

Fossil Arthropods of Great Britain

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Access to the countryside

This volume is not intended for use as a field guide. The description or mention of any site should not be taken as an indication that access to a site is open. Most sites described are in private ownership, and their inclusion herein is solely for the purpose of justifying their conservation. Their description or appearance on a map in this work should not be construed as an invitation to visit. Prior consent for visits should always be obtained from the landowner and/or occupier.

Information on conservation matters, including site ownership, relating to Sites of Special Scientific Interest (SSSIs) or National Nature Reserves (NNRs) in particular counties or districts may be obtained from the relevant country conservation agency headquarters listed below:

Countryside Council for Wales,
Maes-y-Ffynnon,
Penrhosgarnedd,
Bangor,
Gwynedd LL57 2DW.

Natural England,
Northminster House,
Peterborough PE1 1UA.

Scottish Natural Heritage,
Great Glen House,
Leachkin Road
Inverness IV3 8NW.

Conserving our fossil heritage – JNCC policy statement

Fossils are a key part of our natural heritage and a major scientific, educational and cultural resource. They are fundamental to understanding the evolution of life and the character of ancient environments. Fossils also provide a basis for comparing the ages of rocks the world over.

The discovery, collection and study of the fossilized remains of ancient life can be enjoyable and stimulating activities that give people a fascinating insight into the geological and biological history of the Earth. However, the available fossil resource is finite. It is only through maintaining a prudent approach to the management of important fossil sites that future generations will be able to experience, study and enjoy them.

RESPONSIBLE FOSSIL COLLECTING

In most circumstances, responsible fossil collecting is not harmful to the conservation of fossil sites. It can actually benefit our understanding of geology. This is particularly true where the fossils are relatively common or the sites in which they are found are subject to high levels of natural or artificial degradation, such as coastal cliffs that are being eroded, or quarries that are being actively worked. In such situations collecting fossil specimens that might otherwise be destroyed can be beneficial to science, provided that they are properly documented and made available for study. Responsible fossil collecting can therefore be a valuable activity in the sustainable management and safeguard of our fossil heritage.

IRRESPONSIBLE FOSSIL COLLECTING

Irresponsible collecting provides no scientific or educational gain and is therefore an unacceptable activity resulting in irreparable damage to our fossil heritage. It will pose a clear threat where fossils are rare or the fossil source is limited in extent, for example in a cave or a river channel deposit. Collecting without proper recording and curation, inexperienced collecting, over-collecting and inappropriate use of power tools and heavy machinery are likely to reduce or even destroy the scientific value of such sites. Unless the activity is undertaken in an appropriate manner, the statutory nature conservation agencies, the Countryside Council for Wales, Environment and Heritage Service, Natural England and Scottish Natural Heritage, will oppose fossil collecting on the small number of Sites of Special

Fossil collecting – code of good practice

Scientific Interest / Areas of Special Scientific Interest where this activity would cause significant damage to the features of special interest.

CODE OF GOOD PRACTICE

Adopting a responsible approach to collecting is essential for conserving our fossil heritage. The basic principles set out below should be followed by all those intending to collect fossils.

Access and ownership – permission to enter private land and collect fossils must always be gained and local bylaws should be obeyed. A clear agreement should be made over the future ownership of any fossils collected.

Collecting – in general, collect only a few representative specimens and obtain these from fallen or loose material. Detailed *scientific* study will require collection of fossils *in situ*.

Site management – avoid disturbance to wildlife. Many invertebrates and lower plants live on or under loose rocks that should be replaced in their original positions whenever possible. Do not leave the site in an untidy or dangerous condition for those who follow.

Recording and curation – always record precisely the locality at which fossils are found and, if collected *in situ*, record relevant details of the position of the rock layer from where the fossil was collected. Ensure that these records can be directly related to the relevant specimens. Where necessary, seek specialist advice on specimen identification and care. Fossils of prime scientific importance should be placed in a suitable repository, normally a museum with adequate curatorial and storage facilities.

MANAGEMENT OF OUR FOSSIL HERITAGE

In order to achieve the successful management of the fossil heritage of the United Kingdom, the statutory nature conservation agencies will:

- Promote the responsible approach outlined in the *Code of Good Practice*, above.
- Encourage the placement of scientifically important fossils into a suitable repository (such as a museum) in order to ensure their proper curation, longterm security and accessibility.
- Recognize the contribution that responsible fossil collectors can make to geological and palaeontological study.
- Encourage collaboration within the geological community to ensure that maximum educational and scientific gain is made from our fossil resource.
- Support and encourage initiatives that increase awareness and understanding of the value of our fossil resource and the need to conserve it.
- Increase awareness and understanding of the differing management needs of fossil sites. In particular, encourage landowners and occupiers to become advocates for conservation of the fossil resource.
- Review the need for export and import controls on the international trade in fossil specimens.

JNCC, 1997

Preface

There is such a diversity of rocks, minerals, fossils and landforms packed into the piece of the Earth's crust we call 'Britain' that it is difficult to be unimpressed by the long, complex history of geological change to which they are testimony. But if we are to improve our understanding of the nature of the geological forces that have shaped our islands, further unravel their history in 'deep time' and learn more of the history of life on Earth, we must ensure that the most scientifically important Earth science sites are conserved for future generations to study, research and enjoy. Moreover, as an educational field resource and as training grounds for new generations of geologists on which to hone their skills, it is essential that such sites continue to remain available for study. The first step in achieving this goal is to identify the key sites, which is a primary aim of the Geological Conservation Review (GCR).

The GCR, launched in 1977, is a world-first in the systematic selection and documentation of a country's best Earth science sites. No other country has attempted such a comprehensive and systematic review of its Earth science sites on anything near the same scale. After three decades of site evaluation, consultation with the scientific community, and site documentation, we now have an inventory of over 3000 GCR sites, selected for 100 categories covering the entire range of the geological and geomorphological features of Britain.

The minimum criterion for GCR site selection is that sites should offer the finest and/or the most representative feature for illustrating a particular aspect of geology or geomorphology. The resulting GCR sites are thus, at the very least, of national scientific importance and many of these include features regarded as either 'classic' (i.e. a 'textbook example'), internationally important, or simply 'unique'. Some are, in addition, visually spectacular.

The present volume is the 35th to be published in the GCR series of books, which, when complete, will stretch to more than 40 volumes and provide a vast geoconservation information resource. The volume, in describing the ultimately selected GCR sites, represents the results of that part of the GCR assessment and selection programme for Fossil Arthropods and Palaeoentomology. Both of these palaeontological themes provided the basis for site selection categories for the GCR. This volume summarizes the considerable research that has been undertaken on the localities and will be invaluable as an essential reference source for those engaged in their study and aims to provide a stimulus for further investigation. It will also be helpful to teachers and lecturers and for those people who,

Preface

in one way or another, have a vested interest in the GCR sites: owners, occupiers, planners and those concerned with the practicalities of site conservation. The conservation value of the sites is mostly based on a specialist understanding of the Earth science features present and is, therefore, of a technical nature. The account of each site ends, however, with a brief summary of the geological interest, framed in less technical language, in order to help the non-specialist. The first chapter of the volume, used in conjunction with the glossary, is also aimed at a less specialist audience.

This volume deals with the state of knowledge of the sites available at the time of writing, and it must be seen in this context. There is still much to learn about the GCR sites documented here, in increasing our knowledge and understanding of geological history and processes. Geological studies, like any other science, are ever-developing, with new discoveries being made, and existing models being subject to continual testing and modification as new data comes to light. While the existing sites continue to enable us to add to our geological knowledge, increased or hitherto unrecognized significance may be seen in new sites. Indeed, during the writing of this volume, a number of additional localities were considered for inclusion and, after a period of assessment, were ultimately deemed to be worthy of GCR status and were included in this account. That fact is almost inevitable when one considers that some of the original networks of sites were drawn up over two decades ago.

Therefore, it is possible that further important sites will be identified in future years for the GCR as research continues. However, it must be stressed that the GCR is intended to be a *minimalist* scheme, with the selection of only the best, most representative, example of a geological feature, rather than the selection of a series of sites showing closely analogous features.

This account clearly demonstrates the value of the GCR sites to the study of fossil arthropods and their importance within the wider context of Britain's outstanding scientific and natural heritage, and I am grateful to the authors for their valuable contribution in assisting JNCC in its conservation goals.

N.V. Ellis,

GCR Publications Manager and Geoconservation Adviser, JNCC

January 2010

Chapter 1

An introduction to the fossil arthropods of Great Britain

D. Palmer

INTRODUCTION

Today, creatures as seemingly diverse as barnacles and beetles, fleas and flies, land crabs and horseshoe 'crabs', trilobites and woodlice are all recognized as 'arthropods' (from the Greek 'arthron' (joint), and 'podos', (foot)) and were long thought to share a single unifying body plan. Arthropods occupy most of the Earth's environments from the deep oceans to high mountains, deserts and forests. From their marine origins they were amongst the first animals to venture into freshwater and on to the land, the first to take to the air with powered

flight, and they have penetrated deep underground habitats. Consequently, the arthropods are generally considered to be one of the most successful natural groupings of multi-celled organisms that have ever lived. Today, the arthropods comprise some two-thirds of all living species (Figure 1.1).

The fossil record of the arthropods suggests that they were probably the first group of invertebrates to undergo a major diversification. That event happened in late Precambrian times, well over 550 million years ago (Ma). Despite this success, there is a question over the extent to which the fossil record reflects the evolution,

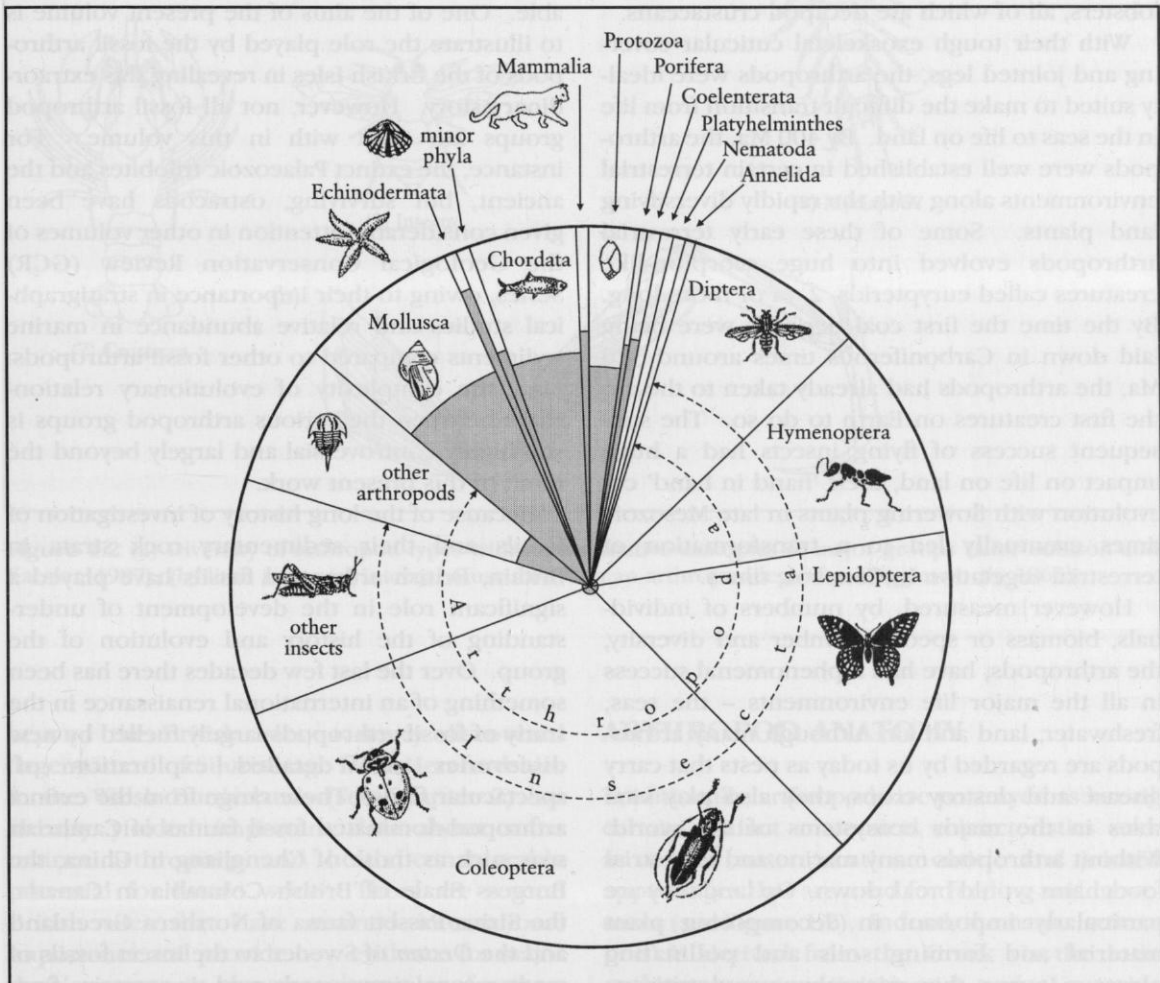


Figure 1.1 The relative numbers of living and extinct species of animals. The percentage of extinct species is shown by the relative size of the grey area for each taxon. Including the other species, Grimaldi and Engel (2005) record 925 000 living species of insects, 123 000 non-insect species, 43 000 chordates, 116 000 'other animals', 30 000 protists, 4800 monerans, 1000 viruses, 69 000 fungi, 27 000 algae and 248 400 vascular plants. (After Muller and Campbell, 1954.)

Introduction to British fossil arthropods

overall diversity and abundance of the group. The body materials of most arthropods are organic and have a low-preservational potential (it is especially low in terrestrial arthropods) except where they have been mineralized, as in the marine trilobites and many aquatic crustaceans.

More than 500 Ma, the oceans of Cambrian times teemed with a huge diversity of trilobites and other extinct arthropods. It may have been predatory arthropods that led the marine 'arms race' and resulted in so many soft-bodied creatures developing hard shells and retreating into sea-bed sediments for defence. Over geological time, these early marine arthropod groups were replaced by ones that are more familiar today such as the shrimps, crabs and lobsters, all of which are decapod crustaceans.

With their tough exoskeletal cuticular covering and jointed legs, the arthropods were ideally suited to make the difficult transition from life in the seas to life on land. By 400 Ma, the arthropods were well established in certain terrestrial environments along with the rapidly diversifying land plants. Some of these early terrestrial arthropods evolved into huge scorpion-like creatures called eurypterids, 2 m or more long. By the time the first coal deposits were being laid down in Carboniferous times around 320 Ma, the arthropods had already taken to the air, the first creatures on Earth to do so. The subsequent success of flying insects had a huge impact on life on land, their 'hand in hand' co-evolution with flowering plants in late Mesozoic times eventually led to a transformation of terrestrial vegetation in Cenozoic times.

However measured, by numbers of individuals, biomass or species number and diversity, the arthropods, have had a phenomenal success in all the major life environments – the seas, freshwater, land and air. Although many arthropods are regarded by us today as pests that carry disease and destroy crops, they also play vital roles in the major ecosystems of the world. Without arthropods many marine and terrestrial foodchains would break down. On land they are particularly important in decomposing plant material and forming soils and pollinating plants. It was this microphagous detritivore habit that played such an essential role in the establishment of the first land communities in Late Silurian times around 418 Ma.

Despite this phenomenal success, there is little detailed understanding or agreement over

how they achieved it, mainly because their early evolutionary pathways are little understood and the significance of what is known is still highly disputed.

Members of the arthropod group can generally be recognized by some basic features such as the segmentation of their bodies with at least some of those segments bearing paired and jointed limbs or other kinds of appendages (Figure 1.2). They all share a cuticular covering to the body made of chitin, proteins, and fats in insects. Consequently, they show a degree of similarity that is often lacking in other major groups.

If it were not for their fossil record however, the story of how arthropods became so successful would be completely obscure and unknowable. One of the aims of the present volume is to illustrate the role played by the fossil arthropods of the British Isles in revealing this extraordinary story. However, not all fossil arthropod groups are dealt with in this volume. For instance, the extinct Palaeozoic trilobites and the ancient, but surviving, ostracods have been given considerable attention in other volumes of the Geological Conservation Review (GCR) Series, owing to their importance in stratigraphical studies and relative abundance in marine sediments compared to other fossil arthropods. Also, the complexity of evolutionary relationships between the various arthropod groups is still highly controversial and largely beyond the remit of this present work.

Because of the long history of investigation of fossils and their sedimentary rock strata in Britain, British arthropod fossils have played a significant role in the development of understanding of the history and evolution of the group. Over the last few decades there has been something of an international renaissance in the study of fossil arthropods largely fuelled by new discoveries and detailed exploration of spectacular finds. These range from the extinct arthropod-dominated fossil faunas of Cambrian seas such as those of Chengjiang in China, the Burgess Shale of British Columbia in Canada, the Sirius Passett fauna of Northern Greenland and the *Orsten* of Sweden to the insect fossils of more-recent times preserved in certain fine-grained terrestrial deposits and the extraordinary amber fossil resin of various ages throughout Mesozoic and Cenozoic times.

Although most of these sites of special preservation (technically known as 'lagerstätten') lie

Arthropod anatomy

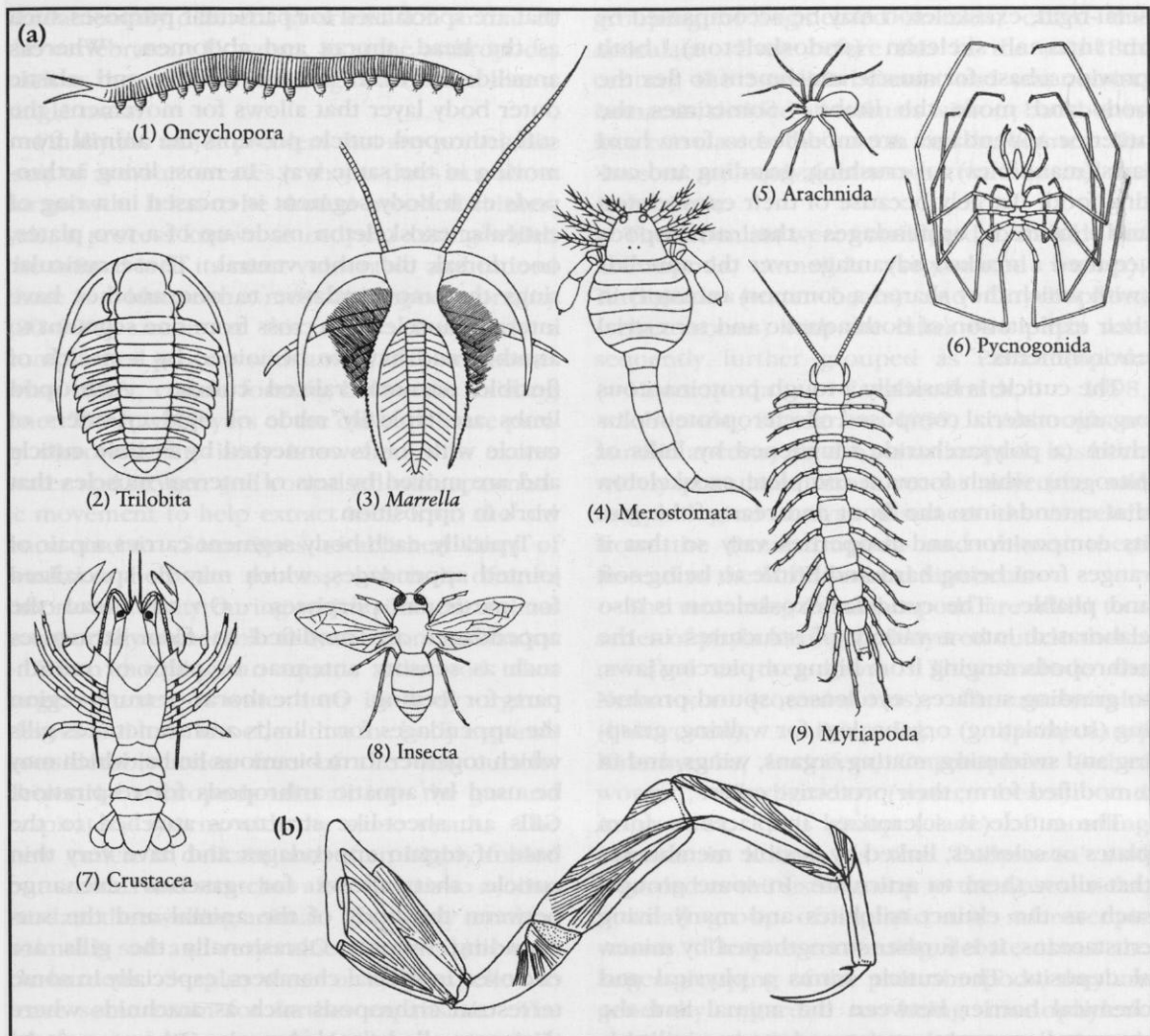


Figure 1.2 (a) Diversity of arthropod types with representative examples of major groups (after Robison and Kaesler, 1987); (b) limb joint and internal musculature in an arthropod leg (after Wigglesworth, 1965).

beyond the British Isles, a newly discovered 'lagerstätten' of Silurian age from Herefordshire in the Welsh Borderlands (see Chapter 2) has already yielded important data about some extinct arthropods and holds considerable potential for future work. There are several British sites that have attained international importance and provide new evidence for major developments in the changing role of arthropods in the history of life. This is especially true for the Scottish Devonian age GCR site of Rhynie (see Chapter 2), which preserves the first early terrestrial ecosystem of plants and animals to be described.

ARTHROPOD ANATOMY

Traditionally, arthropods are portrayed as having certain distinct anatomical characteristics such as a hard outer 'coat' or cuticle and jointed appendages that are used for feeding and movement (see Figure 1.2). Indeed, the name 'arthropod' is derived from the Greek via the Latin *arthron* meaning 'joint' and *podos* meaning 'foot'. The possession of a tough cuticle that is further strengthened by mineralization in some groups has helped increase the fossilization potential of many, but not all, arthropods (see section on 'Fossilization', below). This rigid, or

Introduction to British fossil arthropods

semi-rigid, exoskeleton may be accompanied by an internal skeleton (endoskeleton); both provide a base for muscle attachment to flex the body and move the limbs. Sometimes the anterior appendages are modified to form hard jaws (mandibles) for crushing, grinding and cutting food. Largely because of their exoskeleton and jointed appendages the arthropods acquired a marked advantage over the annelids (with which they shared a common ancestor) in their exploitation of both aquatic and terrestrial environments.

The cuticle is basically a tough proteinaceous organic material composed of scleroprotein plus chitin (a polysaccharide toughened by links of nitrogen) which forms a complete exoskeleton that extends into the front and rear of the gut. Its composition and properties vary so that it ranges from being hard and brittle to being soft and pliable. The cuticular exoskeleton is also elaborated into a variety of structures in the arthropods ranging from biting or piercing jaws, to grinding surfaces, eye lenses, sound producing (stridulating) organs, legs for walking, grasping and swimming, mating organs, wings, and in a modified form, their protective cases.

The cuticle is sclerotized in places to form plates or sclerites, linked by flexible membranes that allow them to articulate. In some groups, such as the extinct trilobites and many living crustaceans, it is further strengthened by mineral deposits. The cuticle forms a physical and chemical barrier between the animal and the surrounding environment and its versatility is probably one of the key innovations that helped promote the success of the arthropods. When toughened it can act as a 'suit of armour' to help prevent attack by predators and physical damage in high-energy environments. On land, the cuticle helps prevent dessication and damage from ultra-violet light, but its general lack of elasticity can also create problems for the animal in obtaining oxygen from its surroundings (respiring), growing and moving. However, the waxy or scaly insect cuticle is flexible. In addition, the inert and insensitive cuticle tissue has to be perforated by fine pores or canals linked to the nervous system so that the animal can sense the surrounding environment.

The arthropod body, like that of the annelids, is divided into segments but unlike annelids, which have very similar body segments, most arthropods show varying degrees of differentiation of the body into specific regions or tagma

that are specialized for particular purposes such as the head, thorax and abdomen. Whereas annelids have an overall flexible and elastic outer body layer that allows for movement, the stiff arthropod cuticle prevents the animal from moving in the same way. In most living arthropods each body segment is encased in a ring of cuticular exoskeleton made up of a two plates, one dorsal, the other ventral. Those cuticular rings that move relative to one another have internal muscles that cross from one segment to another and have to be joined by a stretch of flexible non-mineralized cuticle. Arthropod limbs are typically made of rigid cylinders of cuticle with joints connected by flexible cuticle and are moved by sets of internal muscles that work in opposition.

Typically, each body segment carries a pair of jointed appendages, which may be specialized for particular purposes. On the head the appendages are modified to form structures such as sensory antennae or palps or mouthparts for feeding. On the thorax or trunk region the appendages form limbs and sometimes gills which together form biramous limbs, which may be used by aquatic arthropods for respiration. Gills are sheet-like structures attached to the base of certain appendages and have very thin cuticle that allows for gaseous exchange between the body of the animal and the surrounding water. Occasionally the gills are enclosed in special chambers, especially in some terrestrial arthropods such as arachnids where they are called 'book lungs'. Other terrestrial arthropods breathe by means of branched tracheae – spirally thickened tubes that bring air direct to the tissues. Appendages on the tail or abdomen are often absent but when present may fulfill a number of purposes, for example reproduction.

The body space between the gut and the outer body wall is a blood-filled cavity called a haemocoel, which surrounds the organs and suffuses the tissues. The blood is circulated either by an open-ended dorsal heart or, in large and active arthropods, has specific vessels and a circulation system. The arthropod nervous system is basically comprised of ventral paired nerve cords joined by a ring of nervous tissue around the gut usually to form a single dorsal 'brain' of anterior ganglia. This arrangement is similar to that of the annelids and molluscs, indeed in some primitive arthropods it is barely distinguishable from that of the annelids and

fundamentally different in orientation to that of the vertebrates. However, in some arthropods, such as the mites all the ganglia are fused into a single mass.

Finally the major problem that any non-elastic 'suit of armour' creates is that it does not allow for growth. It has to be shed or moulted at intervals, a process known as ecdysis, during which the animal is at its most vulnerable and indeed there is evidence that most arthropod mortality (80–90%) occurs at this time. Ecdysis is a complicated process with a new, soft, and somewhat larger, cuticle forming below the existing one. The lower layers of the old cuticle are partly dissolved, the body is swollen with excess water and oxygen and convulsed with spasmodic movement to help extract itself from the old encasement. Sometimes established lines of weakness help the process, but it is often a laborious activity during which time the animal is especially vulnerable to attack from predators.

When moulting, an aquatic arthropod takes large volumes of water into its body organs, tissues and haemocoel, so that the body expands considerably once free of the old cuticle. Terrestrial arthropods take air into the gut and respiratory system with the same result. The new cuticle is delicate and often highly folded but unfolds and stretches after ecdysis to accommodate the swelling animal. The newly moulted animal is soft and very vulnerable until the cuticle hardens. Surplus water or air is expelled to leave some room for further expansion. The whole process is expensive in energy, especially as much of the organic material of the old cuticle is wasted but it has proved something of a boon to palaeontologists since it greatly enhances the chances of fossilization. Whole series of the several moult stages are known for many arthropods, especially important groups such as trilobites, ostracods and numerous crustaceans. However, most insects do not have more than one adult moult and confiostracans develop growth lines around the carapace.

ARTHROPOD SYSTEMATICS AND EVOLUTION

Taxonomically, the biological grouping and ranking of the arthropods has been recognized as the phylum Arthropoda since 1848, when the name was introduced by Carl T.E. von Siebold. Since then they have been placed in a larger

grouping of segmented animals, called the Articulata. Even before this in the mid-18th century, the Swedish botanist and taxonomist, Linnaeus, divided all animals without backbones into two classes: the Insecta and the Vermes. His 'Insecta' are equivalent to what we now call the Arthropoda.

The Articulata were considered to include the Arthropoda, Annelida (segmented worms), Tardigrada (water bears) and Onychophora (velvet worms) with the latter two phyla subsequently further grouped as Panarthropoda (=Haemopoda, Cavalier-Smith, 1998, =Lobopoda, Snodgrass, 1938). Although an annelid ancestry for the panarthropods has been widely postulated, more recent molecular and morphological analysis distances the Annelida from the Panarthropoda and relates them instead to the Mollusca and Sipuncula.

The remaining Panarthropoda are allied to a series of phyla having a tri-layered cuticle that is moulted as they grow. They include the Nematoda (roundworms), Nematomorpha (hairworms), Priapulida (priapulans) Kinorhyncha, Loricifera, Onychophora (velvet worms), Tardigrada (water bears) and Arthropoda. This group (clade) of moulting animals is known as the 'Ecdysozoa' and regarded as the sister group to the Gastrotricha, a small group of aquatic and microscopic worms. Despite continuing debate about the larger grouping of the panarthropods, they are generally regarded as being monophyletic although this has also been questioned. However, modern molecular analyses have not supported any of these claims for polyphyly but rather have strengthened the concept of a monophyletic Arthropoda.

Today the arthropods include not only those living and fossil insects, crustaceans, myriapods and chelicerates (spiders and scorpions) but also numerous extinct fossil groups such as the trilobites and eurypterids. There are some arthropod body forms and morphologies that exist only in extinct fossil groups and although many of these fossils are difficult to interpret, without them the overall evolutionary story would be incomplete, simplistic and untrue.

Altogether, the living and fossil arthropods can be placed in at least four major lineages (at the subphylum level), namely the Marello-morpha (the lace crabs), Arachnomorpha (trilobites, arachnids and relatives), Crustaceomorpha and Atelocerata, comprised of the

Introduction to British fossil arthropods

Hexapoda (six-legged arthropods) and Myriapoda (Figures 1.3 and 1.4). There is considerable difference of opinion about the inter-relationships of these groups and the topic is beyond the scope of this introduction. For an overview of the arguments see the contributions to the Systematics Association Special Volume 'Arthropod Relationships' (Fortey and Thomas, 1998).

HISTORY OF INVESTIGATION

The early development of investigation of Arthropods was part of the wider discovery of the fossil record prior to the mid-19th century. There were very few specialist investigators and it was still possible for a competent palaeontologist to have a good grasp of the whole field of palaeontology and to describe almost any new fossil taxa irrespective of their biological affinities. However, the rapid growth of neontology soon made specialization inevitable and this trend eventually impacted upon the study of palaeontology in the 19th century.

The history of investigation of the Arthropods does not have a simple history of progression mainly because the wide palaeontological range of animals involved, from eurypterids to insects, cuts across several specializations. Of these, palaeoentomology has perhaps been the most clearly defined specialization and will be considered first. The history of investigation of the other arthropod groups considered in this volume is dealt with in the following section on the 'Early arthropod evolution and the Cambrian explosion'.

More-detailed information can be found in the recent historical summaries of Rasnitsyn (2002), Grimaldi and Engel (2005) and Smith, R.F. (1973).

It was the invention of the microscope that stimulated some of the first serious investigations of living insects especially some of the small creatures, such as fleas and flies, that played a not insignificant role in the lives of 17th

Figure 1.3. Hierarchical classification of Phylum Arthropoda.

a: includes Cirripedia (barnacles); b: includes orders Arthropleurida, Eoarthropleurida and Microdecemplicida. +: extinct groups. (After Grimaldi and Engel, 2005.)

- Phylum Arthropoda
 - Subphylum †Marellomorpha
 - Subphylum Arachnomorpha
 - Infraphylum †Trilobita (trilobites)
 - Infraphylum Cheliceriformes
 - Superclass †Sidneylida
 - Superclass †Emeraldellida
 - Superclass †Sanctacarida
 - Superclass Chelicerata
 - Epiclass Pycnogonida (sea spiders)
 - Epiclass †Aglaespida
 - Epiclass Euchelicerata
 - Class Xiphosura (horseshoe crabs)
 - Class †Eurypterida (sea scorpions)
 - Class Arachnida
 - Subclass Micrura
 - Order Palpigradi
 - Order †Haptopoda
 - Order †Trigonotarbita
 - Order Araneae (spiders)
 - Order Amblypygida (whip scorpions)
 - Order Uropygida (vinegaroons)
 - Order Schizomida
 - Order Ricinulei (ricinuleids)
 - Order Acari (mites, ticks)
 - Subclass Dromopoda
 - Order †Phalangiotarbida
 - Order Opiliones (harvestmen)
 - Order Scorpiones (scorpions)
 - Order Pseudoscorpionida
 - Order Solfugida (sun scorpions)
- Subphylum Mandibulata
 - Infraphylum Crustaceomorpha
 - †*Martinsonia et al.*
 - Superclass Crustacea
 - Epiclass †Phosphatocopida
 - Epiclass Eucrustacea
 - Class Branchiopoda
 - Subclass Sarsotraca
 - Subclass Phyllopoda
 - Class Remipedia
 - Class Cephalocarida
 - Class Maxillopoda
 - Subclass Thecostraca^a
 - Subclass †Ascothoracida
 - Subclass †Orstenocarida
 - Subclass Tantulocarida
 - Subclass Branchiura (fish 'lice')
 - Subclass Pentastomida
 - Subclass †Skaracarida
 - Subclass Mystacocarida
 - Subclass Copepoda
 - Class Ostracoda
 - Subclass Myodocopa
 - Subclass Podocopa
 - Class Malacostraca (crabs, isopods, etc.)
 - Subclass †Nahecarida
 - Subclass Phyllocarida
 - Subclass Hoplocarida
 - Subclass Eumalacostraca
 - Infraphylum Atelocerata (= Tracheata)
 - Superclass Myriapoda
 - Class Chilopoda (centipedes)
 - Progoneata
 - Class Symphyla
 - Epiclass Dignatha
 - Class Pauropoda
 - Class Diplopoda (millipedes)
 - Subclass Pselaphognatha (polyxenids)
 - Subclass †Arthropleuridea^b
 - Subclass Chilognatha
- Superclass Panhexapoda
 - †*Devonohexapodus et al.*
 - Epiclass Hexapoda
 - Class Entognatha
 - Class Insecta (Ectognatha)

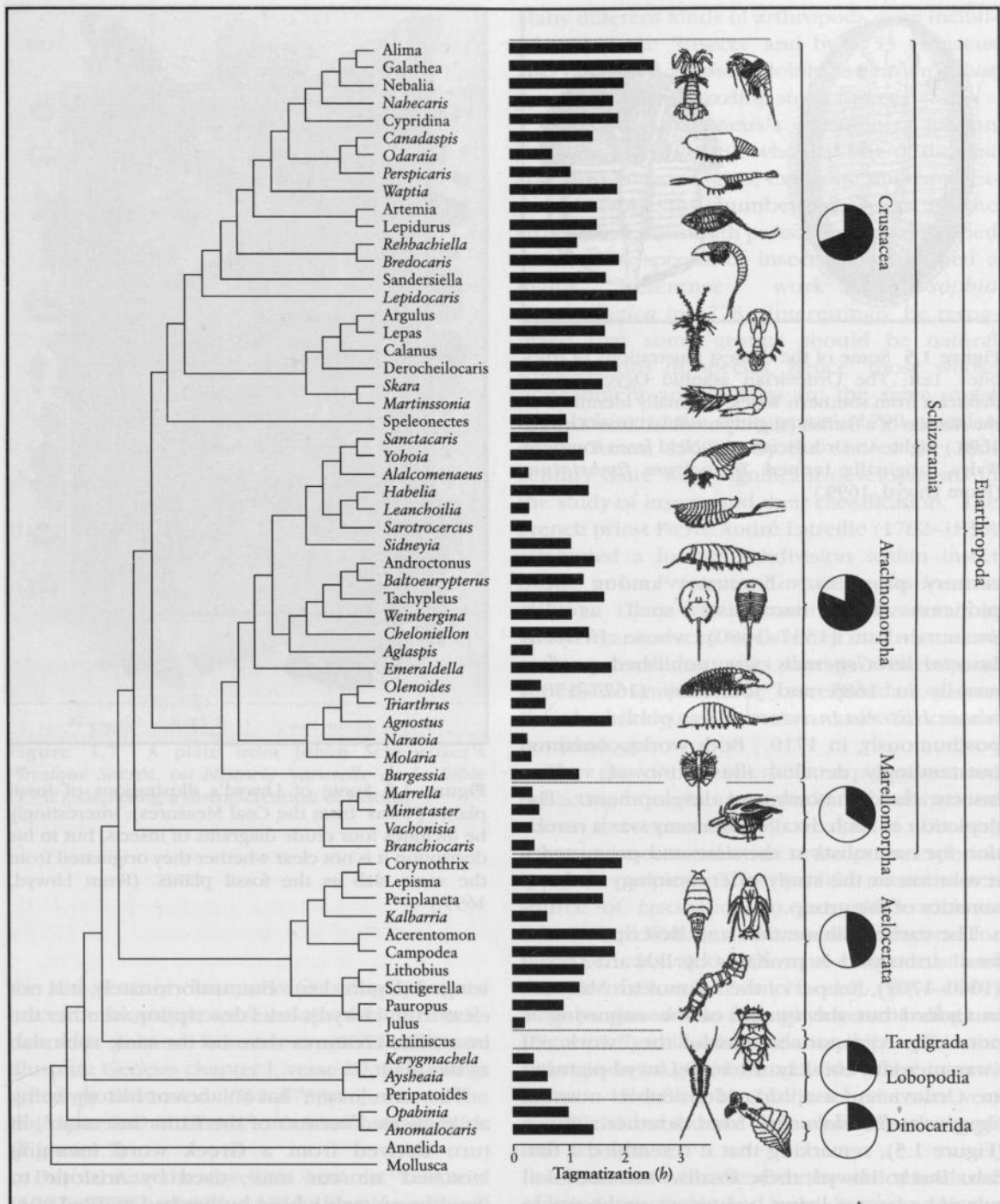


Figure 1.4 Cladogram of fossil (italic type) and Recent (roman type) arthropods. The bar charts illustrate the degree of appendage differentiation and diversity (b) for each taxon. The pie charts indicate the disparity of selected major clades (the sum of ranges on the first 25 principal co-ordinates as a fraction of the value for all arthropods). (After Wills *et al.*, 1997.)

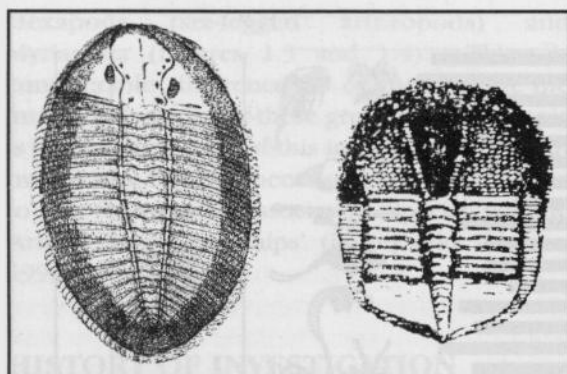


Figure 1.5 Some of the earliest illustrations of trilobites. Left: The Ordovician asaphid *Ogygiocarella debuchii* from southern Wales, originally identified as the skelton of a flatfish (slightly modified from Lhwyd, 1698.) Right: An Ordovician trinucleid from southern Wales, originally termed *Trinucleum fimbriatum* (From Lhwyd, 1699.)

century pioneers. Foremost among these pioneers were naturalists such as Jan Swammerdam (1637–1680) whose *Historia Insectorum Generalis* was published posthumously in 1685 and John Ray (1627–1705) whose *Historia Insectorum* was published, also posthumously, in 1710. Both works contained outstandingly detailed illustration of various insects, their anatomy and development. The depiction of such detailed anatomy was a revelation for naturalists at the time and prompted a revolution in the study of entomology and systematics of the group.

The earliest illustration and description of a fossil arthropod is probably by Edward Lhwyd (1660–1709), Keeper of the Ashmolean Museum in Oxford but the quality of the engraving is poor by comparison with the work of Swammerdam and Ray. In 1698 Lhwyd pictured an Ordovician asaphid, identifiable now as *Ogygiocarella debuchii* from southern Wales (Figure 1.5), remarking that it resembled a flatfish. But to Lhwyd, these fossils were not fossil remains of once living organisms, as he wrote ‘not that I conclude that either of these, or any other Marine-terrestrial bodies, were ever really, either Parts or *Exuviae* of animals’. The following year he published what might be the earliest illustration of fossil insects in his 1699 *Lithophylacii Britannici Ichnographia*. Here an engraving of a Coal Measure plant from the Gloucester region is accompanied by four crude illustrations of insects, one of which is clearly



Figure 1.6 Some of Lhwyd's illustrations of fossil plants ('ferns' from the Coal Measures); interestingly he includes four crude diagrams of insects, but in his description it is not clear whether they originated from the same slab as the fossil plants. (From Lhwyd, 1699.)

winged (Figure 1.6). But, unfortunately, it is not clear from Lhwyd's brief description whether the insect-like creatures were on the same rock slab as the plant.

The term 'insect' has an ancient history, being an anglicized version of the Latin 'insectum', in turn derived from a Greek word meaning 'notched' or 'cut into', used by Aristotle to describe animals whose bodies had marked constrictions or segments such as flies, ants and many worms. Seventeenth century translations of Pliny's works on natural history into the English language, promoted the common use of the word 'insect'. However, the prevailing Judeo-Christian orthodoxy of the Old Testament texts on the creation of life still held a cultural and intellectual stranglehold on the interpretation of the new discoveries of natural history in

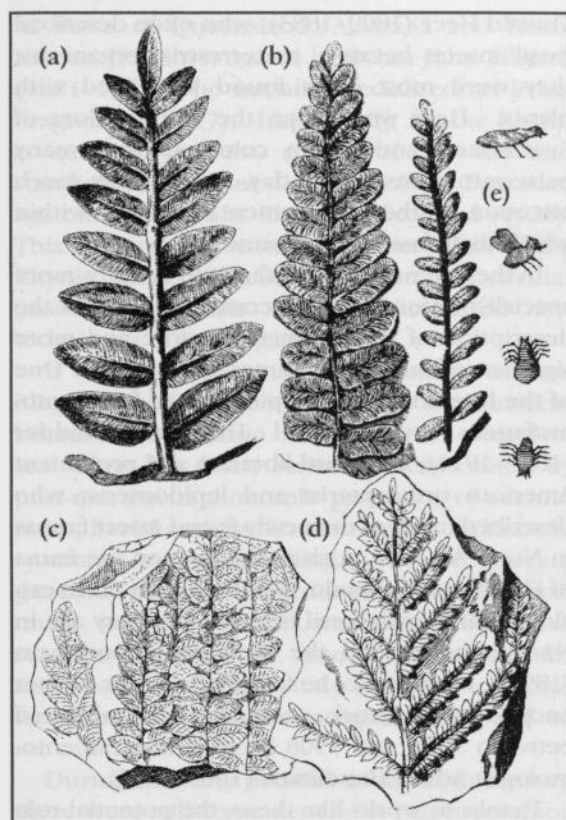


Figure 1.7 A plate from Johan Scheuchzer's *Physique Sacrée, ou Histoire Naturelle de la Bible* (1732), depicting a divine creation of insects.

the 18th century. Swammerdam's illustrations of insect development were co-opted by the Swiss naturalist Johann Scheuchzer (1672–1733) to illustrate Genesis chapter 1, verse 20, in his magnificently illustrated 1732–1733 volume on the *Physique Sacrée Histoire Naturelle de la Bible* (Figure 1.7).

But it was the Swedish botanist Linnaeus (1707–1778) who in 1735 first formalized 'Insecta' as a taxonomic Class of invertebrate animals. He further subdivided the group into orders, such as Aptera, Diptera, Hymenoptera and Neuroptera based on the number and appearance of wings and some other structural features. His classification was solely a matter of 'ordering' what he regarded as fixed immutable species as part of his search for an underlying design and had no evolutionary significance.

Many different kinds of arthropods were included within the 'Insecta' and by 1753 Linnaeus also described a fossil trilobite as *Entomolithus paradoxus* – or 'puzzling stone insect'.

However, Linnaeus's student Johann Fabricius (1745–1808), who was one of the first specialist entomologists, extended the classification beyond the number of wings to the structure of the mouth parts. Fabricius described some 9776 species of insect and published a major reference work *Philosophia Entomologica* in 1778. Interestingly, he recognized that some groups should be natural combinations of species, hence 'those whose nourishment and biology are the same, must then belong to the same genus' (1790, translated by Tuxen, 1967). By the end of the 18th century there were significant developments in the study of insects and their classification. The French priest Pierre André Latreille (1762–1833) attempted a further subdivision within insect orders in his *Précis des Caractères des Insectes* (1796). There was a growing realization that many organisms can be classified into what seem to be natural groupings that go well beyond superficial similarities or 'correspondances' into their underlying anatomy and functional morphology.

The growth of scientific exploration and collecting brought an explosion of information about the extraordinary wealth of diversity amongst insects and other arthropods, especially in the tropics. Their prolific nature was a source of fascination to naturalists such as Darwin and Wallace and a source of income for the latter. It was the German evolutionist and disciple of Darwin, Ernst Haeckel (1834–1919) who produced the first phylogenetic diagram (Figure 1.8) to illustrate relationships within the arthropods in general and with other invertebrates. However, Haeckel's scheme was very superficial and did not take any fossil arthropods into account.

In contrast with the diversity and abundance of living insects that had been discovered by the mid-19th century, their extinct fossil antecedents were apparently impoverished in their diversity and abundance. The one exception was the insect fauna entombed in Baltic amber which had been collected and valued for centuries. The first scientific description of fossil insects, using the Linnean binomial scheme for nomenclature, was published by the German naturalist Marcus Elieser Bloch (1723–1799) in 1799. The

Introduction to British fossil arthropods

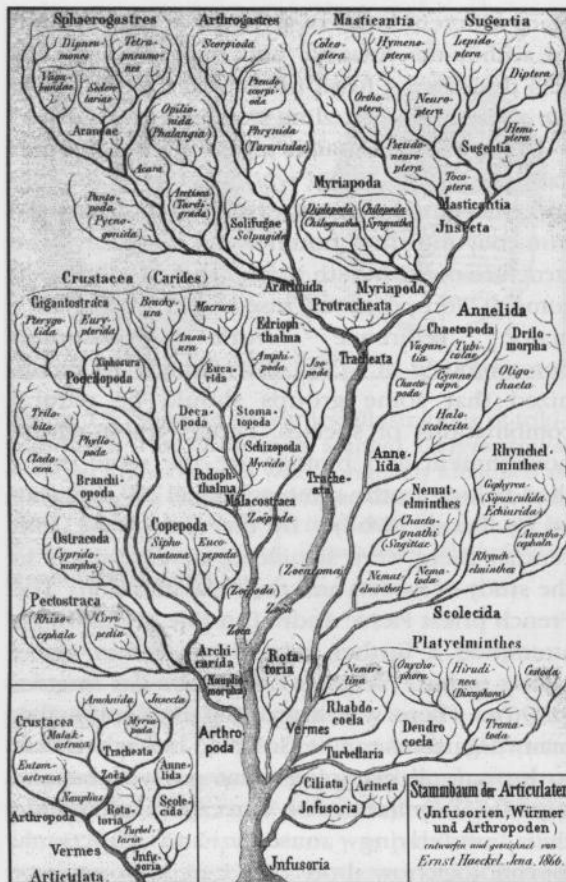


Figure 1.8 The first phylogenetic diagram depicting relationships among insects and other arthropods. Insects were divided into Masticantia and Sugentia for the masticating and sucking insects in this interpretation. (From Haeckel, 1866.)

relative richness of fossil insects, associated with this amber source, was first illustrated in the 1830s by another German, Ernst Friedrich Germar (1786–1859), who was a professor of mineralogy in Halle. Germar was also one of the first to describe in detail the remarkable fossil insects that were being found in increasing numbers from Carboniferous strata.

It was the French entomologist Charles Brongniart (1859–1899) who made the most significant contribution (1893) to the study of the Carboniferous (Stephanian age) insects from Commentry in France. Such descriptions by specialist entomologists such as Brongniart was not particularly common at the time and fossil insects tended to be described among other fossils with which they were found. Indeed, it was fossil plant specialists, such as the botanist

Oswald Heer (1809–1883), who often described fossil insects because, as terrestrial organisms, they were most often found associated with plants. Heer worked on the Tertiary flora of Switzerland and, as in common with many palaeontologists of the day, did not pay much attention to the environmental context within which their fossils were found.

In the latter decades of the 19th century, more specialist entomologists became involved in the description of fossil insects as more and more significant fossil insect faunas were found. One of the foremost of these pioneers of fossil entomofaunas was Samuel Hubbard Scudder (1837–1911), a Harvard librarian and prominent American orthopterist and lepidopterist who described many of the newly found insect faunas in North America, such as the Eocene age fauna of Florissant, Colorado. Scudder went on to catalogue all known fossil insects of Tertiary age in North America and the literature about them (1890). In doing so, he laid the basis for further encyclopaedic work such as that published between 1906 and 1908 by the Viennese entomologist Anton Handlirsch (1865–1935).

Thanks to works like these, the potential role of fossil insects in understanding the phylogeny of the group as a whole was much better appreciated by the early decades of the 20th century. In 1925, the Russian entomologist Andrey Vassilievich Martynov (1879–1938) proposed a new classification of the Insecta that raised questions about their phylogeny and prompted his interest in their fossils. However, Martynov's work was not fully appreciated in the West, despite being deliberately multilingual.

One entomologist who did know of Martynov's work was the American, Harvard-based entomologist, Frank Morton Carpenter (1902–1994) who generated another of the great milestones in the study of palaeoentomology with his two volumes on insects for the *Treatise on Invertebrate Palaeontology* (1992). Carpenter had initially specialized in living Neuroptera but became increasingly interested in a wide range of fossil insects, especially the phylogenetically important Permian-age entomofauna of Kansas on which he published a number of studies. Both Carpenter and Martynov set new standards in the description and illustration of fossil insects.

The importance of Palaeozoic and Permian-Triassic fossil insects was increasingly appreciated as new entomofaunas were discovered, such

as those of Queensland, Australia and Elmo, Kansas, USA investigated by Robin John Tillyard (1881–1937) who initially specialized on living dragonflies (1917). Importantly, for the British context, Tillyard also commented on the outstandingly important discovery of the Devonian age entomofauna at Rhynie in Scotland (1928). This site and the nature of preservation of the Rhynie fossils in chert presented particular problems for their study and required new techniques of investigation.

It was a not uncommon problem for entomologists who became interested in fossil insects, because preservation is hardly ever complete and often has been seriously deteriorated by post-mortem taphonomic processes of recruitment, burial and fossilization within sedimentary strata. An understanding of such processes is generally necessary in order to extract the maximum amount of information from fossil remains. Additionally, insects are too big for micropalaeontological study and often too small for normal macropalaeontological study and so are often overlooked.

During the early decades of the 20th century, there were still some generalist palaeoentomologists such as the American T.D.A. Cockerell (1866–1948). He continued the publication of the Florissant entomofauna, but also described a large range of different fossil insect faunas of differing age in some 4000 publications during his lifetime. But this 'natural history' stage, as it has been called, in the history of investigation, during which the emphasis on description and the amassing as much data as possible, gradually became less important. As a result, many species remained undescribed and taxonomic lists are only now being updated. Interest grew in specific faunas that were important phylogenetically and in phylogeny and systematics in general as well as a variety of topics within fossil insect ecology, such as insect–plant interactions, the reconstruction of past insect communities and topics such as palaeobiogeography.

Of particular importance in the development of palaeoentomological study was the establishment of the Arthropoda laboratory in the Palaeontological Institute of the USSR Academy of Sciences in Moscow which was briefly led by Martynov before his death in 1938. Many new sites with rich fossil entomofaunas were discovered across the various republics of the old Soviet Union and numerous outstanding Russian specialists from Martynov's laboratory

worked on them, such as Boris Borisovich Rohdendorf (1904–1977) and A.P. Rasnitsyn, especially after the Second World War. Because the Russians could not travel beyond the former USSR, they had to study their own fossil faunas, including the insects, and produce comprehensive monograph on them.

Meanwhile the study of all aspects of insect biology and ecology had made significant advances, especially with the development of genetic studies. Such were the advances in comparative anatomy that numerous problems arose in the study of insect systematics and phylogeny.

Most influential in tackling these problems was the German entomologist Willi Hennig (1913–1976) whose new cladistic approach to systematics was to produce the first significant revolution in the whole approach to systematics since Linnaeus introduced the Latin binomial scheme in the mid-18th century. Hennig's major works on insect phylogeny (1953, 1969, see Figure 1.9) took some time to gain a foothold, but by the latter decades of the 20th century, when they had been translated into English, Hennig spawned a whole new methodology called cladistics that incorporated linnaean classification. From his extensive knowledge and experience of entomology, Hennig rightly stressed that similarities do not necessarily equal natural (i.e. evolutionary) relationships and offered a precise definition of biological relationship based on advanced characteristics. His lead has now been followed by many palaeontologists but problems remain, especially for the interpretation of different kinds of information derived from living and fossil organisms.

Recent decades have seen a renaissance in entomological studies with an assimilation of fossil and neontological work (Figure 1.10) epitomized by two recent encyclopaedic works that review the whole field of study, namely the Russian compilation edited by Rasnitsyn and Quicke (2002) and the American volume *Evolution of the Insects* written by David Grimaldi and Michael S. Engel (2005).

The British Context

Of the British naturalists who were pioneer investigators of fossil insects during the middle and latter part of the 19th century, the Rev. Peter Brodie and Herbert Goss were pre-eminent. Brodie's 1845 book *A History of the Fossil*

History of investigation

Insects in the Secondary Rocks of England was a seminal work and is 'still a significant work today' according to Jarzembowski (1989, p. 440), in his review of the investigation of British fossil insects. By comparison Goss did not originate much new work but over the 12 years from 1878 to the turn of the century he produced a series of articles that reviewed progress in palaeontology becoming Goss and Brodie and these were collected in a 1900 synopsis. Jarzembowski's 1989 review continues the tradition established by Goss and is addressed to entomologists and palaeontologists.

By the turn of the 19th century British palaeontological interest was including the study of older insects, especially those of Carboniferous times. Since Upper Carboniferous Coal Measure strata included terrestrial deposits, fossil insects stood a better chance of being preserved and found than in the predominantly marine Lower Carboniferous rocks. Discovery of coal measure insects went hand in hand with the exploitation of coal. Bolton's monograph of the fossil insects of the British Coal Measures (1921–2) is still a key work on British Palaeozoic insects since no insects have been found yet in British Permian strata. Interest in, and investigation of, British Coal Measure insects and other arthropods has been re-stimulated in recent decades by the re-working of colliery tip rock debris from the Writhlington Geological Nature Reserve (Jarzembowski, 1989a, 2004).

The only British fossil insects of pre-Carboniferous age are those discovered in the early Devonian age Rhynie Chert by the Reverend W. Cran and described in 1926 by Hirst and Maulik. Nevertheless, this particular species *Rhyniella praecursor* is of enormous importance as the earliest known insect (hexapod) and was apparently well adapted for life in a semi-aquatic environment and must have had as yet unknown precursors.

After Brodie's pioneering work, no further comprehensive study of British Mesozoic insects has appeared. However, as Jarzembowski relates in his review (1989a), there have been a

Figure 1.10 Geological range of major insect groups. (After Harland *et al.*, 1982 and Jarzembowski, 1989.)

Apterygota auct.		
Order	Collembola (Springtails)	Devonian–Recent
Order	Diplura (Two-tailed Bristletails)	Carboniferous–Recent
Order	Protura	Recent (only)
Order	Thysanura auct. (Three-tailed Bristletails)	Devonian–Recent
Pterygota: Palaeoptera		
Order	Diaphanopteroidea	Carboniferous–Permian
Order	Ephemeroptera (= Plectoptera; Mayflies)	Carboniferous–Recent
Order	Megaseoptera	Carboniferous–Permian
Order	Odonata (Dragonflies and Damselflies)	Permian–Recent
Order	Palaeodictyoptera	Carboniferous–Permian
Order	Protodonata auct. (Giant Dragonflies)	Carboniferous–Permian
Pterygota: Neoptera: Polyneoptera		
Order	Blattodea	Carboniferous–Recent
Order	Caloneuroidea	Carboniferous–Recent
Order	Dermaptera (Earwigs)	Jurassic–Recent
Order	Embioptera (Web-spinners)	Palaeogene–Recent
Order	Grylloblattodea	Recent (only)
Order	Isoptera (Termites)	Cretaceous–Recent
Order	Mantodea (Praying Mantises)	Palaeogene–Recent
Order	Miomoptera	Carboniferous–Permian
Order	Orthoptera (Crickets, Grasshoppers and Locusts)	Carboniferous–Recent
Order	Phasmida (Stick Insects)	Triassic–Recent
Order	Plecoptera (Stoneflies)	Permian–Recent
Order	Protelytroptera	Permian (only)
Order	Protothoptera	Carboniferous–Permian
Pterygota: Neoptera: Paraneoptera		
Order	Anoplura (Sucking Lice)	Quaternary (only)
Order	Hemiptera ([True] Bugs)	Permian–Recent
Order	Mallophaga (Biting and Bird Lice)	Recent (only)
Order	Psocoptera (Book and Barklice)	Permian–Recent
Order	Thysanoptera (Thrips)	Permian–Recent
Order	Zoraptera	Recent (only)
Pterygota: Neoptera: Oligoneoptera (= Endopterygota = Holometabola)		
Order	Coleoptera (Beetles)	Permian–Recent
Order	Diptera ([True or Two-winged] Flies)	Permian–Recent
Order	Glosselytroidea	Permian–Jurassic
Order	Hymenoptera (Wasps, Ants and Bees)	Triassic–Recent
Order	Lepidoptera (Moths and Butterflies)	Jurassic–Recent
Order	Mecoptera (Scorpionflies)	Permian–Recent
Order	Neuroptera auct. (Lacewings, Alderflies and Snakeflies)	Permian–Recent
Order	Siphonaptera (Fleas)	Cretaceous–Recent
Order	Strepsiptera (Stylopids)	Palaeogene–Recent
Order	Trichoptera (Caddisflies)	Permian–Recent

number of detailed studies of some of the Triassic and Jurassic orders of British fossil insects. Since the Stonesfield Slate quarries ceased production, the supply of new mid-Jurassic age insects has all but ceased, although the classic Lower Liassic outcrops along the coast at Charmouth continue to provide a trickle of specimens. The late James Jackson was the main collector from this source since the late 1940s and his material was described by Zeuner (1962) and Whalley (1985). Our knowledge of the insect life of Cretaceous times in Britain continues to be enhanced by numerous recent discoveries from several sites especially within the Weald Clay (e.g. Jarzembowski, 1977, 1987, 1989a, 1995).

By comparison, British insects of Tertiary age have never been comprehensively studied or monographed. Few fossils were recovered from British Tertiary strata until the 20th century and then were recovered from rocks of early Tertiary age because no late Tertiary age strata are preserved. The oldest insect fauna was found in the Palaeocene age Ardtun Leaf Beds of Mull in the Western Isles of Scotland. A small insect fauna of crickets (orthopterans), beetles (coleopterans), bugs (hemipterans), caddis flies (trichopterans) and flies (dipterans) was recovered from these 54 Ma plant-rich clays (see Emeleus and Gyopari, 1992, p 153–6; Daley and Balson, 1999, p 4–5; Cleal *et al.*, 2001, p. 181–4) interbedded with basalt lavas within the British Igneous Province and first described by Zeuner (1941). Some beetles and insect traces (e.g. leaf mines) have been recovered from the late Palaeocene age Woolwich and Reading Beds from various localities in southern England. However, the most famous and abundant insect fauna has been recovered from the Lower Eocene age London Clay outcrop on the foreshore at Bognor Regis in Sussex. Known as the 'Beetle Bed' it was collected over many years by E.M. Venable (1963). Venable and Taylor (1963) suggested that other coastal exposures of the London Clay in southern England might also contain similarly preserved faunas and they have indeed been subsequently found at Herne Bay in Kent (Cooper, 1977). An important fossil fauna of 250 species of hymenopterans and dipterans and at least a dozen other orders have also been recovered from the so-called 'Insect Limestone' in the Bembridge Marls of late Eocene/early Oligocene age in the Isle of Wight. This most important fauna is actively being re-investigated.

EARLY ARTHROPOD EVOLUTION AND THE CAMBRIAN 'EXPLOSION'

In recent years fossil arthropods have come to play an increasing role in discussions and arguments about the early evolution of shelled organisms, the so-called 'Cambrian Explosion' (for a review see Fortey *et al.*, 2004, and Budd and Jensen, 2004). For over a century, palaeontological investigation of the fossil record seems to have shown that around 545 Ma, at the beginning of Cambrian times, most types of animals (phyla) suddenly appeared. Since then new discoveries have extended the fossil record much deeper back into Precambrian times. But most of that older record is microscopic, until around 580 Ma, when macroscopic organisms appear in Vendian times. The evolutionary relationships of these Vendian fossil organisms, the so-called 'Ediacaran Fauna' (named after the Ediacara Hills in the Flinders Range of South Australia from where the fossils were first described), which were soft-bodied organisms, is still disputed. Some of them may belong to living groups such as the sea-pens (Pennatulacea) and the annelids, but others appear to be completely extinct. Others have even been claimed to be ancestral to the arthropods. But the shelled record of most surviving invertebrate phyla, such as molluscs, echinoderms and arthropods, all seems to begin suddenly about 545 Ma (Figures 1.11 and 1.12).

If this sudden appearance of the shelled record is true, then there must have been an extraordinary burst in evolutionary activity over a period of not much more than 10 million years (Conway Morris, 1997). However, since the 1990s a number of discoveries has led to an overhaul of this view. Is such rapid evolution possible or is the fossil record of these times somehow distorted? There have been claims that the rock record at this interval is unusually condensed and actually represents a longer period of time than previously thought. However, a more favoured view is that the sudden event was the acquisition of mineralized skeletons by a variety of already established soft-bodied organisms whose fossilization potential was suddenly enhanced. If this were true, then the earlier evolution of the macroscopic invertebrates in late Precambrian times could well be hidden or obscured in the fossil record, simply because they were not being fossilized.

Detailed description of the exceptionally pre-

Early arthropod evolution and the Cambrian 'Explosion'

Taxa (number of genera)	Observed geological ranges
Superclass Trilobitomorpha	Proterozoic(?); Cambrian–Permian
Class Trilobita (1401)	Cambrian–Permian
Class(es) uncertain (16)	Proterozoic(?); Cambrian–Devonian
Superclass Crustacea	Proterozoic(?); Cambrian–Holocene
Class Branchiopoda (119)	Proterozoic(?); Cambrian–Holocene
Class Malacostraca (586)	Cambrian–Holocene
Class Ostracoda (1900)	Cambrian–Holocene
Class Cirripedia (107)	Silurian–Holocene
Class Euthycarcinoidea (2)	Triassic
Class Copepoda (2)	Miocene–Holocene
Class Cephalocarida (1)	Cambrian–Holocene
Class Mystacocarida	Holocene
Class Branchiura	Holocene
Superclass Chelicerata	Cambrian–Holocene
Class Merostomata (89)	Cambrian–Holocene
Class Arachnida (289)	Silurian–Holocene
Superclass Pycnogonida	Devonian–Holocene
Class Pantopoda (1)	Devonian–Holocene
Superclass Onychophora	Cambrian–Holocene
Class(es) uncertain (2)	Cambrian–Holocene
Superclass Myriapoda	Silurian–Holocene
Class Archipolypoda (8)	Silurian–Pennsylvanian
Class Arthropleurida (1)	Pennsylvanian
Class Diplopoda (23)	Pennsylvanian–Holocene
Class Chilopoda (5)	Cretaceous–Holocene
Class Symphyla (1)	Oligocene–Holocene
Class Pauropoda	Holocene
Superclass Hexapoda	Devonian–Holocene
Class Collembola (25)	Devonian–Holocene
Class Insecta (±5000)	Pennsylvanian–Holocene
Class Protura	Holocene
Class Diplura	Tertiary–Holocene
Superclass Pentastomida	Holocene
Class Linguatulida	Holocene
Superclass Tardigrada	Holocene
Class Eutardigrada	Holocene
Class Heterotardigrada	Holocene

Figure 1.11 Classification of Arthropoda (after Boardman, 1987) with number of fossil genera known in 1987 for each class and thus illustrating the bias of the fossil record towards preservation of some groups rather than others.

served early Cambrian biotas (lagerstätten) of Chenjiang in China, Sirius Passet in northern Greenland and the younger, mid-Cambrian Burgess Shale of British Columbia in Canada and the late Cambrian *Orsten* of southern Sweden have all revealed a remarkable diversity of organisms. Not only had the whole range of invertebrate phyla evolved by early Cambrian times, but also the early chordates and even perhaps the vertebrates (Conway Morris, 2000).

However, within these early established invertebrates, the arthropods show the greatest diversity with representatives from three major groups, the onychophorans (velvet worms, such as the living *Peripatus* and the Cambrian *Aysheaia*), extinct trilobites and chelicerates all present. Even the crustaceans were thought to be represented by *Canadaspis* in the Burgess Shale but this affiliation has since been disputed. Recently however, another more secure fossil crustacean has been found in early Cambrian strata in Britain (see below).

Not only is there high level taxonomic diversity but ecological analysis of individual species of arthropods suggests that niche diversification was already highly developed in these marine communities, all of which suggests that their

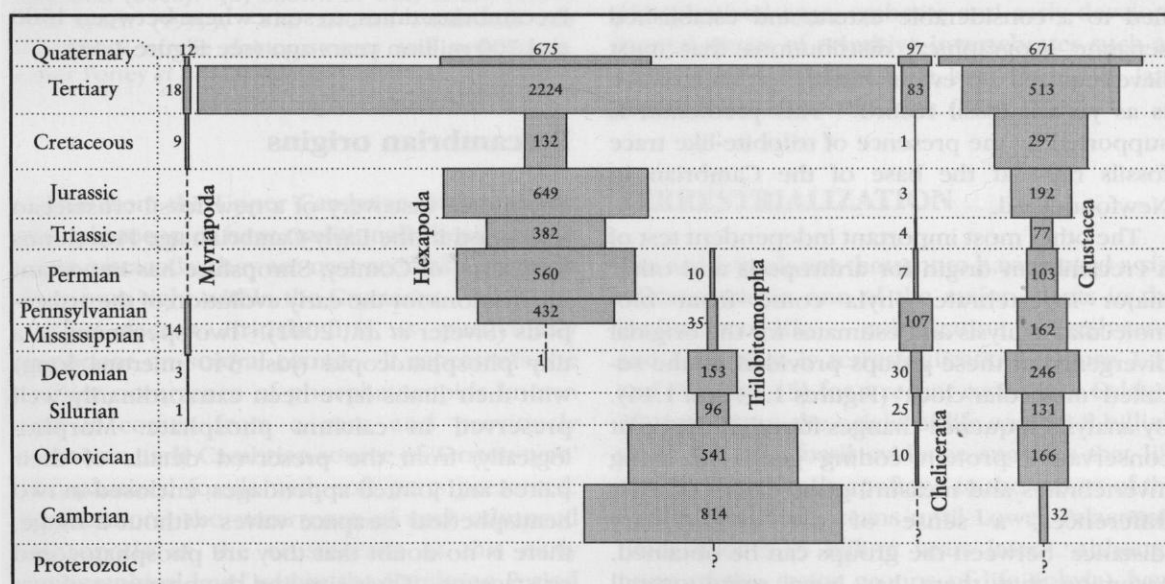


Figure 1.12 Geological distribution of the major arthropod superclasses based mostly on data compiled from the *Treatise on Invertebrate Paleontology* (Moore, 1955–1969). Numbers indicate the fossil genera in each superclass. Data on generic diversity of the Hexapoda was supplied by F.M. Carpenter. (After Robison and Kaesler, 1987.)

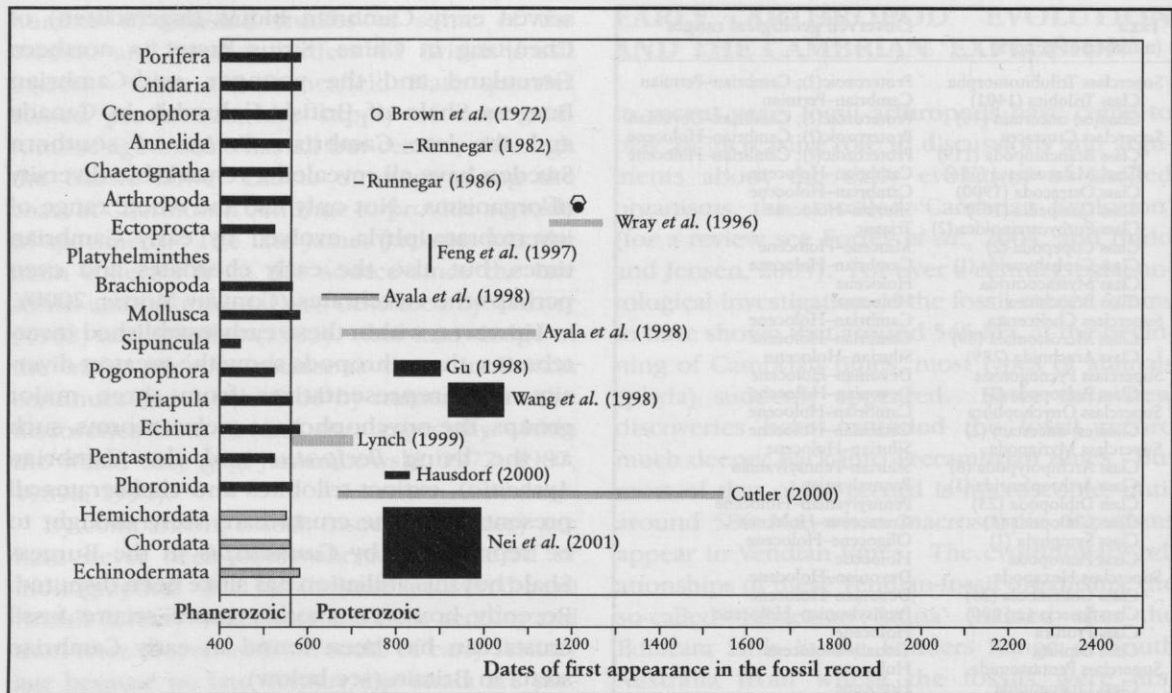



Figure 1.13 The confidence intervals on times of divergence between protostome and deuterostome phyla as measured by recent studies. Estimates are sorted in chronological order; dots indicate point estimates. Line thickness indicates number of genes analysed; black lines, grey lines and the ribosome image  indicate nuclear, mitochondrial and 18S genes used in the analyses respectively. (After Fortey *et al.*, 2004.)

ancestry must pre-date the start of Cambrian times and the ‘shelly’ fossil record (Whittington, 1980). In addition trilobites had already diversified to a considerable extent and established separate geographical distributions that must have required a previous history for which there is as yet no fossil record. This prediction is supported by the presence of trilobite-like trace fossils right at the base of the Cambrian in Newfoundland.

The other most important independent test of a Precambrian origin for arthropods and other major invertebrate phyla come from bio-molecular analysis and estimates for the original divergence of these groups provided by the so-called ‘molecular clock’ (Figures 1.13 and 1.14). By analysis sequence changes found in the most conservative protein coding genes of living invertebrates and measuring the extent of their differences, a sense of the evolutionary ‘distance’ between the groups can be obtained. Assuming that there has been some overall clock-like regularity in these changes and knowing the average rate of change, it is possible to calculate the timing of their divergence.

Although these are very crude measures and

there is considerable argument about their methods and reliability, nevertheless their divergence times all descend well into Precambrian times, to somewhere between 1500 and 700 million years ago (see Figure 1.13).

Precambrian origins

The recent discovery of a new fossil crustacean arthropod in the Early Cambrian age Protolenus Limestone of Comley, Shropshire has important implications for the early evolution of the arthropods (Siveter *et al.*, 2001). Two specimens of a tiny phosphatocopid (just 340 microns long) with their limbs have been extraordinarily well preserved in calcium phosphate. Morphologically, from the preserved details of their paired and jointed appendages, enclosed in two hemispherical carapace valves without a hinge, there is no doubt that they are phosphatocopid crustaceans. Their size and the presence of just four pairs of limbs suggest that the specimens represent an early instar (developmental stage) and they may even be the first instar, closely comparable to the first instars of phosphato-

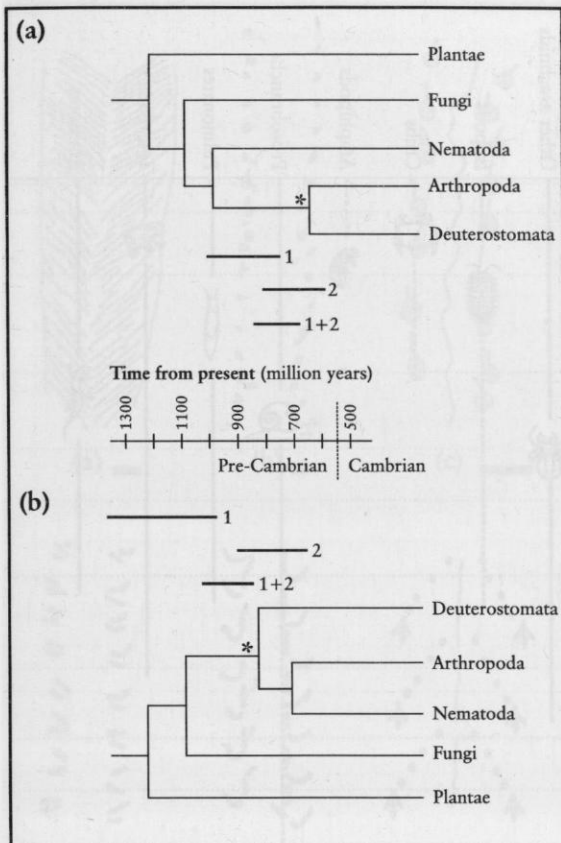


Figure 1.14 Alternative topologies that have been used in divergence time estimation papers. (a) Shown in Wang *et al.*, 1998, Nei *et al.* (2001) and Hausdorf (2000). (b) Shown in Wray *et al.*, (1996) and Lynch (1999). The asterisk symbolizes the divergence of the deuterostomes and arthropods. (After Fortey *et al.*, 2004.)

copids from the Upper Cambrian. Although the phosphatocopids have traditionally been regarded as ostracods, they are now seen as a group in their own right within the Crustacea.

This recent British find is particularly important on several counts. It represents the earliest occurrence of phosphatocopids known and it comes from a rare and previously unknown early Cambrian source of 'Orsten-type' phosphatized fossils with soft parts preserved. Furthermore, the occurrence of such advanced arthropods as the crustaceans at this early stratigraphical level within the Cambrian Period has implications for the early diversification of the arthropods as a whole.

The Crustacea comprise one of the major groups of living arthropods and include such

diverse animals such as crabs, shrimps, lobsters, ostracods and slaters. As a group they are generally regarded as being among the more advanced arthropods and more closely related to the insects than to more primitive groups such as the trilobites, chelicerates (scorpions, horseshoe crabs and spiders), millipedes and centipedes. This evidence for the presence of crustaceans so early in the fossil record of arthropods strongly suggests that the earlier evolutionary steps to the crustacean form must have been even earlier, that is, in Precambrian times.

It is now becoming increasingly clear that the enormous diversity of arthropods is descended from a common ancestor. The onychophorans (velvet worms) are probably the most closely related group to the arthropods and the two must have diverged earlier than their first appearance in the fossil record. In addition, the arthropods may be part of an even bigger grouping called the ecdysozoans, animals which habitually moult in order to grow. Again, the origin and early divergences of the ecdysozoans must extend even further back in late Precambrian times. The search for the cryptic ancestors of the arthropods and other invertebrates is now well under way. Strata bearing primary phosphate deposits are being targeted since the discovery of preserved soft tissues within phosphatized fossils. In recent years remarkable discoveries of phosphatized eggs, embryos and early developmental stages of primitive invertebrates such as sponges and cnidaria have been found in late Precambrian strata of China (Xiao 1998).

TERRESTRIALIZATION

The arthropods are thought to have played a significant role in one of the major events in the evolution of life – colonization of freshwater and land, that is terrestrialization (Figure 1.14 and Figure 1.15) for a recent review see Selden, 2001a). Since the origin of life some 3.8 billion years ago, the fossil evidence suggests that life was predominantly confined to the waters of the Earth's seas and oceans until Lower Palaeozoic times over 3.35 billion years later. Although none of the major groups of life (phyla) have originated on land equally, none of the major groups of land living organisms have become extinct. So it would seem that although the transition from water to land was very difficult,

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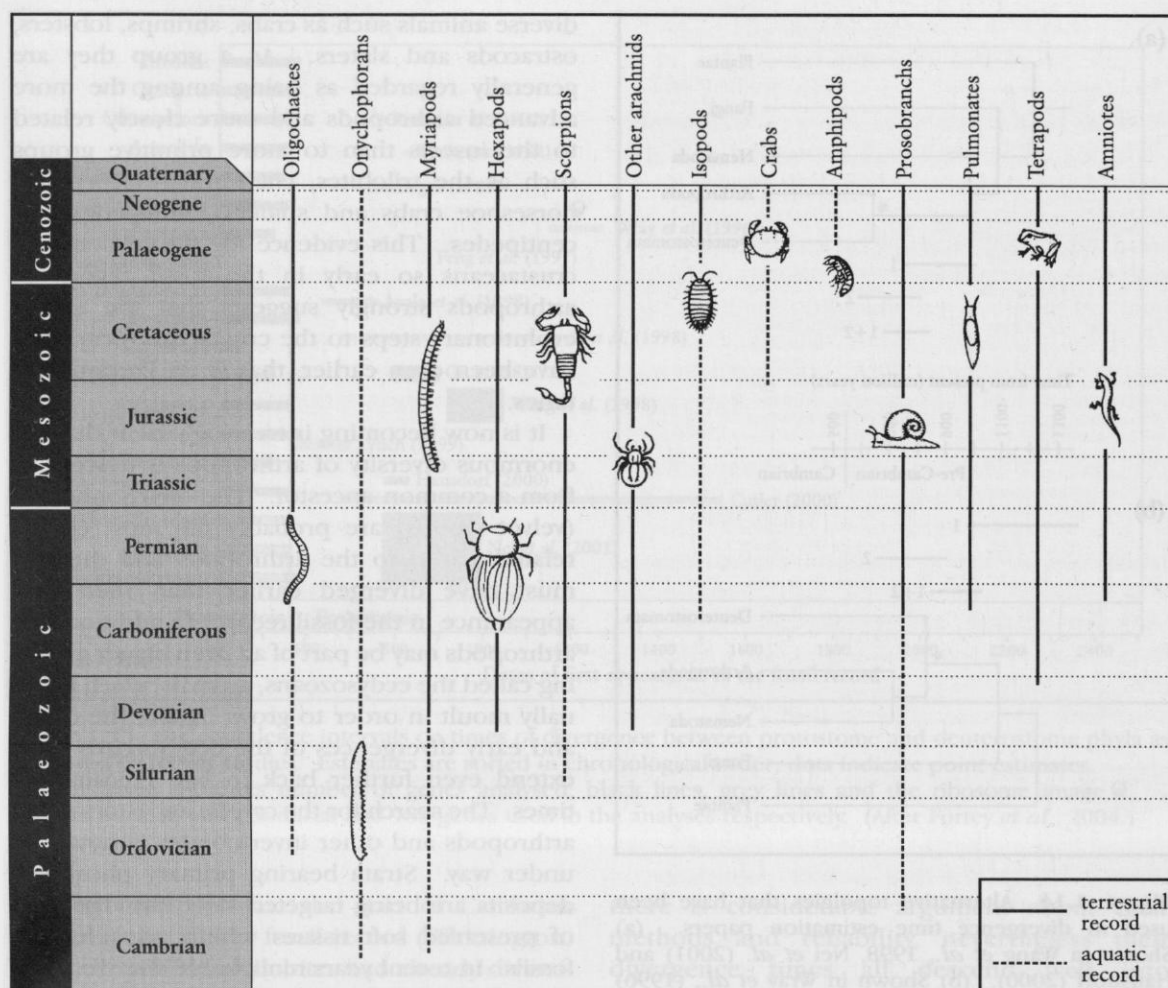


Figure 1.15 Approximate sequence of major events in the invasions of the land by animals, as known from the fossil record. (After Selden and Edwards, 1989.)

once life was adapted to the rigours of *terra firma*, it became securely established there. The interesting questions have always been why, when and how did that terrestrialization event happen and what organisms were able to make the transition first?

Animals moving from water to land have to cope with very different environments and circumstances which demand profound changes in their biology and ways of life. Water is a relatively stable, dense and supportive medium compared with air. Most aquatic environments experience less change in their physical and chemical parameters than does any given sub-aerial environment mainly because the temperature, pressure and humidity of air is in constant flux, at least on a daily basis (except in caves).

Any organism moving out of the water is confronted with life in a light, relatively dry gas and is subjected to fluctuating temperatures, dessication, oxidation and bombardment by ultra-violet rays. To move, the animal has to struggle against gravity to support its own weight and overcome the very varying friction and topography of the ground surface. Vision in air, which has a different refractive index from water, is another difference, but one of the few compensations is that in air, high frequency sound vibrations can be more easily detected. All life processes from breathing and feeding to reproduction impose new demands and difficulties on land. Viewed in this light, it seems surprising that life left the water at all, but after 3.35 billion years of evolution life in the seas and

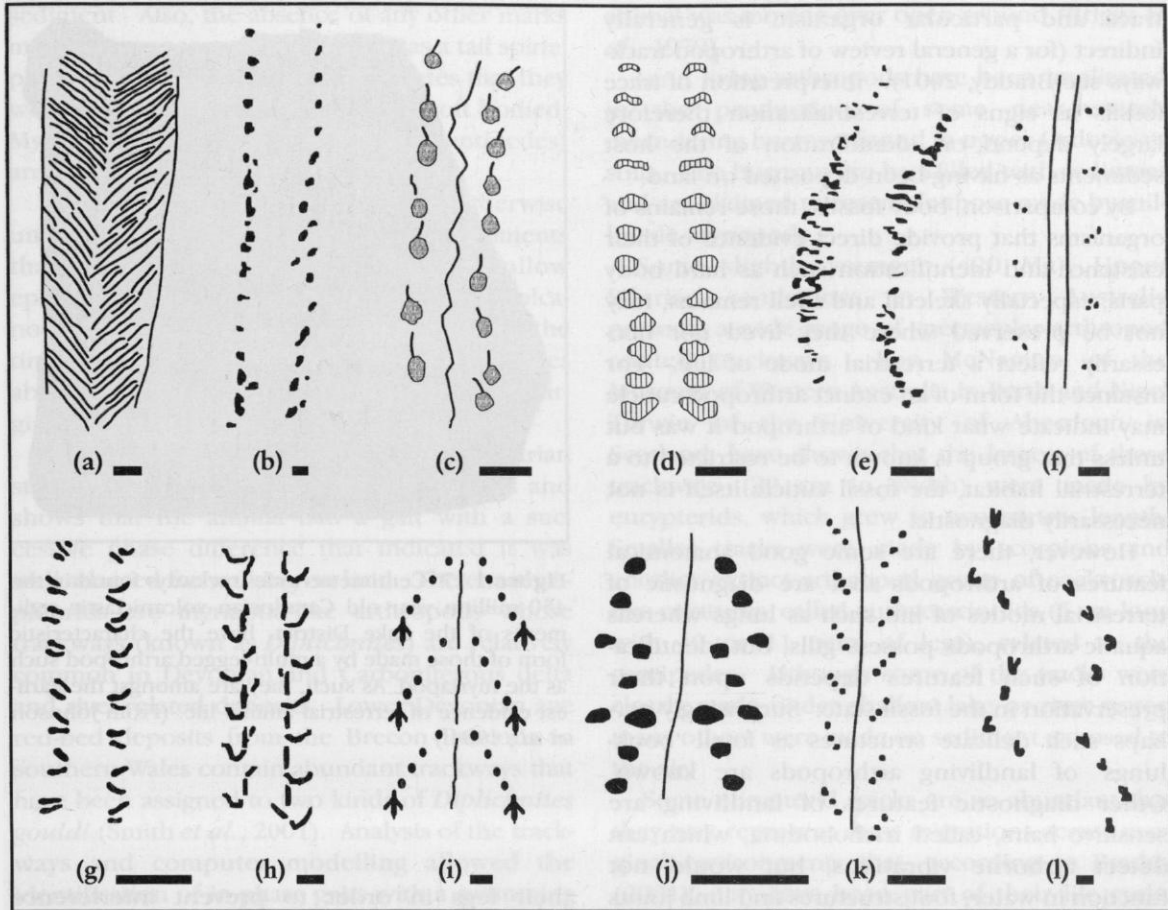


Figure 1.16 Selected arthropod trackway ichnotaxa (a) *Cruziana simplicata*, (b) *Petalichnus brandenburgensis* and (c) *Angulichnus alternipes* attributed to trilobites; (d) *Umfolozia sinuosa* attributed to a crustacean; (e) probable arthropleurid tracks *Diplichnites cuthensis*; attributed to insects are (f) *Siskemia bipediculus*, (g) *Permichnium voelckeri* and (h) *Lithographus hieroglyphicus*. (i) *Kouphichnium variabilis*, (j) *Palmichnium antarcticum*, (k) *Paleobelcura tridactyla* and (l) *Octopodichnus didactylus* are attributed to chelicerates. Scale bar = 1 cm, except for (e) and (j) where it is 10 cm. (After Braddy, 2001.)

oceans had probably diversified as far as it could.

The animals that were able to make this transition most easily were those that were pre-adapted by possession of waterproof 'skins' (cuticular coverings) that were able to retain as much body moisture as possible and resist rapid dessication such as the insects, arachnids and some isopods and, with further adaptations, the molluscs and vertebrates. In addition some groups, such as isopods, myriapods, insect larvae and (nonarthropod) slugs, flatworms and amphibians managed to avoid dessication by inhabiting moist terrestrial environments such as soils and the litter of forest floors. The pathways these various animals took from the water to dry land were mainly via the seashore or freshwater and

floodplains (see for example, Stormer, 1977, fig. 5.1).

British sites of Late Silurian age in the Welsh Borders and of Early Devonian age from Scotland, especially that of Rhynie, are of international importance in the discussion of terrestrialization. The oldest fossil evidence for terrestrial life consists of trace fossils (Figure 1.16), those preserved marks within sedimentary strata that record some life activity and vary enormously from sediment surface footprints or trackways to burrows, feeding traces on food items and faecal debris. The problem with most trace fossils is that they are not directly associated with the fossil remains of the organism that made them and so the link between a particular

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trace and particular organism is generally indirect (for a general review of arthropod trackways see Braddy, 2001). Interpretation of trace fossils as signs of terrestrialization therefore largely depend on identification of the host sediments as having been deposited on land.

By comparison, body fossils, those remains of organisms that provide direct evidence of their existence and identification such as hard body parts, especially skeletal and shell remains, may not be preserved where they lived nor necessarily reflect a terrestrial mode of life. For instance the form of an extinct arthropod cuticle may indicate what kind of arthropod it was but unless that group is known to be restricted to a terrestrial habitat, the fossil cuticle itself is not necessarily diagnostic.

However, there are some good anatomical features of arthropods that are diagnostic of terrestrial modes of life such as lungs whereas aquatic arthropods possess gills; but identification of such features depends upon their preservation in the fossil state. Surprisingly perhaps such delicate structures as fossil 'book-lungs' of landliving arthropods are known. Other diagnostic features of landliving are sensitive hairs, called trichobothria, which can detect airborne vibrations, but would not function in water; foot structures and limb joints typical of land but not aquatic locomotion and, copulatory equipment that is necessary for reproduction on land but not in water.

Terrestrial trace fossils

The earliest known fossil trackways that are thought to have been produced by arthropods date back to some 450 Ma and Caradocian times within the late Ordovician Period. They were found in 1993 (Figure 1.17, Johnson *et al.*, 1994) within the Borrowdale volcanic rocks of England's Lake District. The prints consist of two closely spaced parallel lines, less than 1 cm apart, resembling miniature tank tracks. Each line consists of tiny paired and triangular indentations, made by a number of similarly sharp pointed and sized feet.

In the absence of any body fossil remains, the creatures responsible can only be identified by analysis of the trackways and comparison with similar tracks made by living organisms. For successful and efficient locomotion, arthropods have to combine and regulate the movement of

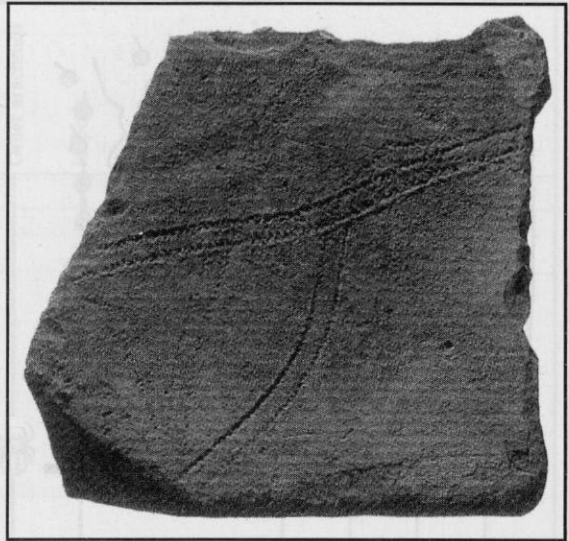


Figure 1.17 Centimetre-wide trackways found in the 450 million year old Caradocian volcanoclastic sediments of the Lake District, have the characteristic form of those made by a multi-legged arthropod such as the myriapod. As such, they are amongst the earliest evidence of terrestrial animal life. (From Johnson *et al.*, 1994.)

their legs in order to prevent interference between them. They can use different walking techniques in response to different circumstances. For example, a myriapod running over soft sand will employ a different gait from one that is pushing through the leaf litter on a forest floor. There has been considerable work on the functional mechanics of their leg movement, which has helped with the interpretation of fossil trackways (Trewin, 1994a).

Analysis of trackways can show whether the maker had walking limbs of similar morphology (homopodous) or different morphology (heteropodous). Since prints of the aforementioned tend to be similar it may be impossible to tell how many legs the animal had. Also, the nature of the substrate, the presence of a slope or current and subsequent preservational processes may produce sets of prints that can look quite different even though they originate from the same animal. Palaeontologists Jill Wright and Derek Briggs, (then at Bristol University), have showed that the Borrowdale tracks were made by multi-legged homopodous creatures, whose paired limbs were strong enough to lift their bodies clear of the soft

sediment. Also, the absence of any other marks made by carapace structures, such as a tail spine, plus the multiplicity of limbs, indicates that they were segmented creatures and not soft bodied. Myriapod arthropods (like modern centipedes) are the most likely candidates.

The tracks were found within the otherwise unfossiliferous pile of lavas, ashes and sediments that were originally deposited in shallow ephemeral lakes and rivers lying between volcanoes and lava plateaux. The Lake District at the time was part of an active island arc of volcanoes above a subduction zone on the south-east margin of the Iapetus Ocean.

A myriapod trackway from Upper Silurian strata of Newfoundland has been analysed and shows that the animal had a gait with a successive phase difference that indicated it was well adapted for walking on land. The coarthropleurids are myriapod-like arthropods whose trackways (known as *Diplichnites*) are relatively common in Devonian and Carboniferous delta and river-related deposits. Lower Devonian age red-bed deposits from the Brecon Beacons in southern Wales contain abundant trackways that have been assigned to two kinds of *Diplichnites* *gouldi* (Smith *et al.*, 2001). Analysis of the trackways and computer modelling allowed the identification of in-phase gaits with a swimming stroke-like motion by both coarthropleurid and kampecarid myriapods. The combined behavioural and sedimentological evidence indicates that these trackways were produced subaqueously in non-marine waters.

Similar tracks have been found in strata of similar age and facies in Pembrokeshire, South Wales (Morrissey and Braddy, 2001). Here fluvial deposits of ephemeral streams within a semi-arid environment preserve abundant meniscate back-filled burrows (*Beaconites barretti*) which are thought to represent periodic colonizations of subaerially exposed sediments by a population of amphibious coarthropleurid myriapods, burrowing down to the water table to aestivate and/or moult. Associated tracks indicate that there was an active and gregarious arthropod fauna that also included arachnids (*Palaeochlura*).

Some remarkably large myriapod trackways have been recorded such as those of a Namurian, Carboniferous age *Arthropleura* from the island of Arran off the west coast of Scotland. These are 36 cm wide and their reconstructed gait shows that the metre-or-so long

animal was moving over open ground (Briggs *et al.*, 1979).

Land living arthropods have been implicated in the production of some near-vertical, meandering burrows found in upper Ordovician soils. The burrows are backfilled with sediment and are claimed to resemble those made by millipede myriapods.

Some slightly younger (420 Ma), Upper Silurian sandstones in Western Australia preserve a wide range of spectacular arthropod related trackways. Ken McNamara of the Museum of Western Australia in Perth and Nigel Trewin of the University of Aberdeen in Scotland, have shown that the largest of these trackways (20 cm in width) were made by eurypterids, which grew to two metres length. Smaller tracks were made by scorpions and another extinct arthropod group of cockroach-like creatures, called euthycarcinoids (5 cm long with 10 or 11 pairs of legs), related to the centipedes. Although some of the tracks were clearly made under shallow lake or river water, many others were made on sediment exposed to the air.

Some eurypterid tracks are so abundant that they may represent mass migrations across marginal environments that, according to Braddy (2001), may have been part of their life cycle. Most of the eurypterids seem to have walked with in-phase gaits like the horseshoe crabs but most of them were not well adapted for walking on land. Braddy characterizes their amphibious locomotion as 'an ungainly subaerial flop, hauling themselves forward with repeated in-phase lunges' (Braddy, 2001, p. 393). But underwater they could use a half-swimming in-phase subaqueous flop. By comparison the stylonurid eurypterids were better adapted for walking on land with a more stable in-phase gait.

Scorpion tracks (*Stiaria*) have been identified as far back as early Devonian times from Old Red Sandstone strata in Scotland (Walker, 1985) and by early Permian times are widespread (e.g. *Paleobelcura*, Figure 1.16) in both marginal marine and continental interior environments as are the tracks of spiders (e.g. *Octopodichnus*). Their asymmetric tracks indicate gaits that are clearly out-of-phase.

Insect tracks are rare in Palaeozoic strata but trace fossils of Early Devonian age from Scotland (Walker, 1985) show similarities to tracks made by modern diplurans and thysanurans (silverfish). Following the Carboniferous radiation of

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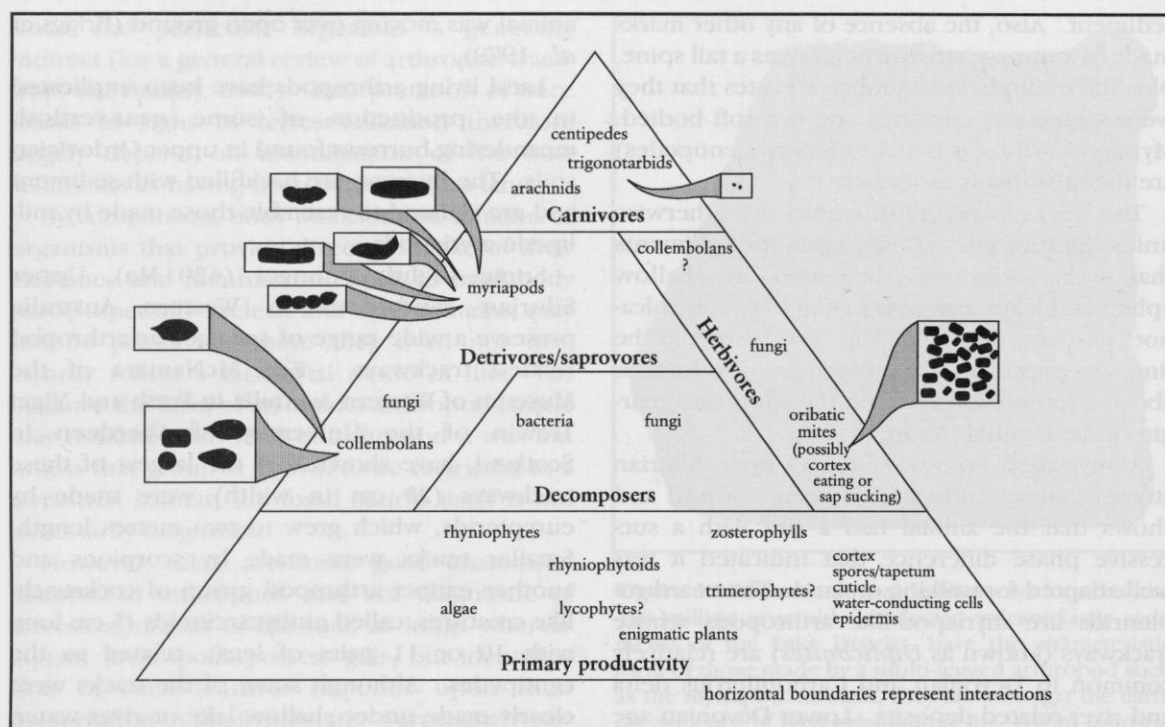


Figure 1.18 A representation of an early terrestrial ecosystem based upon the Rhynie chert terrestrial community. Analysis of the form and origin of abundant fossil coprolites from the site demonstrates the existence of diverse consumers that differed in life habitat and diet. Black shapes show variation in coprolite morphology. (After Habgood *et al.*, 2004.)

the insects, their trace fossils become more abundant with trackway ichnospecies being described from the Permian strata of Germany (Figure 1.16). Jurassic tracks from the Connecticut Valley in America (Figure 1.16) were among the earliest to be attributed to insects and were described by Edward Hitchcock in the mid-nineteenth century. Analysis shows that these insects used similar alternating (tripodal) gaits for maximizing their stability, just as their modern counterparts do.

Trackways made by horseshoe crabs (xiphosurans) are relatively common in certain environmental settings such as the Carboniferous Coal Measure delta swamps and lagoonal carbonate muds of the Jurassic lagoon of Solenhofen in Bavaria and from both marine and nonmarine carbonates of the Cleveland Basin of Yorkshire (Romano and White, 2001). Analyses of these trackways show that as with their modern counterparts, these ancient horseshoe crabs walked with their five pairs of heteropodous legs moving in phase to produce a

lurching-like gait with the tail (telson) dragging on the substrate, and were capable of other modes of locomotion such as half-swimming. The presence of horseshoe crab trackways in deposits which have a mixture of marine and freshwater influences suggests that these essentially marine arthropods were euryhaline and tolerant of freshwater, for example at the Writhlington GCR site.

Coprolites, which are fossil faeces, provide another kind of trace fossil evidence for terrestrialization and plant-animal interactions in early terrestrial ecosystems (see Figure 1.18). Microscopic coprolites found (Edwards *et al.*, 1995) in Upper Silurian and Lower Devonian strata of the Welsh Borderlands are packed full of a variety of plant spores and other plant debris, showing that some small terrestrial animal was ingesting the plant matter. The tough spores with their waxy coats survived the passage through the animal's gut but much of the other plant material had been macerated. This type of herbivory is typical of litter-feeding

arthropod detritivores, such as millipedes.

Despite fossil remains of the actual animals, all of these trace fossils indicate that arthropods were able to move into fresh water and then on to dry land and survive exposure to the atmosphere in late Ordovician times, much earlier than was previously thought. This capability of the arthropods clearly provided the critical stepping stone between the sea and complete terrestrialization.

The body fossil record of terrestrialization

The multi-celled animals that occupy land environments today range from nematode, oligochaete annelids and flat-worms through various arthropods to vertebrates. When exactly these disparate groups first *stepped* on to *terra firma* is not known with any great confidence but what evidence there is from the fossil record is reviewed by Selden (2001a) and suggests that they each made the transition independently and at different times. Most groups have long aquatic records that precede their terrestrialization but some, especially the arthropod myriapods, hexapods, arachnids and also the molluscan pulmonates, have no earlier marine records and are essentially adapted for life on land.

Of the worms, most of the nematodes and flatworms have no fossil record. The first fossil record of annelids is marine and they do not appear to have invaded land until Carboniferous times and then sought protection from rigours of life in these environments by adopting a cryptic existence within soils and forest floor litter. The earliest body fossils of land-living animals follows that of trace fossils and is comprised of arthropod remains. Although there have been claims of myriapod remains from Cambrian marine sediments they have not been confirmed and the earliest undoubted terrestrial arthropod body fossils are those of two myriapod groups, the scutigeromorph centipedes (Jeram *et al.*, 1990) and the archidesmid millipedes (Wilson and Anderson, 2001) both of Silurian age.

The first archidesmid millipede *Archidesmus macnicoli* was described from Lower Devonian strata of Tayside in Scotland by B.N. Peach (1882a). Peach was able to show that *A. macnicoli* was a flat-backed millipede with tuberculate ornament and paranota and suggested that the fossils had an affinity with the living poly-

desmids. New specimens collected from Tillywhandland Quarry near Forfar preserve some previously unknown details of their anatomy that links other archidesmid-like fossils remains from the Cowie Formation of the Stonehaven Group (see GCR site report). Dated by fossil spores to a mid-Silurian age, these Stonehaven fossils are considered to be the oldest millipedes and indeed the oldest terrestrial arthropods known according to Wilson and Anderson (2001). Although these are the oldest known millipedes, apparently they are not the most primitive since they have a relatively derived body plan. Myriapod diversity subsequently boomed in Devonian times with more orders than survive today and by Carboniferous times some of them had reached giant proportions (up to 2 m in length).

The chelicerates include merostomes, such as the extinct eurypterids and surviving horse-shoe crabs (xiphosurans) and the arachnids (spiders, scorpions and mites) of which the eurypterids are by far the most ancient group originating at least as far back as Early Ordovician times but in marine environments. The eurypterids remained primarily aquatic until it became extinct in Early Permian times. However, there is evidence from fossilized secondary lungs and trackways that from the Silurian Period onwards some members were amphibious and capable of moving out of the water but do not appear to have become independent of water.

By comparison their close relatives, the scorpions did manage to make the transition to independent life on land by converting the gills of their Silurian aquatic ancestors into the book lungs of their Devonian descendent forms which could obtain oxygen directly from air. The earliest terrestrial arachnids with booklungs were the trigonotarbid, extinct and primitive relatives of the spiders. Their fossil remains have been found late Silurian age deposits of Shropshire and thereafter they became common in most early terrestrial ecosystems. Spiders, harvestmen, mites and pseudoscorpions all appear in Devonian times and by the Carboniferous Period there were more orders of arachnids than there are today.

All living hexapods (insects) are terrestrial or secondarily aquatic (according to the orthodox view) and the earliest fossils of wingless insects (apterygotes) are of Devonian age while remains of winged insects (pterygotes) do not appear in the record until Carboniferous times. According

to Selden (2001a) the evolution of their air-breathing respiratory organs appears to have evolved independently a number of times, perhaps related to separate terrestrialization events. This suggests that the group is polyphyletic, a suggestion denied by many entomologists. For a detailed review of the ecological history of terrestrial insects see V.V. Zherikhin (in Rasnitsyn and Quicke, 2002).

Some crustacean groups have also taken up land living and have until recently been regarded as the last of the arthropod groups to do so. However, discoveries of two new crustaceans from the Early Devonian age Rhynie Chert have forced this idea to be reconsidered. The first crustacean element to be found was the enigmatic lipostracan *Lepidocaris rhyniensis* but more recently associated with it some 36 almost complete specimens of a new branchiopod have been found (Fayers and Trewin, 2001). Accompanying charophytes indicate that the assemblage was living in a subaqueous non-marine environment, probably a temporary pool (for a recent review of the Rhynie biota see Trewin and Rice, 2004).

The isopods are the most ancient of the extant crustaceans, appearing in the marine fossil record in Upper Carboniferous strata, but their terrestrial members, the oniscideans are only known from Eocene times onwards. Marine decapod crabs and crayfish appear in Jurassic times but true land-living forms do not appear until Neogene times. Finally, marine amphipods appear in Upper Eocene strata but their living terrestrial members, the talitrid beach fleas, sand hoppers and the Southern hemisphere leaf-litter hoppers, all of which can be incredibly numerous, appear to have no fossil record. They are thought to have become land living when the first angiosperm forests developed in coastal regions.

FOSSIL EVIDENCE FOR HERBIVORY IN ARTHROPODS

Despite the ancient history of life's dependence on plants for food at the bottom of the food chain, there is very little direct evidence in the fossil record for specific links between particular herbivores and particular plants. The role of arthropods in the evolution of terrestrialization and development of terrestrial food chains, as discussed, is likewise hard to pin down to direct evidence in the fossil record. Nevertheless, there

are various indications that terrestrial arthropods were intimately associated with the consumption and degradation of plant matter and consequently the formation of soils from at least late Silurian and early Devonian times and that some of this evidence has been derived from British localities (Figure 1.18; for a review see Ash, 2001).

Most of our understanding of arthropod herbivory comes from the discovery of fossil faeces (coprolites) produced by these plant eaters, along with occasional feeding marks preserved on fossil leaves, wood borings, and comparisons with living herbivorous arthropods. Arthropod coprolites are typically small cylindrical or ovoid structures, mostly less than 1 mm in length. Their preservation as fossils requires rapid sedimentation in low-energy environments and typically they are found in fossil soils or have been re-sedimented in fine-grained, quiet-water deposits before they have had time to disintegrate.

The earliest arthropod coprolites indicative of herbivory are late Silurian in age (Edwards *et al.*, 1995) and consist of ovoid pellets packed with a variety of species of plant spores and other plant debris. The spores have survived their passage through the gut remarkably well thanks to their tough waxy coat which is an adaptation for survival in the harsh physical and chemical conditions of the terrestrial environment. But much of the other plant material has been macerated beyond recognition. The arthropods responsible for this herbivory are thought to have been myriapods such as millipedes.

The oldest indications of herbivory that can be more strongly linked with a particular group of arthropods are lesions on fossil plant stems recovered from early- and mid-Devonian sites, especially that of aerial shoots of *Rhynia* from the Rhynie Chert (Kevan *et al.*, 1975; Cleal and Thomas, 1995, p. 92, and the rhynie biota has most recently been reviewed by several papers in Trewin and Rice, 2004). It has also been argued that the cortex of this primitive vascular plant is thickened as a strategy to protect the stele from arthropod predation (Cleal and Thomas, 1995, p. 85). The form of the lesions is similar to that produced by modern piercing and sap-sucking insects, but the body-fossil record of such insects does not begin until Permian times.

Some of the clearest marks on leaves left by arthropod feeding are excisions and these can be differentiated from accidental damage by the

Fossil evidence for herbivory in arthropods

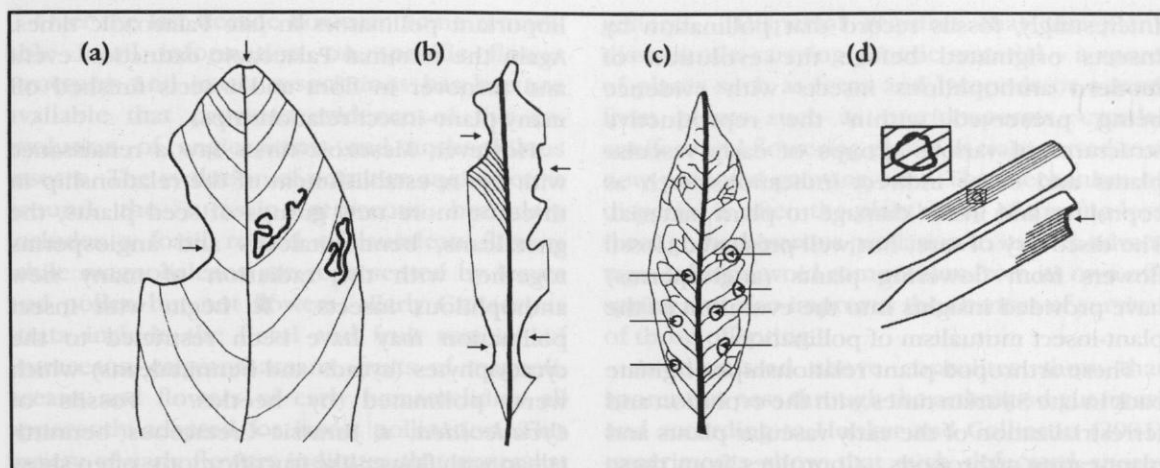


Figure 1.19 Examples of feeding marks on fossil leaves. Marginal feeding marks are arrowed. (a) Feeding marks and leaf mines on an angiosperm leaf from Eocene deposits of Australia $\times 0.5$; (b) marks on *Glossopteris* from Permian deposits of South Africa, $\times 0.5$; (c) hole-feeding marks on an angiosperm leaf from Eocene deposits of England $\times 1$; (d) evidence of window and marginal feeding on two pinnae of the bennettitalean leaf *Zamites* from Triassic deposits in Utah, $\times 1$. (After Boucot *et al.*, 1990, Stephenson and Scott, 1992 and Ash, 2001.)

presence of reaction rims where the leaf tissue has responded to the damage and shows that it occurred while the leaf was still alive and attached to the parent plant. The different forms of such excisions indicate that many of the leaf-eating strategies used by living insect groups appeared during the Palaeozoic Era. Marginal feeding (Figure 1.19) first appeared in late Carboniferous times; hole feeding (Figure 1.19c), skeletonizing and window feeding (Figure 1.19d) during Permian times. Leaf mining not only provides the arthropod responsible with food but also shelter and typically consists of sinuous bands on the lamina of fossil leaves (Figure 1.19a). Fossil examples first appear in late Carboniferous times (Stephenson and Scott, 1992) but are not common until Palaeocene times, on angiosperm leaves. Borings in plant material first appear in Carboniferous times. By Cretaceous times some contain coprolites similar to those produced by living termites, suggesting that these insects were present by this time but most borings are likely to result from beetle activity.

Altogether these trace fossils indicate that arthropod herbivory has an antiquity stretching back to late Silurian times and the early evolution of the vascular plants. A considerable diversification during Carboniferous times partly reflects a greater abundance of plant fossils from that time but also a real response to the evolution of land floras by increasing numbers and

kinds of plant-eating arthropods, especially the insects. Despite the extinction of many of the Palaeozoic arthropods at the Permo-Triassic boundary, the patterns of herbivory recorded by fossil plant material stay very much the same, showing that the newly evolved arthropods replacing those that had become extinct continued to follow the same feeding strategies.

Pollination

The success of plant reproduction is fundamental to the continuance of life on Earth. Much of that reproduction is mediated through the transport and dispersal of pollen and spores through a variety of mechanisms. However, insect pollination is one of the most energy efficient of these mechanisms and has evolved a complex set of mutualistic relationships between plants and their insect pollinators that are important for ecological, economic and evolutionary reasons. Crepet, in a review of the subject (2001), points out that 'pollination by highly faithful pollinators provides a mechanism for increasing the rate of plant speciation'.

Flowering plants are the main beneficiaries of insect pollination and most pollinators belong to four orders of insects which are consequently known as 'anthophilous' (flower loving) insects, namely coleopterans (beetles), dipterans (flies), lepidopterans (butterflies and moths) and hymenopterans (sawflies, wasps, ants, bees).

Interestingly, fossils record that pollination by insects originated before the evolution of modern anthophilous insects with evidence being preserved within the reproductive structures of various groups of early vascular plants and other indirect indications such as coprolites and insect damage to plant material. The discovery of rare, but well-preserved, fossil flowers from flowering plants (angiosperms) have provided insights into the evolution of the plant-insect mutualism of pollination.

These arthropod-plant relationships originate back in late Silurian times with the evolution and terrestrialization of the early vascular plants and plant-eating arthropods. Coprolites from these arthropods show that they targeted and ate a variety of spore bodies from different plants. Importantly, the spores themselves emerged unscathed from their passage through the arthropod gut so perhaps in return from the food provided by eating the spore capsule the plants benefitted from having their spores dispersed. From this primitive sporivory there was a transition to pollen feeding and then to insect pollination of more evolved and complex plants.

Long before the evolution of the angiosperms other plant groups had to attract potential pollinators. While pollen itself provided a nutritious attraction to some arthropods, there had to be some other attractant associated with the ovules to complete the reproductive cycle, such as nutritious ovule tissue which according to Crepet (2001) 'today serves as a substrate for larval development in beetle-pollinated cycads'.

Insect pollinivory is recorded as early as Carboniferous times by fossil coprolites which are linked to orthopteroids (cricket-relatives) and hemipteroids (bug-relatives). There is anatomical evidence, such as large and complex pollen organs, to suggest insect pollination in pteridosperm plants had evolved by Permian times. The curculionid beetles that pollinate modern cycads appear in the fossil record only by Mesozoic times whereas cycads, the most primitive of seed plants, originate in late Palaeozoic times and so there must have been a historic shift in their insect pollinators. The fossil record of insects has considerable potential for providing further understanding of the evolution of plant-insect relationships and their shifts in 'allegiances'. Grimaldi (1999) has suggested that some extinct insect groups (e.g. the palaeodictyopteroids) may have been

important pollinators in late Palaeozoic times. Again the terminal Palaeozoic extinction event and turnover in flora and insects finished off many plant-insect relationships.

However, Mesozoic times saw a renaissance with the re-establishment of the relationship in three or more new groups of seed plants, the gnetaleans, bennettitaleans and angiosperms together with the radiation of many new anthophilous insects. To begin with insect pollination may have been restricted to the cycadophytes (cycads and bennittaleans) which were pollinated by beetles. Fossils of *Cycadeoidea*, a Jurassic-Cretaceous bennittitalean with flower-like fructifications, often show insect damage typical of pollen feeding beetles.

Evolutionary patterns of anthophilous insects are, according to Crepet (2001), consistent with the appearance of gnetaleans and angiosperms in latest Jurassic and earliest Cretaceous times. While important families of pollinating flies (dipteran) such as the Acroceridae and Bombyliidae have evolved by late Jurassic times, anatomical structures associated with anthophily are not found in their fossil record until Cenozoic times. According to Grimaldi (1999), the fossil record suggests a Cretaceous-Cenozoic radiation of the syrphid 'flower-flies', while nemestrinid flies appear in late Jurassic times and might indicate flower-feeding as early as this.

The relationship of the pollinating insects with the flowering plants transcends all other plant-insect relationships in scope and importance. There are fundamental and unresolved questions about the role of the insects in the early evolution of the angiosperms and whether they co-evolved or whether one preceded the other. As discussed by Crepet (2001), the problems largely revolve around the difficulties associated with the incomplete nature of the fossil record and resolving the fossil data to an appropriate level of detail. If significant insect pollinators evolved before the flowering plants the implication is that the pollinators were not as Crepet says 'causally related to the massively successful diversification of the flowering plants'. More information is required on the first appearances of groups such as the bees (apids) who are thought to have evolved in late Cretaceous times. But in addition, the early evolution and radiation of the angiosperms themselves is still not well resolved by the fossil record.

Over the last decade however, some remarkable fossil information on specific flower structures and insect associations has become available that provides evidence of the co-evolution of angiosperms and anthophilous insects. The evolution of primitive angiosperms around the Jurassic–Cretaceous boundary includes a fossil record of lauralean flowers while magnoliales are represented by leaves and pollen but not flowers. Early Cretaceous strata include the floral and fruit remains of lauraceans, calycanthaceans; fruits of magnoliaceans and flowers of early hamamelidids all apparently adapted for insect pollination. This variety of early flowers indicates that generalist insects such as beetles, various flies, short-tongued moths and sphecids were the pollinators. This diversity of dipterans suggests that they were more important in this early phase of angiosperm evolution than previously recognized. By the beginning of late Cretaceous times (Cenomanian Stage) the angiosperms literally bloom with a huge increase in floral diversity from magnoliids to rosids and asterids associated with highly derived insect pollinators such as bees. Late Cretaceous times saw a further development and modernization in both floral structures and insect pollinators.

Plant–arthropod interactions: Dispersal

The second element to the success of the angiosperms following pollination is dispersal. As with pollination, a variety of animals, including arthropods, have evolved a role in several ways ranging from burial to consumption and defecation (for a general discussion, see Hooker and Collinson, 2001). As discussed above, arthropods played a vital role in the success of the land-living vascular plants right from the start in late Silurian times. Detritus feeding arthropods, such as myriapods, were important in the formation of early soils through recycling of organic material through the gut and re-deposition as coprolitic material within sediment where it is often further degraded by bacterial and fungal activity and contributes to soil formation.

Dispersal of plant reproductive material to new growth sites is crucial to their survival and expansion as species, members of communities and the spread of terrestrial vegetation in

general. Dispersal requires that the plant disseminule carrying genetic material – a spore of plants such as ferns and lycopods or a seed from plants such as pteridosperms, cycads, conifers and flowering plants, is transported to a new potential growing site. The mechanism of dispersal is often the plant's way of turning loss through herbivorous predation to its own advantage. It helps avoid competition from its own offspring and also improves the chances of survival of those offspring.

As discussed above coprolites show that spores can pass through the arthropod gut intact and according to Hooker and Collinson (2001) experiments show that such defecated spores are still viable. At least 6% of ingested bracken spores were still viable in giant millipede and locust faecal pellets. Palaeozoic spore-containing coprolites are rare but some important late Silurian and early Devonian sites have provided abundant specimens containing a variety of spores associated with the earliest terrestrial vascular plants. Similarly some Coal Measure deposits from Carboniferous tropical swamps have yielded herbivorous arthropod coprolites. It thus seems likely that spore dispersal by arthropods originated almost as soon as the plants and arthropods first invaded the land.

Consumption of fresh plant material is as difficult for arthropods as it is for any other animal and requires the mediation of gut bacteria, but the arthropod first have to acquire the bacteria. By feeding on plant litter rather than fresh, living plant matter, digestion is aided by the bacterial decay and the arthropods ingest the bacteria that can establish a gut flora. Thus detritivory is thought to be the initial step in the co-evolution of this dispersal mechanism.

Barbed and hooked spores evolved in Devonian times and may have aided dispersal by arthropods who unwittingly carry them. Similarly, fossil pollen has been found lodged between the exoskeletal plates of the giant late Carboniferous myriapod *Arthropleura* and was probably dusted onto the animal as it moved through dense vegetation. Surfaces of other early arthropods such as mites, collembolans, trigonotarbids and later millipedes may have provided similar substrates for the entrapment of plant spores but there is no direct evidence for such a mode of transport and dispersal from the fossils of these arthropod groups yet.

Today ants are important dispersers of plant seeds. Special ant-attracting tissues are present

on the seeds of certain plants that encourage the ants to carry the seeds away to their nests but not to eat them. Thus the seeds are buried in a situation that promotes their germination. It is likely that this relationship co-evolved between the plants and the ants a long time ago. The oldest fossil ants are early Cretaceous (Aptian) in age and thus not much younger than the earliest angiosperms but there is no direct fossil evidence for the existence of such a relationship at this time. Seeds are also buried in ideal circumstances for germination by the activity of dung beetles (scarabaeids). The fossil record of their dung-ball burying habit is essentially of Tertiary age, but extends back to late Cretaceous times (Collinson, 1999a).

Insect-angiosperm co-evolution

Because of the major role that pollinating insects play in the continuing reproductive success of the flowering plants (angiosperms), it has been hypothesised that insects may even have played a fundamental role in the initial evolutionary radiation of the angiosperms during Early Cretaceous times, some 135 million years ago. However, insects are not the only groups of animals that might have assisted the early evolution and spread of the angiosperms; dinosaurs, mammals and birds may all have played a role, but only the dinosaurs and insects have been implicated in the early evolution of angiosperms. Herbivorous dinosaurs have also been thought to have mediated the tempo and pattern of angiosperm radiation through the changes in their browsing behaviour associated with evolutionary changes in their jaw mechanisms. However, a review by Barrett and Willis (2001) has downplayed the role of the dinosaurs by showing that there are no good correlations between the timing and distribution of changes in dinosaur feeding habits and angiosperm evolution, although there might have been some co-evolutionary interactions between the two groups in Late Cretaceous times.

There has also been considerable re-assessment of the role of the insects in early angiosperm evolution. Fossil angiosperms first appear during the Early Cretaceous Epoch within the tropical realm of North Africa, which was still part of the southern supercontinent of Gondwana, although it was breaking up by this time as the southern Atlantic Ocean opened up.

Within a relatively brief period of time, a few million years, the angiosperms were well distributed throughout the tropical and subtropical realm across the Tethys Ocean to China. Direct fossil evidence for insect predation on Cretaceous angiosperms is sparse but insect herbivory can be inferred from fossil traces of feeding activity such as leaf mines and other distinctive damage. Another approach is through the study of the functional morphology of insect mouthparts. However, again there are no good correlations between the timing of such insect activities and innovations in feeding habits with angiosperm radiation to support a strong co-evolutionary link between the two groups. Neither is there any marked correlation between the timing of insect diversification and the origin of the angiosperms (Labadieira and Sepkoski, 1993).

Nevertheless, the ecological and taxonomic diversification of the angiosperms is thought to have been aided by insect pollinators (Crepet, 1996). Mid Cretaceous angiosperms are characterized by the appearance of floral features that indicate a high degree of pollinator specificity and the origin and radiation of many pollen eating (anthophilous) insects especially bees and pollen wasps (hymenopterans), various flies (dipterans) and butterflies (lepidopterans). By Late Cretaceous times insect herbivory, especially by aphids and beetles, also seems to have been well established (Wilf *et al.*, 2000). Pollination by insects is thought to have developed from pollen eating by insects with chewing mouthparts and it is possible that a number of key angiosperm characteristics such as closed carpels were adaptations that provide some protection from the ovules from such insect predation.

ARTHROPODS – THE DEVELOPMENT OF FLIGHT

As described above, arthropods were the first animals to leave the sea and set foot on land, some 450 Ma and were the first to eat land-living plants. It is likely that they could only do this because they had already acquired a gut flora of bacteria that helped digest tough plant cellulose. So began an intimate association between insects and plants. An association of such importance to life on land, that without it the land would not have been 'greened' and then

coloured in the way we see today. The flowering plants depend to a large extent on insects to transport their genetic material, that is, pollen. And in order to do this over any significant distance requires insects that can fly.

However, the ability to fly also, more fundamentally, fulfills several different functions for insects. Firstly, it allows for the dispersal of the insects themselves so that they can move into new ecospace. Such dispersal can also distance potential mates but with other adaptations for mate location in place, for example pheromones, such distances can be overcome by flight. And, as the word 'flight' also suggests, the mechanism can be used to escape from predators. The 'fight or flight' option established a new kind of 'arms race' in which predators also took to the air and so arose many different modes of flight along with camouflage, mimicry, and so on. Further functions include thermoregulation, protection, and auditory communication. Indeed, it can be argued that wings and flight are the most important morphological innovation in the overall evolutionary success of the insects (for an extended discussion of this innovation, see Alexander, 2002 and Grimaldi and Engel, 2005).

It was the insects that 'invented' flight but the how and why of that original achievement has been surprisingly elusive. Since no legs have been lost in wing development, wings are not just modified legs and there is no other readily identifiable and adaptable pre-existing structure to account for the appearance of wings. That over 99% of living insects can fly shows how important this evolutionary innovation and adaptation has become for them. Traditionally insects used to be divided into two main groups, the wingless apterygotes and the winged pterygotes. It is generally considered that wings have never evolved in the apterygotes but that in some of the pterygotes they have been secondarily lost, nevertheless their true taxonomic relationships are revealed by other characteristics.

The earliest known winged insects include representatives of at least four different insect groups and are found in Early Bashkirian (Namurian) strata of Germany. They include the polyneopteran Paoliidae such as *Kemperala*, palaeodictyopterans such as *Stenodictya*, megasecopterans such as *Mischoptera* (Figure 1.20) and geropterans such as *Eugeropteron*. The contemporaneous appearance of such a diversification of winged insects implies a signif-

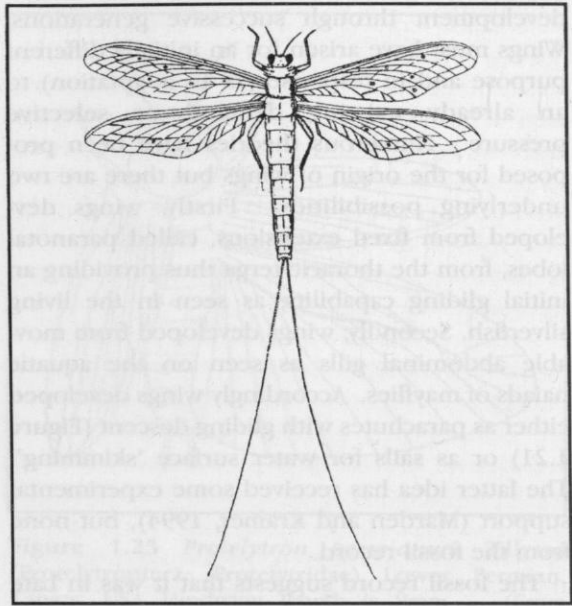


Figure 1.20 *Mischoptera woodwardi* Brongn. Stephanian; Commeny, France $\times 0.5$. (After Handlirsch, 1908.)

icantly earlier origination for winged flight in Early Carboniferous or perhaps Late Devonian times. Indeed Engel and Grimaldi (2004) claim that the discovery of metapterygote features in *Rhyniognatha hirsti* from the Rhynie Chert supports an Early Devonian (Pragian) age for the origin of flight. Although relationships between these first winged insects are disputed it is still generally argued that there was a single origin for winged insects.

The origin of wing-powered flight is a classic problem in evolutionary studies that applies not only to insects but to all other flying animals like the extinct pterosaurs, bats and birds, who have independently 're-invented' the technique of powered flight using wings at various subsequent times through geological history.

Functional flying wings have to be relatively large and complex structures but must have started out small and incapable of providing lift-off, even for such a tiny creature as an insect. So initially the evolution of early 'wings' must have provided some other advantage. As with so many evolutionary innovations, the problem is more complicated than it might at first appear because animals cannot predict a need for a structure like wings nor predetermine their

Introduction to British fossil arthropods

development through successive generations. Wings must have arisen for an initially different purpose and in response (as an adaptation) to an already existing demand or selective pressure. Numerous theories have been proposed for the origin of wings but there are two underlying possibilities. Firstly, wings developed from fixed extensions, called paranotal lobes, from the thoracic terga thus providing an initial gliding capability, as seen in the living silverfish. Secondly, wings developed from movable abdominal gills as seen on the aquatic naiads of mayflies. Accordingly wings developed either as parachutes with gliding descent (Figure 1.21) or as sails for water surface 'skimming'. The latter idea has received some experimental support (Marden and Kramer, 1994), but none from the fossil record.

The fossil record suggests that it was in Late Carboniferous times when insects first really took off and dominated the airways without any competition from flying vertebrates. There are remarkable fossils from this period, like

Meganeura, a giant predatory dragonfly first described by the great French naturalist Adolphe Brongniart in 1885 (Figure 1.22). But the dragonflies dominance of the skies was relatively short-lived because they lacked an important technical device, necessary for aerial warfare. Just as birds, bats and indeed humans have found out, control of the airspace is vital in territorial conflict. Like most aeroplanes, dragonflies could not – and still cannot – fold their wings back when at rest they tilt the base or bend them instead. However, today over 99% of all living winged insects can fold their wings, which both protects the wings and greatly improves manoeuvrability on the ground, allowing them to hide from their enemies. Once that technical hurdle was overcome, there was no holding back for the flying insects.

Fossil neopteran pterygotes such as *Gerarus* show that the wing folding adaptation soon evolved, by Westphalian (Upper Carboniferous) times. In many neopterans, the front pair of wings was stiffened and toughened to form what

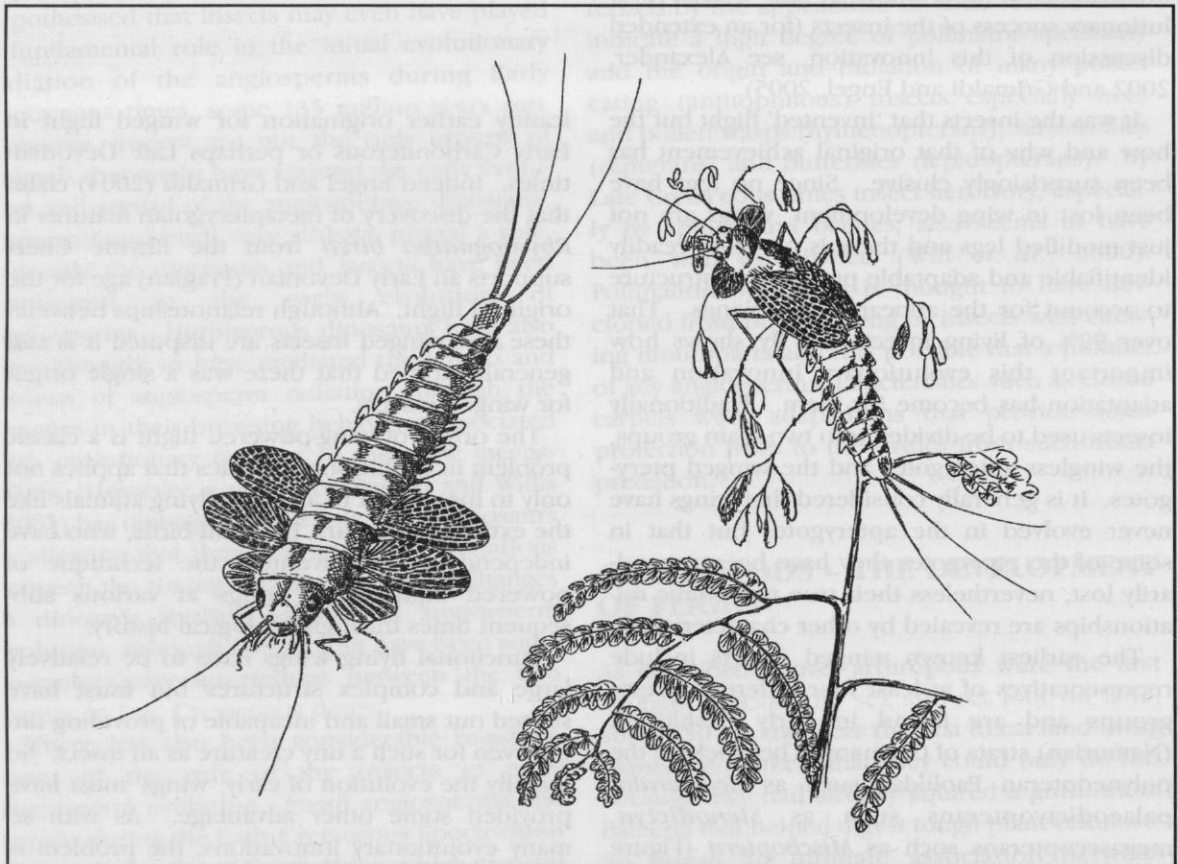


Figure 1.21 Hypothetical ancestral winged insects as reconstructed by A. G. Ponomarenko. (From Rohdendorf and Rasnitsyn, 1980.)

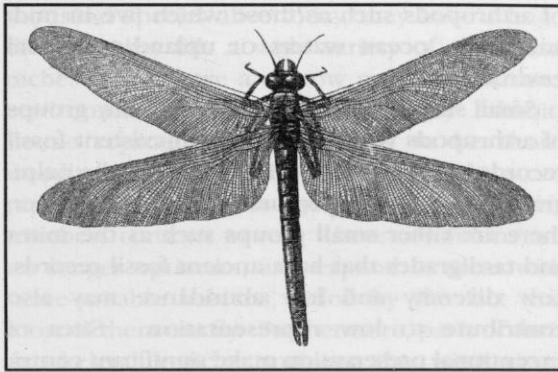


Figure 1.22 *Meganeura monyi* Brongniart Stephanian; Upper Productive Coal Measures, Commentry, France $\times 1/12$. (From Handlirsch, 1908.)

are known as elytra or tegmina. These form a protective case or covering to the more delicate and membranous hind (flying) wings when the insect has landed, as seen in the extinct protelytroterans such as the early Permian age *Protelytron* (Figures 1.23) as well as in beetles (coleopterans) and cockroaches (blattodeans).

TAPHONOMY AND PRESERVATION POTENTIAL

Arthropods are often cited as an example of the problematic nature of the fossil record. Despite their enormous diversity and success throughout much of Phanerozoic time, there is a question over the extent to which this is reflected in the record. According to Wills (2001) 'even the thickest cuticle is unlikely to be preserved as a fossil in all but the most exceptional circumstances', although a thick cuticle should stand a better chance of being preserved than a thin cuticle. Consequently, there is an expectation that only those arthropods with mineralized cuticle, such as the trilobites and some crustaceans, are likely to have been preserved. Nevertheless, the moulting behaviour of arthropods enhances the fossil record of those animals with mineralized skeletons by multiplying the chances of the moulted exoskeleton being buried and preserved thus biasing the record in their favour. However, the discovery of several fossil sites around the world with exceptional preservation (Konversat Lagerstätten) has opened some windows on the past diversity of

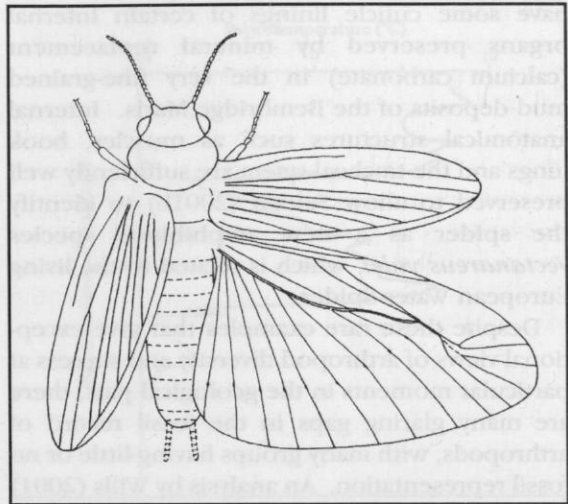


Figure 1.23 *Protelytron permianum* Tillyard (Protelytroptera: Protelytridae) Lower Permian, Kansas, USA Hindwing length is 8mm. (From Carpenter, 1971.)

the arthropods. In these sites, arthropod cuticle has been preserved in various ways to reveal remarkable levels of anatomical detail. They also give a much more faithful view of the relative abundance of different arthropods in the past, especially many extinct forms whose existence would not otherwise be known about.

Preservation of arthropod cuticle in these sites varies from thin organic films and layers of diagenetic alumino-silicate clay minerals, such as is found in the Cambrian Burgess Shale, to the three-dimensional phosphatized forms from the Cambrian *Orsten* of Sweden, the pyritized material of the Devonian age Hunsrück Slate of Germany, which requires X-rays to reveal its detail, the near-perfect preservation within Mesozoic and Cenozoic amber and rare silica permineralization of important sites such as the Rhynie Chert GCR locality. More recently, a British locality of Silurian age has been found in Herefordshire (Sutton *et al.*, 2001) which preserves a variety of arthropods in three-dimensions within carbonate nodules. By detailed sectioning and computer imaging, the body form of the animals can be reconstructed in sufficient detail to reveal diagnostic characters. Younger British strata have also yielded some remarkable examples of high quality preservation. For instance, well-preserved insects and spiders have been found (Selden, 2001b) in Oligocene age lagooned deposits from the Isle of Wight. There are spiders that even

Introduction to British fossil arthropods

have some cuticle linings of certain internal organs preserved by mineral replacement (calcium carbonate) in the very fine-grained mud deposits of the Bembridge Marls. Internal anatomical structures such as muscles, book lungs and the tracheal system are sufficiently well preserved to allow Selden (2001b) to identify the spider as a new amphibious species *Vectanareus yulei*, which is related to the living European Water Spider.

Despite these rare examples that give exceptional views of arthropod diversity and success at particular moments in the geological past, there are many glaring gaps in the fossil record of arthropods, with many groups having little or no fossil representation. An analysis by Wills (2001) tried to assess the overall quality of the arthropod record by focussing on the gaps between the first occurrences of sister groups. The premise here is that if the fossil record were complete then sister taxa should appear as fossils at the same time in the stratigraphical record. But if the record is not complete then the first occurrences of sister taxa will be separated in time and ghost ranges need to be hypothesised to fill in the gap between the two points of origin. The better the fossil record of a group of organisms then the better the congruence between their fossil ranges and the fewer or shorter the ghost ranges. Wills compared differences in congruence for large samples of arthropods against a wide range or other fossil groups ranging from echinoderms and other non-arthropod invertebrates and vertebrate groups such as the fish, reptiles, birds and mammals.

Overall these statistical analyses show that arthropods are indeed under-represented in the fossil record compared with other major groupings such as the fish, reptiles or all taxa taken together and that this applies both during Palaeozoic and post-Palaeozoic times. They conclude that there is probably no single reason for the apparent incompleteness of the arthropod record but a number of factors can be suggested with low preservation potential almost certainly playing a major part. However, even some groups with resilient and mineralized cuticles such as the trilobites, which therefore should have relatively high preservation potential, actually have low indices of congruence as measured by Wills. Another important factor is the very low availability of sediments representative of some life habitats for particular groups

of arthropods such as those which live in mid- and deep- ocean waters or upland terrestrial environments.

Small size is another factor with many groups of arthropods with sparse or non-existent fossil records being typically minute such as the palpi-grade arachnids or proturan insects. However, there are other small groups such as the mites and tardigrades that have ancient fossil records. Low diversity and low abundance may also contribute to low representation. Sites of exceptional preservation make significant contributions by preserving occasional rare forms even among higher taxa. Exploration of the stratigraphical record is still undeveloped in many parts of the world, consequently discovery of new Konservat-Lagerstätten is still highly likely along with whole new fossil arthropod faunas. It takes the discovery of only one well-preserved new fossil to establish the minimum divergence age for an entire taxon whether at the family or phylum level.

Some arthropod groups that should theoretically have reasonable fossil records because of their abundance and habitats, such as the abundant and widespread amphipods with over 5500 living species (including the common beach hoppers), many of which are marine or, the equally diverse and abundant isopods with their 4000 species (including the familiar terrestrial woodlice) distributed amongst 98 families, actually have some of the patchiest and least satisfactory fossil records.

INSECTS AS CLIMATE INDICATORS

It is well known that most lifeforms are sensitive to variations in climate. The global distribution of living organisms, both plants and animals, is to a large extent controlled by the present climate zones, but it is also well known that some organisms are much more sensitive to climate than others. Humans and some birds are remarkably good at tolerating a wide range of climate, whereas many insects and plants are severely constrained in their geographical ranges by narrow climate tolerances. Indeed, study of Quaternary ice-age deposits and fossils has utilized the restricted climate-tolerance of beetles to provide detailed information about climate change.

Beetles are very common insects in terrestrial environments and with some three hundred

thousand species alive today, they have a huge diversity that fills a wide variety of ecological niches. Most have a narrow range of diet and environmental conditions that they inhabit. Beetle reproductive cycles tend to be short, usually less than a year, so that populations can rapidly respond to changing conditions. Their numbers contract in areas where conditions are no longer optimum, and expand in areas with more-suitable habitats, aided by the fact that most of them can fly. Furthermore, parts of their exoskeletal cuticle, such as the wing cases (elytra) are very tough and not easily degraded once the animal has died. Consequently, the fossil record of beetles in certain terrestrial depositional environments such as bogs and lakes, is remarkably good.

Fortunately, individual beetle species can be identified even from their wing cases and many species have changed very little over the last million or so years. Thus known habits and tolerances of living species, especially those of northern Eurasia and other cool areas can be reliably extrapolated back into the immediate past and used to reconstruct past climates. In the 1960s, Russell Coope and his co-workers at Birmingham University pioneered the use of beetle remains as particularly sensitive recorders of climate change throughout the Quaternary period, often in conjunction with fossil pollen records (Coope, 1979).

Some Quaternary deposits contain the remains of up to 200 beetle species and can provide a very exact climate assessment of a very narrow window in time with temporal ranges of tens to hundreds of years. Beetles found in British glacial deposits now live in Siberia or central Asia and so interpretation of the climatic significance of the fossils requires knowledge of present-day beetle distribution throughout the world. Figure 1.24 shows an average temperature curve for Britain over the last 14 000 years since the last glacial maximum, based on beetle fossils found in successive glacial and interglacial deposits.

As described by Wilson *et al.* (2000, p.173–4) the beetle record of different assemblages of beetles with different climate tolerance reveals that winters were less severe during the glacial maximum than during the rest of the glacial and may explain the higher snowfall. The transition from Arctic to temperate beetle assemblages is sudden about 13 000 years ago when the polar front moved north and produced summers

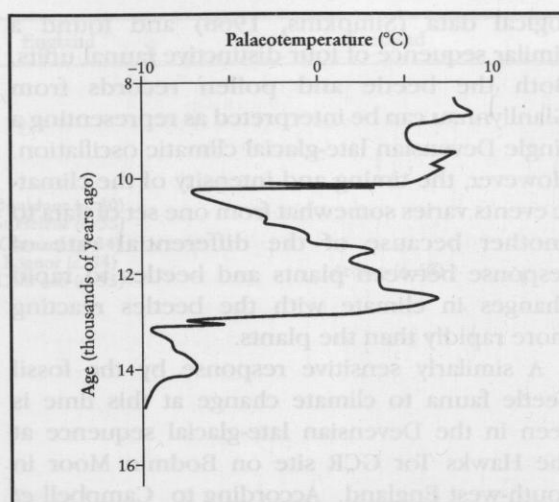


Figure 1.24 The average temperature curve for Britain for the glacial maximum to early Holocene times, as assessed from beetle remains. (After Wilson *et al.*, 2001.)

similar to those of today. Beetle records from Yorkshire show that around 13 ka temperatures rose dramatically by 12–14°C for July and 19–21°C for January to a summer maximum of 20°C and winter minimum of 5°C. The rapid deterioration of climate into the Younger Dryas around 11 ka is marked by the appearance of wholly Arctic beetles in the British fossil record, and beetles are so rare in Scottish deposits at this time that the landscapes were probably similar to polar deserts.

One of the best-known and most intensively studied Quaternary sites in the British Isles for its beetle record is the GCR site of Glanllynau in the Llyn Peninsula of northern Wales, described by Campbell and Bowen (1989). This coastal Devensian age site shows evidence for a fluctuating ice front and glacial retreat as recorded by both sediments and its fossil record. Sediment infills to originally waterfilled kettle holes have yielded a sequence of fossiliferous clay layers rich in organic material which have been radiocarbon dated. Pollen fossils were used to divide the succession into four main pollen zones from a horizon equivalent to the Older Dryas up through the Younger Dryas to Holocene time. Radiocarbon dates provided a timeframe from around $14\,468 \pm 300$ ka to mark the beginning of the Late Devensian late glacial sequence through to $11\,300 \pm 300$ ka. In 1972, Coope and Brophy compared their interpretation of the beetle record of environmental change with the previously published palyno-

logical data (Simpkins, 1968) and found a similar sequence of four distinctive faunal units. Both the beetle and pollen records from Glanllynau can be interpreted as representing a single Devensian late-glacial climatic oscillation. However, the timing and intensity of the climatic events varies somewhat from one set of data to another because of the differential rate of response between plants and beetles to rapid changes in climate with the beetles reacting more rapidly than the plants.

A similarly sensitive response by the fossil beetle fauna to climate change at this time is seen in the Devensian late-glacial sequence at the Hawks Tor GCR site on Bodmin Moor in south-west England. According to Campbell *et al.* (1998, p. 37) Coleoptera from Hawks Tor show that the period of maximum interstadial warmth may have been somewhat earlier than the thermal maximum adduced from pollen evidence. It is also probable that the transition from Arctic to Interstadial conditions was vastly more rapid than suggested from the pollen data: this is in keeping with pollen and insect evidence from other areas of the British Isles (e.g. Coope and Brophy, 1972; Coope, 1977).

GCR SITE SELECTION

This volume describes 34 sites (see Figure 1.25) that were selected for the GCR because of their special significance in the study of certain important groups of fossil arthropods. They are sites that have yielded important specimens of arthropod groups, including extinct aquatic eurypterids, phyllocarid crustaceans, synxiphosurane chelicerates, eumalacostracan crustaceans, early scorpions and primitive terrestrial arthropods such as millipedes, kampecarid myriaopods, euthycarcinoid and trigonotarbid arachnids, early mite taxa and diverse insects, which have not received specific attention throughout the other palaeontological and stratigraphical volumes of the GCR series.

The GCR project aims to identify the most important geological sites and provide the scientific arguments and evidence on which a case for conservation can be built. The documentation presented here becomes a matter of public record with the ultimate aim of formal notification as Sites of Special Scientific Interest (SSSIs) many of which are already notified. The notification of SSSIs under the Wildlife and

Countryside Act 1981 (amended in 1985 and substantially modified in 2000 by the Countryside and Rights of Way Act 2000 in England and Wales, and in Scotland by the Nature Conservation (Scotland) Act 1991) is the main mechanism of legal protection in Great Britain.

The origins, aims and operation of the review, together with comments on the law and practical considerations of Earth-science conservation, are fully explained in volume 1 of the GCR series, (Ellis *et al.*, 1996). The GCR has identified three fundamental site selection criteria; firstly, international importance, secondly, the presence of exceptional features that are scientifically important, and thirdly the presence of representative features that are essential for characterizing the fossil record of the organisms in question. Each site must satisfy at least one of these criteria but many of them satisfy two and some include all three categories.

Many of the sites described in the present volume have also been selected for other categories of the GCR, especially biostratigraphical ones and for their representation of other major groups of fossils such as the plants (Cleal and Thomas, 1995, Cleal *et al.* 2001), fishes (Dineley and Metcalf, 1999), reptiles (Benton and Spencer, 1995), and mammals and birds (Benton *et al.*, 2005). However, the emerging importance of some of these fossil arthropods within these sites has greatly increased their overall importance, and in a few instances become the most significant aspect of the palaeontology of the site.

The general international importance of some of the British fossil arthropods, particularly their contribution to the understanding of the evolutionary and ecological aspects of the initial terrestrialization of life on Earth, has already been stressed. Ten sites fall in this category, many of which have a strong historical component (such as Ludford Lane, Ardtun and Stonesfield) and are not as accessible and productive as they once were, but others such as Rhynie still have potential for further research but require excavation for adequate access.

There are exceptional features to the fossil arthropod faunas of most of the sites and there are a number of different kinds of features. These include the national importance of the site; a significant historic interest in the site; the diversity of its fauna; a significant palaeobiological interest in some aspect of the fauna, such

GCR site selection

				England	Scotland
Cenozoic	Quaternary	Holocene	0		
		Pleistocene	0.01		
	Neogene	Pliocene	1.8		
		Miocene	5.3		
	Tertiary		23.0		
		Oligocene	33.9	Bouldnor (c. 30) St Helens (c. 33) Gurnard (c. 34) Bognor (c. 54) Cold Ash (c. 55)	Ardtun (c. 55)
Mesozoic	Cretaceous	Palaeocene	55.8		
			65.5		
		Maastrichtian	70.6		
		Campanian	83.5		
		Santonian	85.8		
		Coniacian	89.3		
		Turonian	93.5		
		Cenomanian	99.6		
		Albian	112		
		Aptian	125	Smokejacks (c. 125)	
		Barremian	130	Clockhouse, Auclaye (c. 130)	
		Hauterivian	136		
		Valangian	140		
		Berriasian	145		
	Jurassic		145	Dinton (c. 143) Teffont (c. 144) Poxwell, Durlston (c. 145)	
		Tithonian	151		
		Kimmeridgian	156		
		Oxfordian	161		
		Callovian	165	Stonesfield (c. 166)	
		Bathonian	168		
Mesozoic	Jurassic	Aalenian	176		
		Toarcian	183	Dumbleton (c. 182)	
		Pleinsbachian	190		
		Sinemurian	196	Stonesfield (c. 195)	
		Hettangian	200	Aust (c. 200)	
			204		
	Triassic	Rhaetian	216		
		Norian	228		
		Carnian	228		
		Ladinian	245		
		Anisian	251		
		Scythian	271		
Palaeozoic	Permian	Zechstein	271		
		Rotliegendes	299		
			305	Writhlington (c. 307)	
	Carboniferous	Stephanian	315		
		Westphalian	326		East Kirkton (c. 328) Granton (c. 332)
		Namurian	345		Glencartholm (c. 340)
		Visean			

Figure 1.25 (continued overleaf). Chronology of GCR sites described in the present volume, with dates based on the timescale of Gradstein *et al.* (2004).

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			England	Scotland
P a l a e o z o i c	Carboniferous	Tournaisian		Foulden (c. 348)
	Devonian	Emsian	360	
		Pragian	407	
			411	Rhynie (c. 410) Turin Hill (c. 411)
		Lochkovian		
	Silurian		416	
		Pridoli	Bradnor, Perton, Tin Mill (c. 417) Ludford (c. 418) Whitcliffe (c. 419) Church Hill (c. 420)	
		Ludlow	419	
				Stonehaven (c. 422)
		Wenlock	423	
			428	Slot Burn (c. 426) Gutterford (c. 428) Dunside (c. 430)
		Llandovery		
	Ordovician	Ashgill	444	
		Caradoc	456	
		Llanvirn	461	
		Arenig	472	
		Tremadoc	479	
	Cambrian		488	
		Late	501	
		Mid	513	
		Early		
			542	

Figure 1.25 – continued. Chronology of GCR sites described in the present volume, with dates based on the timescale of Gradstein *et al.* (2004).

as the presence of unique taxa and unusual preservational circumstances.

National importance can refer to various aspects of the fauna. For instance the Church Hill arthropods are not only unique to the Welsh basin but are also of importance for correlation and comparison with contemporaneous but different arthropods within the Midland Valley of Scotland with its different palaeogeography and depositional environments. In contrast Aust Cliff, Durlston, Charmouth and Clock House are of national importance because of the richness of their arthropod faunas and include internationally important stratotypes.

Six sites are of especial historic interest, such as Gutterford Burn in the Pentland Hills of the Midland Valley of Scotland. The site was excavated in the 19th century especially for its fossil agnathan fish and associated eurypterid arthropods. It is now supplemented by a network of other sites in the region such as Dunside

near Lesmahagow which have potential for future development. An even older historic fauna was recovered from Stonesfield in Oxfordshire, extensively worked for so-called ‘Stonesfield slate’. This thin-bedded and fissile limestone was used particularly as roofing material up until the late 19th century. Many of the workings were pits and some extended underground; most of them are now inaccessible. However, the process of quarrying the stone exposed a wonderful variety of different fossils ranging from dinosaur bones to insects.

Mostly, the exceptional features of sites refer to the diversity of their arthropod faunas and other aspects of palaeobiological interest and importance. There are 16 sites that preserve a significant diversity of fossil arthropods, ranging from Perton Lane in the Welsh Borders to the Weald Clay site of Auclaye in southern England which also has fine preservation in phosphate. Fourteen sites have features of palaeobiological

interest. For instance, Church Hill has an ecologically important association of arthropods with a marine invertebrate fauna, and several GCR sites preserve associations of arthropods with jawless fish (e.g. Turin Hill and Slot Burn). Other sites such as Rhynie, Ludford Lane, East Kirkton, Granton Shore, Charmouth, Durlston Bay, Ardtun and Gurnard have unique taxa as indeed most fossil insect sites do.

In addition there are several instances of exceptional preservation, which has allowed the survival of delicate tissues normally degraded by a whole range of post-mortem processes prior to fossilization. For instance, the microarthropods of the Rhynie Chert GCR site are exceptionally preserved with astonishing anatomical detail in the finely crystalline silica mineral chert. The deposits of the Scottish Carboniferous GCR sites of East Kirkton and Granton Shore also had somewhat unusual sedimentary and post-depositional environments that resulted in preserved important arthropod faunas.

All of the sites together fulfil the requirement of *representativeness* and as such are part of a network of sites connected primarily by their similar stratigraphical age and linked palaeoenvironments. Six separate networks have been established: the Silurian network in the Midland Valley of Scotland (e.g. Gutterford Burn), where arthropods are associated with agnathan fish; the late Silurian network of the Welsh Borders (e.g. Whitcliffe), where eurypterid arthropods are associated with a variety of other invertebrates and record the terrestrialization of environments and faunas; the Scottish network of Lower Carboniferous 'Oil Shale' sites that includes Foulden, Glencartholm, Granton Shore and East Kirkton; the late Jurassic network in Dorset of Poxwell and Durlston Bay preserve a considerable diversity of insects associated with the freshwater or lagoonal deposits of the Purbeck Beds; similarly, the early Cretaceous network of the Wealden area (e.g. Clockhouse) and the Eocene–Oligocene network in the Isle of Wight also preserve diverse insect faunas associated with freshwater or lagoonal environments; finally, the two Isle of Wight sites of Gurnard and St Helens which represent the Eocene–Oligocene boundary deposits in the Hampshire Basin.

Many of the sites described in the present volume are important in several contexts both biostratigraphical and palaeobiological (see below). From the latter point of view several are

described in other GCR volumes for the importance of two or more other major taxonomic groups. A number of arthropod sites are co-located with GCR sites listed for fossil fishes, plants, reptiles and mammals. For instance Turin Hill is a Palaeozoic Palaeobotany GCR site, (Cleal and Thomas, 1995) for the importance of its Lower Devonian plants, as well as for fossil fishes (Dineley and Metcalf, 1999, where the site is called 'Tillywhanland Quarry') for its jawless and primitive jawed fish. In the present volume, it is listed for its eurypterid and early myriapod arthropods. Durlston Bay is an even more diverse site being listed for its diverse early Cretaceous fish fauna, which includes 32 species (Dineley and Metcalf, 1999), its 40 reptile species (Benton and Spencer, 1995), and its mammal fauna (Benton *et al.*, 2005) as well as for its stratigraphical context (Allen *et al.*, in prep). In the current context Durlston Bay is also one of the most productive sites for fossil insects of late Jurassic age in Europe with some 200 new insect species belonging to 12 orders represented, ranging from beetles to dragonflies.

The GCR arthropod sites vary greatly in their size, extent and character from a network of linked coastal cliff sections in dipping strata such as those of Durlston Bay, Charmouth, and the Isle of Wight, to a finite 'dump' of old mine spoil such as Writhlington. Writhlington is comprised of the tip debris from an old Radstock coal mine and has produced a number of important xiphosurids, phalangiotarbid arachnids and insect fossils of Carboniferous 'Coal Measure' age. The internationally renowned Rhynie Chert GCR site with its exceptionally preserved Devonian microarthropods is unusual in that it does not crop out naturally at the surface but has to be excavated to gain access to the fossiliferous strata. However, this has had the beneficial effect of protecting the site from irresponsible overcollecting or irresponsible commercial collecting (see the JNCC Fossil Collecting Policy Statement in the preliminary pages of the present volume). Originally the site was located through the identification of fossiliferous 'float' boulders from the subcrop that had been built into local drystone walls. The original Stonesfield fauna was also largely obtained from underground workings for 'slate'; the site is of historical interest for the description of British fossil insects, since the fossiliferous horizons are no longer accessible. And finally, Bognor Regis,

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internationally famous for early Eocene age insects is only exposed at low spring tides and then is often covered with shifting sand deposits. However, it is from the sands that pyritized fossils can be sieved.

Selection of the GCR arthropod sites was originally made some 20 years ago and was based on the state of knowledge at that time. The declared aim of the GCR is to identify 'the minimum number and area of sites needed to demonstrate the current understanding of the diversity and range of features within each block or network'. Inevitably new potential sites have emerged since that time and of these, Stonehaven (Grampian, Scotland) is described herein as just such a potential site because of the recent discovery of the earliest known millipede fossils from its mid-Silurian age strata, fossils which have given it an international importance.

GCR sites described in the present volume

The following sites are generally arranged in ascending chronological order but also clustered into related networks that have temporal and environmental links within specific palaeogeographical regions. This arrangement forms the scheme for the chapters of the present book and the order of site reports within each chapter. For each site the GCR number is given along with its Ordnance Survey grid reference, regional location and summary of the main criteria for which it has been selected, and finally, there are cross references to other GCR volumes in which the site is also described for other features of geological interest, such as stratigraphy, fossil plants, fishes and reptiles.

Lower Palaeozoic sites – Scotland – a network of Midland Valley sites of Silurian age

GCR 1598. Dunside (NS 748 368), Lesmahagow, Strathclyde, Scotland.

The diverse fauna of Silurian (Early Silurian, upper Llandovery, Telychian age *c.* 430 Ma) arthropods is particularly rich in eurypterids, several species of phyllocarid crustaceans and a very rare synxiphosurane chelicerate associated with agnathan fish. This site has also been selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999).

GCR 1582. Gutterford Burn (NT 158 591), Pentland Hills, Lothian, Scotland.

This is a key historic site for Early Silurian (upper Llandovery, Telychian age *c.* 428 Ma) arthropods, especially a diversity of eurypterids including stylonuroids, rare synxiphosurine chelicerates and one of the earliest scorpions associated with agnathan fish. The site has also been selected as a GCR site for its stratigraphical value (Aldridge *et al.*, 2000).

GCR 2804. Slot Burn (NS 681 321–NS 680 321), Lesmahagow, Strathclyde, Scotland.

From this nationally important site a diversity of mid Silurian (early Wenlock age, *c.* 426 Ma) eurypterid arthropods and agnathan fish has been found. The site has also been selected as a GCR site for its fossil fish (Dineley and Metcalf, 1999) and stratigraphical value (Aldridge *et al.*, 2000).

GCR 2797. Turin Hill (NO 526 551, NO 491 523, NO 494 535), Forfar, Tayside, Scotland.

A historic and internationally renowned site for the palaeobiological study of Lower Devonian (early Gedinnian age, *c.* 411 Ma) eurypterids, especially stylonuroids, very rare early terrestrial millipede and kampecarid myriapods have also been found here. The site has also been selected as a GCR site for its fossil fish (Dineley and Metcalf, 1999), fossil plants (Cleal and Thomas, 1995) and its stratigraphical value (Barclay *et al.*, 2005).

GCR Stonehaven (NO 881 866), Aberdeenshire, Scotland.

Recent discoveries of some of the earliest known terrestrial millipede species, associated with eurypterids and phyllocarids have given this Silurian site of latest Wenlock–?earliest Ludlow age (*c.* 422 Ma), international importance.

Lower Palaeozoic sites – Welsh Borderlands – including the network of late Silurian–early Devonian sites

GCR 2799. Church Hill (SO 412 738), Hereford and Worcester, England.

The truly marine eurypterid and phyllocarid fauna with rare xiphosurans of this Upper Silurian, Ludlow Series (Ludfordian age, *c.* 420 Ma) site is unique to the Welsh basin and of

national importance for comparison with near contemporary faunas of the Midland Valley of Scotland. This site has also been selected as a GCR site for its fossil fish (Dineley and Metcalf, 1999) and stratigraphical value (Aldridge *et al.*, 2000).

GCR 2802. The Whitcliffe (SO 506 744–SO 512 741), Shropshire, England.

This Welsh Borderland Silurian site of Ludlow Series, Ludfordian age (c. 419 Ma) is the type locality for three of the four eurypterid species recorded from here. This site has also been selected as a GCR site for its stratigraphical value (Aldridge *et al.*, 2000).

GCR 1597. Ludford Lane and Ludford Corner (SO 5124 7413–SO 5120 7410), Shropshire, England.

A classic locality that defines the Ludlow Series and Downton Group (late Silurian Pridoli age, c. 418 Ma). It is internationally renowned for its flora and fauna, including some of the earliest direct evidence of terrestrial animals (trigonotarbid arachnid and centipede remains), together with eurypterids, arthropleurid and kampecarid myriapods. This site has also been selected for the GCR for its fossil fishes (Dineley and Metcalf, 1999) and stratigraphy (Aldridge *et al.*, 2000).

GCR 2798. Tin Mill Race (SO 460 754), Hereford and Worcester, England.

Compared with others, this site of late Silurian (Pridoli age, c. 417 Ma) has yielded important eurypterid remains within recent decades and is still available for research. This site has also been selected as a GCR site for its fossil fish (Dineley and Metcalf, 1999).

GCR 1584. Perton Lane (SO 596 406), Hereford and Worcester, England.

An important historic site from which a diverse fauna of late Silurian (Ludlow–Pridoli age, c. 417 Ma) eurypterids have been collected. This site has also been selected as a GCR site for its fossil plants (Cleal and Thomas, 1995) and its stratigraphical value (Aldridge *et al.*, 2000).

GCR 2800. Bradnor Hill (SO 291 577), Kington, Hereford and Worcester, England.

This historically important site of Ludlow–Pridoli age (c. 417 Ma) yielded a diversity of eurypterid arthropods in the 19th century. This site has also been selected as a GCR site for

its fossil fishes (Dineley and Metcalf, 1999).

Upper Palaeozoic sites – Scotland – with a network of Lower Carboniferous sites

GCR 1581. Rhynie Chert (NJ 494 277), Aberdeenshire, Scotland.

An internationally important site of Early Devonian (Pragian) age (c. 410 Ma) for the study of terrestrial arthropods, their palaeobiology and evolution. The fauna includes crustaceans, including the first Devonian euthycarcinoid also trigonotarbid arachnids, the oldest mites, the earliest collembolan insect (hexapod) and a myriapod all associated with a world renowned fossil flora. This site has also been selected as a GCR site for its fossil plants (Cleal and Thomas, 1995) and its stratigraphical value (Barclay *et al.*, 2005).

GCR 2801. Foulden (NT 921 552), near Berwick-on-Tweed, Borders, Scotland.

The earliest known Carboniferous (Tournasian, Courceyan age, c. 348 Ma) non-marine arthropods have been found at this site including the earliest limuloid and an unusual eurypterid all associated with plant and fish remains. This site has also been selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999).

GCR 1583. Glencartholm (NY 376 796), Dumfries and Galloway, Scotland.

A key site for the study of early Carboniferous (Viséan, Holkerian–Asbian age, c. 340 Ma) arthropods with remarkable diversity including eurypterids, xiphosurans, scorpions and crustaceans, including the greatest diversity of Lower Carboniferous shrimps in the world. The site still has potential for further detailed research. This site has also been selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999), fossil plants (Cleal and Thomas, 1995).

GCR 2805. Granton Shore (NT 245 771), Lothian, Scotland.

This exposure of the Lower Carboniferous Granton ‘Shrimp Bed’ (Upper Viséan, Asbian age, c. 332 Ma) is internationally famous, mainly for fossils of the conodont animal found here, but it also has a unique arthropod fauna of eumalacostracan crustaceans, especially the shrimps *Tealliocaris woodwardi*, *Waterstonella grantonensis* and *Crangopsis socialis*. The sequence adjacent to this site has also been

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selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999).

GCR 2803. East Kirkton (NS 990 690), Lothian, Scotland.

This internationally important site of Lower Carboniferous (Upper Viséan, Brigantian, c. 328 Ma) age has provided a unique fauna which includes arthropods such as eurypterids, scorpions, and the oldest known harvestman (opilionid). This site has also been selected as a GCR site for its fossil fishes and tetrapods (Dineley and Metcalf, 1999).

Upper Palaeozoic sites – England

GCR 2977. Writhlington (ST 703 553), Radstock, Avon (Somerset), England.

This site, of Upper Carboniferous 'Coal Measure' (late Asturian) age c. 307 Ma, is of international importance. Comprised of the tip debris from an old Radstock coal mine, it has produced the largest number of fossil insects of any site in the UK, including the oldest known damselfly and the greatest number of phalangiotarbid arachnid fossils. It provides an exceptional resource for studying Upper Carboniferous terrestrial life.

Mesozoic sites – England

GCR 0799. Aust Cliff (ST 565 895), Avon (Somerset), England.

Of national importance, this Rhaetian age (late Triassic–earliest Jurassic, c. 200 Ma) site is the most productive in Britain for Triassic age insects of which scorpionflies (mecopterans) are most abundant with some of the fossils preserving original colour patterning. The site is also famed for its fossil necrotauliid insects from the Cotham Marble. The site also has considerable potential for further investigation. This site has also been selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999) and fossil reptiles (Benton and Spencer, 1995).

GCR 0794. Charmouth (SY 359 931 and SY 369 930), Charmouth–Pinhay Bay, Dorset, England.

Lying within a World Heritage Site inscribed for its geology, this is one of the most productive sites for fossil insects of Liassic (Lower Jurassic, Sinemurian, c. 195 Ma) age in Britain with some unique species. These terrestrial arthropods are

fossilized in marine deposits and include dragonflies (odonatans), bugs (hemipterans), beetles (coleopterans) and crickets (orthopterans), some of which are unique to the site. This site has also been selected for the GCR for its fossil fishes (Dineley and Metcalf, 1999) and fossil reptiles (Benton and Spencer, 1995).

GCR 1683. Dumbleton (SP 006 345), Alderton Hill, Gloucester, England.

This key site for the study of Lower Jurassic (early Toarcian age, c. 182 Ma) insects has provided the types specimens of important genera of Mesozoic dragonflies *Heterophlebia* and *Gomphites*, which provide links with Liassic sites in continental Europe.

GCR 1486. Stonesfield (SJ 392 172, SJ 387 168, SJ 379 172 and SJ 387 171), Oxfordshire, England.

Although largely inaccessible today, this internationally renowned mid-Jurassic (Bathonian, c. 166 Ma) site is of particular historic interest for the description of British fossil insects. Its fauna includes beetles (coleopterans), dragonflies (odonatans) and bugs (hemipterans). This site has also been selected as a GCR site for its fossil fishes (Dineley and Metcalf, 1999) and fossil reptiles (Benton and Spencer, 1995), fossil mammals (Benton *et al.*, 2005) and its stratigraphical value (Cox and Sumbler, 2002).

GCR 0806. Poxwell (SY 740 835), near Weymouth, Dorset, England.

This important site is one of two linked sites (see also Durlston Bay) from the Lower Purbeck Beds of late Jurassic age (Portlandian, c. 145 Ma) that has provided a diversity of terrestrial insects (some 20 species) including fossil cockroaches (blattodeans), dragonflies (odonatans), bugs (hemipterans), beetles (coleopterans), true flies (dipterans) and caddis flies (trichopterans).

GCR 0793. Durlston Bay (SZ 035 772–SZ 039 786), Swanage, Dorset, England.

Britain's richest Berriasian (early Cretaceous) fossil insect site, this is one of a network, including Poxwell, of Late Jurassic sites (Portlandian–Berriasian age, c. 145 Ma) preserving insects from within the Middle and Late Purbeck Beds. This is also one of the most productive sites for insects of this age in Europe. Some 200 new insect species belonging to 12 orders are represented, ranging from beetles to

cockroaches. This site has also been selected as a GCR site for its fossil fish (Dineley and Metcalf, 1999) and fossil reptiles (Benton and Spencer, 1995), fossil mammals (Benton *et al.*, 2005) and its stratigraphical value (Wright and Cox, 2001).

GCR 0808. Teffont Evias (ST 990311 and ST 994309), Wiltshire, England.

A key site in the history of British palaeoentomology, this Lower Cretaceous site (Berriasian *c.* 144 Ma) is now a disused quarry, but produced a diverse fauna of fossil insects (including representatives of five insect orders) in the past described in the first major study of British fossil insects by P.B. Brodie.

GCR 1487. Dinton (SU 006 307), Wiltshire, England.

This historically important basal Cretaceous site in Middle Purbeck limestones (Berriasian, *c.* 143 Ma) has provided some 60 fossil insects including the type specimens of a number of species belonging to some eight different orders. They were the main source of the 'Wealden' (Purbeck) insects described by Brodie in 1845, the earliest major work on British palaeoentomology.

Early Cretaceous age sites

GCR 0823. Clockhouse Brickworks

(TQ 176 383), near Capel, Surrey, England.

This early Cretaceous site in the Weald Clay (Hauterivian, *c.* 130 Ma) is of national importance. It has produced an abundant (several thousand fossils) and diverse insect fauna (11 orders present) including one of the earliest described social insects, a termite.

GCR 0824. Smokejacks Brickworks

(TQ 112 374), Ockley, Surrey, England.

This early Cretaceous site in the Weald Clay is slightly younger (Barremian, *c.* 125 Ma) than Clockhouse Brickworks. Fossil representatives of some six orders of insects have been found here. This site has also been selected as a GCR site for its fossil reptiles (Benton and Spencer, 1995).

GCR 1525. Auclaye (TQ 168 388), Surrey, England.

This early Cretaceous (Barremian) site, *c.* 130 Ma, has produced a diverse fauna of insects belonging to 8 different orders including the beetles (coleopterans), dragonflies (odonatans),

cockroaches (blattodeans and blattarians), crickets (orthopterans), lacewings (neuropterans), caddisflies (trichopterans), true flies (dipterans), wasps hymenopterans and bugs (hemipterans).

Cenozoic sites – Scotland

GCR 0797. Ardtun (NM 379 248), Island of Mull, Strathclyde, Scotland.

This site on the island of Mull in the Western Isles of Scotland is internationally renowned for its early Cenozoic (Lower Eocene, *c.* 55 Ma) age plant-rich sediments interbedded with lavas. The accompanying fauna of a few insect species includes the homopteran cicada *Eotettigarcata scotica* and crickets (orthopterans) and has no equivalent in southern Britain. This site has also been selected as a GCR site for its fossil plants (Cleal *et al.*, 2001) and associated igneous rocks (Emeleus and Gyopari, 1992).

Cenozoic sites – England

GCR 0798. Cold Ash (SU 500 714), Berkshire, England.

This key site in the Reading Formation (Eocene age, *c.* 55 Ma) is the only collectable one in the British Isles to have preserved evidence of leaf mining by insects and the evolution of this aspect of plant–insect relationships. This site has also been selected as a GCR site for its fossil plants (Cleal *et al.*, 2001) and its stratigraphical value (Daley and Balson, 1999).

GCR 1488. Bognor Regis (SZ 918 984), West Sussex, England.

This internationally famous site for early Eocene age (*c.* 54 Ma) insects has provided a remarkably well-preserved fauna of pyritized insects especially beetles, some of which are related to modern subtropical genera. The terrestrial insects are preserved in marine sediments. This site has also been selected as a GCR site for its fossil plants (Cleal *et al.*, 2001), fossil fishes (Dineley and Metcalf, 1999), fossil mammals and birds (Benton *et al.*, 2005) and its stratigraphical value (Daley and Balson, 1999).

GCR 0796. Gurnard (SZ 462 943), Isle of Wight, England.

A key site for a diversity of fossil insects in Britain with some 250 species known, of which the most common is a tree ant *Oecophylla* and the best-known, a relief termite *Mastotermes*

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anglicus. The arthropods are found within the Bembridge Marls of late Eocene–early Oligocene age (34 Ma) and the site is linked in a small network with St Helens also in the Isle of Wight.

GCR 0795. St. Helens (SZ 638 899), Isle of Wight, Hampshire, England.

One of a small network of sites (see also Gurnard) of late Eocene–early Oligocene (c. 33 Ma) age in the Hampshire Basin, from which a diversity of fossil insects and the first British clam shrimp (conchostracan) have been found within the Bembridge Marls.

GCR 0807. Bouldnor (SZ 382 907), Isle of Wight, England.

One of the most promising sites in Britain of early Oligocene age (c. 30 Ma) insects, the Hamstead Beds here on the Isle of Wight have yielded fossil flies (dipterans), beetles, (coleopterans) and ants and wasps (hymenopterans) associated with freshwater ostracods and some plant remains. This site has also been selected as a GCR site for its fossil plants (Cleal *et al.*, 2001), fossil mammals and birds (Benton *et al.*, 2005), fossil reptiles (Benton and Spencer, 1995) and its stratigraphical value (Daley and Balson, 1999).

GCR SITES IN A PALAEO-GEOGRAPHICAL CONTEXT

The stratigraphical distribution of the sites itemized in the previous section is clearly clustered both palaeogeographically and temporally. Since most of the arthropod fossils discussed herein lived in marginal marine to terrestrial environments it is inevitable that most of these clusters reflect times and places in which these environments are well represented by deposits that are preserved in the British stratigraphical record. Such preservation requires particular geological conditions especially regional structural ones, such as basin development and these are discussed in detail in the introductory sections. Here the sequence of sites are briefly considered within the overall geological framework of the formation of the British Isles as the geological entity we recognize today.

The oldest cluster of sites (Dunside, Gutterford Burn, Slot Burn and Stonehaven) is Silurian (upper Llandovery–Ludlow) in age and is situated in Scotland north of the Southern

Uplands Fault and south of the Highland Boundary Fault. Thus they are part of the Early Palaeozoic development of the eastern Laurentian margin and were separated from England, Wales and southern Ireland (Avalonia) by the southern hemisphere Iapetus Ocean. The latter was finally being closed by plate movements and subduction as Avalonia moved north towards Laurentia.

Plate convergence, collision and the resulting Caledonian orogeny produced regressive successions within Silurian inliers of the Midland Valley of Scotland. They record a transition from marine into shallow marginal marine and fluvial conditions. These strata preserve important fossil faunas, including agnathan fish and arthropods that reflect the changing environmental conditions. Additionally, the early Devonian (Old Red Sandstone) strata and fossils of Turin Hill reflect the onset of terrestrial conditions and accumulated during the later stages of deposition within the Silurian to Early Devonian basins of the region. Latterly these were accompanied by extensive volcanism.

The Rhynie site, lying some 50 km west-north-west of Aberdeen, is the one Palaeozoic site that lies outside the Midland Valley of Scotland. Its Old Red Sandstone (Early Devonian, Pragian age) strata represent a unique terrestrial ecosystem of international importance. The Rhynie deposits and organisms accumulated around hydrothermal springs within a small subsiding asymmetrical fault basin (half-graben) whose development on the Ordovician and Late Proterozoic (Dalradian) basement rocks was related to basin formation within the Early Devonian strike-slip system of the region. Due to plate tectonic motion, this region was located south of the equator at the time.

A separate network of six Siluro-Devonian sites (Church Hill, The Whitcliffe, Ludford Lane and Ludford Corner, Bradnor Hill, Perton Lane and Tin Mill Race) represents the development of environments and life on the Avalonian crustal fragment that converged with Laurentia during the Silurian Period. There was a marine regression as the Welsh Basin finally shallowed and was transformed into a region of non-marine environments and sedimentation. Global sea levels were falling from Late Ludlow into Prídolí times, there was increasing sediment supply from an uplifted hinterland in the collision zone and basinal extension and subsidence gave

way to crustal shortening and uplift. Again arthropod related faunas that record these changing environmental conditions are preserved within the strata of the region. Their particular importance lies in the co-incidental timing of the evolution of arthropods and adaptation for freshwater and terrestrial environments for the first time and their preservation in appropriate sediments that have subsequently been recruited to the stratigraphical record.

By Early Carboniferous times major palaeogeographical changes had taken place following the closure of the Rheic Ocean and the collision of Armorica with the southeastern margin of Laurentia to produce the Acadian Orogeny (c. 400 Ma). Subsequently, the collision of the main Gondwanan continent of Africa produced the Variscan orogeny in north-west Europe (Laurussia, c. 370–290 Ma). Although Britain lay to the north of the main collision zone, orogenic events controlled the tectonic evolution of the region within which a number of separate provinces can be recognized.

An Early Carboniferous age network of sites, including Foulden, Granton and East Kirkton all lie within the Fife Midlothian Basin of the eastern part of the Midland Valley of Scotland. Again, deposition here was influenced by volcanism, eustasy, crustal extension, and strike-slip movements along the Highland Boundary and Southern Uplands Faults. Topographical development was highly influenced by volcanic eruptions and the formation of separate basins of deposition in the east and west of the Midland Valley. Outside the Midland Valley and separated from it by the Southern Uplands and Mid-North Sea Highs, is the Glencarholm site. It lies within the Solway Basin that had intermittent connection with the Northumberland Basin to the north-east. Overall, the stratified waters and restricted circulation of these basins produced ideal conditions for the preservation of organic matter and the formation of oil shales and accompanying carbonates. Alternating lacustrine and marginal marine conditions preserved a unique biota including vertebrates and arthropods.

The only English site of Upper Carboniferous age with a significant arthropod fauna of concern here is Writhlington in Avon (Somerset), lying within the Culm Basin to the south of the Wales–London–Brabant High. The development of this basin was strongly influenced by the

Variscan orogeny as it propagated northwards and developed into flexural foreland basins. Writhlington is particularly unusual in that its preservation is solely the result of human mining activity and conservation following the closure of the coal mines. Recognition that the Westphalian 'Coal Measure' deposits here contained an important arthropod fauna led to rock debris from the mines being set aside purely for their palaeontological interest and value. The fauna preserves an important record of Upper Carboniferous terrestrial life when the British Isles lay close to the equator within the Pangean supercontinent.

Despite the persistence of terrestrial environments throughout much of Permian and Triassic times in the British Isles, there was a prevalence of arid tropical environments throughout much of this 100 million year long period. Predominant oxidizing conditions prevented the deposition of suitable environments in which the arthropods of concern here were fossilized. Not until the very end of Triassic times does the British stratigraphical record preserve a site with an arthropod fauna of significance in this context – Aust Cliff in Avon, south-west England.

Late Triassic and Early Jurassic times saw the final agglomeration of Pangea but no sooner had the supercontinent reached its greatest extent than it began to break up. From Late Triassic into Early Jurassic times widespread lithospheric extension and crustal sagging allowed shallow seaways to flood across north-west Europe and the ocean was being newly created in the central Atlantic region by Mid-Jurassic times. By this time, the British Isles lay in the Northern Hemisphere and had undergone profound changes in palaeogeography and climate with the establishment of a latitudinally zoned pattern of climate.

The Triassic–Jurassic boundary (Rhaetian) sequence at Aust cliff in the Bristol Channel basin developed upon an inherited Variscan tectonic basement control of predominantly east-west faults. Aust preserves a marginal marine, quiet water, environment of deposition in which a diversity of land derived fossil material is preserved including a nationally important insect fauna among other invertebrate, reptile and fish remains.

Jurassic times are sampled by three GCR sites in southern England (Charmouth, Dumbleton, and Stonesfield). These, along with the remaining 13 younger sites, have been primarily

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selected for their palaeoentomology. Although most insects are primarily terrestrial organisms, their fossil record has to a considerable extent accumulated in low-energy, marginal marine and estuarine type deposits that are sufficiently fine-grained to preserve relatively delicate fossil remains. This applies especially to the British geological context during Mesozoic and Cenozoic times because there is a general lack of terrestrial deposits such as fine-grained fluvial and lacustrine sediments which might otherwise accumulate insect and other arthropod remains. The exception is the Scottish Cenozoic site of Ardtun (see below).

In general the British Jurassic strata accumulated in a number of sedimentary basins separated by topographic 'highs' that developed on extensional fault systems related to regional stretching of the lithosphere. Deposition was also controlled by a series of transgressions and regressions that produced alternating marine and terrestrial influences within individual basins. And, there were many minor fluctuations in sea level, but overall there was a rise in sea level throughout Jurassic times with the result that there are no Late Jurassic sites that preserve significant palaeoentomological faunas.

Latterly, sea levels fell from the end of Jurassic times into the Early Cretaceous only to rise again so that there are no Cretaceous sites recorded here that are younger than Aptian in age. Nevertheless, seven Early Cretaceous GCR sites in southern England (Poxwell, Durlston Bay, Teffont Evias, Dinton, Clockhouse Brickworks, Auclaye, and Smokejacks Brickworks) do pre-

serve highly significant and diverse insect faunas.

Similar environments of deposition were present in Palaeogene times and five GCR sites in southern England (Cold Ash, Bognor Regis, Gurnard, St Helens and Bouldnor) preserve fossil insects. All but one of these sites lie within the Hampshire–Dieppe Basin but Cold Ash lies to the north-east across the Weald–Artois High within the London Basin. Outer ripples of Alpine orogenic events far to the south produced pulses of uplift in southern England and fluctuating facies changes in the basins of deposition. Bognor, for instance preserves marginal marine sediments into which terrestrial insect remains have been recruited, whereas Bouldnor records brackish to freshwater lagoonal conditions that possibly include some sub-aerial deposits. The Gurnard and St Helens GCR sites form a small network that records the lagoonal succession across the Eocene–Oligocene boundary.

In contrast, the Scottish GCR site of Ardtun on Mull in the Western Isles was fully terrestrial. The insect- and plant-bearing strata here owe their preservation to deposition within an active volcanic environment and being interbedded within a thick sequence of Upper Palaeocene–Lower Eocene age lavas.

Arrangement of the present volume

In the chapters that follow, the palaeogeographical settings are described in detail, the chapters themselves being arranged by geological time.