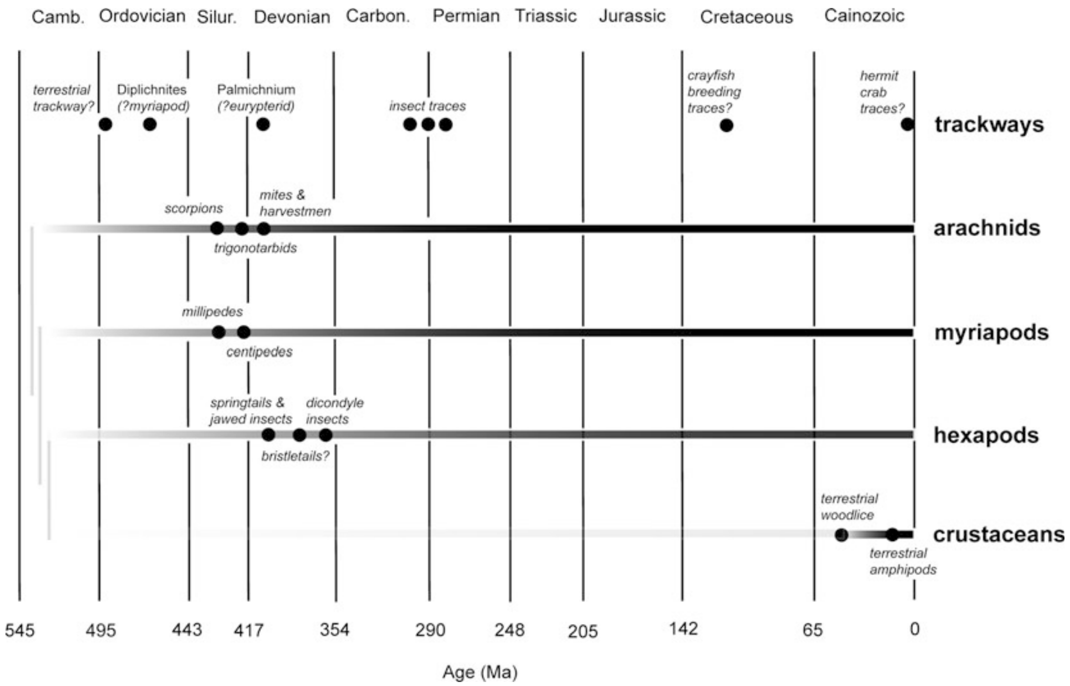

Fig. 16.1 A time framework for terrestrialisation based on trace fossils and the body fossil record of the four major arthropod lineages. Note that, hexapods are now conventionally regarded as having evolved from within the crustaceans

evidence for early life on land can be found in Braddy (2004), and a recent comprehensive case study based on the Siluro–Devonian Old Red Sandstone of Britain was published by Morrissey et al. (2012). Ichnologists refer to trackways made in a terrestrial environment (Fig. 16.2) as ‘subaerial’, differentiating them from those left in sediments under water. Subaerial trackways can be recognised by, for example, the footprints of the animal crossing desiccation cracks, which imply that the original animal (named the producer) walked across mud which was already exposed to the air and was in the process of drying out. Other examples can involve animals walking over ash falls. However, in both cases, we must exclude the possibility that the trackway (or ash fall) was made in water and was later exposed as the mud or ash dried out.

The oldest putative record of an arthropod walking across land comes from the Cambrian–Ordovician Nepean Formation in Ontario, Canada (MacNaughton et al. 2002). Dating to around 488 Ma, these trackways assigned to the ichnogenera *Diplichnites* and *Protichnites* were interpreted as having been made in a near-shore environment and as having possibly been produced by an enigmatic group of extinct arthropods known as the Euthycarcinoidea (see also Chap. 15). Collette et al. (2012) provided further model-based experimental evidence that Cambrian *Protichnites* traces could have been made by euthycarcinoids. These extinct (Cambrian–Triassic) mandibulate arthropods have multiple pairs of uniramous trunk limbs, but in the absence of unequivocal respiratory organs, it is unclear whether euthycarcinoids were aquatic, amphibious or terrestrial creatures.

Considerably younger trackways from the Ordovician Borrowdale Volcanic Group of England (Johnson et al. 1994) were again assigned to *Diplichnites*, and to another ichnogenus *Diplopodichnus*. These trackways were interpreted as non-marine, with millipedes tentatively suggested as a possible producer. Again, it is unclear whether they were left by fully terrestrial animals. Retallack and Feakes (1987)

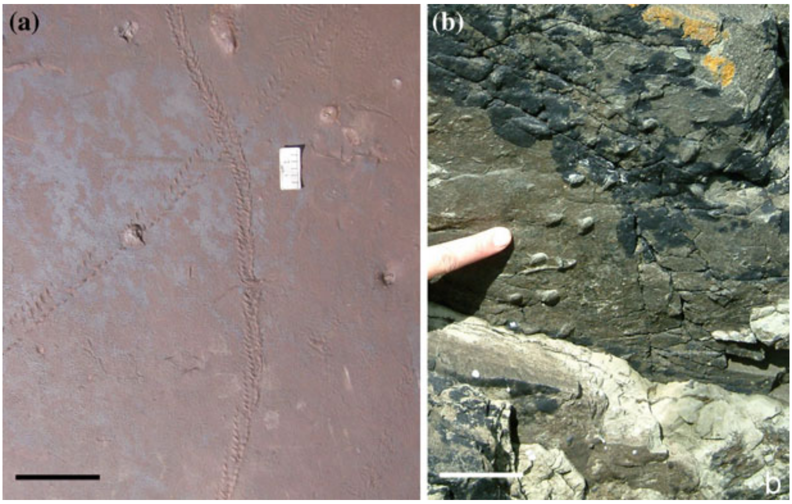

Fig. 16.2 Arthropod trackways can imply life on land. **a** *Diplichnites*, a terrestrial trail probably made by a millipede-like animal, from the Early Devonian of Wales; **b** *Palmnichnium*, thought to be a semi-terrestrial eurypterid trackway, from the late Silurian of Wales. Scale bars equal 50 mm. Images courtesy of Rob Hillier and Lance Morrissey

documented supposed terrestrial burrows in fossil soils from late Ordovician Juniata Formation of central Pennsylvania, USA. Millipedes were inferred as the possible producers of these impressions, but this was disputed by Wilson (2006) and others, and the terrestrial palaeoenvironment of the Juniata Formation has now been comprehensively disproved by sedimentological analysis (Davies et al. 2010).

From the Silurian onwards, there are further records of terrestrial (millipede?) trackways (e.g. Wright et al. 1995; Morrissey et al. 2012). The latter authors also noted examples of a putative scorpion trace named *Paleohelcura* in the Old Red Sandstone of South Wales. Both these localities and the similarly aged Alken an der Mosel in Germany yield another ichnogenus called *Palmichnium*, recovered from sediments probably lain down in the intertidal zone. These impressions have been ascribed to the walking activities of sea scorpions (Eurypterida). The scenario implied here is that at least some eurypterids might have been semi-terrestrial (see also below) and perhaps clambered onto beaches to mate in a similar fashion to the modern horseshoe crabs (Poschmann and Braddy 2010).

Trackways unequivocally produced by insects first appear rather later in the fossil record, first being picked up in the Permo-Carboniferous (e.g. Braddy and Briggs 2002). Trace fossils assignable to terrestrial crustaceans are also very rare and so far do not belong to the Cambrian–Devonian phase of radiation either. Genise et al. (2008) described putative terrestrial breeding traces from the mid-Cretaceous (ca. 125 Ma?) of Patagonia in Argentina which they believed to be consistent with the activities of crayfish. Barely counting as fossils, Walker et al. (2003) described trackways from the Holocene (i.e. less than 12,000 years old) of the West Indies which they interpreted as the activities of a terrestrial hermit crab (Decapoda: Paguroidea).

There are two general problems with at least the older trace fossil discoveries. First, we cannot be exactly sure which arthropod produced a given trackway. Inferences can be made, for example three pairs of impressions would suggest a hexapod, four an arachnid and multiple pairs or groove-like furrows a myriapod. However, it is extremely rare to find a trackway with the producer (quite literally) stopped dead in its tracks at the end, such as in the aquatic ‘death marches' of horseshoe crabs from the Jurassic of Solnhofen (Malz 1964). PreSilurian trackways have sometimes been ascribed to a myriapod-like animal, but it would be premature to accept them as explicit evidence for crown-group Myriapoda. As with the euthycarcinoids mentioned above, it is conceivable that there were other extinct arthropods around at this time with multiple limbs capable of leaving such impressions. Second, as discussed by Johnson et al. (1994), we cannot be certain that an arthropod walking across dry land in the mid-Palaeozoic was habitually terrestrial. These may represent (semi)-aquatic animals capable of brief excursions onto land, but who were trying to cross from one body of water to another, or were trying to escape a drying pool.

To recap, from the end of the Cambrian through to the Ordovician and Silurian, it appears that some arthropods—possibly including myriapods and eventually also arachnids—could walk across land, but it is unclear from the trace fossils alone whether they lived in this environment on a long-term basis. Apart from some possibly semi-aquatic crustacean burrows from the Devonian (Morrissey et al. 2012), there is no convincing trace fossil evidence for terrestrial locomotion by insects or crustaceans prior to the Carboniferous and Cretaceous, respectively.

16.4.2 Body Fossils

A general overview of the arthropod fossil record can be found in Chap. 15. Although there is a dubious record of an Ordovician mite, the oldest arthropod fossil which can be assigned with confidence to a terrestrial habitat is the millipede (Diplopoda) *Pneumodesmus newmani* from the Silurian (ca. 428 Ma) of Scotland (Wilson and Anderson 2004). Significantly, this fossil (Fig. 16.3d, arrow) reveals the putative openings of spiracles which imply a tracheal system (see also 16.5.5). There is also an enigmatic group called Kampecarida—probably millipedes of some description—known from a range of Siluro–Devonian localities. They were last reviewed by Almond (1985) and would merit further study. A small number of scorpions (Scorpiones) also occur in strata dating from the mid-to-late Silurian. Laurie's (1899) species *Dolichophonus loudonensis* is stratigraphically the oldest known arachnid and is approximately the same age as the oldest terrestrial millipede *Pneumodesmus*; both fossils incidentally coming from Scotland. Note that there has been a long debate about whether the early scorpions (Fig. 16.3a) were terrestrial or aquatic, the latter hypothesis championed by Kjellesvig-Waering (1986) in particular. However, as critiqued by Scholtz and Kamenz (2006) and Kühl et al. (2012), these views have rarely been supported by convincing morphological features. The trend seems to be shifting towards interpreting all fossil scorpions as potentially terrestrial animals.

16.4.2.1 Ludford Lane

Late Silurian fossils from the ca. 419 Ma Ludford Lane consist of cuticle remains acid-macerated out of the sediment. These include fragments of the oldest centipede (Chilopoda), which can be provisionally assigned to the Scutigeromorpha (Jeram et al. 1990; Shear et al. 1998). Scutigeromorphs (Fig. 16.3e) are widely perceived as sister group of all other centipedes. There is also a millipede belonging to the extinct Arthropleurida group (Shear and Selden 1995). A further interesting Ludford Lane find is the oldest non-scorpion arachnid which belongs to an extinct spider-like order called Trigonotarbida (Fig. 16.3b). Since younger trigonotarbids are demonstrably terrestrial (see below), this habitat has been assumed for the Ludford Lane fossil too. Finally, there are also examples of fossil faeces, or coprolites (Fig. 16.3c), which may have been produced by a detritivore such as a millipede (Edwards et al. 1995).

16.4.2.2 Rhynie

The next oldest localities are from the Early Devonian. Prominent among these are the Rhynie and adjacent Windyfield cherts of northwest

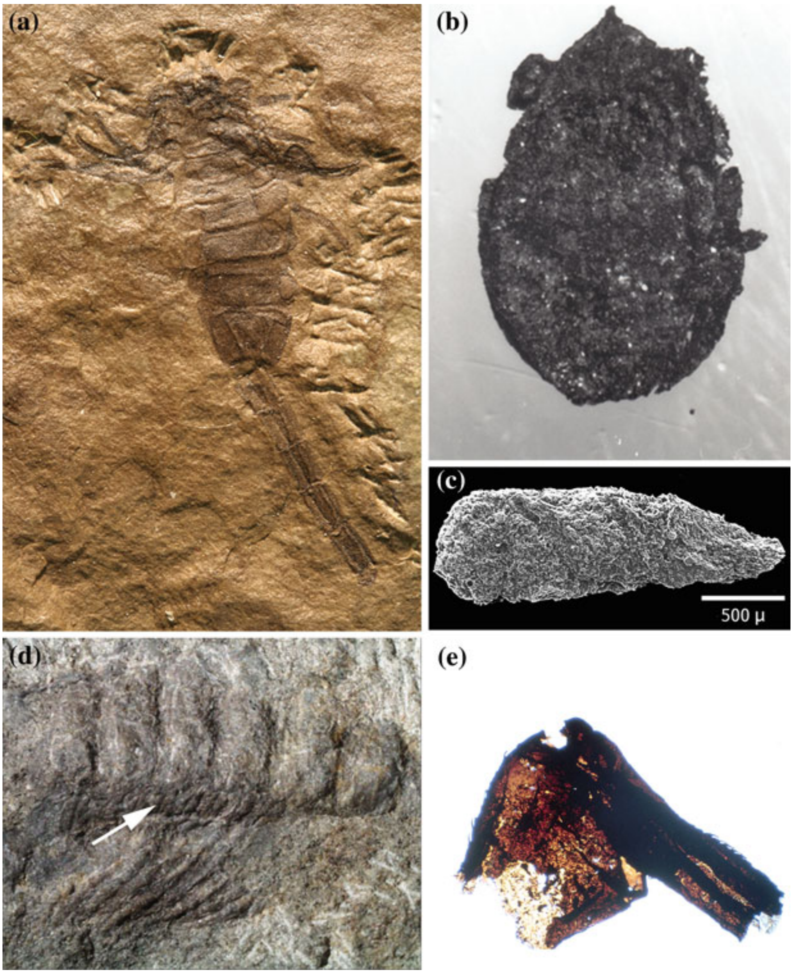

Fig. 16.3 Terrestrial arthopod life in the Silurian. **a** the scorpion *Proscorpius osborni* from the 'Bertie Waterlime' of the USA (note that, some authors have interpreted early scorpions as aquatic); **b** the trigonotarbid arachnid *Palaeotarbus jerami* from Ludford Lane, UK; **c** scanning electron micrograph of a coprolite, possibly from a myriapod, from Ludford Lane, UK; **d** the millipede *Pneumodesmus newmani* from Cowie Harbour, Scotland with slit-like spiracles arrowed (used with permission by the Paleontological Society); **e** femur–tibia articulation of a scutigeromorph centipede, *Crussolum* sp., from Ludford Lane, UK

Scotland which are dated to ca. 410 Ma and preserve an entire terrestrial ecosystem of early plants and animals with extraordinary three-dimensional fidelity. Rhynie has yielded more trigonotarbid arachnids (Hirst 1923), as well as the oldest unequivocal mites (Acari), such as *Protacarus crani* and some further species named later from among Hirst's original specimens (Fig. 16.4a). From the same locality, Dunlop et al. (2004) described the oldest harvestman (Opiliones) as *Eophalangium sheari*. Further significant finds at Rhynie are the oldest terrestrial hexapods. These include a springtail (Collembola) *Rhyniella praecursor* described by Hirst and Maulik (1926) and Scourfield (1940) (Fig. 16.4b). Perhaps, even more significant is *Rhyniognatha hirsti*, a fossil primarily known from its mandibles (Tillyard 1928). It was later reinterpreted as the oldest true insect (Engel and Grimaldi 2004); the authors even speculating that this animal may have borne wings. Other Rhynie/Windyfield records include euthycarcinoids, centipedes and an additional hexapod of uncertain affinity (Anderson and Trewin 2003; Fayers and Trewin 2005).

16.4.2.3 Alken and Other Sites

Marginally, younger than Rhynie are a number of localities in the German Rhineland, the most famous of which is Alken an der Mosel (cf. Størmer 1970, 1976). As well as semi-terrestrial eurypterid trace fossils (see above), these sites have yielded early terrestrial arthropods

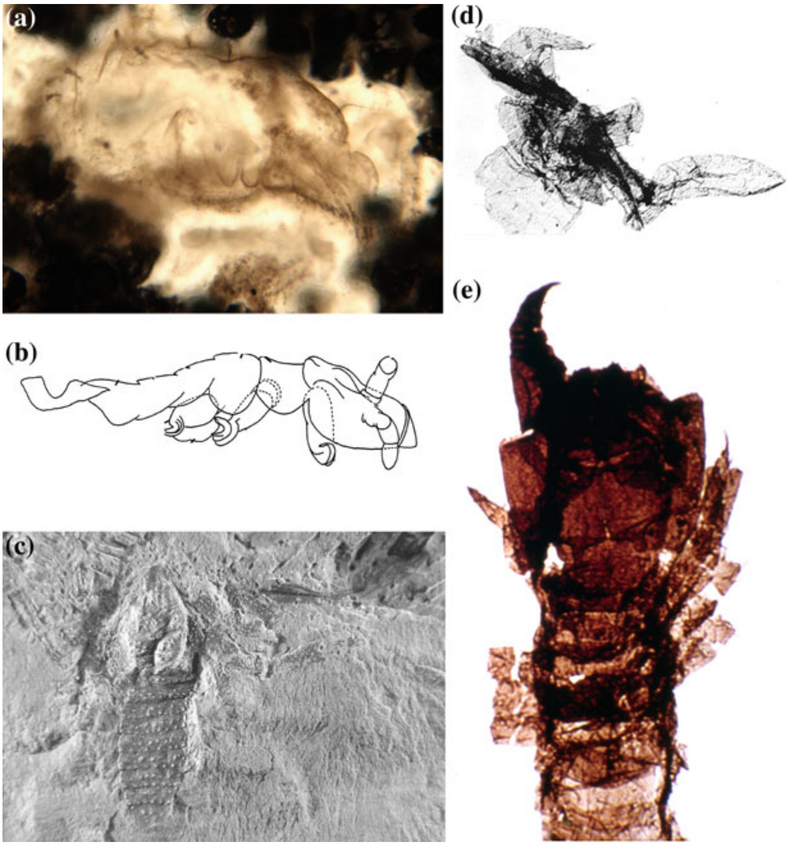

Fig. 16.4 Terrestrial arthropod life in the Devonian. **a** a mite, possibly *Protospeleorchestes pseudoprotacarus*, from the Rhynie chert, Scotland; **b** drawing of the collembolan *Rhyniella praecursor* (after Scourfield 1940), also from the Rhynie chert; **c** the trigonotarbid arachnid *Alkenia mirabilis* from Alken an der Mosel, Germany; **d** the oldest pseudoscorpion *Dracochela deprehendor* from Gilboa, New York, USA; **e** the centipede *Devonobius delta*, also from Gilboa

such as trigonotarbids (Fig. 16.4c), scorpions and arthropleurids, as well the oldest example of another extinct arachnid order named Phalangiotarbida (Poschmann et al. 2005). More generally, a number of early Devonian sites have yielded records of scorpions reviewed by Kjellesvig-Waering (1986), but as noted above, his interpretations must be treated with caution. Kjellesvig-Waering assumed that almost all Palaeozoic scorpions were aquatic and at least one set of scorpion 'gills' later turned out to be part of an arthropleurid millipede (Shear and Selden 1995). In general, millipedes are also quite well represented at this time. Numerous Devonian examples belonging to the juliform group—the classic, long-bodied millipedes which burrow through soil and litter—were critically reviewed by Wilson (2006).

16.4.2.4 Gilboa

The Middle Devonian, in particular the ca. 390 Ma Gilboa locality near New York, has produced more trigonotarbid arachnids, as well as both oribatid and alicorhagiid mites (Norton et al. 1988; Kethley et al. 1989). Other notable finds at Gilboa include the oldest pseudoscorpion (Schawaller et al. 1991, revised as a stem-group taxon by Judson 2012) (Fig. 16.4d). Also significant is *Attercopus fimbriunguis*. This fossil was first thought to be a trigonotarbid (Shear et al. 1987), but was later reinterpreted as the oldest spider (Araneae). More recently, it has been shown to be an example of an extinct, spider-like order called Uraraneida (Selden et al. 2008). These animals probably resembled spiders, albeit with a flagelliform tail like that of a whip scorpion (Uropygi). The well-preserved cuticle fragments suggest that *Attercopus* could produce silk, but lacked the discrete spinnerets which define the true spiders. Gilboa also hosts centipedes (Shear and Bonamo 1988; Shear et al. 1998) including another scutigeromorph, together with a further record assigned to an extinct group (Fig. 16.4e).

16.4.2.5 Other Ancient Insects and Crustaceans

A contemporary find (Labandeira et al. 1988) from the mid-Devonian of Gaspé in Québec, Canada, is a bristletail (Insecta: Archaeognatha). After the Rhynie mandibles (see above), this fossil would be only the second oldest example of a true insect. However, the fossiliferous nature of this find was seriously questioned by Jeram et al. (1990) shortly after its publication and unless more specimens or evidence are forthcoming, it would be unwise to accept this as an unequivocal insect record. Recently, Garrouste et al. (2012) reported the discovery of a putative terrestrial insect from the Late Devonian (ca. 365 Ma) of Belgium. *Strudiella devonica* was assigned to the Dicondylia clade and noted for having 'orthopteroid' mouthparts suitable for an omnivorous diet.

What should by now be apparent is the preponderance of arachnid and myriapod fossils making up these Siluro–Devonian terrestrial assemblages, as compared to the relative paucity of hexapods/insects and the complete absence of any demonstrably terrestrial crustaceans. The hexapods—and in particular the pterygote (winged) insects—only really seem come into their own from the Carboniferous onwards (e.g. Prokop et al. 2005) by which time land-based communities of plants and animals were already well established.

Body fossils of unequivocally terrestrial crustaceans are much younger. The oldest terrestrial woodlice (Isopoda: Oniscoidea) are currently known as fossils from Eocene (ca. 49 Ma) Baltic amber (reviewed by Schmidt 2008), although the larger clade to which they belong—the Scutocoxifera—can be traced back to the Jurassic. The oldest known Amphipoda referable to the (semi-)terrestrial family Talitridae are even younger, being first recorded from the Miocene (ca. 16 Ma) Chiapas or Mexican amber (Bousfield and Poinar 1994). It has also been suggested (Bousfield 1983) that since modern Talitridae live in, and feed on, angiosperm litter then the group is unlikely to be older than the flowering plants which themselves radiated in the mid-Mesozoic.

Fossils of a number of land crabs (Decapoda, Brachyura) can be found in the Quaternary (ca 2–3 Ma). These include fossils assignable to Gecarcinidae from the Caribbean (Donovan and Dixon 1998), Potamidae from Japan (Naruse et al. 2004) and Grapsidae from Hawaii (Paulay and Starmer 2011). The last of these is an interesting case study in which the species was probably driven extinct by human activity. However, for all these remains, we do not know whether they are indicative for a fully terrestrial lifestyle according to our definition. There is currently no body fossil record of the terrestrial hermit crabs (Coenobitidae), although a possible trace fossil of this group was mentioned above.

16.4.3 Molecular Clocks

An alternative way to infer the age of terrestrial crown-group clades is to use the molecular clock. If we assume—and it is an assumption—that arachnids, hexapods and myriapods each had a common terrestrial ancestor, then determining when each of these groups separated off from their nearest relatives (i.e. the time of cladogenesis) would yield an approximate date by which the clade may have come onto land. The problem here comes if the split occurred far back in time in an aquatic environment, and if the crown-group terrestrial arthropods had a stem group of aquatic ancestors which continued living for millions of years in the water and about which we know little or nothing from the fossil record. In essence, how tightly is cladogenesis coupled to terrestrialisation? How soon did the last common ancestor make it onto land?

The principal value of the fossils here is in imposing constraints on these models. For example, terrestrial millipedes must have evolved by the mid-Silurian at the very latest (Wilson and Anderson 2004). In another case study, Dunlop and Selden (2009) pointed out that, at 428 Ma, fossil scorpions are older than a published estimate of 393 ± 23 Ma for the split between spiders and scorpions based on a mitochondrial phylogeny. In this particular example, the fossil showed that the split based on molecular data was an underestimate. In this context, well-preserved fossils whose systematic position is robust can act as calibration points, helping to improve the overall reliability of molecular-based phylogenies. Further discussion of the strengths and limitations of molecular dating—such as the risks of treating stem-group fossils as calibration points for crown-group organisms—can be found in Kenrick et al. (2012).

More usually, molecular methods suggest older dates (sometimes substantially so) for life on land, as compared to the direct evidence of the fossil record. This is unsurprising as it is unlikely that we will ever find a fossil of the very first terrestrial animal in a given clade. Problems come when there is large discrepancy between the fossil and molecular dates. A prime example would be the study of Schaefer et al. (2010) who calibrated their tree using data for oribatid mites; a group with a reasonable fossil record thanks to their often quite tough and resilient bodies. Their data suggested that oribatid mites—and by inference interstitial soil microarthropods in general—originated and began moving onto land as early as the late Precambrian (571 ± 37 Ma). By contrast, the oldest fossil oribatids from the Gilboa locality are considerably younger, being Devonian (390 Ma) in age. Realistically, a Precambrian date for land arthropods seems much too early. As noted by Kenrick et al. (2012), most Precambrian fossils are barely recognisable as animals, let alone members of crown-group arthropod clades, and these authors suggested that the discrepancy in this case may be due to an analysis which relied on only a single gene.

Authors such as Pisani et al. (2004) recovered somewhat younger dates of 475 ± 53 Ma for the split between xiphosurans and arachnids, and 442 ± 50 Ma for a split between millipedes and centipedes. These dates (Fig. 16.5) are more consistent with the fossil record since the oldest arachnids and myriapods are Silurian (and thus about 430 Ma). However, for the crustacean–hexapod split, a very old (i.e. Precambrian) date of 666 ± 58 Ma was recovered in this paper. Alternatively, Regier et al. (2004) published a younger date of ca. 488–461 Ma for crown-group hexapods—this is still about 50 million years before the first body fossil—while Sanders and Lee (2010) found an older date of ca. 504 Ma. In another study, Rehm et al. (2011) recovered a ca. 555 Ma split for myriapods and chelicerates—with a ca. 500 Ma split for millipedes and centipedes—and a ca. 480 Ma split for spiders and horseshoe crabs; in their scheme, mites were their sister clade coming off at ca. 495 Ma. The hexapods and crustaceans were dated to a split of ca. 520 Ma (Rehm et al. 2011, Fig. 16.1). As noted above, elucidating the sister group of hexapods among the crustaceans is crucial to dating their origins. Future developments in this field will hopefully refine the methods further and reduce the gap between the inferred (molecular) and observed (fossil) data.

16.5 Challenges and Solutions

As we have argued above, the major arthropod groups almost certainly moved onto land independent of one another, but once they did they all faced an identical set of problems. These animals developed similar, sometime even identical, responses to these challenges. The example of tracheae arising in parallel in insects, myriapods and arachnids has already been discussed. It is a prime example of how moving onto land automatically creates homoplastic characters among different groups of arthropods exposed to the same selective pressures. The physiological challenges faced by animals moving from an aquatic to a terrestrial environment have been summarised in some detail

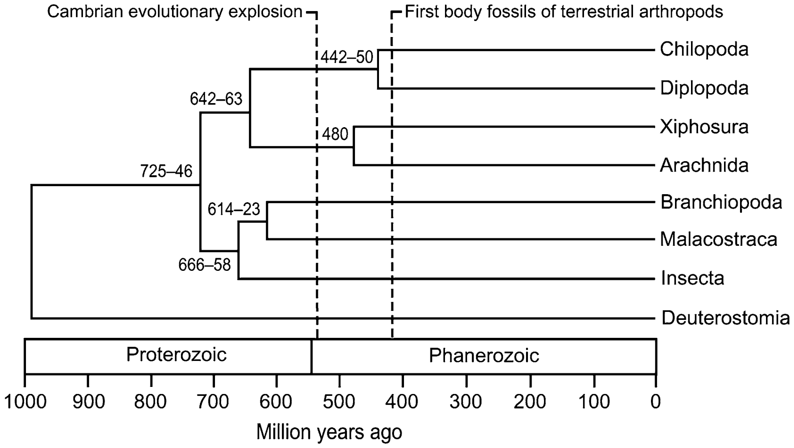

Fig. 16.5 A fossil-calibrated timescale of arthropod evolution based on two nuclear genes, reproduced from (Pisani et al. 2004, Fig. 2). Numbers associated with nodes are divergence times (Ma) and their standard errors. Molecular clocks offer an alternative approach for estimating when terrestrial arthropod clades first appeared (see text for details)

by Little (1990). In brief, these relate primarily to gas exchange, reproduction, osmoregulation and exposure to ultraviolet radiation. Likewise, sensory structures have to be modified for life on land (e.g. Stensmyr et al. 2005). Changes in locomotory biology would also have been important and—on a related point—it is interesting to speculate whether smaller or larger arthropods were better able to make the initial transition onto land?

16.5.1 Body Size

If terrestrialisation did take place via the interstitial route, then tiny microarthropods would have been better adapted to exploit such environments. They could easily occupy wet spaces between soil or sand particles and, like many such organisms in modern soil ecosystems (Villani et al. 1999), they could burrow deeper into the substrate in search of moisture when the upper layers dried out. However, minute organisms are highly dependent on local conditions—they are less able to walk far or fast—and if there is a major change in the environment, they run the risk of drying out more quickly. Larger animals, with a lower surface area to body size ratio, would have been more resilient against such fluctuations in the environment, but would presumably have been more exposed to such changes.

Palaeontology does not, as yet, yield a clear picture about which of these scenarios is correct. Smaller, less strongly sclerotised arthropods are, in principle, less likely to be preserved as fossils, and so key components of the early land fauna may simply not be visible. In any case, different taxa may have adopted different strategies. The oldest (Silurian) trigonotarbid arachnid is only ca. 1.5 mm long, and most of the Rhynie arachnids described so far have body lengths from less than 1 mm (the mites) up to about 4 mm (trigonotarbids). By contrast, scorpions seem to have been at least a few centimetres long throughout their known geological history (cf. Kjellesvig-Waering 1986). Indeed, in the Devonian a few became huge, with body lengths approaching a metre!

The known Silurian juliform millipedes preserve body lengths in the 35–45 mm range (Wilson and Anderson 2004), comparable to modern temperate species found in soils today. However, the Devonian also yields tiny arthropleuridean millipedes less than 5 mm long (Wilson and Shear 2000). This is interesting given that Carboniferous arthropleurids achieved enormous body lengths of two metres or more (Kraus and Brauckmann 2003). The earliest hexapods also tend towards a small body size, whereas (Shear et al. 1989) documented some fairly large early terrestrial arachnids and myriapods from the early Devonian of Canada.

An origin from small-sized aquatic ancestors is also likely for terrestrial ostracods (De Deckker 1983). The various malocostracan terrestrial crustacean lineages reveal, however, a different pattern of land colonisation. For instance, it is obvious that among true land crabs and the various 'amphibious' hermit crabs and brachyurans, it was relatively large animals which gave rise to terrestrial populations starting from a variety of marine and freshwater origins. In the case of the proper land brachyurans, it seems apparent that they colonised land from a freshwater habitat (Diesel et al. 2000). In contrast to this, the monophyletic oniscoid isopods invaded land only once and most likely from the sea, since the *Ligia* species—which serve as model for the transition—mostly occur on sea shores (see Schmalfuss 1978; Carefoot and Taylor 1995; Schmidt 2008). Again, it is apparent that the first terrestrial isopods were animals in the centimetre range (Schmidt 2008).

16.5.2 Locomotion

We have already argued that the presence of jointed legs in ancestral arthropods was probably an important factor in facilitating a smooth transition from water onto land. Many aquatic arthropods live on (or in) the substrate, and it was presumably fairly straightforward to adapt such a body plan to a terrestrial environment. Although quantitative data are lacking, when we compare the walking legs of purely aquatic arthropods with their (semi-)terrestrial relatives (insects, spiders and certain crabs), there seems to have been a tendency for the legs to become larger and often thicker in proportion to the rest of the body. Terrestrial animals are no longer supported by the buoyancy of water, and larger, thicker legs can accommodate a more extensive musculature to support the animals and overcome the effects of gravity on land; see, for example, discussion in (Dalingwater 1985).

Related to this, authors such as Selden and Jeram (1989)—based on the studies of Manton (1977)—proposed the presence of a plantigrade foot in scorpions as one of the criteria for recognising terrestrial animals. The idea here is that marine animals, supported by the buoyancy of water, can effectively walk on the tips of their toes (digitigrade stance), but terrestrial animals would have little purchase on the substrate, and abrade their toes, without the larger surface area of a foot on the ground. Manton (1977) showed how rocking joints in the leg allowed the foot to remain stable while the body and leg moved forwards during locomotion. Terrestrial arthropods hang from their legs, which have rocking joints at the bases of the leg and the tarsus. Note that this applies better to insects and arachnids, which have relatively few legs, than to the multi-limbed millipedes and centipedes who can still use a digitigrade stance on land today as their weight is distributed across many more individual appendages. Another interesting point of convergence between arachnids and insects is the tendency (there are exceptions in both groups) to have two large claws, or ungues, at the end of the leg. In some arachnids, a smaller third claw may be present and both insects and arachnids may have a fleshy (adhesive) pad between the claws. It is interesting to speculate whether this two-clawed pattern evolved in parallel as an advantageous feature for gripping the substrate and/or clambering through the early vegetation.

16.5.3 Osmoregulation

Water balance—and specifically water loss—is one of the main challenges facing primarily terrestrial animals. The presence of a cuticular exoskeleton in arthropods (cf. Chap. 8) was undoubtedly a major advantage here, and most terrestrial groups have a waxy epicuticle layer which reduces water loss directly over the cuticle. Behavioural adaptations should also be mentioned here, and numerous arthropods avoid desiccation by favouring damp, humid habitats or by burrowing deeper into the substrate. Another option is to avoid activity during daylight; groups like scorpions are predominantly nocturnal. In tracking the evolution of relevant features, the fossil record is less helpful. Even the best preservation (e.g. Rhynie) does not yield structures such as Malphigian tubules. Other osmoregulatory organs, such as coxal glands, are also hard to detect in fossils.

Osmoregulation is also highly relevant to the question about the route taken onto land, specifically did the ancestors of a given terrestrial arthropod group come directly from a marine environment or did they go first via fresh water? Little (1990) concluded that because intertidal animals could tolerate a greater range of salinities—as well as being better adapted to variable water supply, temperature, etc.—they were thus better adapted to move onto land than those which became highly adapted to freshwater or interstitial habitats.

16.5.4 Reproduction and Development

As discussed above, we suggest here that the ability to complete the life cycle without having to return to water is a reasonable definition of a fully terrestrial arthropod. Achieving this imposes major constraints upon the organism. Sperm can no longer simply be released over the eggs as in an aquatic environment, but must be delivered directly to the eggs or the female genital opening. This can either be done directly, for example, via an intromittent organ such as a penis or the palpal organ of spiders, or indirectly via a sperm package (Witte and Döring 1999). These packages, or spermatophores, can either be deposited on the substrate to be discovered later by the female, or they can be deposited as part of a controlled mating ritual in which the female is usually led directly over the sperm package by the male (Witte and Döring 1999). Similarly, the eggs now have to be provided with a protective layer to prevent them from drying out (see below). A few groups such as scorpions (reviewed by Warburg 2012) have adopted live-birth strategies instead.

16.5.4.1 Mating Chelicerates and Myriapods

Tracing the evolution of reproductive systems in the fossil record can be challenging, but under optimal conditions of preservation, key developments can still be identified. Kamenz et al. (2011) argued that at least some Silurian eurypterids had arachnid-like spermatophores, the precursors of which are occasionally fossilised as the eurypterid ‘horn-organs’ (Fig. 16.6a). While eurypterids are thought to have been primarily aquatic—with some speculation about trends towards an amphibious mode of life (see Sect.16.4.1)—the evolution of spermatophores in the common ancestor of eurypterids and arachnids would have provided a useful way for the first arachnids to transfer their sperm on land. It is tempting to speculate about eurypterids practising some sort of scorpion-like mating dance. Other arachnids have taken indirect sperm transfer further and developed direct techniques. The Rhynie chert harvestman preserves both a male penis and female ovipositor (Dunlop et al. 2004), which implies that by the early Devonian, these animals had already developed a mechanism for impregnating females directly and then laying eggs (Figs. 16.6b, c) without the need for water.

Among the myriapods, the oldest evidence for direct copulation is the millipede *Cowiedesmus eroticopodus* from the Silurian of Scotland (Wilson and Anderson 2004). Most modern millipedes belong to the derived clade Helminthomorpha, which is characterised by the presence in the male of modified appendages a short distance behind the head called gonopods. These are actively used in sperm transfer, and their presence in a Silurian fossil (Fig. 16.6d) shows that the helminthomorph mating strategy of direct insemination was already present in some of the oldest millipede fossils.

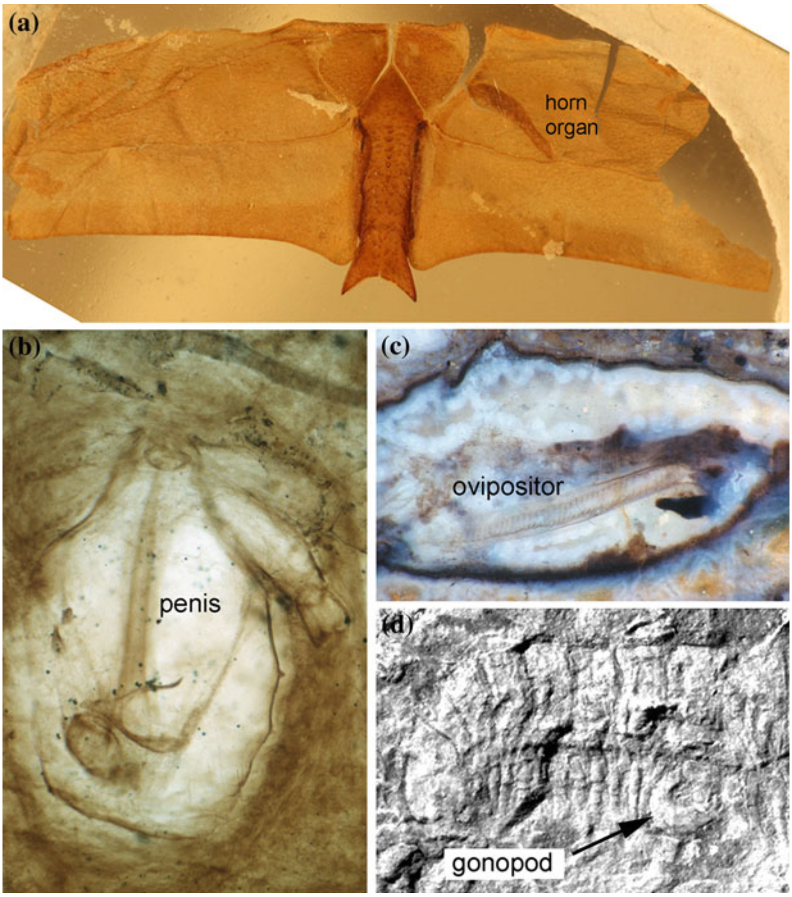

Fig. 16.6 Fossil reproductive organs. **a** the genital operculum of a eurypterid (*Eurypterus* sp. from the Silurian of Sareema in Estonia) with its genital appendage, whereby the associated horn organ was recently interpreted as a precursor of a (male) spermatophore; **b–c** the penis and ovipositor of male and female harvestmen, respectively, from the Devonian Rhynie chert of Scotland (after Dunlop et al. 2004); **d** the millipede *Cowiedesmus eroticopodus*, which preserves limbs modified into gonopods, from Cowie Harbour, Scotland (used with permission by the Paleontological Society)

16.5.4.2 Brooding Crustaceans

Among crustaceans, there are no fossil data for changes in reproductive strategies, but the developmental biology and physiology of today's semi-terrestrial species offers some interesting insights into a shift onto land which is still in progress (e.g. Greenaway 2003). The study by Cannicci et al. (2011) stressed the role of the embryo and maternal care in the terrestrialisation of crabs. In particular, they focussed on the fact that developing embryos in amphibious and shallow water species can be bimodal in their respiration, with oxygen uptake possible both from water and air. This can affect brooding strategies since the relative ease of extracting oxygen from air compared to water can reduce the level of parental care required—such as the mother having to create water currents to ventilate the eggs. The authors stressed that these crab embryos are still not independent of water, and parental effort is still needed to maintain a suitable microhabitat. For example in some genera, brooding mothers tend to remain in their burrows, which limits their offspring's exposure to desiccation.

16.5.4.3 Arthropod Eggs

The major leap forward for vertebrates getting onto land was the evolution of the amniote egg, which freed previously amphibious tetrapods from their reproductive link to the water by providing a miniature pond (the amniotic cavity and fluid) within the egg itself in which the embryo develops. To protect the egg and embryo from evaporation either leathery or calcified shells enclose the egg, or as a secondary evolutionary step, the eggs develop inside the mother. Similar solutions have been realised in arthropods, as reviewed by Zeh et al. (1989) who argued that adaptations for life on land affecting the egg stage were key to freeing up a wider range of niches for these animals to exploit. In particular, in the fully terrestrial arachnids, myriapods and hexapods, the eggs are generally enclosed in thick outer envelopes, and in some cases, such as scorpions, eggs undergo development within the maternal uterus. Additional brood care devices such as silken cocoons in spiders or maternal brood chambers (e.g. pseudoscorpions, whip spiders) have also evolved. The more derived centipedes enrol themselves around their eggs and millipedes produce a protective coat for the eggs, the nematomorphans specifically using silk to build a nesting chamber.

As in other aspects of their biology, terrestrialisation in relation to egg protection in crustaceans took a different pathway. Most ‘terrestrial’ crustaceans, such as the decapod land crabs and land hermit crabs including the robber crab *Birgus latro*, are effectively still at the ‘amphibian’ stage in that their larvae develop in water (Türkay 1987). The only fully terrestrial crustaceans are found among decapods and peracarids, namely within brachyurans and within isopods and amphipods. All these taxa are characterised by complex maternal brood care structures which already evolved partly or completely in the marine environment.

In the pleocyematan decapods, the eggs are attached to the maternal pleopods and, in particular, in brachyuran crabs, the ventrally folded pleon forms a protecting structure which encapsulates a tightly closed brood chamber. This is the structural prerequisite for terrestrialisation, since only a slightly increased degree of tightness between the pleon margin and the sternites allows for the generation of a humid or water-filled chamber for the embryos. In combination with increasingly embryonised larval stages—that is, a direct development, which evolved in freshwater crabs—this leads to a complete terrestrial life cycle in the few true land crab species (see e.g. Diesel et al. 2000).

A comparable but convergent solution to the problem of egg protection occurs within the peracarid crustaceans. Terrestrial isopods and amphipods maintain the eggs in a ventral brood pouch—the marsupium (Fig. 16.7)—which effectively acts as a mobile pond (Hoese and Janssen 1989). This peracarid marsupium is formed by a number of plates, the oostegites, originating from the coxae of a number of thoracopods. Interestingly, the marsupium as such is not an adaptation to a terrestrial life style, but was already present in the marine peracarid stem species (Richter and Scholtz 2001). Hence, terrestrial isopods and amphipods inherited this structure form their marine ancestors. Likewise, the direct development and the absence of distinct larval stages that we observe in terrestrial isopods and amphipods were also already present in their marine ancestor. Again, they cannot be regarded as unique terrestrial adaptations. Nevertheless, the marsupium of terrestrial isopods in particular is a very effective structure for brood protection and even allowed the colonisation of desert habitats.

16.5.5 Gas Exchange

Terrestrial arthropods presumably evolved from aquatic, gill-bearing forebears. In the standard arthropod Bauplan, the trunk limbs originally comprised a leg-like branch for locomotion and a flap-like branch with numerous blade-like lamellae for gas exchange and/or swimming. External gills of this form are impractical in air, where they would collapse under their own weight and/or dry out far too quickly. Terrestrial arthropods were thus faced with two options: adapt or innovate. An example of adaptation would be to internalise an existing system, which appears to have been the case in the book lungs of the pulmonate arachnids.

16.5.5.1 Book Lungs

Arachnid book lungs are widely regarded as homologous with the book-gills of horseshoe

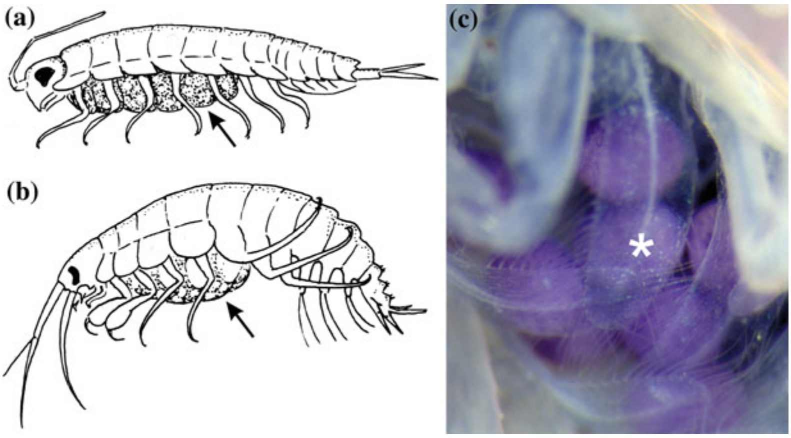

Fig. 16.7 The marsupium of peracarid crustaceans. **a** schematised isopod showing the position of the marsupium (*arrow*) in the pereon region; **b** schematised amphipod showing the position of the marsupium (*arrow*) in the pereon region; **c** photograph of ventral aspect of the marsupium of the (semi) terrestrial amphipod *Orchestia cavimana*. The embryos are enclosed and protected by plate-like coxal structures, the oostegites (*asterisk*), which form the marsupium. Line drawings modified from Dohle (1976)

crabs (e.g. Kingsley 1885). For a recent study, comparing and contrasting lung and gill development see Farley (2012). In essence, one can argue that arachnids have largely retained the leg branch in the prosoma for locomotion, but in groups like spiders and scorpions, they have lost the legs and retained the gill branch on the opisthosoma for gas exchange. Fossil book lungs (Fig. 16.8b) can be observed in the Devonian Rhynie chert trigonotarbids (Claridge and Lyon 1961; Kamenz et al. 2008). The quality of preservation even allows us to identify the small cuticular struts keeping adjacent lung lamellae apart. It is worth reiterating that these fossilised respiratory systems are anatomically indistinguishable from the lungs and tracheae of living arachnids. Shear et al. (1989) and Kühl et al. (2012) also documented putative book lung material preserved in Devonian scorpions from Canada and Germany, respectively.

The Devonian also throws up some unusual morphologies. Fossil scorpions in the genus *Waeringoscorpio* from both Alken an der Mosel and a nearby locality have unusual projections from the sides of the opisthosoma (Størmer 1970; Poschmann et al. 2008). These are associated with the lung-bearing body segments in living scorpions. Poschmann et al. (2008) likened these scorpion structures to the gills seen today in some (secondarily) aquatic insect larvae. It raises the intriguing possibility that these early terrestrial faunas included animals with unique respiratory systems, and perhaps even animals which secondarily re-entered water.

16.5.5.2 Modified Branchial Chamber Walls and Gills

As noted above, some authors have speculated that the extinct eurypterids were to a certain extent amphibious. One line of evidence in favour of this is some well-preserved fossils expressing paired structures on the opisthosoma referred to as 'gill tracts' or Kiemenplatten (Fig. 16.8a). These appear to have been modified areas of spongy tissue with a fine microornament of conical projections occupying the upper walls of the gill chambers (Selden 1985; Manning and Dunlop 1995). In this scenario, eurypterids are hypothesised to have relied on these gill tracts during brief excursions onto land. Analogies have been drawn with the branchial lungs of certain (semi-) terrestrial brachyuran crabs and hermit crabs, whereby a folded gill chamber wall creates an increased surface area for gas exchange (e.g. Farrelly and

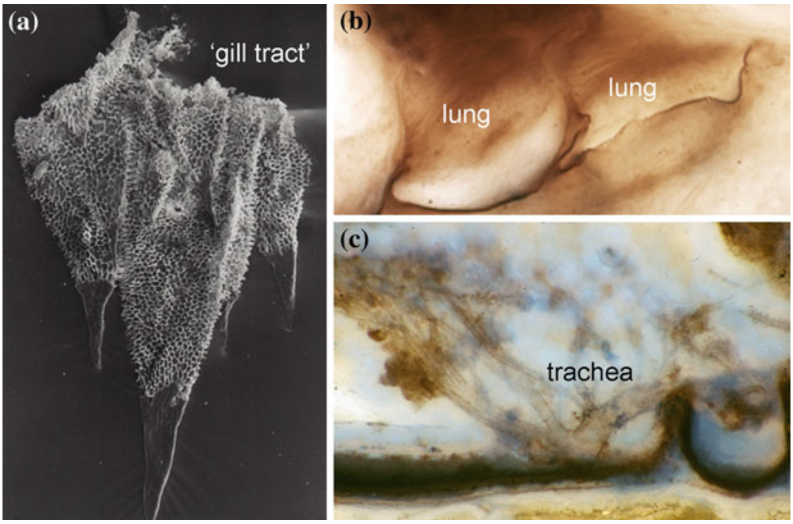

Fig. 16.8 Fossil respiratory organs. **a** scanning electron micrograph of 'gill tract' tissue from a eurypterid (after Manning and Dunlop 1995); modified regions of the gill chamber wall interpreted as potentially analogous to the branchial lungs of certain modern terrestrial crabs; **b** the oldest book lungs (after Kamenz et al. 2008), from a Devonian Rhynie chert trigonotarbid arachnid; **c** the oldest tracheal tubes (after Dunlop et al. 2004), from a Rhynie chert harvestman

Greenaway 1993; 2005). This is often accompanied by adaptive modifications of gill structures such as stiffening and the presence of nodules, which prevent the gill lamellae from collapsing, and a functional shift from a predominant role in gas exchange to more ion-regulation (Farrelly and Greenaway 1992).

Terrestrial oniscoid isopods still use their gills for respiration. These are, uniquely in malacostracans, formed by the pleopodal endopods (Gruner 1993). The use of gills in a terrestrial environment was made possible due to a complex water-conducting system, which constantly supplies the ventral side of the pleon with a water flow (Hoese 1981). In addition, within some oniscoidean groups, the anterior exopods are equipped with invaginations forming lung-like structures (Hoese 1981, 1983; Gruner 1993). These are additional examples of animals modifying an existing structure for terrestrial respiration.

16.5.5.3 Tracheae

Alternatively, arthropods could innovate and evolve an entirely new respiratory system. The best example here would be the branching tracheae which evolved independently in multiple arthropod groups (Hilken 1997) and supply the tissues with oxygen directly. Both book lungs and tracheae open through small rounded or slit-like spiracles which reduce the amount of water lost over the respiratory organs via evaporation. The specific discontinuous gas exchange cycle used by many tracheate arthropods—essentially the cycle in which the spiracles are opened and closed—was investigated by Klok et al. (2002), who again concluded that this essentially identical physiological process must have evolved in different groups simultaneously. The oldest direct evidence for unequivocally terrestrial respiration (Sect. 16.4.2) is the spiracle openings preserved in a Silurian millipede (Fig. 16.3d). The oldest example of the actual tracheal tubes themselves (Fig. 16.8c) comes from the Devonian Rhynie chert harvestman (Dunlop et al. 2004). The branching pattern observed here is almost identical to that seen in modern harvestmen today. Thus, both lung-based and tracheal systems for gas exchange were already clearly established by the Devonian.

16.6 Concluding Remarks

If we step back and take a broad view of the arthropod fossil record (see also Chap. 15), it is notable that crustaceans appear quite early as a recognisable group, alongside trilobites and various other Cambrian marine arthropods. By contrast, contemporary fossils assignable to today's primarily terrestrial groups (arachnids, myriapods and hexapods) are unknown. A major challenge has been to identify convincing stem-group representatives of all three primarily terrestrial clades back in their original marine environment in the early to mid-Palaeozoic. Arthropods called megacheirans may have given rise to the chelicerates, but fossils proposed as potential hexapod or myriapod ancestors have invariably proved to be highly controversial; see Haas et al.'s (2003) supposed marine Devonian hexapod with its reinterpretation by Kühl and Rust (2009). At this point, it is worth remembering that, according to current phylogenies, the hexapods were merely the first—and by a considerable margin the most successful—of a number of attempts by crustaceans throughout their geological history to colonise the land.

Despite the success of the insects as a megadiverse branch of now largely land-living crustaceans, much of the focus in the present chapter has instead been on early fossils of myriapods and arachnids. Both groups were likely to have been on land from about 430 million years ago and have been recorded, often with quite modern-looking body plans, from an increasing number of Siluro–Devonian fossil assemblages. If the fossil record does reflect the composition of the original ecosystem, it is tempting to envisage them together as part of an early detritivore/carnivore association. Arachnids and centipedes today do not commonly eat millipedes and one could speculate whether millipedes evolved defence mechanisms such as calcified cuticle and noxious secretions in response to predator attacks back in these early terrestrial ecosystems.

Although hexapods are numerically the most significant terrestrial arthropod group today, the fossil record suggests that their transition onto land may have begun slightly later. They were present both as collembolans and as early jawed insects by at least 410 million years ago, but their early evolution is less well understood, being based on only a handful of (sometimes controversial) precarboniferous records. By the time of the Carboniferous Coal Measures, about 300 million years ago, a truly diverse fauna of winged insects begins to appear. Yet, the origins—or at least the principal radiations—of the most diverse modern clades among the holometabolus insects (beetles, flies, wasps, etc.) did not take place until the early part of the Mesozoic. Some authors (e.g. Grimaldi 1999) point to the rise of the flowering plants, as part of a so-called Cretaceous Terrestrial Revolution about 100 million years ago. This may have created new ecological niches (e.g. as pollinators) which further facilitated insect diversification. Thus, one hypothesis could be that insects came late, but gradually came to dominate terrestrial ecosystems from the end of the Palaeozoic onwards, supplanting the myriapods and arachnids in both diversity and abundance.

Finally, the non-hexapod crustaceans have also attempted to invade the land on more than one occasion. Precise dates for the origins of groups like land crabs and (terrestrial) woodlice are unfortunately not well constrained, but we should reiterate that there is no evidence for any of these groups living on land during the Palaeozoic. Physiologically, none of these terrestrial crustaceans is as well adapted for life on land as the insects, myriapods and arachnids. Thus, it is tempting to see today's amphibious crustaceans as living models for the problems—and solutions—faced by all terrestrial arthropods having to evolve the mechanisms which they need to free themselves completely from their aquatic ancestry.

Acknowledgments We thank C. Oliver Coleman for advice on fossil amphipods; and Lyall Anderson, Wolfgang Dohle, Diane Edwards, Hagen Hass, Rob Hillier, Carsten Kamenz, Andrew Jeram and Lance Morrissey for making images used here available. The editors and a reviewer provided valuable comments on an earlier version. PAS's visit to Berlin was funded by the Alexander von Humboldt Foundation.

References

Almond JE (1985) The Silurian-Devonian fossil record of the Myriapoda. Phil Trans R Soc B 309:227–237

Anderson LI, Trewin N (2003) An Early Devonian arthropod fauna from the Windyfield cherts, Aberdeenshire, Scotland. Palaeontology 46:467–509

Armonies W, Reise K (2000) Faunal diversity across a sandy shore. Mar Ecol Prog Ser 196:49–57

Bartsch I (1989) Marine mites (Halacaroidea: Acari): a geographical and ecological survey. Hydrobiologia 178:21–42

Bayartogtokh B, Chatterjee T (2010) Oribatid mites from marine littoral and freshwater habitats in India with remarks on world species of *Thalassozetes* (Acari: Oribatida). Zool Stud 49:839–854

Benton MJ (2010) The origins of modern biodiversity on land. Phil Trans R Soc B 365:3667–3679

Bousfield EL (1983) An updated phyletic classification and palaeohistory of the Amphipoda. In: Schram F (ed) Crustacean Phylogeny (Crustacean Issues 1). Balkema, Rotterdam, pp 257–277

Bousfield EL, Poinar GO Jr. (1994) A new terrestrial amphipod from Tertiary amber deposits of Chiapas province, southern Mexico. Hist Biol 7:105–114

Braddy SJ (2004) Ichnological evidence for the arthropod invasion of land. Fossils Strata 51:136–140

Braddy SJ, Briggs DEG (2002) New Lower Permian nonmarine arthropod trace fossils from New Mexico and South Africa. J Palaeont 76:546–557

Cannicci S, Simoni R, Giomi F (2011) Role of the embryo in crab terrestrialization: an ontogenetic approach. Mar Ecol Prog Ser 430:121–131

Carefoot T, Taylor B (1995) *Ligia*: a prototypal terrestrial isopod. In: Alikhan MM (ed) Terrestrial Isopod Biology (Crustacean Issues 9). Balkema, Rotterdam, pp 47–60

Claridge MF, Lyon AG (1961) Lung-books in the Devonian Palaeocharinidae (Arachnida). Nature 191:1190–1191

Collette JH, Gass KC, Hagadorn JW (2012) *Protichnites eremita* unshelled? experimental model-based neoichnology and new evidence for a euthycarcinoid affinity for this ichnospecies. J Palaeont 86:442–454

Condé B (1965) Présence de Palpigrades dans le milieu interstitial littoral. C r Acad Sci Paris 261:1898–1900

Dalingwater JE (1985) Biomechanical approaches to eurypterid cuticles and chelicerate exoskeletons. Trans R Soc Edinb Earth Sci 76:359–364

Davies NS, Rygel MC, Gibling MR (2010) Marine influence in the Upper Ordovician Juniata Formation (Potters Mills, Pennsylvania): implications for the history of life on land. Palaios 25:527–539

De Deckker P (1983) Terrestrial ostracods in Australia. Austr Mus Mem 18:87–100

Diesel R, Schubart CD, Schuh M (2000) A reconstruction of the invasion of land by Jamaican crabs (Grapsidae: Sesarminae). J Zool 250:141–160

Dohle W (1976) Zur Frage des Nachweises von Homologien durch die komplexen Zell- und Teilungsmuster in der embryonalen Entwicklung höherer Krebse (Crustacea, Malacostraca, Peracarida). Sitzungsber Ges Naturf Freunde Berlin 16:125–144

Dohle W (1988) Myriapoda and the ancestry of insects. Manchester Polytechnic, Manchester

Donovan SK, Dixon HL (1998) A fossil land crab from the late Quaternary of Jamaica (Decapoda, Brachyura, Gecarcinidae). Crustaceana 71:824–826

Dunlop JA, Anderson LI, Kerp H, Hass H (2004) A harvestman (Arachnida: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland. Trans R Soc Edinb Earth Sci 94:341–354

Dunlop JA, Selden PA (2009) Calibrating the chelicerate clock: a paleontological reply to Jeyaprakash and Hoy. Exp Appl Acarol 48:183–197

Edwards D, Selden PA, Richardson JB, Axe L (1995) Coprolites as evidence for plant–animal interaction in Siluro-Devonian terrestrial ecosystems. Nature 377:329–331

Engel MS, Grimaldi D (2004) New light shed on the oldest insect. Nature 427:627–630

Farley R (2012) Ultrastructure of book gill development in embryos and first instars of the horseshoe crab *Limulus polyphemus* L (Chelicerata, Xiphosura). Front Zool 9:4. doi:10.1186/1742-9994-9-4

Farrelly CA, Greenaway P (1992) Morphology and ultrastructure of the gills of terrestrial crabs (Crustacea, Gecarcinidae and Grapsidae): adaptations for air breathing. Zoomorphology 112:39–49

Farrelly CA, Greenaway P (1993) Land crabs with smooth lungs: Grapsidae, Gecarcinidae, and Sundathelphusidae ultrastructure and vasculature. J Morph 215:245–260

Farrelly CA, Greenaway P (2005) The morphology and vasculature of the respiratory organs of terrestrial hermit crabs (*Coenobita* and *Birgus*): gills, branchiostegal lungs and abdominal lungs. Arthropod Struct Dev 34:63–87

Fayers SR, Trewin NH (2005) A hexapod from the Early Devonian Windyfield Chert, Rhynie, Scotland. Palaeontology 48:1117–1130

Garrouste R, Clément G, Nel P, Engel MS, Grandcolas P, D'Haese C, Lagebro L, Denayer J, Gueriau P, Lafaite P, Olive S, Prestianni C, Nel A (2012) A complete insect from the Late Devonian period. Nature 488:82–85

Garwood RJ, Edgecombe GD (2011) Early terrestrial animals, evolution and uncertainty. Evol Edu Outreach 4:489–501

Genise JF, Bedatou E, Melchor RN (2008) Terrestrial crustacean breeding trace fossils from the Cretaceous of Patagonia (Argentina): palaeobiological and evolutionary significance. Palaeogeo Paleoclim Palaeoecol 264:128–139

Glenner H, Thomsen PF, Hebsgaard MB, Sørensen MV, Willerslev E (2006) The origin of insects. Science 314:1883–1884

Greenaway P (2003) Terrestrial adaptations in the Anomura (Crustacea: Decapoda). Mem Mus Vict 60:13–26

Grimaldi D (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. Ann Miss Bot Gard 86:373–406

Gruner H-E (1993) Klasse Crustacea, Krebse. In: Gruner H-E (ed) Lehrbuch der speziellen Zoologie, Band I, 4.Teil Arthropoda. Gustav Fischer, Jena, pp 448–1030

Haas F, Waloszek D, Hartenberger R (2003) *Devonohexapodus bocksbergensis*, a new marine hexapod from the Lower Devonian Hunsrück Slates, and the origin of Atelocerata and Hexapoda. Organ Divers Evol 3:39–54

Hilken G (1997) Vergleich von Tracheensystemen unter phylogenetischem Aspekt. Verh Naturwiss Ver Hamburg 37:5–94

Hirst S (1923) On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire). Ann Mag Nat Hist 12(70):455–474

Hirst S, Maulik S (1926) On some arthropod remains from the Rhynie Chert (Old Red Sandstone). Geol Mag 63:69–71

Hoese B (1981) Morphologie und Funktion des Wasserleitungssystems der terrestrischen Isopoden (Crustacea, Isopoda, Oniscoidea). Zoomorphology 98:135–167

Hoese B (1983) Struktur und Entwicklung der Lungen der Tylidae (Crustacea, Isopoda, Oniscoidea). Zool Jb Anat 109:487–501

Hoese B, Janssen HH (1989) Morphological and physiological studies on the marsupium of terrestrial isopods. Monit zool ital (NS) 4:153–173

Jeram AJ, Selden PA, Edwards D (1990) Land animals from the Silurian: arachnids and myriapods from Shropshire, England. Science 250:658–661

Johnson EW, Briggs DEG, Suthren RJ, Wright JL, Tunnicliff SP (1994) Non-marine arthropod traces from the subaerial Ordovician Borrowdale Volcanic Group, English Lake District. Geol Mag 131:395–406

Judson MLI (2012) Reinterpretation of *Dracochela deprehendor* (Arachnida: Pseudoscorpiones) as a stem-group pseudoscorpion. Palaeont 55:261–283

Kamenz C, Dunlop JA, Scholtz G, Kerp H, Hass H (2008) Microanatomy of Early Devonian book lungs. Biol Lett 4:212–215

Kamenz C, Staude A, Dunlop JA (2011) Sperm carriers in Silurian sea scorpions. Naturwissenschaften 98:889–896

Kenrick P, Wellman CH, Schneider H, Edgecombe GD (2012) A timeline for terretrialization: consequences for the carbon cycle in the Palaeozoic. Phil Trans R Soc B 367:519–536

Kethley JB, Norton RA, Bonamo PM, Shear WA (1989) A terrestrial alicorhagiid mite (Acari: Acariformes) from the Devonian of New York. Micropaleontology 35:367–373

Kingsley JS (1885) Notes on the embryology of *Limulus*. Q J Microsc Sci 25:521–576

Kjellesvig-Waering EN (1986) A restudy of the fossil Scorpionida of the world. Palaeontographica Am 55:1–287

Klok CJ, Mercer RD, Chown SL (2002) Discontinuous gas-exchange and its convergent evolution in tracheated arthropods. J Exp Biol 205:1019–1029

Kraus O, Brauckmann C (2003) Fossil giants and surviving dwarfs. Arthropleurida and Pselaphognatha (Atelocerata, Diplopoda): characters, phylogenetic relationships and construction. Verh naturwiss Ver Hamburg (NF) 40:5–50

Kraus O, Kraus M (1994) Phylogenetic system of the Tracheata (Mandibulata): on "Myriapoda"–Insecta interrelationships, phylogenetic age and primary ecological niches. Verh naturwiss Ver Hamburg (NF) 34:5–31

Kühl G, Bergmann A, Dunlop JA, Garwood RJ, Rust J (2012) Redescription and palaeobiology of *Palaeoscorpius devonicus* Lehmann, 1944 from the Lower Devonian Hunsrück Slate of Germany. Palaeontology 55:775–787

Kühl G, Rust J (2009) *Devonohexapodus bocksbergensis* is a synonym of *Wingertshellicus backesi* (Euarthropoda)—no evidence for marine hexapods living in the Devonian Hunsrück Sea. Org Divers Evol 9: 215–231

Labandeira CC, Beall BS, Hueber FM (1988) Early insect diversification: evidence from a Lower Devonian bristletail from Québec. Science 242:913–916

Laurie M (1899) On a Silurian scorpion and some additional eurypterid remain from the Pentland Hills. Trans R Soc Edinb 39:575–590

Levi HW (1967) Adaptations of respiratory systems of spiders. Evolution 21:571–583

Little C (1990) The Terrestrial Invasion—an Ecophysiological Approach to the Origins of Land Animals. Cambridge University Press, Cambridge

Macnaughton RB, Cole JM, Dalrymple RW, Braddy SJ, Briggs DEG, Lukie TD (2002) First steps on land: arthropod trackways in Cambrian–Ordovician eolian sandstone, southeastern Ontario, Canada. Geology 30:391–394

Malz H (1964) *Kouphichnium walchi*. Die Geschichte einer Fährte und ihres Tieres. Nat Mus 94:81–97

Manning PL, Dunlop JA (1995) The respiratory organs of eurypterids. Palaeontology 38:287–297

Manton SM (1977) The Arthropoda: Habits, Functional Morphology, and Evolution. Oxford University Press, Oxford

Morrissey LB, Hiller RD, Marriott SB (2012) Late Silurian and early Devonian terrestrialization: ichnological insights from the Lower Old Red Sandstone of the Anglo-Welsh Basin, U.K. Palaeogeog Palaeoclim Palaeoecol 337–338:194–215

Naruse T, Karasawa H, Shokita S, Tanaka T, Moriguchi M (2004) A first fossil record of the terrestrial crab, *Geothelphusa tenuimanus* (Miyake and Minei 1965) (Decapoda, Brachyura, Potamidae) from Okinawa Island, Central Ryukyus, Japan. Crustaceana 76:121–1218

Norton RA, Bonamo PN, Grierson JD, Shear WA (1988) Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. J Paleontol 62:259–269

Olesen J (2009) Phylogeny of Branchiopoda (Crustacea) – character evolution and contribution of uniquely preserved fossils. Arthrop Syst Phylog 67:3–39

Paulay G, Starmer J (2011) Evolution, insular restriction, and extinction of oceanic land crabs, exemplified by the loss of an endemic *Geograpsus* in the Hawaiian Islands. PLoS ONE 6(5):e19916. doi:10.1371/journal.pone.0019916

Pisani D, Poling LL, Lyons-Weiler M, Hedges SB (2004) The colonization of land by animals: Molecular phylogeny and divergence times among arthropods. BMC Biology 2:1; doi:10.1186/1741-7007-2-1

Poinar GO Jr., Kerp H, Hass H (2008) *Palaeonema phyticum* gen. n., sp. n. (Nematoda: Palaeonematidae fam. n.), a Devonian nematode associated with early land plants. Nematology 10:9–14

Poschmann M, Anderson LI, Dunlop JA (2005) Chelicerate arthropods, including the oldest phalangiotarbid arachnid, from the Early Devonian (Siegenian) of the Rhenish Massif, Germany. J Paleontol 79:110–124

Poschmann M, Braddy SJ (2010) Eurypterid trackways from early Devonian tidal facies of Alken an der Mosel (Rheinisches Schiefergebirge, Germany) Palaeobiodivers Palaeoenvir 90:111–124

Poschmann M, Dunlop JA, Kamenz C, Scholtz G (2008) The Lower Devonian scorpion *Waeringoscorpio* and the respiratory nature of its filamentous structures, with a description of a new species from the Westerwald area, Germany. Paläont Ztschr 82:418–436

Prokop J, Nel A, Hoch I (2005) Discovery of the oldest known Pterygota in the Lower Carboniferous of the Upper Silesian Basin in the Czech Republic (Insecta: Archaeorthoptera). Geobios 38:383–387

Regier JC, Shultz JW, Kambic RE (2004) Phylogeny of basal hexapod lineages and estimates of divergence times. Ann Entomol Soc Am 97:411–419

Regier JC, Shultz JW, Zwick A, Hussey A, Ball B, Wetzer R, Martin JW, Cunningham CW (2010) Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463:1079–1083

Rehm P, Borner J, Meusemann K, von Reumont BM, Simon S, Hadrys H, Misof B, Burmester T (2011) Dating the arthropod tree based on large-scale transcriptome. Mol Phyl Evol 61:880–887

Retallack GJ, Feakes CR (1987) Trace fossil evidence for Late Ordovician animals on land. Science 235:61–63

Richter S, Scholtz G (2001) Phylogenetic analysis of the Malacostraca (Crustacea). J Zool Syst Evol Res 39:113–136

Ripper W (1931) Versuch einer Kritik der Homologiefrage der Arthropodentracheen. Z wiss Zool 138:303–369

Rolfe WDI (1985) Early terrestrial arthropods: A fragmentary record. Phil Trans R Soc B 309:207–218

Sanders K, Lee MSY (2010) Arthropod molecular divergence times and the Cambrian origin of pentastomids. Syst Biodivers 8:63–74

Schaefer I, Norton RA, Scheu S, Maraun M (2010) Arthropod colonization of land – linking fossils in oribartid mites (Acari, Oribatida). Mol Phyl Evol 57:113–121

Schawaller W, Shear WA, Bonamo PM (1991) The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). Amer Mus Novit 3009:1–17

Schmalfuss H (1978) *Ligia simony*: a model for the evolution of terrestrial isopods. Stuttg Beitr Naturk A 317:1–5

Schmidt C (2008) Phylogeny of the terrestrial Isopoda (Oniscidea): a review. Arthropod Syst Phyl 66:191–226

Scholtz G, Kamenz C (2006) The book lungs of Scorpiones and Tetrapulmonata (Chelicerata, Arachnida): Evidence for homology and a single terrestrialisation event of a common arachnid ancestor. Zoology 109:2–13

Scourfield DJ (1940) The oldest known fossil insect (*Rhyniella praecursor* Hirst and Maulik). Further details from additional specimens. Proc Linn Soc 152:113–131

Selden PA (1985) Eurypterid respiration. Phil Trans R Soc B 309:209–226

Selden PA (2001) Terrestrialization (invertebrates). In:Briggs DEG, Crowther PR (eds). Palaeobiology II. Blackwell, Oxford, 71–74

Selden PA (2012) Terrestrialisation (Precambrian–Devonian) (Version 3.0).In: Encyclopedia of Life Sciences. Wiley, Chichester.doi: 10.1002/9780470015902.a0001641.pub3

Selden PA, Edwards D (1989) Chapter 6. Colonisation of the land. In: Allen KC, Briggs DEG (eds) Evolution and the fossil record. Belhaven, London, pp 122–152

Selden PA, Jeram AJ (1989) Palaeophysiology of terrestrialisation in the Chelicerata. Trans R Soc Edinb Earth Sci 80:303–310

Selden PA, Shear WA, Sutton MD (2008) Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order. Proc Natl Acad Sci USA 105:20781–20785

Shear WA (1991) The early development of terrestrial ecosystems. Nature 351:283–289

Shear WA, Bonamo PM (1988) Devonobiomorpha, a new order of centipeds (Chilopoda) from the Middle

Devonian of Gilboa, New York State USA, and the phylogeny of centiped orders. Amer Mus Novitat 2927:1–30

Shear WA, Bonamo PM, Grierson JD, Rolfe WDI, Smith EL, Norton RA (1984) Early land animals in North America: evidence from Devonian age arthropods from Gilboa, New York. Science 224:492–494

Shear WA, Gensel PG, Jeram AJ (1989) Fossils of large terrestrial arthropods from the Lower Devonian of Canada. Nature 384:555–557

Shear WA, Jeram AJ, Selden PA (1998) Centiped legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and North America. Amer Mus Novitat 3231:1–16

Shear WA, Kukalová-Peck J (1990) The ecology of Palaeozoic terrestrial arthropods: the fossil evidence. Can J Zool 68:1807–1834

Shear WA, Selden PA (1995) *Eoarthropleura* (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America. N Jahrb Geol Paläont Abh 196:347–375

Shear WA, Selden PA (2001) Rustling in the undergrowth: animals in early terrestrial ecosystems. In: Gensel PG, Edwards D (eds) Plants invade the land: Evolutionary and environmental perspectives. Columbia University Press, New York, pp 29–51

Shear WA, Selden PA, Rolfe WDI, Bonamo PM, Grierson JD (1987) New terrestrial arachnids from the Devonian of Gilboa, New York. Amer Mus Novitat 2901:1–74

Stensmyr MC, Erland S, Hallberg E, Wallén R, Greenaway P, Hansson BS (2005) Insect-like olfactory adaptations in the terrestrial giant robber crab. Curr Biol 15:116–121

Størmer L (1970) Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 1: Arachnida. Senckenberg Leth 51:335–369

Størmer L (1976) Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on the fauna and problems regarding invasion of land by arthropods. Senckenberg Leth 57:87–183

Strother PK, Al-Hajri S, Traverse A (1996) New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. Geology 24:55–58

Strother PK, Wood GD, Taylor WA, Beck JH (2004) Middle Cambrian cryptospores and the origin of land plants. Mem Ass Australas Palaeontol 29:99–113

Thibaud J-M (2007) Recent advances and synthesis in biodiversity and biogeography of arenicolous Collembola. Ann soc Entomol France NS 43:181–185

Tillyard RJ (1928) Some remarks on the Devonian fossil insects from the Rhynie chert beds, Old Red Sandstone. Trans Ent Soc Lond 76:65–71

Türkay M (1987) Landkrabben. Nat Mus 117:143–150

Van Roy P, Orr PJ, Botting JP, Muir LA, Vinter J, Lefebvre B, el Hariri K, Briggs DEG (2010) Ordovician faunas of Burgess Shale type. Nature 465:215–218

Villani MG, Allee LL, Díaz A, Robbins PS (1999) Adaptive strategies of edaphic arthropods. Ann Rev Entomol 44:233–256

von Reumont B, Burmester T (2010) Remipedia and the evolution of hexapods. In: Encyclopedia of Life Sciences (ELS). Wiley, Chichester. doi/10.1002/9780470015902.a0022862

von Reumont BM, Jenner RA, Wills MA, Dell'Ampio E, Pass G, Ebersberger I, Meyer B, Koenemann S, Iliffe TM, Stamatakis A, Niehuis O, Meusemann K, Misof B (2012) Pancrustacean phylogeny in the light of new phylogenomic data: support for Remipedia as the possible sister group of Hexapoda. Mol Biol Evol 29:1031–1045

Walker SE, Holland SM, Gardiner L (2003) *Coenobichnus currani* (new ichnogenus and ichnospecies): fossil trackway of a land hermit crab, early Holocene, San Salvador, Bahamas. J Paleontol 77:576–582

Warburg MR (2012) Pre-and post-parturial aspects of scorpion reproduction: a review. Eur J Entomol 109:139–146

Wilson HM (2006) Juliformian millipedes from the Lower Devonian of Euramerica: implications for the timing of millipede cladogenesis in the Paleozoic. J Paleontol 80:638–649

Wilson HM, Anderson LI (2004) Morphology and taxonomy of Paleozoic millipedes (Diplopoda: Chilognatha: Archipolypoda) from Scotland. J Paleontol 78:169–184

Wilson HM, Shear WA (2000) Microdecemplicida, a new order of minute arthropleurideans (Arthropoda, Myriapoda) from the Devonian of New York State, U.S.A. Trans R Soc Edinb Earth Sci 90:351–375

Witte H, Döring D (1999) Canalized pathways of change and constraints in the evolution of reproductive modes of microarthropods. Exp Appl Acarol 23:181–216

Wright JL, Quinn L, Briggs DEG, Williams SH (1995) A subaerial arthropod trackway from the upper Silurian Clam Bank formation of Newfoundland. Can J Earth Sci 32:304–313

Zeh DW, Zeh JA, Smith RL (1989) Ovipositors, amnions and eggshell architecture in the diversification of terrestrial arthropods. Quart Rev Biol 64:147–168

Zhang Z-Q (2011) Phylum Arthropoda von Siebold, 1848. In: Zhang Z-Q (ed) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 4138:99–103