Fossil Fishes of Great Britain

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Acknowledgements

The initial task to identify, inspect and assess the condition of sites from which notable fossil fishes had been collected in the past began under the auspices of the Nature Conservancy Council (NCC) in the 1980s. Miss S. Turner and, later, Miss M.A. Rowlands set the work in motion for the NCC, visiting localities and corresponding with many individuals with local knowledge or expertise in the field of palaeoichthyology. An appreciable fund of data was established for Palaeozoic sites, and the task of GCR site selection from the list of potential localities had been largely completed by the late 1980s. Work towards publication of the results of this part of the GCR was initiated and Miss Rowlands prepared the draft of a text on the pre-Mesozoic sites. The work was then delayed for some time. In 1995 the present senior author (D.L.D.) was engaged by the Joint Nature Conservation Committee (JNCC) to revise and extend the account of the Palaeozoic sites and, with the assistance of S.J.M., to complete the task of examining localities within the Mesozoic and Cenozoic formations and to prepare this report. Subsequently it was agreed to add an account (Chapter 15) of fossil amphibian tetrapod sites.

Almost all of the sites described in this volume have been visited and assessed relatively recently, but it is possible that the condition of some of them may have changed in the ensuing two years. Many sites may be visited only with the express permission of third parties. Whenever sought by the present authors, this was immediately forthcoming, and it is pleasant to record our gratitude for this.

A large number of people have contributed to and helped in the work at all stages, and to them sincere thanks are extended. Professor M.J. Benton has been staunch in his support throughout. He and the following friends and colleagues have read parts of the draft text: Dr M.I. Coates, Mr R. Davidson, Dr C. Duffin, Dr P.F. Forey, Prof. B.G. Gardiner, Dr E.J. Loeffler, Dr A.R. Milner, the late Dr C. Patterson, Dr N.H. Trewin, Dr C.J. Underwood and Dr D.J. Ward. Their corrections and comments have much improved the outcome. At the University of Bristol much kind help has also been provided by Mrs P. Baldaro, Dr E. Cook, Dr P. Orr and Mr S. Powell.

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As well as those organizations who have given their kind permission for the reproduction of illustrations and photographs, thanks also go to the many authors named in the figure captions.

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 or that a right of way exists. 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 in no way 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,
Plas Penrhos,
Ffordd Penrhos,
Bangor,
Gwynedd LL57 2LQ.

English Nature,
Northminster House,
Peterborough PE1 1UA.

Scottish Natural Heritage,
12 Hope Terrace,
Edinburgh EH9 2AS.

Conserving our fossil heritage – JNCC policy statement

Fossils are a key part of our natural heritage and form 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 this resource.

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, inexpert 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, English Nature, Environment and Heritage Service and Scottish Natural Heritage, will oppose fossil collecting on the small number of Sites of Special

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.

ACHIEVING POSITIVE MANAGEMENT

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, long-term 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

This book summarizes the results of part of the Geological Conservation Review (GCR), an extensive research programme that aimed to assess the scientific significance of Britain's geological and geomorphological localities so that a representative set of the most important ones could be protected by law. Ultimately, the GCR sites were selected with a view to their designation as Sites of Special Scientific Interest (SSSIs) under the Wildlife and Countryside Act (1981).

In this volume the scientific importance of the set of fossil fish GCR sites is described. The surveys of fossil fish sites were carried out initially for three GCR 'Blocks' – Silurian–Devonian Chordata, Carboniferous–Permian Fish/Amphibia and Mesozoic–Tertiary Fish/Amphibia. In each block, a list of candidate GCR sites was established on the basis of previous research and published material; the list was refined to contain only the most scientifically important localities after consultation with as many people as possible and visits to as many sites as possible. The refined list of GCR sites comprised those nationally and internationally important sites that were needed to reflect the diversity of the fossil fishes of Britain and the history of research and investigation already undertaken.

Because there is potentially a great wealth of sites from which to choose, inevitably reliance has to be placed on those that have already been discovered, documented and researched. Also, while some of the sites described have been the subject of research or study very recently, others have been known for over 100 years, and there may be other classic sites emerging as a result of research under way at the present time. This emphasizes that the sites included in this volume represent what might be thought of as a snapshot at a particular point in time reflecting the way in which the need for a range of sites of different types is reconciled with the background of the information that has become available. It is also important to remember that some potential sites may overlap with sites described in other volumes of the Geological Conservation Review Series which were selected for the GCR for other special interests, such as stratigraphy, fossil mammals (Benton *et al.*, in prep.) or fossil reptiles (Benton and Spencer, 1995).

Most of the SSSI proposals made as a result of the Geological Conservation Review have already been translated into site designations by the appropriate country conservation agencies (the Countryside Council for Wales, English Nature and Scottish Natural Heritage).

This volume is not intended to cover the practical problems involved in future site conservation, but rather to record the scientific justification for conserving particular sites and to demonstrate the character and significance that the sites have against the background of a wider palaeontological context. Although some of the sections necessarily use some technical terms, the accounts (particularly the 'conclusions' sections) have been constructed to be accessible to the non-specialist as far as possible; also the glossary at the end of the volume is compiled with this in mind.

We hope that readers will appreciate this volume as a foundation to describe the sites included but also bear in mind that these are only some of the sites that could have been designated. The purpose of the volume is not only to ensure that the selected GCR sites are available and documented for future generations but to acknowledge that, as further research is undertaken, additional knowledge can be added to that contained in this volume.

Museum abbreviations

BATM, Bath Museum.
BGS(GSM), British Geological Survey, Keyworth (old Geological Survey Museum collection, London).
BMB, Bedford Museum.
BRSMG, Bristol City Museum Geology Collections.
BRSUG, University of Bristol Geology Museum.
CAMMZ, Cambridge University Museum of Zoology.
CAMSM, Sedgwick Museum, Department of Earth Sciences, Cambridge University.
DORCM, Dorset County Museum, Dorchester.
EXEMS, Royal Albert Memorial Museum, Exeter.
GCM, Gloucester City Museum.
GLAHM, Glasgow Hunterian Museum.
LEICSM, Leicester City Museum.
MAIDM, Maidstone Museum.
NHM, Natural History Museum, London.
OUM, University Museum, Oxford.
RSM, Royal Scottish Museum.
SM, Stroud District Museum.
SMLU, Ludlow Museum.
UCL, University College London.
UMXC, Museum of Department of Zoology, University of Cambridge.
WHIMS, Whitby Museum.
YORMS, York Museum.

Chapter 1

British fossil fish and amphibian sites

D.L. Dineley

INTRODUCTION

Britain's heritage of fossils is of international importance in its length, breadth and composition. For the size of the country, the heritage is exceptionally rich. It extends back into the distant Proterozoic part of the Precambrian (or Cryptozoic Eon) and from there to the Recent; it touches every geological period, a time span of more than 600 million years (Ma). Its breadth may be judged from the enormous range of organisms that are present, from unicellular prokaryotes to Man. The great variety and complexity of its composition means that it encompasses marine life from the deep water to the littoral, reefal and boreal, the freshwater aquatic and the terrestrial. Some of the great evolutionary steps taken by life – such as the colonization of the land – are well documented by fossils in Britain.

It is small wonder that fossils attracted early and sustained attention from scholars in these islands and that some of the early palaeontologists were greatly impressed by this wealth of material. While the marine invertebrate fossils are clearly the more numerous, widespread and conspicuous of all major groups, it was some of the fossil vertebrates that stirred not only scientific interest in the early days, but also public interest. Amongst these strange and puzzling fossils attracting attention early in the 19th century were fossil fishes. From the Old Red Sandstone of Scotland came large numbers of fishes that caught the imagination of the young Swiss naturalist Louis Agassiz. His unique intellectual gifts were soon exercised to the full in producing a great scientific work on them (1833–1845) that has influenced palaeontology ever since.

While Agassiz's work was arousing strong interest in these ancient fishes, other collectors were at work in the other Palaeozoic rocks, and the Mesozoic and the Cenozoic rocks elsewhere in Britain. There came countless further fossil fish specimens, and the British students who described, conserved and wove this wealth of fossils into the history of life have been neither few nor unremarkable. Vertebrate palaeontologists have been amongst the most productive and influential biologists throughout the last century and a half. Some have given remarkable interpretations of animals from the preserved remains, while others have added data to the record of Darwinian evolution. The value of fossil fishes as index fossils in biostratigraphy has been developed and, increasingly, they are seen as significant indicators of past environments and ecosystems.

Such a wealth of important fossils as has accumulated, has prompted not a little concern as to how to keep abreast of all the different aspects of natural science it impinges upon. This book sets out to describe and assess the geographical and geological spread of fossil fishes and their significance in (British) palaeontology, not to mention the history of this science itself!

The present volume contains descriptions of some 95 fossil fish localities and two sites selected primarily for their tetrapod fossils; 64 are Palaeozoic in age, 19 in Mesozoic rocks and 14 in Cenozoic beds. It is important to note that a few of the fish sites also contain important tetrapod remains, as indeed do fossil reptile sites (see Benton and Spencer, 1995); these are described in the final chapter. Their distribution is shown in Figure 1.15. Table 1.2 gives the stratigraphical distribution of the sites in Britain. Many sites occur as natural exposures in streams, cliffs and beaches. Quarries, brickpits and mines have added to the total.

The selection of sites was guided by the principles discussed by Benton (1988) when working on localities yielding fossil reptiles. Interest focused upon the number and kinds of fossil fishes present, their preservation and stratigraphical position, and upon the significance of the fossils to science and the history of palaeontology. Early work on the Palaeozoic sites was done by M.A. Rowlands, while M.J. Benton helped reorganize textual materials on the Palaeozoic dates. In 1994 D.L.D. and S.J.M. took over the revision of that work and the description of Mesozoic and Cenozoic sites, including the addition of 33 new sites.

Over 20 000 species of living fishes are known and more are discovered every year. Of all the vertebrates, the fishes are the most numerous and ancient in their lineage. They have been swimming in the waters of the oceans since early Palaeozoic times, and in the smaller realms of freshwater since mid-Palaeozoic days. This geological record of some 500 Ma or more is a long one by any standard, and it is one which shows a continuing successful response to the many changes through which the Earth has passed. It is true to say that just as fishes always live where other forms of life are present, and are to a greater or lesser extent influenced by similar ecological factors, their fossils show this to have been equally so in the past.

The fossil record of the fishes and amphibians emphasizes the sheer diversity of vertebrate life and how from early days these animals were capable of evolving into many different kinds within the same environment. The pattern and progress of all vertebrate evolution is to an extent reflected in the geological history of the fishes and by Late Devonian times these processes had led to the origin of the first animals with limbs, the tetrapods. From then onwards evolution continued with growing significance for the origin and history of our own species.

In this volume we describe and interpret a succession of selected nationally important geological sites at which fossil fishes have been found. There are almost as many different kinds of fishes to be found amongst these as there are sites themselves. These are localities chosen for the Geological Conservation Review (GCR) because of their significance in the history of fishes and/or ancient habitats in which the fishes thrived. Many of them are also important for their place in the scientific exploration of our countryside. All are worth conserving and are chosen as representative of the total available range of sites. Their wealth of fossils may be far from exhausted, though few, if any, can be regarded as inexhaustible.

Many other sites which yield well-preserved fish fossils very nearly qualified as GCR sites, but in seeking to create a representative nationally important site series for the GCR they were excluded from the final lists because their features were better shown elsewhere. Such sites are conserved through the RIGS scheme. The Devonian of South Wales offers many such sites. Notwithstanding, many more important sites remain to be discovered and will need to be considered for the GCR in the future. The study of all of them, whether listed here or not, is far from complete. New techniques in field and laboratory are forthcoming and data handling is improving at a great pace. The story of British fossil fishes has many chapters still to be written and the present small volume must be no more than a brief state-of-the-art account and, perhaps, a stimulus to future geological anglers.

AMPHIBIANS

To the flow of research currently being published on fossil fishes must be added the significant advances concerning the origins of the tetrapods and the early evolution of those animals (Thomson, 1993). Britain continues to yield invaluable material in this connection. Amphibians are the most primitive and geologically the most ancient of the tetrapods. Today's Amphibia are tied to the aquatic environments in the larval stage, but are preponderantly well-adapted to life on dry land as adults. Early tetrapod history is still obscure, despite the material now available. Students of the group are cautious to identify the most ancient of these fossils without ascribing to them the style and modes of life of the modern Amphibia (metamorphosis, aquatic larvae, etc.). Nor is any direct or particular phylogenetic relationship to living frogs, salamanders, etc. envisaged. Indeed, some early fossil tetrapod taxa may be more closely related to the amniotes than to modern amphibians, or may represent some stem group falling outside the diversity of extant tetrapods. Very few traces of amphibian metamorphosis exist in the fossil record, and only recently has a relatively acceptable hypothesis concerning the rise of tetrapods from lobe-finned sarcopterygian fishes been constructed (see Chapter 15).

Very few fossil amphibians feature in the palaeontological record compared to the number of fossil fishes, although a final chapter in this volume is added to represent the very small number of British sites yielding the very early tetrapods and (later) amphibian remains. This links the record of the fishes to the record of the tetrapods, principally the reptiles (Benton and Spencer, 1995), in the present series of GCR volumes.

Several localities selected for their value as fossil fish sites also yield amphibian teeth or bones, and some others are recorded in the reptile site volume (Benton and Spencer, 1995). Nevertheless, the first traces of 'amphibians' in Britain may be trackways in the Old Red Sandstone. British (Palaeozoic) primitive tetrapod faunas from the Carboniferous are some of the earliest and most important in the world.

THE GEOLOGICAL BACKGROUND

The small area that comprises the British Isles has a quite extraordinary geological history. Since late Precambrian time some record of each geological period has become part of the British stratigraphical column. For the most part this is

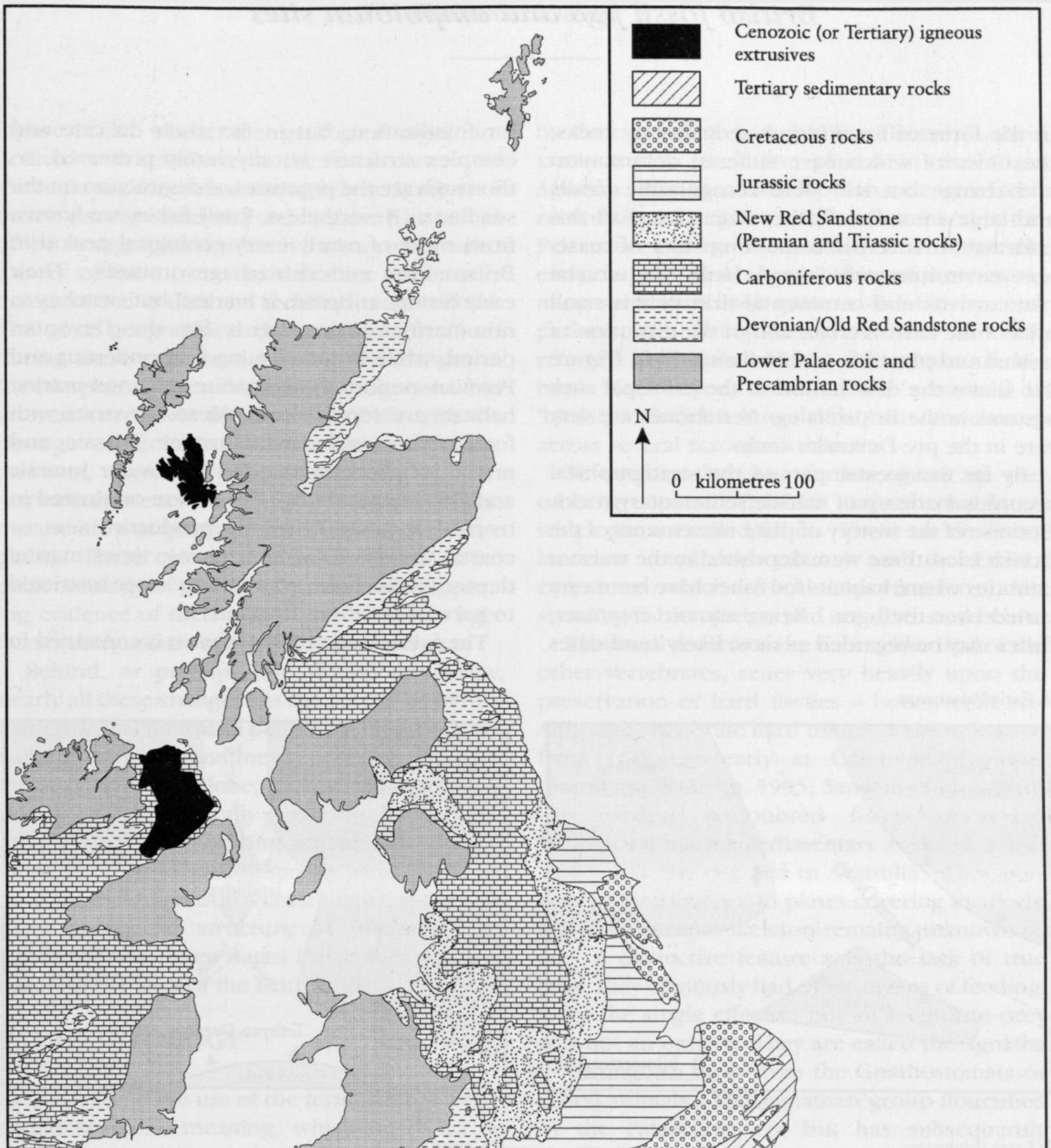

Figure 1.1 Sketch map of the principal outcrops of the main stratigraphical units in the British Isles. The pre-Devonian formations, both sedimentary and crystalline, comprise the Precambrian and the three Lower Palaeozoic Systems. The Devonian rocks include both marine and continental (Old Red Sandstone). The Cenozoic, or Tertiary, sedimentary formations are those of the Hampshire Basin, the London Basin and East Anglia. The flood basalts of the North-west Tertiary Igneous Province are marked, but the many intrusive igneous rocks and various older volcanics are omitted for the purposes of this discussion.

in the form of fossiliferous sedimentary rocks, the older of which have suffered deformation and change but still yield recognizable fossils and large amounts of other data. From all this information is revealed the long story of ceaseless environmental change here, the crustal plate activity and continental drift of this small area of the Earth's crust, and of the evolution of animal and plant life (see Hallam, 1994). Figure 1.1 shows the distribution of the principal rock systems in the British Isles. Vertebrates are very rare in the pre-Devonian rocks.

By far the greater part of the stratigraphical record is made up of marine sedimentary rocks. Because of the history of plate movements of the British Isles, these were deposited in the warmer latitudes where habitats for fishes have been very varied over the ages. Being aquatic creatures, fishes may be regarded as most likely candidates for fossilization, but in fact their delicate and complex structure is only rarely preserved, so thorough are the processes of destruction on the sea floor. Nevertheless, fossil fishes are known from rocks of nearly every geological period in Britain from mid-Silurian age onwards. Their early history in Britain is marine, but switches to non-marine environments for the Devonian period, while in the ensuing Carboniferous and Permian periods both marine and non-marine habitats are represented. Mesozoic strata with fossil fishes include freshwater Triassic and marine, shallow-marine and freshwater Jurassic and Cretaceous strata. All of these originated in tropical, organically highly productive seas or coastal waters. During Cenozoic times marine deposition became progressively more restricted to parts of southern England.

The full extent of this scenario is contained in

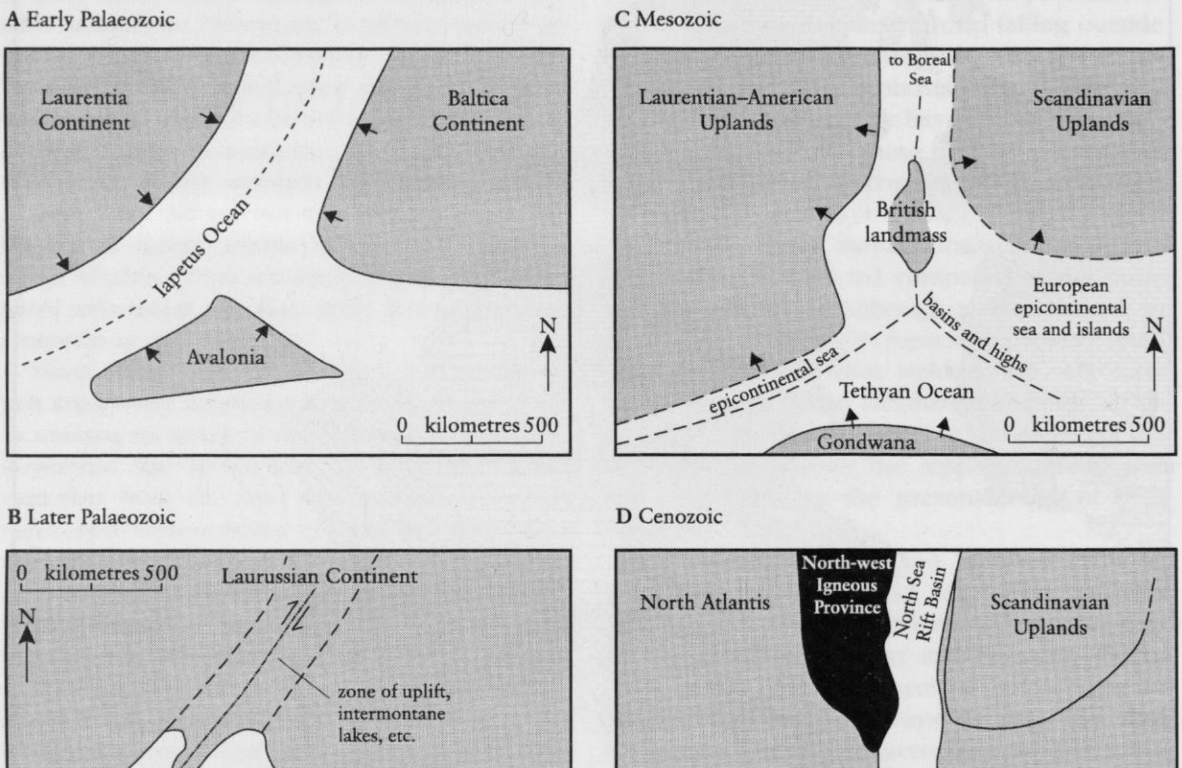

Figure 1.2 A possible scenario of the evolution of the British Isles. (A) Fusion of the continental crustal blocks Laurentia, Avalonia and Baltica in the early to middle Palaeozoic cycle of events. (B) Evolution of middle to late Palaeozoic basins and orogenic uplifts. (C) Mesozoic basin and upland developments. (D) Late Mesozoic–Cenozoic (Alpine) cycle – Atlantic rifting.

Figure 1.14, where the geological ages are defined with reference to the fossil content of the rocks and the actual dating is based on radiometric (isotope analysis) techniques. The names of the stratigraphical column have a complicated history of their own, the dates are continually being revised as data and techniques are refined. The great geographical changes brought about during these eras were matched by changes in the biosphere. There has been a progressive but uneven increase in the diversity of life with the passage of geological time. Now and again, however, there have been relatively sudden 'extinction events' when, for uncertain reasons, marine life was greatly reduced across the entire globe. These events, too, are recorded in the palaeontology of the British rocks, and supporting evidence of their occurrence comes to light from geochemistry and geophysics each year.

Behind, or perhaps one should say below, nearly all these changes lies the Earth's most fundamental mechanism – plate tectonics – continually moving the continents and oceans about the surface of the globe, producing mountains, island arcs and generally powering the 'geological cycle'. This unceasing activity has brought together, from various originally widely separated sources, fragments of crust to give the patchwork geological structure of Britain today. Figure 1.2 illustrates stages in the tectonic evolution of the area of the British Isles.

PALAEONTOLOGY

In this volume the use of the term fish has a particular scientific meaning, which needs to be clarified, especially as the old but still-familiar Linnaean class name Pisces became redundant in the 19th century. The vernacular word 'fish' is cognate with the latin *pisces* and consequently use of the term 'fish' has become both wide ranging and diffuse in its meaning. It generally refers to the most common living bony fishes (the teleosts) and cartilaginous sharks, rays and skates (the chondrichthyans). However, there are also a number of surviving representatives of older groups that were much commoner in the past, such as the coelacanths, dipnoans (lungfishes), myxinoids (hagfishes) and petromyzontids (lampreys), which are also regarded as fishes, in both common and more scientific use.

The hagfishes and lampreys are relatively unfamiliar jawless (agnathan) fishes. These are widely separated from all the living jawed fishes by their anatomy, and this is reflected in their taxonomy as they are placed in the Class Agnatha. The agnathans have an extensive fossil record of extinct groups which flourished in the Palaeozoic and are discussed in detail within the early chapters of this book. Many of these swimming vertebrates look quite un-fish-like by comparison with living fishes, yet they are still referred to as fishes within the context of this book. So, the term fishes, unlike 'mammals' or 'birds', includes a range of aquatic vertebrates across several taxonomic classes.

To confuse the issue further, there are two other groups of 'fish-like' aquatic chordates, which are not called fishes. These are the living lancelets (cephalochordates) and the extinct conodonts, which are both important for understanding fish evolution and are discussed below.

The fossil record of the fishes, like that of the other vertebrates, relies very heavily upon the preservation of hard tissues – bone, teeth etc. Although vertebrate hard tissues are now known from rocks as early as Cambro-Ordovician (Smith and Sansom, 1995; Sansom *et al.*, 1996), the earliest undoubted fishes occur in Ordovician marine sedimentary rocks in North and South America and in Australia. They possessed bony scales and plates covering the body, but their internal skeleton remains unknown so far. A distinctive feature was the lack of true jaws; they obviously had other means of feeding, since the single effective bite of teeth into prey was not an option. They are called the Agnatha to distinguish them from the Gnathostomata or jawed animals. This agnathan group flourished in the Palaeozoic era but has subsequently diminished to a mere couple of forms – hagfishes and lampreys. All the remaining fishes have been and are gnathostomes, and from one group of these were derived the first tetrapods in Mid- and Late Devonian times. While the tetrapods have evolved in spectacular ways since then, the fishes have been equally successful in their diversification and colonizing of every part of the oceans and freshwaters (Hay-Cunningham, 1985).

The question of the origin of the vertebrates remains as fiercely argued as ever (see Janvier, 1996). Nowadays it seems certain that the ancestors of the oldest true vertebrates must lie at least far back in the Cambrian Period if not in the Vendian or other Precambrian time. We have true vertebrate remains from Middle Ordovician rocks in North and South America and Australia, and their anatomies suggest that a relatively long line of ancestors may yet be recovered from the fossil record. Some years ago the problematic sclerite (a protective or supporting plate of hard tissue), *Anatolepis*, was described from several localities ranging in age from Late Cambrian to Arenig in the Ordovician. The original interpretation was of an agnathan vertebrate but it did not meet with widespread acceptance. Research at the University of Birmingham has now revealed its true vertebrate histological affinities and emphasizes the early date of vertebrate radiation and the phylogeny of primitive chordates (Smith and Sansom, 1995; Smith *et al.*, 1995).

One other relatively new line of investigation is the relationship between the early vertebrates and the conodont animals. The latter have a record extending back into the Cambrian period. Conodonts are microscopic phosphatic structures resembling teeth, and are commonly obtained by dissolution of marine limestones in acetic or similar acid. In histology the conodonts are seen to possess structures and materials in common with primitive vertebrates, and a close phylogenetic relationship has been suggested by some students (e.g. Aldridge and Purnell, 1996; Blieck, 1992; Janvier, 1995). It has been equally strongly denied by others (Kemp and Nicoll, 1995; Pridmore *et al.*, 1997). For many years the nature of the animal that bore these hard parts was completely unknown (Aldridge *et al.*, 1995).

Conodonts have a stratigraphical range from Cambrian to Triassic and many forms are biostratigraphically very sensitive. Conodont fossils occur in right- and left-hand forms and in one or more pairs. Pairs of several different form species are found to constitute complex assemblages. In function these assemblages appear to have been part of a pharyngeal mechanism for moving food into the gut. Several instances are known of conodont assemblages being preserved intact within the preserved soft body of the animal (Briggs *et al.*, 1995). The general conodont anatomy has similarities to the hypothetical primal vertebrate, and many cladograms or other 'family trees' postulate a common ancestor. So far as the present discussions are concerned, this is of general interest rather than of importance to our main purpose.

There are other organisms still extant which share some common features with the vertebrates – the Chordata include not only the familiar craniate animals, but also the Urochordates and Cephalochordates. We know, for example, that a cephalochordate animal (Conway Morris and Zhang, 1996), *Pikaia*, lived in Middle Cambrian times; another possibility was *Yunnanozoon* from the Early Cambrian of China (Chen *et al.*, 1995) and early conodonts are recorded from the Late Cambrian. From the Harding Sandstone (Caradocian, Late Ordovician) of Colorado, new discoveries of primitive scales from loganellid thelodonts and chondrichthyid placoid scales have been recently made (Sansom *et al.*, 1996). This effectively pushes back the record of the (agnathan) thelodonts by some 10 Ma and the (gnathostome) sharks by about 25 Ma, and thereby a major radiation of the lower vertebrates is advanced from the Silurian to the late Ordovician. Our diagram (Figure 1.3) shows a phylogenetic scheme of chordates within the geological record.

This diagram also sets out one view of the possible relationships between the different major divisions of vertebrates existing in pre-Carboniferous times. Of these, the Ordovician examples (Richie and Gilbert-Tomlinson, 1977; Gagnier and Blieck, 1992; Gagnier, 1995) are unknown so far in Britain, as are the galeaspids, which are remarkable Chinese primitive agnathan vertebrates. From the very primitive group the anaspids, small, fusiform, naked or clad with small rows of scales, the lampreys are thought to have descended; they were certainly present in the Carboniferous Period. Gnathostomes appear first in the Ordovician and must have originated from an agnathous ancestor well prior to the date of the first Ordovician (Harding Sandstone) gnathostome fossil. To take the story of vertebrate evolution on to further chapters, the first tetrapods entered the stratigraphical record in Late Devonian times. We have both their bones and teeth and their footprints from well before that period was ended.

Towards the end of the Devonian Period came an 'extinction event' of great significance. It involved the total demise of all the older groups of agnathans. Only the myxinoids (hagfishes), lampreys and most of the gnathostomes survived. The disappearance of so many vertebrate kinds made way for the gnathostomes, in particular, to adapt to new habitats, and this they did most vigorously. In fact, it could be said that they have never looked back. The Devonian Period was unmistakably an 'Age of Fishes' with

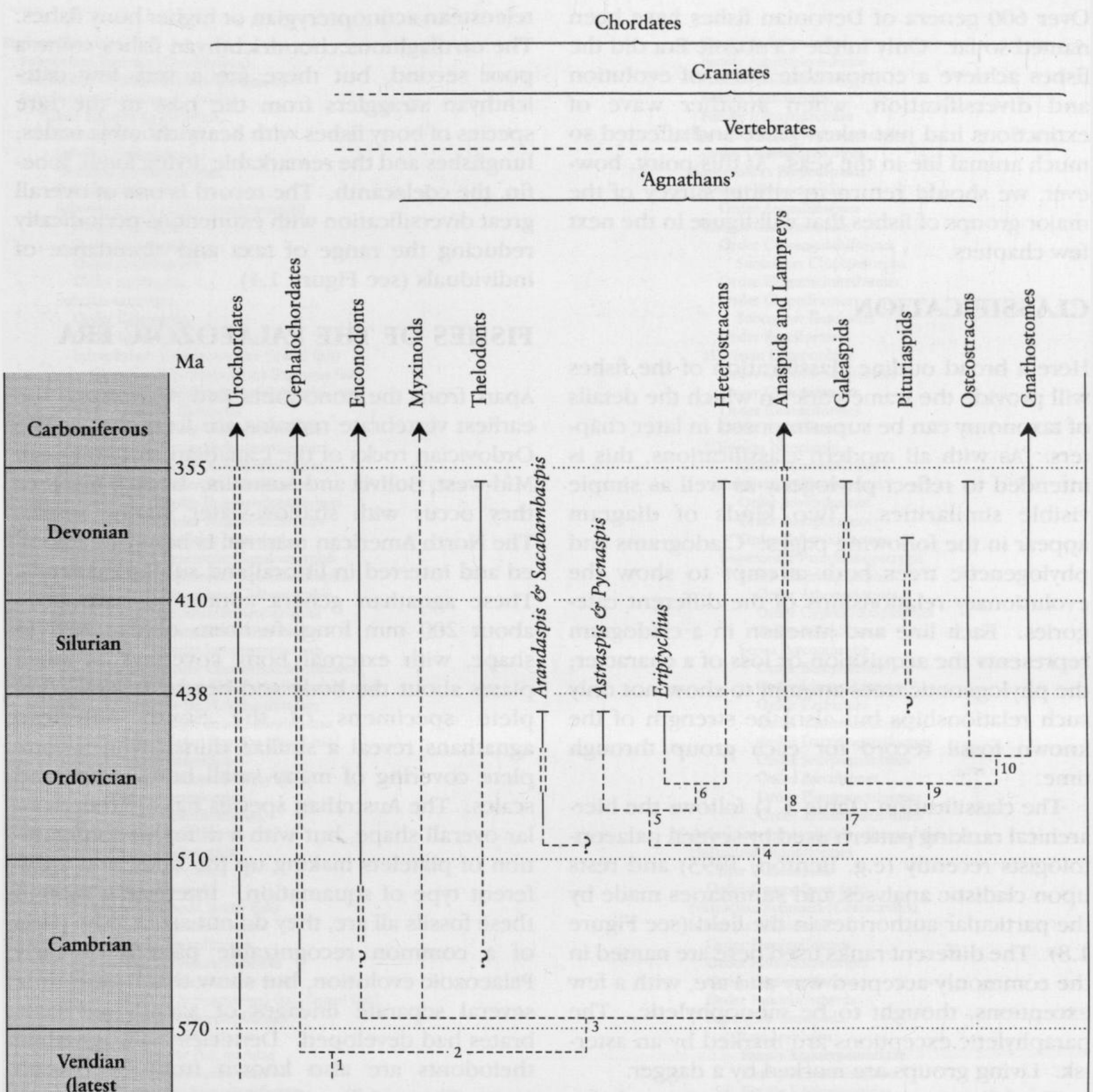

Figure 1.3 A phylogenetic scheme of chordates within the stratigraphical record (after Blieck, 1992). The two known cephalochordates of the Cambrian are *Pikaia gracilis* from the Middle Cambrian Burgess Shale of Canada and *Yunnanozoon lividum* from a Chinese Early Cambrian fauna (*c.* 525 Ma). Thelodonts, as yet undescribed, are known from the Ordovician. Acquisition of vertebrate characters: (1) chordate features (mesoderm, notochord, etc.); (2) somitic characters (somites, creatine phosphate, etc.); (3) craniate features (neural crest, cartilaginous endoskeleton); (4) two semicircular canals, dermal ossification, etc. (5) aspidin present; (6) same four-layered structure of dermal bone; (7) paired fins, etc.; (8) gill openings in a slanted line; (9) cellular dermal bone, perichondral bone etc.; (10) heterocercal tail with change of scale ornamentation at caudal peduncle, pectoral fins, concentrated at base, etc. For full discussion see Blieck (1992), also Chen *et al.* (1995). The Australian group the pituriaspids, the most recently discovered and puzzling, seems to be related to the basic stock from which also came the Chinese galeaspids and the Euramerican osteostracans (see Long, 1995).

its proliferation of species in the marine realm and the entry into fresh waters on all continents. Over 600 genera of Devonian fishes have been named so far. Only in the Cenozoic Era did the fishes achieve a comparable burst of evolution and diversification, when another wave of extinctions had just taken place and affected so much animal life in the seas. At this point, however, we should return to a brief survey of the major groups of fishes that will figure in the next few chapters.

CLASSIFICATION

Here a broad outline classification of the fishes will provide the framework on which the details of taxonomy can be superimposed in later chapters. As with all modern classifications, this is intended to reflect phylogeny as well as simple visible similarities. Two kinds of diagram appear in the following pages. Cladograms and phylogenetic trees both attempt to show the evolutionary relationships of the different categories. Each line and junction in a cladogram represents the acquisition or loss of a character; the phylogenetic trees attempt to show not only such relationships but also the strength of the known fossil record for each group through time.

The classification (Table 1.1) follows the hierarchical ranking pattern used by several palaeontologists recently (e.g. Benton, 1993) and rests upon cladistic analyses and summaries made by the particular authorities in the field (see Figure 1.8). The different ranks used here are named in the commonly accepted way and are, with a few exceptions, thought to be monophyletic. The paraphyletic exceptions are marked by an asterisk. Living groups are marked by a dagger.

The following summaries have been used: for agnathans Forey and Janvier (1993), for placoderms Gardiner (1993a), for chondrichthyans Cappetta *et al.* (1993), for actinopterygians Gardiner (1993b) and Patterson (1993), for sarcopterygians Schultze (1993) and for amphibians Milner (1993a).

The origins of the major taxa (classes and subclasses) are still vigorously debated today. The Gnathostomata, it is generally agreed, must have originated from the Agnatha at a very early date, and the different subclasses of gnathostomes must have appeared not very long afterwards, perhaps by the middle of the Ordovician Period. Unfortunately the fossil record has yet to reveal fossils that show how or when this was achieved. Today the world of fishes is dominated by the teleostean actinopterygian or higher bony fishes. The cartilaginous chondrichthyan fishes come a poor second, but there are a very few osteichthyan stragglers from the past in the rare species of bony fishes with heavy rhombic scales, lungfishes and the remarkable 'living fossil' lobe-fin, the coelacanth. The record is one of overall great diversification with extinctions periodically reducing the range of taxa and abundance of individuals (see Figure 1.4).

FISHES OF THE PALAEOZOIC ERA

Apart from the conodonts and *Anatolepis*, the earliest vertebrate remains are from the Middle Ordovician rocks of the Canadian and American Mid-west, Bolivia and Australia. In each instance they occur with shallow-water marine fossils. The North American material is highly fragmented and interred in littoral and sublittoral sands. These agnathan genera appear to have been about 200 mm long, fusiform or flattened in shape, with external bony coverings of small plates about the body and head. Several complete specimens of the South American agnathans reveal a similar animal with a complete covering of many small bony plates and scales. The Australian species has a rather similar overall shape, but with a different configuration of platelets making up the body, and a different type of squamation. Interesting though these fossils all are, they do not seem to be parts of a common recognizable pattern of early Palaeozoic evolution, but show that by this time several separate lineages of agnathous vertebrates had developed. Denticles from agnathan thelodonts are also known from Ordovician strata (Figure 1.5).

Now that the thelodonts and astraspids have been found accompanied by gnathostome fish scales in the Ordovician of North America (Sansom *et al.*, 1996), it is clear that there was plenty of time for the gnathostomes to become well established by the Early Silurian. The evidence from Silurian rocks is more abundant and significant. The agnathans were by then highly diversified and widely distributed. Silurian Thelodonti, Heterostraci, Galeaspida and Osteostraci each present several families; the Heterostraci and Osteostraci were especially conspicuous around Euramerica. Thelodonts are generally small fossils, with some 'giants'

Table 1.1 Classification of fishes and amphibians (living = †; paraphyletic exceptions = *).

- Phylum Chordata
  - Subphylum Tunicata (Urochordata)
  - Subphylum Cephalochordata (Acraniata)
  - Subphylum Vertebrata (Craniata)
    - *Class Agnatha (jawless fish)
      - †Subclass Myxinoidea
      - Subclass Conodonta
      - †Subclass Petromyzontida
      - Subclass Anaspida
      - Subclass unnamed (Pteraspidomorphi)
        - Order Thelodonti
        - Order Heterostraci
        - Order Arandaspida
        - Order Astraspida
      - Subclass unnamed
        - Order Galeaspida
        - Order Osteostraci
        - Infraphylum Gnathostomata (jawed fish)
          - Class Chondrichthyes (cartillaginous fish)
            - †Subclass Elasmobranchii (sharks, rays)
              - Cohort Euselachii
                  - Order Ctenacanthiformes
                  - Order Hybodontiformes
                  - Order Xenacanthiformes
                  - Order Symmoriiformes
                  - Order Eugeneodontiformes
                  - Order Petalodontiformes
                - †Subcohort Neoselachii
                  - Superorder Squalomorphii
                  - Superorder Squatinomorphii
                  - Superorder Galeomorphii
                  - Superorder Batomorphii
                - Subclass Subterbranchialia
                  - Order Iniopterygiformes
                  - Order Chondrenchelyiformes
                - †Subclass Holocephali (ratfish, etc.)
                  - Order Helodontiformes
                  - Order Bradyodontiformes
          - Class Placodermi (armour-plated fish)
            - Order Stensioellida
            - Order Pseudopetalichthyida
            - Order Ptyctodontida
            - *Order Acanthothoraci
            - Order Petalichthyida
            - Order Phyllolepida
            - Order Arthrodira
            - Order Antiarchi
          - Class Acanthodii (spiny fish)
            - Order Acanthodiformes
            - Order Climatiiformes
            - Order Ischnacanthiformes
          - Class Osteichthyes (bony fish)
            - †Subclass Actinopterygii (ray-finned fish)
              - Family Cheirolepididae
              - Infraclass Cladistia
                - Family Polypteridae
              - Infraclass Actinopteri
                - Order Dorypteriiformes
                - Order Bobasatraniiformes
                - Order Saurichthyiformes
              - †Superdivision Chondrostei
                - Family Acipenseridae
                - Family Polyodontidae
              - †Superdivision Neopterygii
                - Order Palaeonisciformes
                - Order Pholidopleuriformes
                - Order Perleidiformes
                - Order Peltopleuriformes
              - †Division Ginglymodi
                - Family Lepisosteidae
              - Division Halecostomi
                - Family Semionotidae
                - Family Dapediidae
                - Family Macrosemiidae
                - Order Pycnodontiformes
              - †Subdivision Haleomorphi
                - Order Parasemionotiformes
                - Order Amiiformes
            - †Subclass Teleostei
              - Unnamed subdivision
                - Family Pachycormidae
                - Family Aspidorhynchidae
                - Family Pholidophoridae
                - Family Leptolepidae
                - Family Ichthyodectidae
              - †Supercohort Osteoglossomorpha
                - Order Osteoglossiformes
              - †Supercohort Elopocephala
                - Cohort Elopomorpha
                  - Order Anguilliformes
                - Cohort Clupeocephala
                  - Order Crossognathiformes
                    - Subcohort Clupeomorpha
                  - Order Ellimmichthyiformes
                  - Order Clupeiformes
                    - Subcohort Euteleosti
                  - Order Esociformes
                - †Division Ostariophysi
                  - Order Gonorhynchiformes
                  - Order Cypriniformes
                  - Order Characiformes
                  - Order Siluriformes
                - †Division Neognathi
                    - Order Salmoniformes
                  - Subdivision Neoteleostei
                    - Order Stomiiformes
                    - Order Aulopiformes
                    - Order Polymixiiformes
                  - Superorder Paracanthopterygii
                    - Series Atherinomorpha
                      - Order Atheriniformes
                      - Order Cyprinodontiformes
                      - Order Beloniformes
                    - Series Percomorpha
                      - Order Bercyformes
                      - Order Lampridiformes
                      - Order Zeiformes
                      - Order Gasterosteiformes
                      - Order Dactyliopteriformes
                      - Order Scorpaeniformes
                      - Order Perciformes
                      - Order Pleuronectiformes
                      - Order Tetraodontiformes
            - †Subclass Sarcopterygii (lobe-finned fish)
              - †Infraclass Dipnoiformes
                - Order Diabolepida
                - Order Dipnoi (lung fish)
              - †Infraclass Actinistia (Coelacanths)
              - Infraclass Rhipidistia
                - Order Porolepiformes
                - Order Rhizodontiformes
                - Order Osteolepiformes
                - Order Panderichthyida
                - Superclass Tetrapoda
                  - *Class Amphibia
                    - Family Elginerpetontidae
                    - Family Acanthostegidae
                    - Family Ichthyostegidae
                    - Family Tulerpetontidae
                    - Family Crassigyrinidae
                    - Family Baphetidae
                    - †Subclass Batrachomorpha
                      - ?Order Aïstopoda
                      - Order Nectridea
                      - Family Colosteidae
                      - Order Microsauria
                      - Order Temnospondyli
                        - Family Dendrerpetontidae
                        - Family Brachyopidae
                        - Family Rhinesuchidae
                        - Family Capitosauridae
                        - Family Trematosauridae
                      - †Intraclass Lissamphibia
                        - Order Gymnophiona
                        - Order Urodela
                        - Order Anura
                      - Subclass Reptilomorpha
                        - Order Anthracosauria
                        - Order Seymouria
                        - Order Diadectomorpha

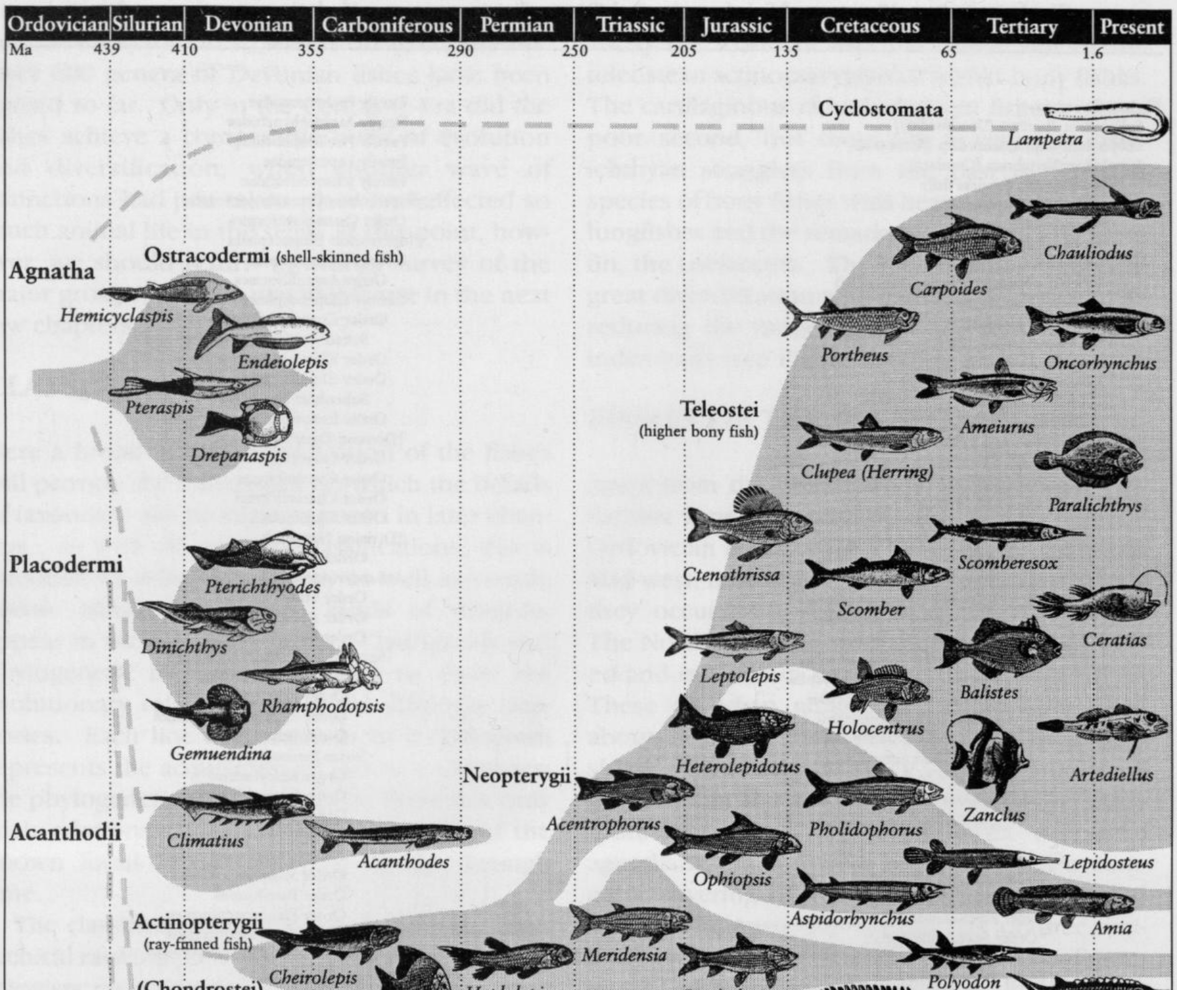

Figure 1.4 A geological history of fishes. The geological periods and the ages of the period boundaries are given at the top. The shaded areas suggest the relative abundance of species within the different classes during each period (after Ommaney, 1963, with data from Benton, 1993).

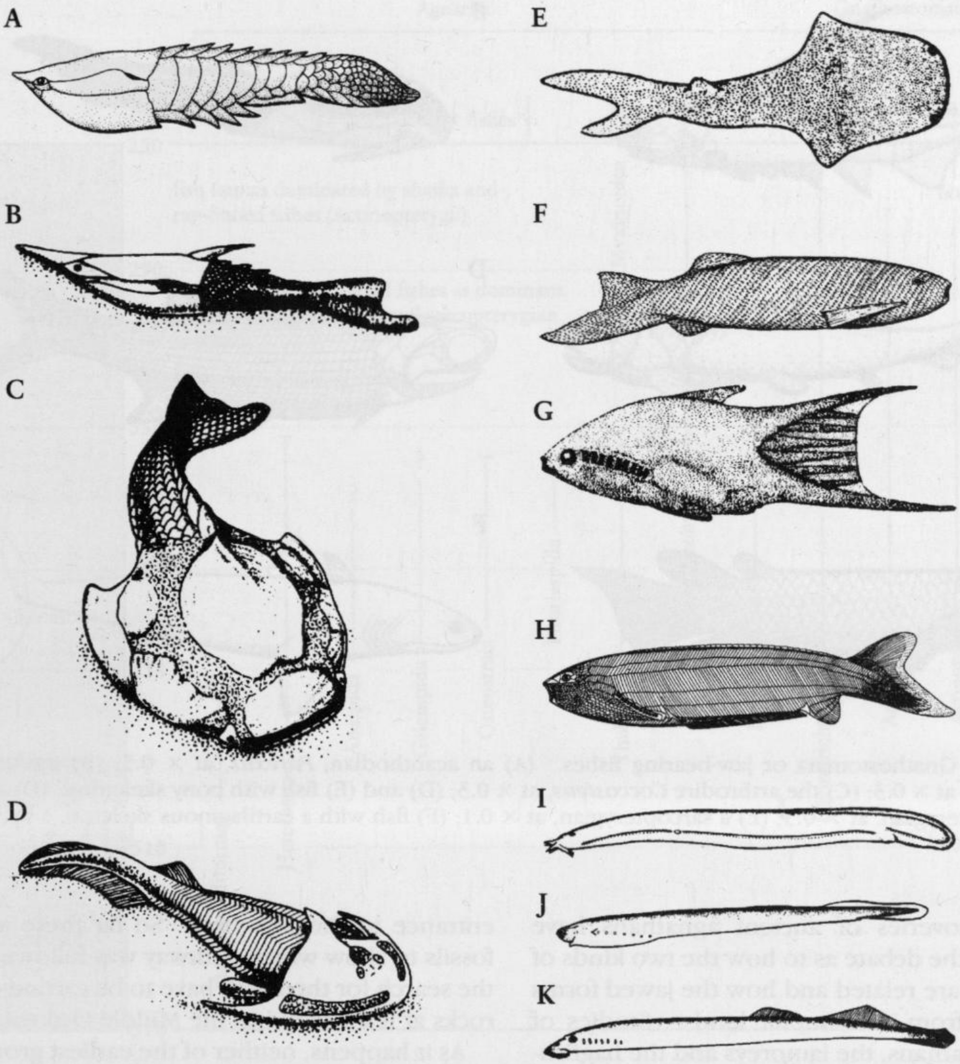

Figure 1.5 The Agnatha; fishes lacking jaws. (A) *Anglaspis*, a heterostracan from the Siluro-Devonian; (B) *Pteraspis* a heterostracan from the Early Devonian; (C) *Hemicyclaspis*, an osteostracan from the Late Silurian; (D) *Psammolepis*, a Late Devonian heterostracan; (E)–(G) Silurian thelodonts, *Thelodus*, *Phlebodus* and an unnamed form from Canada; (H) the Devonian anaspid *Pharyngolepis*; (I) a living lamprey ammocoete larva; (J) an adult living lamprey; (K) the extant adult hagfish. Not shown are the Chinese galeaspid and Australian pituriaspid. All are approximately a third natural size.

reaching perhaps 250 mm long, covered in tiny denticles of bone-like material. New thelodonts from Canada show shapes very different from those previously known, and possess gill openings like those of the anaspids and the lampreys. There are also stomachs in these animals, though no jaws are known. It is therefore possible that the thelodonts are not a natural group. Most heterostracans, about the same size or larger, have a carapace of bony plates about the head and body and small bony scales on the flexible hind part and tail. All were probably microphagous feeders, some perhaps burrowing in sandy substrates or algal mats. The Osteostraci possessed headshields that were more or less rigid boxes of bone with ventral mouths and gill openings. Their bodies were laterally compressed, scale covered and with heterocercal tails. The Galeaspida were rather similar Chinese (and perhaps Australian) animals while the Pituriaspida were distinct if superficially similar Australian forms.

There have been several theories accounting for the origins of the gnathostomes and the

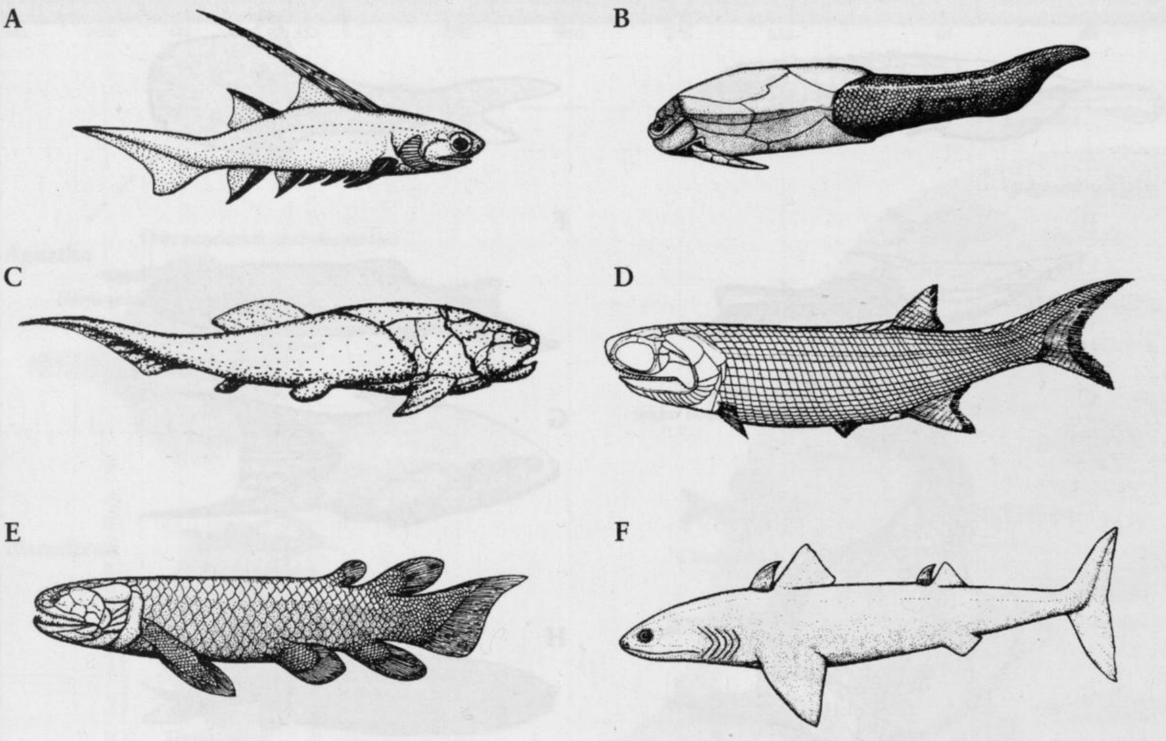

Figure 1.6 Gnathostomata or jaw-bearing fishes. (A) an acanthodian, *Parexus*, at × 0.5; (B) the antiarch *Remigolepis*, at × 0.3; (C) the arthrodire *Coccosteus*, at × 0.3; (D) and (E) fish with bony skeletons: (D) a primitive actinopterygian, at × 0.5; (E) a sarcopterygian, at × 0.1; (F) fish with a cartilaginous skeleton, a hybodont shark, at × 0.1.

recent discoveries of ancient agnathans have stimulated the debate as to how the two kinds of vertebrates are related and how the jawed forms originated from the simpler kinds. Studies of today's agnathans, the lampreys and the hagfishes, reveal their differences and these are thought to go back into early vertebrate history. Forey and Janvier (1993) reviewed the evidence and the hypotheses about early relationships. They pointed out that the hagfishes have less in common with the fossil agnathan groups than with the lampreys. Lampreys share many features with the anaspids, galeaspids and osteostracans while the heterostracans are considered the closest-related agnathan group to the gnathostomes (Figure 1.5). With the latest discoveries of thelodonts, it seems that they may be even closer to the gnathostomes than all the others.

Thus it (also) seems that the agnathans are a paraphyletic group, i.e. some are more closely related to gnathostomes than to other agnathans. It is still commonly held that jaws developed from the foremost of the gill arches or, alternatively, that the jaws developed from the velum (a pumping organ situated at the entrance to the pharynx). So far there are no fossils to show which pathway was followed, but the search for them will have to be carried out in rocks at least as old as the Middle Ordovician.

As it happens, neither of the earliest groups of gnathostomes of which we can restore the anatomy of the head gives very much help in this connection (Figure 1.6).

The Placodermi were a very diverse group and made their appearance during the Silurian Period (Gardiner, 1990). Possessing jaws of a kind, they sported bony head and body armour to a greater or lesser extent. Many were tiny, whereas the largest in Late Devonian time reached a length of 6 m. Their origins are uncertain but many authors have regarded their cranial anatomy and general shape as being related to that of the elasmobranchs. There are, nevertheless, many features of placoderm cranial and jaw structure that are quite unlike any of those in the elasmobranchs. Placoderm origins have also been thought of as relaying back to a common stem with osteichthyans. For now, it is perhaps best to regard placoderms as a sister-group of both bony and cartilaginous fishes, a

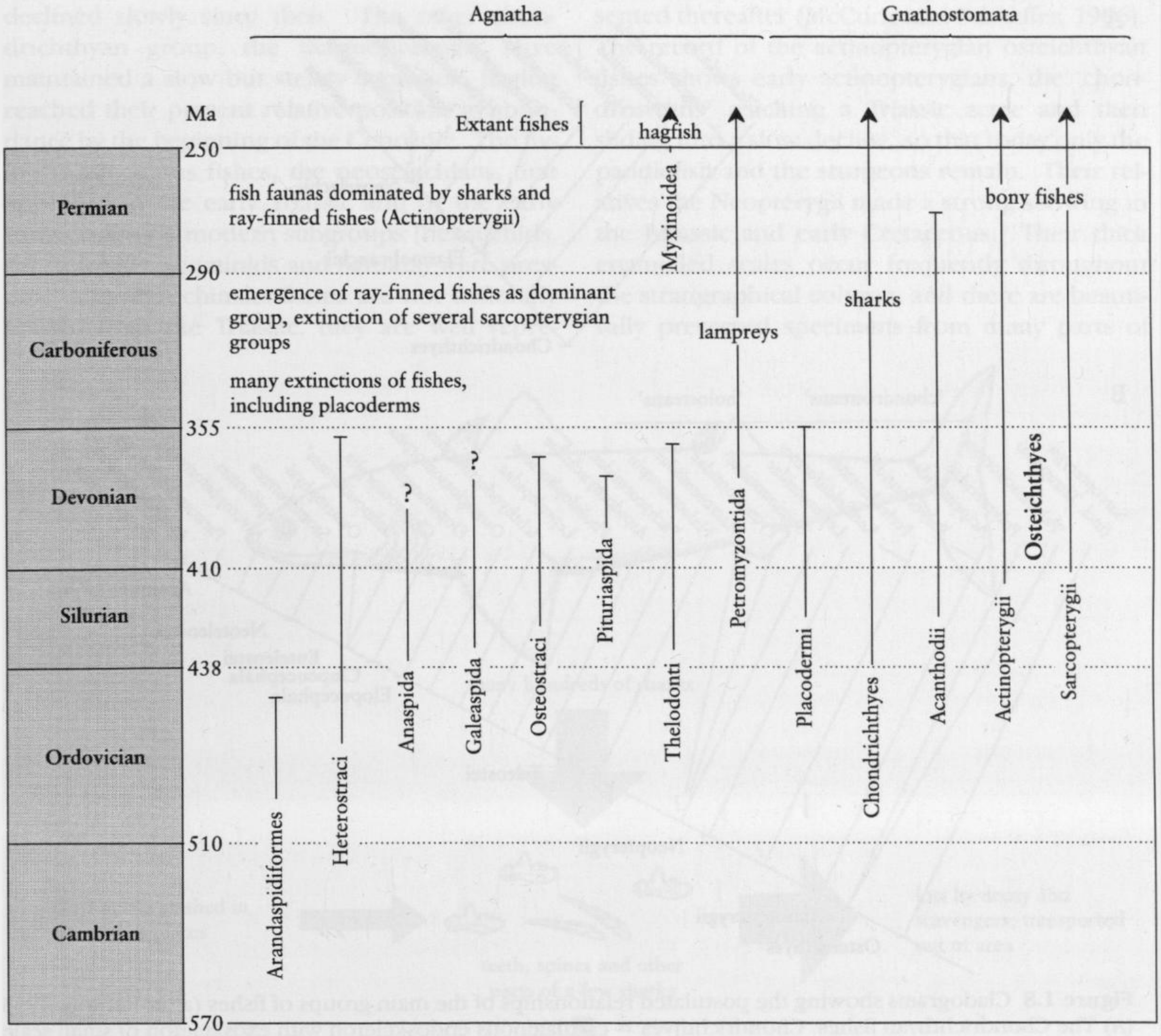

Figure 1.7 Age ranges of Palaeozoic fishes (after Long, 1993).

group that became extinct by the end of Devonian time.

The Acanthodii were a rather more uniform group, with spine-supported fins and rather slender shapes that at first sight suggest kinship to the sharks but not the placoderms. Some had jaws with 'teeth'; all had a covering of tiny scales. They, too, will be discussed below. The Chondrichthyes (cartilaginous fishes) are most conspicuously equipped with jaws and were well established in Devonian seas and are today represented by sharks, rays and chimaeras or rabbit-fishes. They seem to have been unquestionably predatory throughout their long history, but their origins are as difficult to discover as those of the other gnathostomes.

The other groups of gnathostome fishes include many strongly active types. They are broadly divisible into two basic kinds, the cartilaginous skeleton-bearing Chondrichthyes and the bony fishes, the Osteichthyes. The latter include those with ray-supported fins, the actinopterygians, and those with lobe-based fins, the sarcopterygians. Amongst the Sarcopterygii are the lungfishes with their ability to withstand drought conditions that would be lethal to most other fishes. From the Sarcopterygii also comes evidence for the ancestry of the earliest tetrapods. This is surprisingly widespread, occurring in the Late Devonian rocks of Scotland, Europe, Greenland and Canada. These so-called 'missing-link' fossils have fish-like shapes but with structures in limbs and skulls that greatly resemble those of true

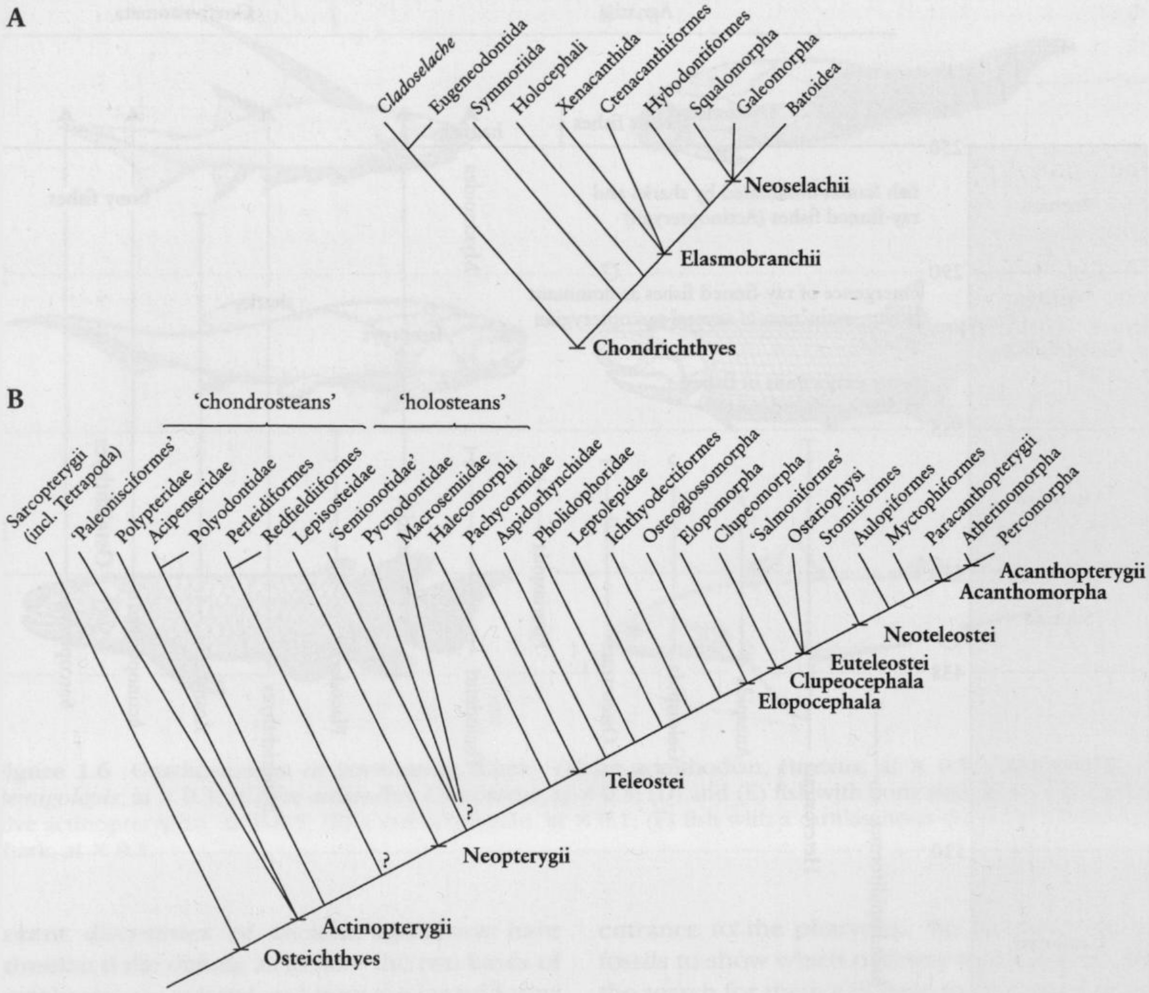

Figure 1.8 Cladograms showing the postulated relationships of the main groups of fishes (after Benton, 1993). (A) The Chondrichthyan fishes. Chondrichthyes = cartilaginous endoskeleton with exoskeleton of small scales, sometimes enlarged into head spines or fin spines. Elasmobranchi = a predaceous group with distinctive jaw suspension and quickly replaced characteristic tooth structure; no operculum, gill slits opening directly to the outside. Neoselachii = modern sharks, skates and rays; characteristic vertebrate and fin structures. (B) The major groups of Osteichthyan (bony) fishes. Actinopterygii = ray-finned fishes; Neopterygii = actinopterygians with distinctive separation of cheek and jaw bones from the opercular. Teleosti = advanced bony fishes. Elopocephala = advanced teleosts. Clupeocephala = a group derived from the Elopocephala. Euteleostei = most are characterized by acellular bone and by features of the skull and caudal skeleton. Neoteleostei = most characterized by stiff fin spines and modifications of the positions of the pectoral and pelvic fins and body proportions. Acanthomorpha = spiny teleosts with modifications for swimming concentrated in the caudal fin. Acanthopterygii = further modifications to the bones around the mouth and caudal vertebrae and fin are found in this group.

amphibian tetrapods (see Chapter 15).

By the end of the Palaeozoic Era all of the jawless forms, save only the lampreys and hagfishes, were extinct. The original ecological niches had, no doubt, been taken over by bony and cartilaginous gnathostome forms (Figure 1.7). Many taxa of Palaeozoic fishes are known only from bony fragments and scales: these isolated items have not only palaeobiological value but also are of increasing value in biostratigraphy.

FISHES OF THE MESOZOIC AND CENOZOIC

At the beginning of the Triassic Period life in the oceans and on the continents was slowly beginning to recover from the Permian global event that decimated the living world. We have little or no record of the holocephalian fishes at that time, but they have left a small number of fossils, chimaeras and rabbitfishes, which seems to have declined slowly since then. The other chondrichthyan group, the Elasmobranchii, have maintained a slow but steady evolution, having reached their present relative position in abundance by the beginning of the Cenozoic. The living cartilaginous fishes, the neoselachians, first appeared in the early Triassic and by the early Jurassic several modern subgroups (hexanchids, orectolobids, squatinids and batoids) were present. Although chimaeriforms are not definitely known from the Triassic, they are well represented thereafter (McCune and Schaeffer, 1986). The record of the actinopterygian osteichthyan fishes shows early actinopterygians, the 'chondrosteans' reaching a Triassic acme and then sliding into a slow decline, so that today only the paddlefish and the sturgeons remain. Their relatives the Neopterygii made a strong showing in the Jurassic and early Cretaceous. Their thick enamelled scales occur frequently throughout the stratigraphical column, and there are beautifully preserved specimens from many parts of

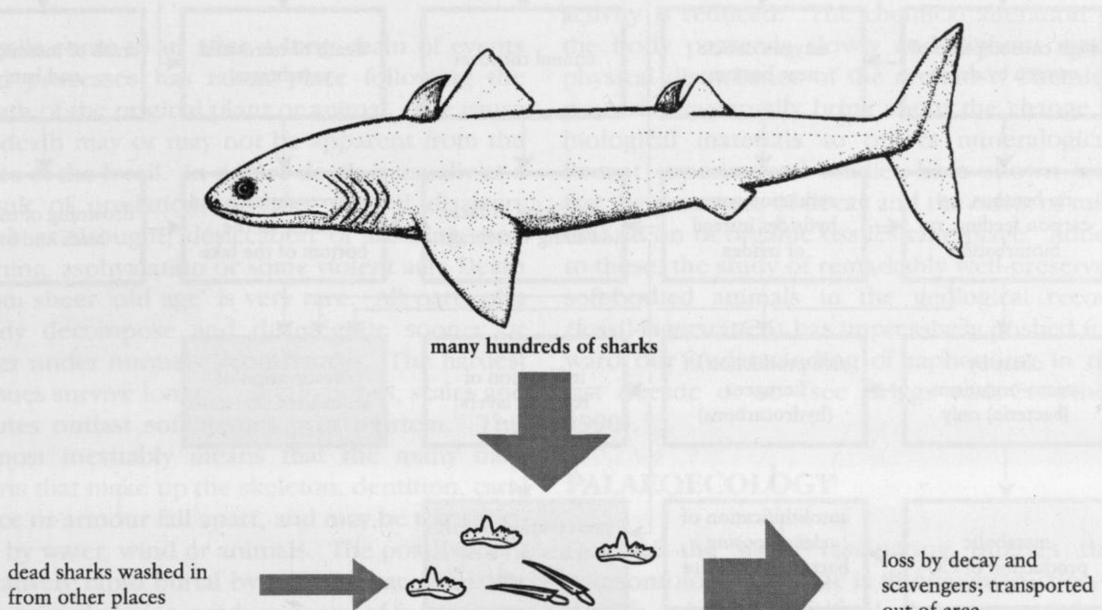

Figure 1.9 Fossilization under most circumstances preserved only a very small percentage of the living world in the fossil record. Most of the animals and virtually all the plants that lived alongside these sharks were not fossilized (after Beerbower, 1960).

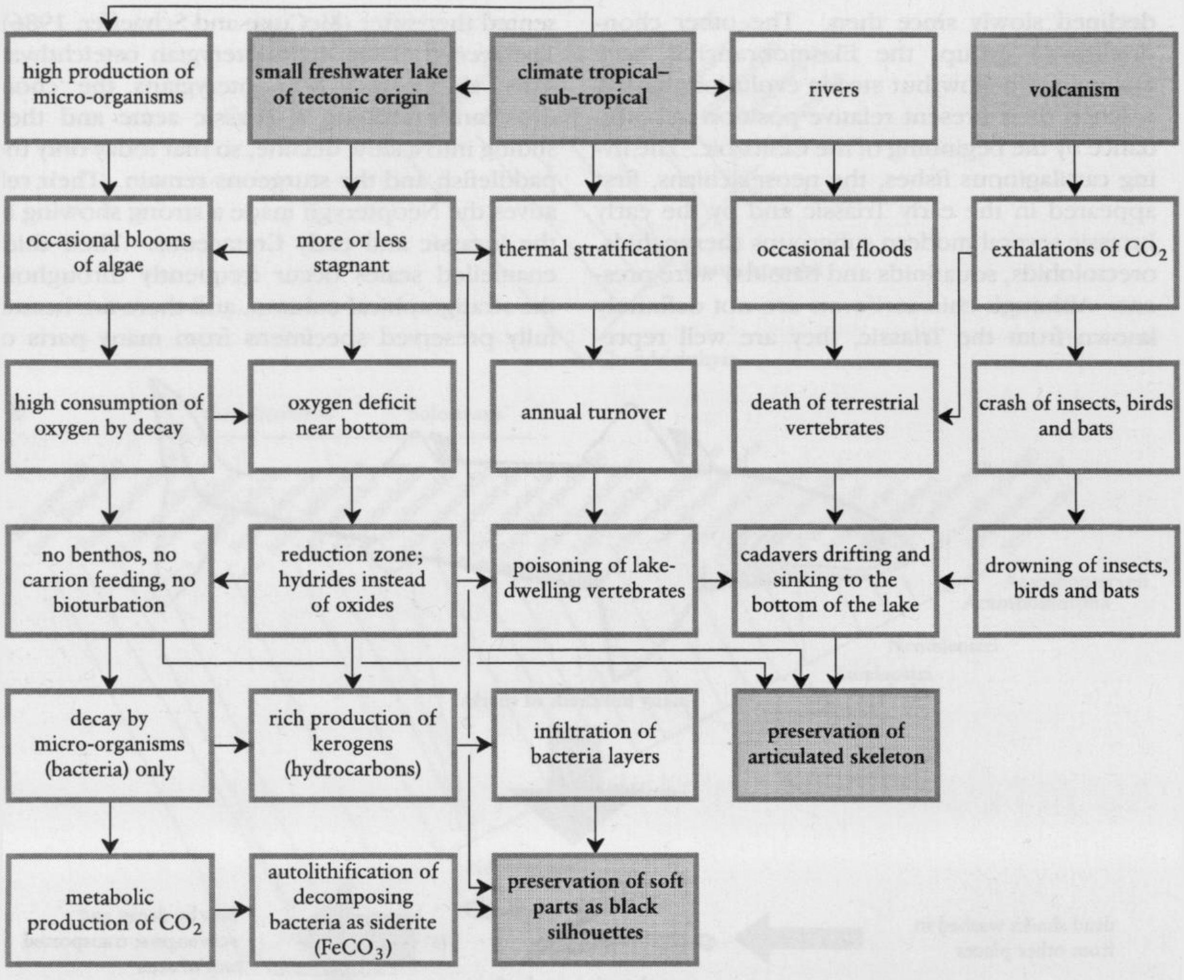

Figure 1.10 Under rare conditions exceptional preservation of articulated skeletons and even so-called soft parts occurs. This diagram shows the factors involved in the preservation of a large Eocene biota in a German lake deposit. Many of these factors and pathways played a part in the preservation of complete fishes in the British Middle Devonian, Carboniferous and Jurassic record (after Franzen, 1985).

the world. The decline of the thick-scaled early actinopterygians in the Cenozoic has presumably been in the face of teleost success. From being widespread in the late Mesozoic they have been reduced to very small numbers today, with only the gar and bowfin fishes as living representatives.

Two of the three divisions of the lobe-finned fishes, i.e. the coelacanths and the lungfishes, have survived to the present. Coelacanths are represented by a small number of early and mid-Mesozoic genera: they were most diverse in the Triassic, less so in the Jurassic and then appeared to have died out in the late Cretaceous; however, about 60 years ago coelacanth fishes were discovered in deep water off the east coast of South Africa. Hailed as a 'living fossil', this species is a relatively large animal, a metre or more in length and viviparous. Lungfishes, on the other hand, have long been known, despite the apparent hazards – even hostility – of their habitat. A mere half-dozen species survive. Ever since the onset of the strongly continental conditions of the Permian period these hardy creatures have existed in seemingly small numbers, but with a greatly restricted range of types compared with previous times. In the Triassic and Jurassic they were represented by the tooth-form genus *Ceratodus* and related genera.

Far and away the greatest numbers of modern fish species belong to the thin-scaled kind known as 'teleosts'. They range in size, habits and habitats to occupy every ocean and river system, and have been set upon this course steadily since Jurassic times. Their success was rapid during the Cretaceous and continued unhindered into the Cenozoic. The global event that changed so much of the terrestrial and shallow-water marine life had no such effect upon teleost fishes. They are models of efficiency, but since their skeletons are commonly reduced to the most economic and fragile structures, they have been well preserved only under rather uncommon conditions (Figures 1.9 and 1.10).

TAPHONOMY

Fossils come to us after a long chain of events and processes has taken place following the death of the original plant or animal. The cause of death may or may not be apparent from the state of the fossil. In nature death is usually as a result of predation, disease, natural disasters such as drought, desiccation or freezing, poisoning, asphyxiation or some violent act. Death from sheer 'old age' is very rare. All parts of a body decompose and disintegrate sooner or later under normal circumstances. The hardest tissues survive longest. Teeth, bones, scales and scutes outlast soft tissues post mortem. This almost inevitably means that the many hard parts that make up the skeleton, dentition, carapace or armour fall apart, and may be transported by water, wind or animals. The possibility of relatively rapid burial by sediment accounts for the overwhelming predominance of fossils of an aquatic origin. Fossil shellfish abound; fossil birds are very rare. Fossil fishes fall somewhere in between. The ideal conditions for their preservation are in environments that are 'quiet', which lack currents or other physical disturbance, where scavengers and degraders cannot function and where the animal body is quickly covered by the finest sediment (Figures 1.9 and 1.10).

Where anoxic (anaerobic) conditions exist, as they do on many lake or sea floors, bacterial activity is reduced. The chemical alteration of the body proceeds slowly and without much physical disturbance of the remains. Chemical processes eventually bring about the change of biological materials to others mineralogical. Recent experimental studies have shown how fast the processes of decay and the onset of mineralization of organic tissues take place. Added to these, the study of remarkably well-preserved soft-bodied animals in the geological record (fossil-lagerstätten) has impressively pushed forward our understanding of taphonomy in the last decade or so (see Briggs and Crowther, 1990).

PALAEOECOLOGY

One of the more fascinating puzzles that palaeontologists pursue is the reconstruction of the life styles of the animals they resurrect from

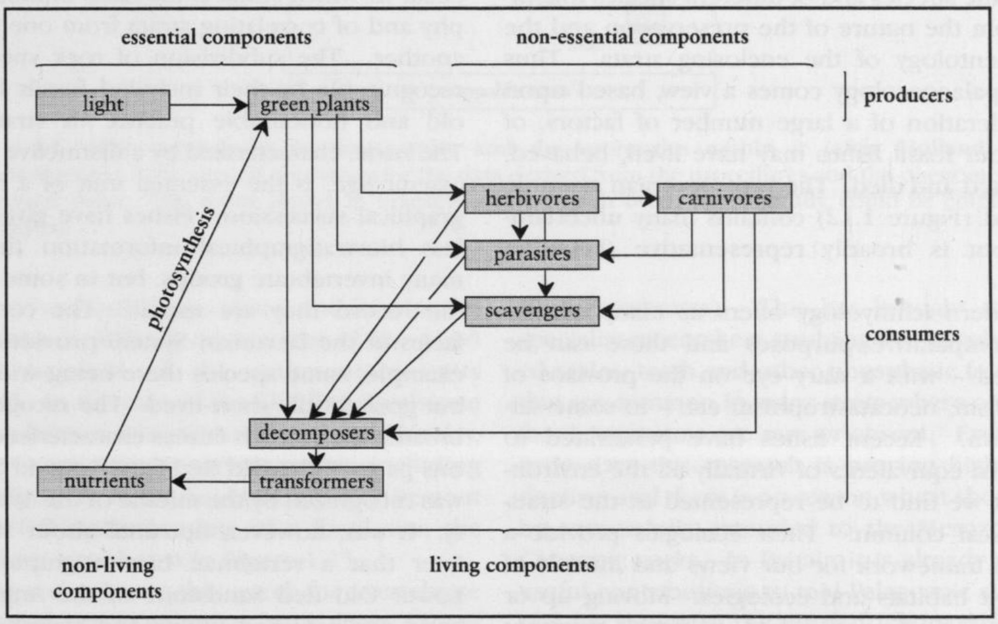

Figure 1.11 The basic channels for the flow of materials through a typical ecosystem. This is elaborated in Figure 1.12 to show the trophic flow in a late Devonian assemblage.

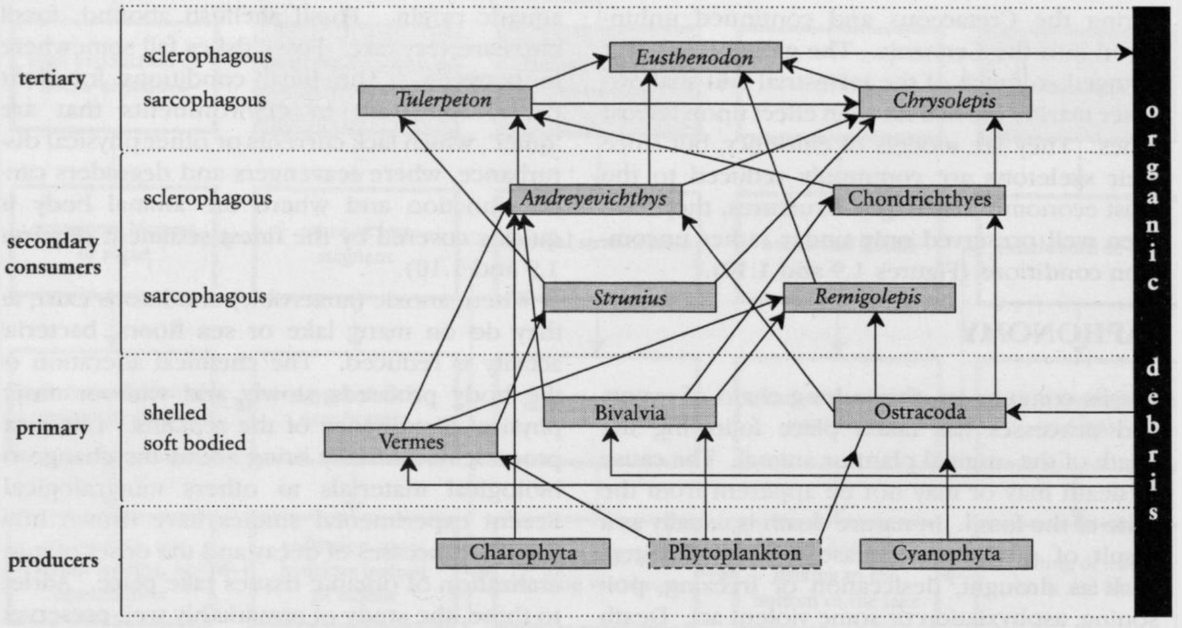

Figure 1.12 A model of the possible trophic flow and connections in the well-preserved *Eusthenodon* assemblage in the Late Devonian of the Tula region of Russia (after Lebedev, 1992). This vertebrate community included chondrichthyes, antiarchs, dipnoi and crossopterygians as well as the tetrapod *Tulerpeton*.

the fossil record. No animal exists within a vacuum but interacts with, and is dependent upon, its environment – a rule that must have operated ever since animals first appeared (Figure 1.11). Much can be gained from a study of the fossil anatomy, from the assemblages of individuals of the same species and of different species together, from the nature of the preservation and the sedimentology of the enclosing strata. Thus from palaeoecology comes a view, based upon consideration of a large number of factors, of how our fossil fishes may have lived, behaved, migrated and died. The Late Devonian example offered (Figure 1.12) contains many uncertainties but is broadly representative (Lebedev, 1992).

Modern ichthyology offers us many models for comparative purposes and these can be applied – with a wary eye on the provisos of actualism, neocatastrophism etc. – to some satisfaction. Recent fishes have penetrated to modern equivalents of virtually all the environments we find to be represented in the stratigraphical column. Their ecologies provide a useful framework for our views and models of ancient habitats and ecologies. Moving up or down the stratigraphical column, frequent palaeoenvironmental changes are discernible; corresponding changes in the palaeoecology occur, and ecostratigraphy is the discipline which orders and interprets all this information.

BIOSTRATIGRAPHY

The simple discipline of recording which fossils occur in which strata is the basis of biostratigraphy and of correlating strata from one place to another. The subdivision of rock successions recognizable by their included fossils is a very old and honourable practice in stratigraphy. The zone, characterized by a distinctive fossil or assemblage, is the essential unit of a biostratigraphical succession. Fishes have given rather less biostratigraphical information than very many invertebrate groups, but in some parts of the record they are useful. The continental facies of the Devonian System provides a good example, some species there being widespread but geologically short-lived. The recognition of broadly distinct fish faunas characteristic of various parts of the Old Red Sandstone in Scotland was recognized by the middle of the 19th century. It was, however, not until about 100 years later that a vertebrate biostratigraphy of the Lower Old Red Sandstone of the Anglo-Welsh basin was achieved (White and Toombs, 1948). In these continental vertebrate-bearing rocks, fossiliferous beds may be separated by many

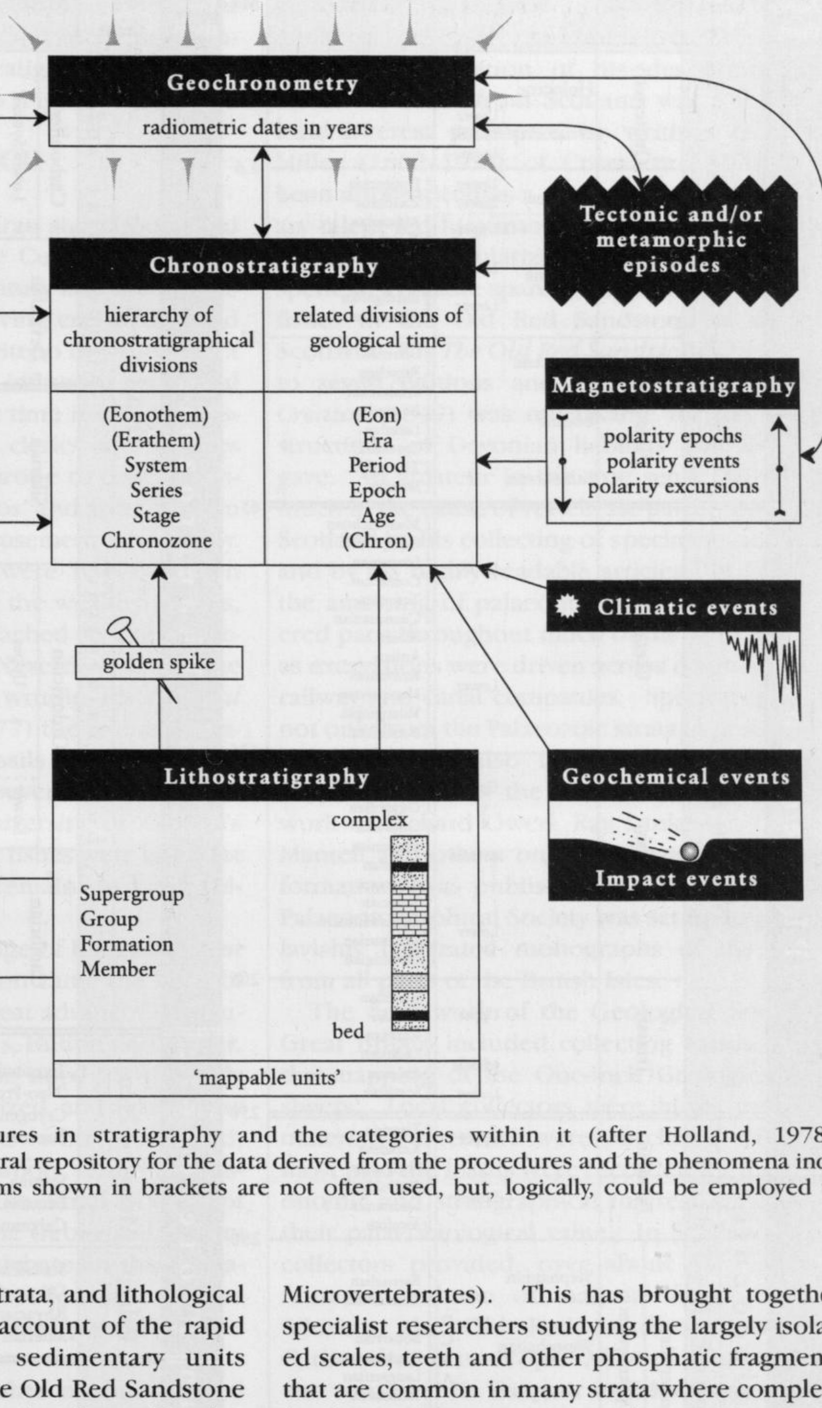

Figure 1.13 The procedures in stratigraphy and the categories within it (after Holland, 1978). Chronostratigraphy is the central repository for the data derived from the procedures and the phenomena indicated around them. The terms shown in brackets are not often used, but, logically, could be employed to greater extent.

metres of unfossiliferous strata, and lithological correlation is difficult on account of the rapid lateral variation of the sedimentary units involved. In the case of the Old Red Sandstone this has been a ubiquitous handicap (Dineley, 1982). Correlation by various means, including biostratigraphy, is the fundamental requirement for the full understanding of a fossil site; the procedures are shown in Figure 1.13.

A new technique in this search for a vertebrate fossil-based stratigraphy has been given a great boost recently by the International Geological Correlation Project No. 328 (Palaeozoic Microvertebrates). This has brought together specialist researchers studying the largely isolated scales, teeth and other phosphatic fragments that are common in many strata where complete fossil organisms are rare or absent. Even in its early days this research is proving highly productive, and there is no reason why it should not be successfully extended to the Mesozoic and Cenozoic rocks. In Britain it is already making useful contributions to mid-Palaeozoic stratigraphy (as shown in the journal *Ichthyolith Issues* from 1989 until present).

The stratigraphical table used in this volume

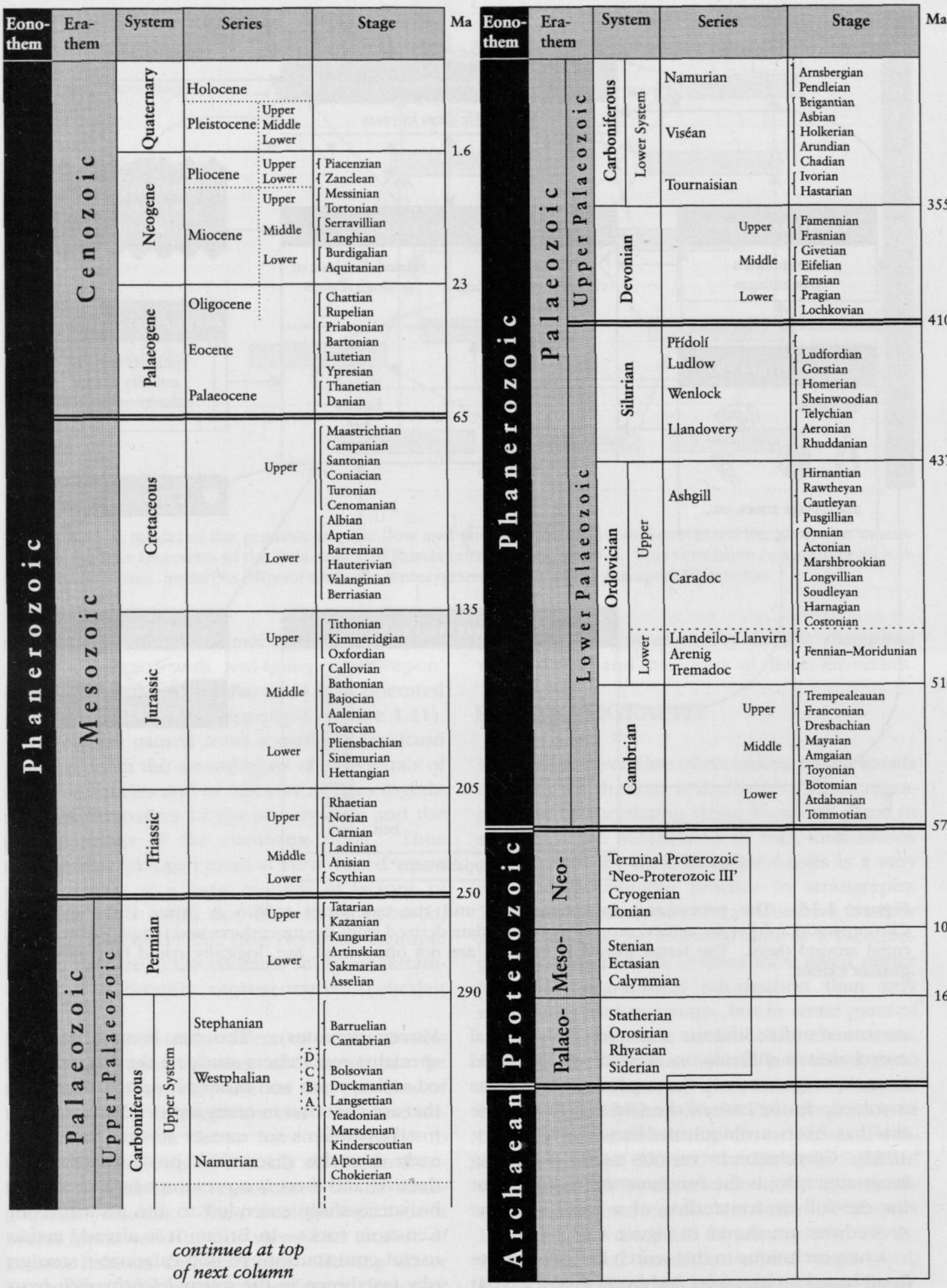

Figure 1.14 The global stratigraphical column, based on that of the International Union of Geological Sciences (Cowie and Bassett, 1989). In the situation where alternative series and stage names are given, the left hand column is usually favoured. The geochronometric dates are based upon published isotope analyses.

is that adopted by the International Union of Geological Sciences (1992) and includes radio-isotope dates tied to biostratigraphically determined points in the column (Figure 1.14).

HISTORY OF RESEARCH

It was the discovery of a large shark tooth and other marine fossils in the Cenozoic rocks of Tuscany in the mid-17th century and the realization that such fossils and living creatures could be linked that led Nicolaus Steno to write one of the most effective books to influence geological scholars of the day. At that time it was the custom of wealthy gentlemen, clerics and scholars in Britain and mainland Europe to collect minerals, fossils and other 'curios' and arrange them in 'cabinets' for their amusement and study. Several of these cabinets were handed down through the generations of the wealthy houses, but the documentation attached to the collections tended to perish. Nevertheless, by the time Dr Robert Plot was writing his *Natural History of Oxfordshire* (1677) the true explanation of the origin of fossils was becoming known. Plot had access to several 'cabinets' and the collections in the University of Oxford's Ashmolean Museum. Fossil fishes were amongst the more obvious organic remains in these collections.

With the coming of the Age of Enlightenment and the Industrial Revolution came the birth of modern geology and the great advances in natural history made by Linnaeus, Buffon and Cuvier. The value of fossils and the need for properly curated collections was realized, and again it was the 'gentlemanly geologists' who prospected, collected and discoursed upon vertebrate fossils. The Royal Society, the Royal Society of Edinburgh and especially the Geological Society of London were centres of debate for these amateurs, and they too housed collections. In due course their collections were passed to the national museums.

In Scotland the fossil fishes of the Old Red Sandstone were a rich source of interest to academics and amateurs. There is a long list of collectors and students who were instrumental in compiling the wonderful resource for Louis Agassiz's great work *(Monographie des poissons fossiles du Vieux Grès Rouge ou Système Dévonien [Old Red Sandstone] des Iles Britanniques et de Russie*, 1833–1845). This publication was a stimulant to the flow of specimens, new taxa and debate, as described by S.M. Andrews (1982). An immediate result of Agassiz's publication of his descriptions of Devonian fishes from Scotland was a flurry of local interest prompted by writings of Hugh Miller (1802–1856) of Cromarty. Miller had been apprenticed as a stonemason but his literary talent led him into journalism. He put this to good use popularizing local geology, and he spent all available spare time searching for fossil fishes in the Old Red Sandstone of eastern Scotland. His *The Old Red Sandstone* (1841) ran to seven editions and his *Footprints of the Creator* (1849) was remarkable for the reconstructions of Devonian habitats and fishes it gave. An amateur in the true sense, Miller did much in the cause of vertebrate palaeontology in Scotland by his collecting of specimens and data and by his highly readable articles. In England the amassing of palaeontological material gathered pace throughout much of the 19th century, as excavations were driven across country by the railway and canal companies. Specimens came not only from the Palaeozoic strata in or near the coalfields, but also from the Mesozoic and Cenozoic rocks of the southern counties. The work of Richard Owen, Ray Lankester, Gideon Mantell and others on fish remains from these formations was published in London, and the Palaeontographical Society was set up to publish lavishly illustrated monographs of the fossils from all parts of the British Isles.

The field work of the Geological Survey of Great Britain included collecting fossils during the mapping of the One-inch Geological Map sheets. Local collectors were hired and local materials sometimes were purchased. For the most part the fossils were recorded for their taxonomic and stratigraphical interest rather than their palaeobiological value. In Scotland these collectors provided, over about 40 years, an immense volume of material from the late Silurian, the Old Red Sandstone and the Carboniferous outcrops. Most of their produce was sent to R.H. Traquair in Edinburgh, one of the most active and shrewd workers in this field during the later decades of the 19th century and the early years of the 20th century. During this time A. Smith Woodward at the Natural History Museum was publishing a continuous and remarkable stream of articles on new fossil vertebrates, including fishes from all parts of the stratigraphical column, both British and foreign. Meanwhile in Europe fossil fishes from many localities were the subject of research in Berlin, Paris, St Petersburg and Moscow and, later, Stockholm and Oslo. In North America in the 19th century, fossil fish bonanzas were being discovered in the late Palaeozoic rocks of Maritime Canada, New York, Ohio and other Appalachian States. In the Mid-West Mesozoic, and in the southern states and the South West Cenozoic, fishes were coming to light in large numbers. All of these were influential in extending our knowledge of the anatomy, habitats and ecology of forms only sparsely known from British localities. Louis Agassiz moved to a professorship in zoology at Harvard University in 1848 and continued there his work on fossil vertebrates, fishes included. Amongst the other more important researchers in North America were C.R. Eastman, J. Leidy, J.S. Newberry and Bashford Dean, and J.F. Whiteaves in Canada.

As in the case of fossil reptiles (Benton and Spencer, 1995, p. 4), collecting during the early half of the 20th century became rather sporadic, much of it being by amateurs. This coincided with the decline of local natural history societies and the loss of skilled collectors with local knowledge. Something of a revival has been achieved since World War II and in the last 20 years local museum standards of conservation and documentation in geology have dramatically improved.

In the latter half of the 20th century there has been no slackening of interest in fossil fishes in Britain. At the Natural History Museum, Smith Woodward, who had published his first paper of fossil fishes (sharks) in 1884, and his last in 1942, was succeeded by E.I. White whose interest was largely in Palaeozoic faunas, as has been that of R.S. Miles and P.L. Forey. Fishes from the later eras have been studied there by C. Patterson. Elsewhere B.G. Gardiner has been concerned with chondrosteans, T.S. Westoll and S.M. Andrews with Devonian faunas, A. Ritchie with Silurian vertebrates in Scotland, S. Turner with thelodonts, and D.L. Dineley with Siluro-Devonian agnatha in Britain and Canada.

Highly influential in the 20th century study of British faunas have been specialists in Scandinavia, Germany, France and the USA. This has been especially so in the case of Palaeozoic occurrences, since the researchers in those countries had access to unusually productive localities. More recently in the Baltic States and Russia, there has been a flourishing of research into mid- and late Palaeozoic vertebrates, much of it having a direct relevance to the understanding of British fossils.

A recent development of significance has been the recognition in Asia, Australia and Antarctica of Devonian genera also known in Britain, and generally regarded as non-marine. International co-operation and liaison in geological research has now reached a very satisfactory level; publication is today comparatively rapid and effective. International bibliographies are produced at regular intervals and are indispensable in a time of such a flood of scientific literature and intellectual activity.

Fossil fishes have figured increasingly in matters of correlation and palaeogeography. Microvertebrate remains in particular are now being utilized and are, in the Palaeozoic, locally referable to conodont zones. In 1962 Dineley began to demonstrate the close similarity and regional correlation between the Siluro-Devonian vertebrate faunas of Britain and eastern and arctic Canada (Dineley, 1964, 1967, 1968, 1990). Triassic non-marine fish faunas had been shown by Brough (1936) to be similar in Britain and eastern North America, but direct biostratigraphical correlation was not attempted. Somewhat later, Young (1981) was able to show the use of Devonian fossil fishes in designating biogeographical provinces and a possible sequence of plate-tectonic movements during mid-Palaeozoic times that affected their distribution (Young, 1993).

PALAEONTOLOGICAL CONSERVATION

The compilation of this and the other palaeontological volumes in the GCR series is possible because of the care with which fossils have been collected, stored and reported. Unfortunately, only a rather small proportion of all the fishes collected from the localities described is still available for study. All too many specimens described in the past have been mislaid. An important and representative fraction is housed in museums where they can be seen and studied. The records of their description and where they came from may be published in scientific journals, books and field guides. The sites from which they came may still be available for the enthusiast to sample. So important are some sites that they have been selected for the Geological Conservation Review and have been designated Sites of Special Scientific Interest under the Wildlife and Countryside Act, 1981, by the statutory nature conservation agencies, and they are afforded a degree of protection by law. Field societies, learned bodies and many educational establishments provide codes of behaviour for those who would collect specimens in the field. Care and restraint are of utmost importance in collecting from what are very finite resources. Volume 1 of the GCR series (Ellis *et al.*, 1996) provides an introduction to the circumstances which indicate a need for conservation and for a strategy to plan and implement geological conservation in Britain. Change to the natural environment continues undiminished; the present exercise is largely one of 'stocktaking' and, although valuable for the moment, is only a stage in an indefinitely extendable process.

THE CHOICE AND DISTRIBUTION OF THE GCR SITES

The prime aim of the Geological Conservation Review (GCR) was to select sites for conservation which are of at least national, that is British, importance to the sciences of geology and geomorphology; more than 3000 sites have been selected. The full rationale of the GCR and the detailed criteria and guidelines used in site selection are given elsewhere (Ellis *et al.*, 1996): this volume presents the detailed scientific justification for the selection of sites representing fossil fishes. A broad categorization of geological and geomorphological subject matter (e.g. the major subdivisions of the geological timescale) was a prerequisite to site selection in the GCR. Of the *c.* 100 site selection categories used by the GCR, 15 are concerned with the palaeontology of significant animal and plant groups. Most invertebrate fossils (e.g. trilobites, echinoderms, ammonites and other molluscs) are addressed within the stratigraphy blocks, owing to their wide use in correlating rock strata and relative abundance when compared to reptile, fish, mammal, bird, terrestrial plant and insect fossils. This volume describes sites selected in three 'blocks' of the GCR: Silurian–Devonian chordata, Carboniferous–Permian Fish / 'Amphibia' and Mesozoic–Tertiary Fish / 'Amphibia'.

As with so many categories of fossils in Britain, there is a very large number of sites from which good specimens have been collected. Some are of national and international importance and have been known for very many years; others, equally interesting, have been discovered recently. There undoubtedly remain many fossil fishes and amphibians yet to be recovered from the outcrop geology of the British Isles. All may contribute to an improvement in our understanding of these fossil vertebrates.

Within the overall rationale of the GCR the choice of sites for inclusion in this volume follows the broad guidelines for sites yielding other fossils. These include:

1. Sites yielding a unique assemblage of species that are significant to the understanding of

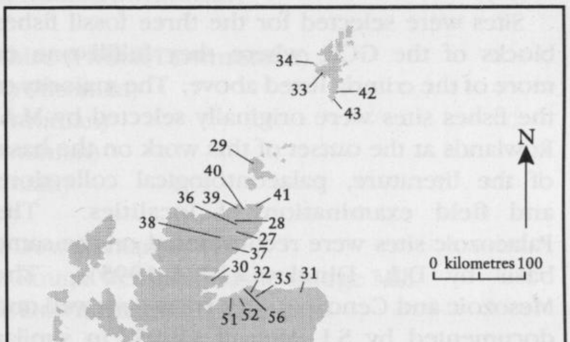

Figure 1.15 Locality map showing the distribution of the 97 fossil fish sites described in this volume. They are principally grouped upon the ancient sedimentary basins: Caledonian and Orcadian (Devonian), Midland Valley of Scotland (Carboniferous), Anglo-Welsh (Devonian), Oxford–Wessex (Triassic–Jurassic) and the Hampshire and London Basins (Cenozoic). See Table 1.2 for key to numbers.

early vertebrates (e.g. Birk Knowes, Scaat Craig).

2. Sites where the fossils are exceptionally well preserved, showing features not seen elsewhere (e.g. Achanarras, Wayne Herbert).

3. The best available sites for major fish/early tetrapod and amphibian assemblages (e.g. East Kirkton, Sidmouth, Kirtlington).

Also included are localities that are of historical importance in the development of our studies of early vertebrates (e.g. Ludford Lane, Lyme Regis).

Sites were selected for the three fossil fishes blocks of the GCR, where they fulfill one or more of the criteria listed above. The majority of the fishes sites were originally selected by M.A. Rowlands at the outset of this work on the basis of the literature, palaeontological collections and field examination of localities. The Palaeozoic sites were reconsidered on the same basis by D.L. Dineley (1994–1995). The Mesozoic and Cenozoic sites were reviewed and documented by S.J. Metcalf (1995) in similar fashion. Many other localities were visited or studied but subsequently rejected from the final GCR list for lack of conservation or collecting potential, or other necessary attributes.

The stratigraphical distribution of the fossil fishes sites described in this volume is as below. Additionally two sites (one Carboniferous and one Cenozoic) are recorded primarily for their amphibian fossils (see discussion below).

Cenozoic	13
Cretaceous	9
Jurassic	8
Triassic	2
Permian	1
Carboniferous	9
Devonian	36
Silurian	17
	95

Figure 1.15 and Table 1.2 shows the distribution of major British fossil fish sites with comparable sites elsewhere in the world. Thus the stratigraphical range of the sites is from the Middle Silurian to the Cenozoic, but may be extended as further discoveries are made.

SITES OF BRITISH FOSSIL AMPHIBIANS

Amphibians and early tetrapods feature to only a small extent in the British fossil record, but contribute much to our understanding of amphibian evolution. They are recognized as the 'biological intermediates between bony fishes and reptiles'. The fossils of early tetrapods, previously regarded as amphibians, have become increasingly important since it has been recognized that they do not fit into traditional concepts of fish to amphibian to reptile evolution. Present evidence suggests that these early extinct tetrapod groups were closer to the amniotes. The first signs of these primitive tetrapods are possibly trackways now found in the Upper Old Red Sandstone of Scotland. There is more positive evidence in the pieces of bone known from Scaat Craig, very high in the Upper Old Red Sandstone of Scotland; other Devonian fossils of like kinds occur in the Baltic, Moscow, eastern Canada and East Greenland regions, but only in the Carboniferous are appreciable skeletal remains of amphibians found.

Many fossil sites of international importance have been lost because they were located in carboniferous coal seams, and the details of the provenance of some Carboniferous fossil 'amphibians' are also now lost, but important discoveries of new material have been made in Scotland in recent years. Mesozoic and Cenozoic occurrences are numerous, most being at sites yielding fossil fishes and/or reptiles. The presence of tetrapod remains at older sites as are described below is mentioned where appropriate, but only a single site, East Kirkton in Lothian, is newly described especially on account of the fossil early tetrapods.

The true amphibia are essentially freshwater in habit, which seems to have limited their distribution and propensities for fossilization. Their evolution is well documented from localities in virtually every continent. The British sites yield taxa that also occur, or are related to others, in Europe and North America. Most seem to have been members of diverse vertebrate communities associated with transient continental environments such as lakes, coal swamps, lagoons and deltas.

Reference to a new rich fauna of amphibians of Late Eocene age at Hordle Cliff, Hampshire is made in Chapter 14.

Table 1.2 Fossil fish sites described in this volume. See also Figure 1.15.

Lower Palaeozoic sites

Silurian

1. Birk Knowes, Lesmahagow, Lanarkshire (Wenlockian)
2. Dunside*, Lesmahagow, Lanarkshire (Wenlockian)
3. Shiel Burn, Hagshaw Hills, Strathclyde (Wenlockian)
4. Dippal Burn*, Lesmahagow, Lanarkshire (Wenlockian)
5. Slot Burn, Lesmahagow, Lanarkshire (Wenlockian)
6. Birkenhead Burn, Lesmahagow, Lanarkshire (Wenlockian)
7. Ardmore–Gallanach, Argyll and Bute (Přídolí/Downtonian)
8. The Toutties, Stonehaven, Kincardineshire (?Přídolí/Downtonian)
9. Cwar Glas, Dyfed (Gorstian, Ludlovian)
10. Church Hill Quarry, Leintwardine, Herefordshire (Přídolí/Downtonian)
11. Ludford Lane, Ludlow, Shropshire (Přídolí/Downtonian)
12. Ledbury Cutting, Herefordshire (Přídolí/Downtonian)
13. Temeside, Ludlow, Shropshire, (Přídolí/Downtonian)
14. Tite's Point, Gloucestershire (Přídolí/Downtonian)
15. Lydney, Gloucestershire (Přídolí/Downtonian)
16. Downton Castle Area, Herefordshire (Přídolí/Downtonian)
    Downton Castle Bridge, Tin Mill Race, Forge Rough Weir and Castle Bridge Mill
17. Bradnor Hill, Kington, Herefordshire (Přídolí/Downtonian)

Upper Palaeozoic Sites

Silurian–Devonian

18. Devil's Hole, Morville, Shropshire (Přídolí–Lochkovian/Downtonian–Dittonian)

Devonian

19. Oak Dingle, Tugford, Shropshire (Lochkovian/Dittonian)
20. Cwm Mill, Abergavenny, Gwent (Lochkovian/Dittonian)
21. Wayne Herbert Quarry, Herefordshire (Lochkovian/Dittonian)
22. Besom Farm Quarry, Burwarton, Shropshire (Lochkovian/Dittonian)
23. Hoel Senni Quarry, Powys (Lochkovian–Pragian/Dittonian–Breconian)
24. Tillywhandland Quarry and Whitehouse Den (two sites) Forfarshire (Lochkovian)
25. Aberlemno Quarry, Forfarshire (?Lochkovian/Dittonian)
26. Wolf's Hole Quarry, Forfarshire (?Lochkovian/Dittonian)
27. Westerdale Quarry, Caithness (Eifelian)
28. Achanarras Quarry, Caithness (Eifelian–Givetian)
29. Cruaday Quarry, Orkney (Eifelian–Givetian)
30. Black Park, Edderton, Sutherland (Eifelian–Givetian)
31. Den of Findon, Ross and Cromarty (Eifelian–Givetian)
32. Tynet Burn, Morayshire (Eifelian)
33. Melby, Shetland (Eifelian–Givetian)
34. Papa Stour, Shetland (Eifelian–Givetian)
35. Dipple Brae, Morayshire (Givetian)
36. Spittal Quarry, Caithness (Givetian)
37. Banniskirk Quarry, Caithness (Givetian)
38. Holburn Head Quarry, Caithness (Givetian)
39. Weydale Quarry, Caithness (Givetian)
40. Pennyland Quarry, Caithness (Givetian)

Table 1.2 – *contd.*

41. John o'Groats, Caithness (Givetian)
42. The Cletts, Exnaboe, Shetland (Givetian)
43. Sumburgh Head, Shetland (Givetian)
44. Bedruthan Steps, Cornwall (?Emsian–Eifelian)
45. Mill Rock, Woolacombe, Devon (Givetian)
46. Afon y Waen*, Breconshire (Famennian/Farlovian)
47. Portishead, Somerset (Famennian/Farlovian)
48. Prescott Corner, Farlow, Shropshire (Famennian/Farlovian)
49. Oxendean Burn, Berwickshire (Frasnian)
50. Hawk's Heugh, Berwiskshire (Famennian)
51. Boghole, Muckle Burn, Nairnshire (Frasnian)
52. Scaat Craig, Morayshire (Frasnian)

Carboniferous

53. Foulden, Berwiskshire (Tournaisian)
54. Wardie, Midlothian (Viséan)
55. Glencartholm, Berwickshire (Viséan)
56. Cheese Bay, Midlothian (Asbian, Viséan)
57. Inchkeith, Fife (?Brigantian, Viséan)
58. Ardross Castle, Fife (Brigantian, Viséan)
59. Abden, Kirkaldy, Fife (Brigantian, Viséan)
60. Steeplehouse Quarry, Derbyshire (?Asbian, Viséan)
61. Bearsden, Glasgow (Pendleian, Namurian)

Permian

62. Middridge*, County Durham (Ufimian)

Mesozoic sites

Triassic

63. Sidmouth*, East Devon (Anisian)
64. Aust Cliff*, Avon (Rhaetian)

Jurassic

65. Lyme Regis Coast, Dorset (Hettangian, Sinemurian)
66. Blockley Station Quarry, Gloucestershire (Pliensbachian)
67. Whitby Coast*, Yorkshire (Toarcian)
68. Stonesfield*, Oxfordshire (Bathonian)
69. Kirtlington Old Cement Works Quarry, Oxfordshire (Bathonian)
70. Watton Cliff, Dorset (Bathonian)
71. Kimmeridge Bay*, Dorset (Kimmeridgian)
72. Durlston Bay, Dorset (Tithonian)

Cretaceous

73. Hastings*, East Sussex (Berriasian–Barremian)
74. Brook–Atherfield Point*, Isle of Wight (Barremian–Aptian)
75. East Wear Bay*, Folkestone, Kent (Albian)
76. Blue Bell Hill Pits, Burham, Kent (Cenomanian–Turonian)
77. Totternhoe, Bedfordshire (Cenomanian)
78. Southerham (Machine Bottom Pit)*, Lewes, East Sussex (Cenomanian–Turonian)

Table 1.2 – *contd.*

79. Southerham Grey Pit, Lewes, East Sussex (Cenomanian)
80. Southerham (Lime Kiln Quarries), Lewes, East Sussex (Turonian)
81. Boxford Chalk Pit, Berkshire (Turonian–Santonian)

Cenozoic sites

Palaeocene and Eocene

82. Pegwell Bay, Kent
83. Herne Bay, Kent (Palaeocene)
84. Upnor, Kent (Eocene)
85. Abbey Wood, Greater London (Eocene)
86. Bognor Regis, West Sussex (Eocene)
87. Maylandsea, Essex (Eocene)
88. Sheppey, Kent (Eocene)
89. Burnham-on-Crouch, Essex (Eocene)
90. Brackelsham Bay, West Sussex (Eocene)
91. Lee-on-Solent, Hampshire (Eocene)
92. Barton Cliff, Hampshire (Eocene)
93. Hordle Cliff*, Hampshire (Eocene)
94. King's Quay, Isle of Wight (Eocene)

Sites described primarily for their tetrapod fossils

95. East Kirkton, West Lothian (Brigantian, Viséan)
96. Headon Hill*, Isle of Wight (Eocene)

*Sites proposed for the GCR on account of their fossil fish and amphibian fauna; many of these localities have already been selected for the GCR on other counts (e.g. fossil reptiles or mammals).