Rhynie Chert, Aberdeenshire

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Introduction

The Rhynie Chert locality; of Early Devonian (Pragian, about 410 million y ears old) age, is the best known Lagerstarte of early terrestrial biota in the world, with its diversity of arthropods, ranging from tiny collembolans (springtails) to predatory trigonotarbid arachnids. Not only is it the longest known Lagerstätte, having been first described scientifically in the 1920s, but also it preserves the biota in such an exquisite manner that current research is still producing new morphological detail (e.g. Shear *et al.,* 1998; Trewin and Rice 2004). The cherts represent fossilized sinter — hot-spring siliceous deposits that were laid down in a complex of rivers, lakes and floodplains within the vast Laurasian continent. The hydrothermal activity centred on a fault system, mineralizing and altering subsurface strata as well as forming hot springs and geysers at the surface in the Rhynie area (see (Figure 2.58)).

The deposits surround both upright and fallen stems and other parts of early land plants (see Cleal and Thomas, 1995, for details of plant studies on the Rhynie Chert) such as *Rhynia* and *Aglaophyton.* Together with the petrified plants, animals were discovered in the 1920s, which remained the oldest-known terrestrial animals until 1990 (Jeram *et al.,* 1990). The arthropods found here and their association with other fossils make this one of the world's most important sites for studies of early terrestrial ecosystems, palaeobiology and evolution.

Crustacea were reported in the Rhynie Chert by Scourfield (1920a,b, 1926, 1940a) and Calman (1926), and arachnids by Hirst (1923). Hirst and Maulik (1926) described a possible eurypterid and collembolan 'insects'. With few exceptions, the accuracy of the descriptions and, especially, the detailed drawings of arthropods in these papers has been corroborated by later workers, and the illustrations have been widely reproduced in the literature. Later published work, for example Claridge and Lyon (1961) and Shear *et al.*, (1987a,b), has only added details to the initial discoveries. Since 1926, new taxa have been described from Rhynie only in the last decade.

Recent work has involved investigation of the stratigraphy, sedimentology, taphonomy, structure, and mineral deposits of the chert (Rice *et al.,* 1995; Trewin 1994b; Trewin and Rice 1992, 2004). This work led to the discovery of a new locality, called the Windyfield Chert', some 700m to the east of the Rhynie site. There is little doubt as to the international importance of the Rhynie site, not only for historical reasons but also for its current research work and future potential. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Palaeozoic Palaeobotany and Non-Marine Devonian selection categories (Cleal and Thomas, 1995; Barclay *et al.,* 2005).

Description

In this Grampian inlier the Devonian strata are surrounded by older Dalradian metamorphic rocks and plutonic igneous rocks of Ordovician age. The Rhynie and Windyfield sediments were deposited in a narrow north-east to south-west trending faulted, half-graben basin within these older rocks. The western edge was marked by an active fault with the resulting sedimentary wedge lying unconformably on the older basement rocks and decreasing in thickness eastwards. Hydrothermal fluids rose along the fault plane and deposited sinter around geysers and hotsprings at the surface. Subsequent earth movements tilted the strata towards the northwest and folded the chert bearing rocks near Rhynie village into a north-eastwards plunging syncline.

The cherts at Rhynie occur as lenses within the Dryden Flags and Shales of Early Devonian (Pragian) age. The sequence was described in detail by Trewin (1994), and summarized below:

Shales with thin sandstones, including the Rhynie cherts/(alluvial plain and lacustrine)	>30 m
Tuffaceous sandstones	to 40 m
Lava-variably altered andesite	to 20 m
Pre-lava sandstones/(local alluvial fan)	*c.* 30 m

The cherts occur as lenses within shales, and represent fossilized sinters from hot springs, within a dominantly fluvial setting on the Old Red Sandstone continent. Modern analogues for the sedimentological setting of siliceous hot springs occur in Yellowstone National Park, Wyoming, USA. The strata are dated by palynology to Pragian, or possibly late Lochkovian, in age (Rice *et al.* 1995).

Trewin (1994b) summarized the Rhynie faunal list: one crustacean (but it is the commonest arthropod fossil at the site), five trigonotarbid arachnids, one mite (possibly five species), one collembolan and a euthycarcinoid (from the Windyfield Chert, Anderson and Trewin, 2003). The poorly preserved remains of a supposed spider and eurypterid described by Hirst (1923) and Hirst and Maulik (1926) have not generally been accepted by later workers (see below). More recently, an opilionid (harvestman) and myriapods have been reported from the chert (Shear *et al.* 1998; Anderson and Trewin 2003; Dunlop *et al.,* 2004). The disputed insect *Rhyniognatha hirsti* was shown to be genuine by Engel and Grimaldi (2004), and new crustaceans have been described (Anderson *et al.,* 2004; Fayers and Trewin 2003). In spite of the low diversity of the fauna (only arthropods are known) their remains are abundant in some horizons, and the exceptionally fine preservation of detailed morphology has established the Rhynie animals as models for elucidating the anatomy and taphonomy of arthropods in other early terrestrial Lagerstätten. The Windyfield chert biota was described in comparison with that of Rhynie by Fayers and Trewin (2004), whose summary gives the most recent list of the biotas. These authors did not consider there to be any significant difference between the two chert biotas.

Crustacea

The commonest arthropod in the Rhynie chert is *Lepidocaris rhyniensis* Scourfield, 1926 (Figure 2.55). Scourfield (1926) erected a new crustacean order, Lipostraca, for the new animal, and later he described some new specimens, including young stages Scourfield (1940a). *Lepidocaris* is a tiny, multi-segmented form with 11 pairs of phyllopods (leaf-like limbs), long branched antennae and a pair of caudal appendages. It lived in water and fed on organic detritus in ephemeral pools within the hot-spring environment much like fairy shrimps do today. More recently, other branchiopod species have been described by Fayers and Trewin (2003) and Anderson *et al.* (2004).

Euthycarcinoidea

Hirst and Maulik (1926) described *Heterocrania rhyniensis,* represented by scattered fragments of body and appendages, and referred it, with considerable doubt, to the Eurypterida. *Heterocrania* was largely ignored by later workers; it was not, for example, included in Waterston's review of Devonian eurypterids (in Rolfe and Edwards 1979). However, the discovery of more-complete specimens in the Windyfield Chert by Anderson and Trewin (2003) revealed that the animal was an euthycarcinoid and was the first known from Devonian rocks. The systematic position of this group is problematic as they have similarities to both crustaceans and insects. Like the crustacean *Lepidocaris,* they lived in ephemeral freshwater pools and were probably detritus feeders.

Arachnida

The remains of trigonotarbids (Figure 2.56) are fairly common in the Rhynie chert and their spider-like appearance was described by Hirst (1923) and Hirst and Maulik (1926). Despite this similarity they lack definitive spider features such as poison glands and silk producing glands. The discovery of well-preserved book-lungs in Rhynie trigonotarbids (Claridge and Lyon 1961, see also Størmer 1976) removed any possible doubt that these were truly terrestrial air-breathers. Further morphological details were added by Shear *et al.,* (1987) and Dunlop (1994a). Trigonotarbids belong to the arachnid taxon Tetrapulmonata, as the sister group to spiders, amblypygids, uropygids and schizomids. They occur in all of the main early terrestrial Lagerstätten.

Trigonotarbids, like almost all arachnids, were carnivores and presumably fed on any animals they could catch. Having caught their prey they would have injected it with digestive enzymes through the wounds made by their biting chcliceral fangs. The enzymes would liquefy the flesh of the prey so that it could be sucked out.

Palaeocteniza crassipes, described as a spider by Hirst (1923), was re-studied by Selden *et al.* (1991) who concluded that it was not a spider but probably the moult of a juvenile trigonotarbid. The oldest known spider is therefore the Upper Devonian *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (Shear *et al.,* 1987a,b).

The oldest known mites (Acari) occur in the Rhynie chert and like trigonotarbids and spiders, mites are arachnids. Hirst (1923) thought the specimens were conspecific; he named them *Protacarus crani* which he placed, with some doubt, in the modern family Eupodidae. Dubinin (1962) considered they represented five species belonging to four families: *Protacarus crani* (Pachygnathidae), *Protospeleorchestes pseudoprotacarus* (Nanorchestidae), *Pseudoprotacarus scoticus* (Alicorhaglidae), and *Paraprotacarus hirsti* and *Palaeotydeus devonicus* (Tydeidae). John Kethley (Field Museum of Natural History, Chicago) has restudied the specimens and questioned the alicorhagiid affinity of *Pseudoprotacarus scoticus* because of its pre-tarsal morphology (in Kethley *et al.,* 1989). He considered all to belong to the family Pachygnathidae (pers. comm. in Norton *et al.,* 1989) except the nanorchestid (a family which is nevertheless included in the superfamily Pachygnathoidea). They all appear to belong to the Prostigmata (=Actinedida).

The mites, like the *Lepidocaris* crustaceans, were probably saprophagous and fed on dead organic matter but being terrestrial it was plant litter and other soil organic detritus. However, it is also possible that some mites were sap-suckers who sucked juices from living plant tissue.

Myriapoda

A short piece of leg probably belonging to a predatory scutigerimorph centipede was identified in a piece of RhyMe chert by Shear *et al.,* (1998) and Anderson and Trewin (2003). Detritivorous eoarthropleurids have also been found (Fayers and Trewin (2004).

Hexapoda

The earliest known hexapod, the collembolan *Rhyniella praecursor* Hirst & Maulik, 1926 (Figure 2.57), 1.5 mm long was described from multiple specimens originally found by the Revd W Cran (Jarzembowski, 1989). *R. praecursor* had a furca as in living Collembola and evidently belongs to the extant family Isotomidae (Whalley and Jarzembowski 1981; Greenslade and Whalley 1986). Such an early (Pragian) date for *Rhyniella* and the mite *Protacarus* has been controversial (Crowson 1970; Greenslade 1988), but there is no evidence that *Rhyniella* is anything other than an extinct genus and species of early Devonian springtail. *Rhyniella* was probably adapted for walking on water as it has elongate claws, which are characteristic of Collembola, which live in a semi-equatic environment. Collembola are the most abundant hexapods on Earth with up to 250 million individuals per acre.

A hexapod mandible, *Rhyniognatha hirsti,* found alongside *rhyniella* and interpreted by Tillyard (1928) as insectan but without any firm placement, was re-described recently by Engel and Grimaldi (2004) who showed it to be an ectognath (true insect), and not necessarily a primitive form, and thus the oldest known fossil insect. Their interpretation suggests that primitive insects should be found in older strata, at least of Silurian age.

Trace fossils

Trace fossils attributed to arthropods, in the form of coprolites, have been described from the Rhynie chert (Habgood *et* W., 2004). These authors found a variety of coprolite types ranging in size and shape from larger, elongate forms with identifiable organic and inorganic contents, somewhat similar to those described from the Siluro-Devonain of the Welsh Borderland (Edwards *et al.,* 1990), down to smaller, round faecal masses formed of amorphous organic matter. The producers of the larger coprolites were considered to be mainly detritivores, whereas the smaller masses were likely to have been produced by microherbi-vores (e.g. collembolans and mites, feeding on microbes and fungi).

Interpretation

Taphonomy and palaeoecology

The Rhynie arthropods appear as thin films of cuticle, which may be preserved complete or as irregular patches. Maceration of the chert in hydrofluoric acid can yield complete podomeres, but the preservation differs from bed to bed (Trewin, 1994b). Both complete and disarticulated arthropod remains occur, including a trigonotarbid specimen showing leg podomeres inside the abdomen; this is presumably a moult. Crowson (1970, 1985) put forward the idea that the Rhynie arthropods could be much younger animals that crawled into fissures in the chert and were sealed in by re-mobilization of the silica, perhaps in Tertiary times, since their modern aspect might not be expected in such ancient rocks. Rolfe (1980), Kane and Schluter (1985), and Greenslade (1988) have argued persuasively on geological and palaeontological grounds that the Rhynie fauna is genuinely Devonian in age, and finds of very similar Devonian faunas from elsewhere support this (for example, terrestrial Lagerstätten reported, from Germany (Størmer, 1977), New York (Shear *et al.*, 1987a,b), and Shropshire (leram *et al.,* 1990)).

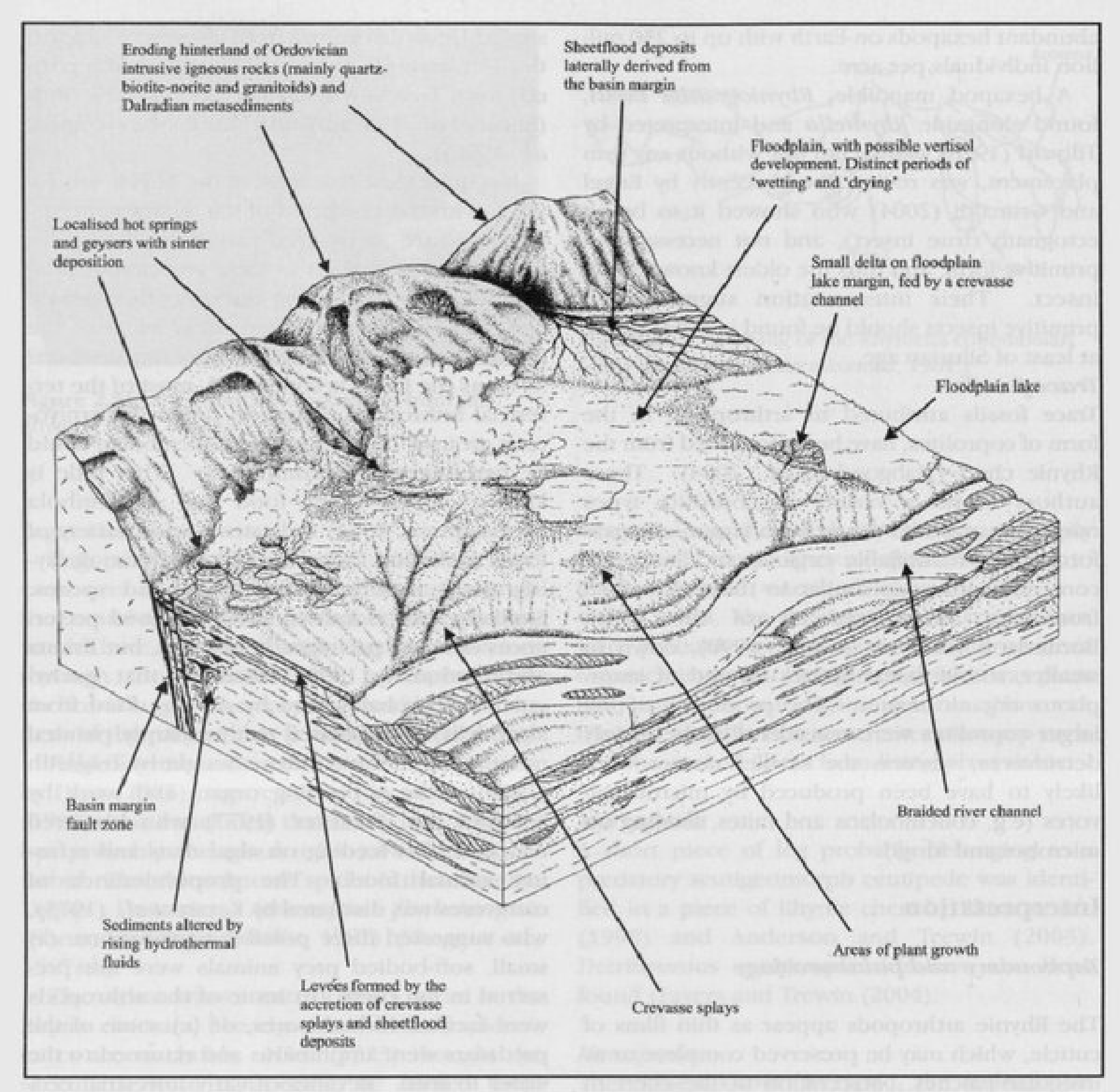
It is quite clear that most of the Rhynie arthropods, with the exception of the freshwater crustaceans, are terrestrial animals, living in Devonian times much as their present-day relatives do. An interesting question then arises: how much of the total terrestrial biota of the area at the time is preserved in the Rhynie chert? As far as the fauna is concerned, most of the terrestrial arthropods belong to primarily carnivorous groups. The mites and collembolan could be herbivores or decomposers. What little is known about the food of Collembola (Christiansen, 1964) indicates a wide variety of foods including fungal hyphae, bacteria, decaying plant material, frass, algae and spores. Similarly, little is known about the food preferences of living pachygnathoid mites, but Krantz and Lindquist (1979) reasoned that pachygnathoids probably feed by sucking fluid from algal cells; they pointed to the sharply pointed mouthparts of these mites, thought by Tragardh (1909) to be a piercing organ, and work by Schuster and Schuster (1977) who observed nanorchestids feeding on algal mats and refusing animal food. The preponderance of carnivores was discussed by Kevan *et al.* (1975), who suggested three possible explanations: (a) small, soft-bodied prey animals were not preserved in the chert; (b) some of the arthropods were facultative herbivores; or (c) some of the predators were amphibious and returned to the water to feed. Reviews of early terrestrial ecosystems by Shear (1991), Edwards and Selden (1993) and Shear and Selden (1999) concluded that the decomposer/microherbivore food chain, such as occurs in modern soil and litter communities, predominated in Devonian terrestrial Lagerstätten. The Rhynie fauna may be a litter community; on the other hand, macroherbivory may not have been widespread. at the time.

The unique preservation of the arthropods in the Rhynie chert, as three-dimensional moulds, means that they complement, and in most cases help to interpret, studies on similar arthropods from the other contemporaneous localities yielding terrestrial biotas. Interestingly, the studies on these other localities have confirmed the lack of macroherbivores among these early arthropods (see above).

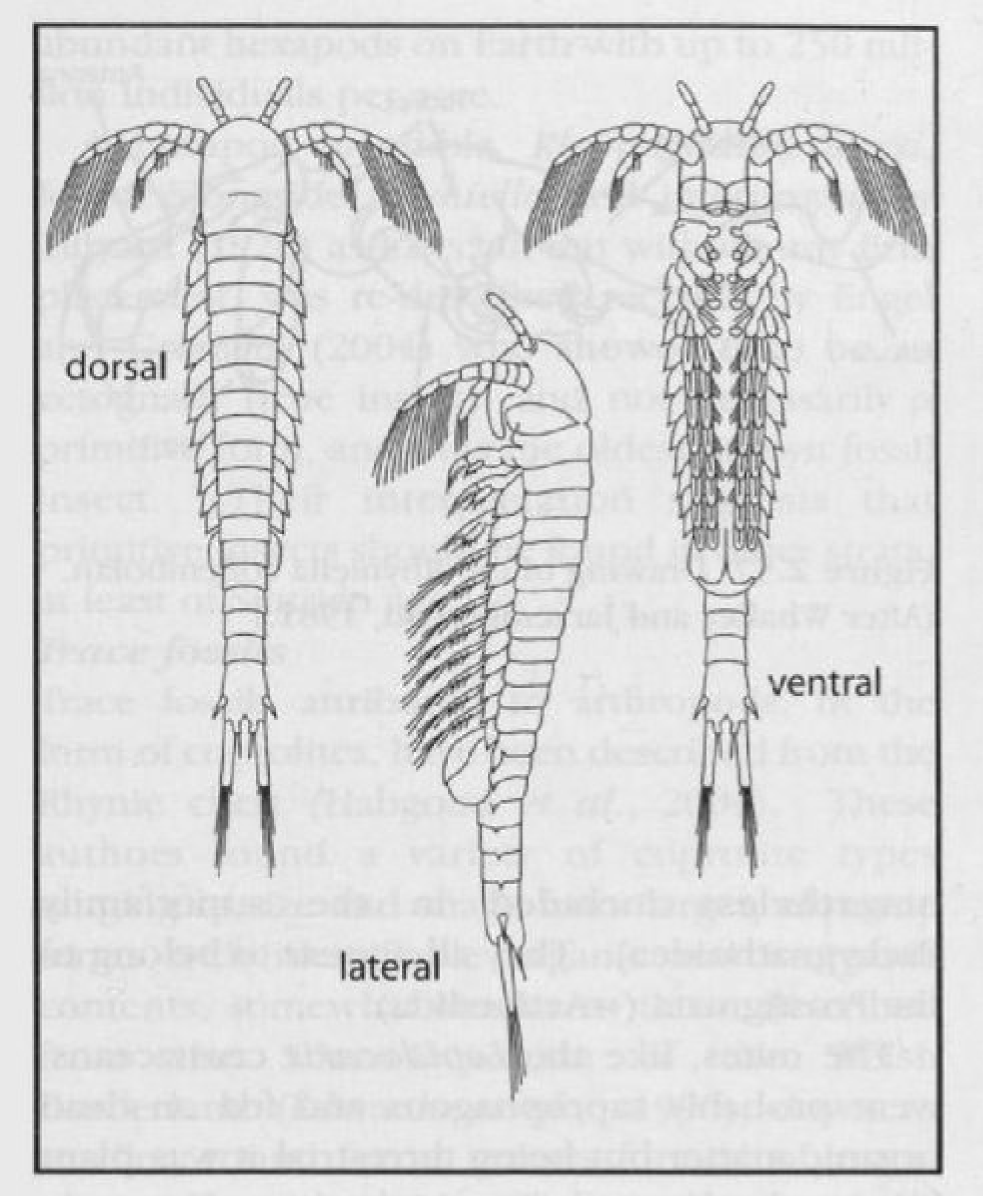
Conclusions

The Rhynie Chert locality is of international importance for the study of terrestrial arthropods, being the first discovered locality, yielding the best-preserved fossils, showing a relatively diverse fauna, and being readily accessible for future work. Apart from some small, concealed sites nearby, the Rhynie chert is unique; no other site in the world has yielded the same types of animals with the same type of high quality preservation in three dimensions. Conservation of the site is essential both for historical interest and to support current and future work being carried out in laboratories throughout the world.

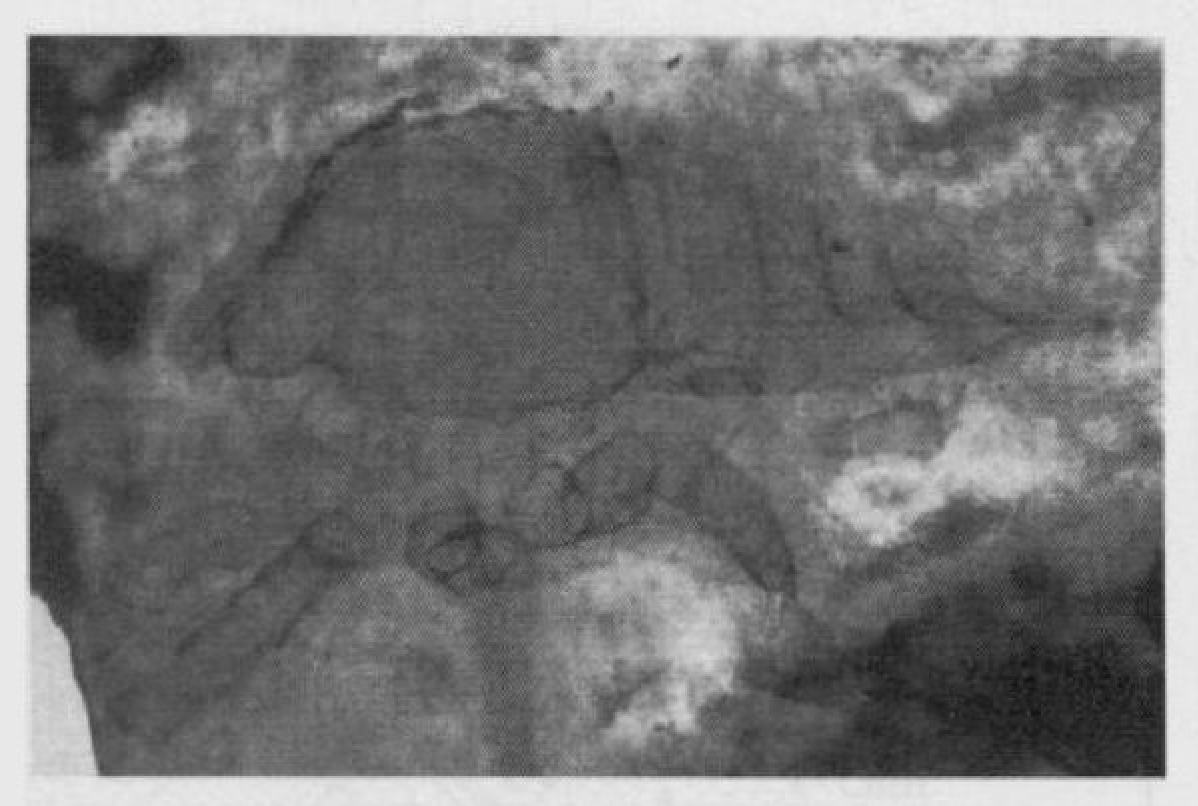
References



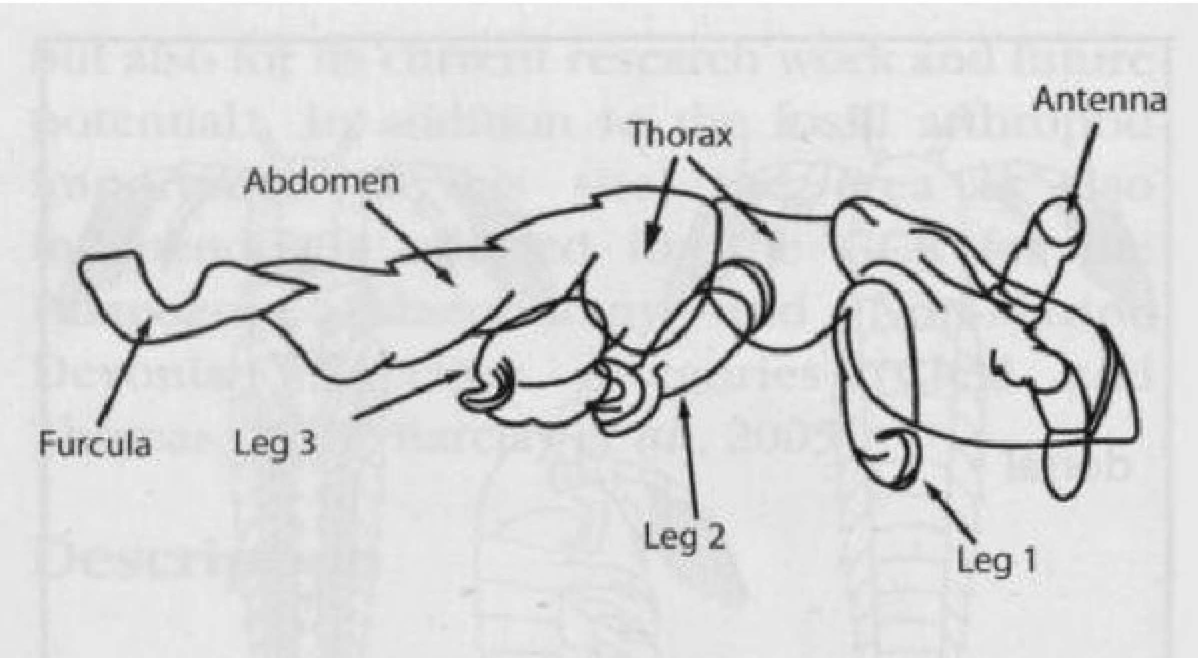
(Figure 2.58) Reconstruction of the Rhynie environment. (After Payers and Trewin, 2004.)



(Figure 2.55) Lepidocaris rhyniensis reconstruction, based on specimens from the Rhynie Chert. (From Scourfield, 1940.)



(Figure 2.56) A triognotarbid specimen from the Rhynie Chen. (Photo: P. Selden.)



(Figure 2.57) Drawing of the Rhyniella collembolan. (After Whalley and Jarzembowski, 1981.)