Mesozoic and Tertiary Palaeobotany of Great Britain

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Chapter 2

The Triassic palaeobotany of Great Britain

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INTRODUCTION

At the end of the Palaeozoic Era there was a dramatic change in the world's vegetation. The tropical swamp forests that had been dominated by giant clubmosses disappeared. The higher northern latitudes also lost their covering of the ancestral conifers, the cordaites (see Cleal and Thomas (1995) and Thomas and Cleal (1993) for details of British Palaeozoic vegetation and GCR sites respectively). This was part of the massive Permo–Triassic extinction event that caused some 96% of all the known species of plants and animals to die out (Wignall and Hallam, 1996).

Triassic floras are generally impoverished, both taxonomically and numerically, worldwide, the most notable exceptions being in parts of Gondwana such as South Africa (e.g. Anderson and Anderson, 1983, 1989). Dobruskina (1994) has given a general description of the Triassic floras of Europe and Asia. The poverty of the British floras was further enhanced by desert conditions having prevailed over much of the country during the Triassic Period. Only in Upper Triassic (Rhaetian) deposits is there any significant palaeobotanical record in Britain and both of the GCR sites are in rocks of this age.

HISTORY OF RESEARCH

Because of the prevailing aridity at the beginning of the Mesozoic Era, early Triassic plants are for the most part poorly preserved. Plant remains have been recorded from the Upper Sherwood Sandstone Group of Bromsgrove and other areas in Worcestershire and Warwickshire since 1837 when R.I. Murchison and H.E. Strickland published the first geological paper on the area. Other notable collectors include the Reverend P.B. Brodie, the Reverend W.S. Symonds and, more recently, L.J. Wills (1910) who reviewed the 'Lower Keuper' rocks (= Upper Sherwood Sandstone Group). Since then very little work has been done on the 'Keuper' and very few specimens have been collected.

The plant fossils from the British Rhaetian deposits, although more abundant than those from the stratigraphically lower beds, tend to be fragmentary. Early studies on the floras of this age were by Buckman (1850), Gardner (1886b) and Sollas (1901), on the bryophytes. However, our understanding of the British Rhaetian floras has been largely through the efforts of Tom Harris. He re-examined the bryophytes described by earlier authors, enlarging significantly on details such as the reproductive organs (Harris, 1938, 1939). He also described remains of bennettite foliage, *Otozamites bechei* Brongniart, from south-western Britain (Harris, 1961c) and contributed greatly to the study of the Rhaetian fissure fills in South Wales (Harris, 1957, 1958; Lewarne and Pallot, 1957).

PALAEOGEOGRAPHICAL AND STRATIGRAPHICAL SETTING

During the Triassic Period, most of the continents were joined together to form the Supercontinent of Pangea, which had been in existence since Permian times (Figure 2.1). Britain was drifting north during the Triassic Period, so that by Rhaetian times it had reached about 30°N and was thus outside of the tropical belt.

European Triassic rocks belong to one of two successions: the south European 'Alpine', which is largely marine in origin, and the 'Germanic', which is largely continental. Nearly all the information on Triassic plants comes from the latter. Low-lying land during Early Triassic times was covered by a low-diversity vegetation dominated by such clubmossses as Pleuromeia, Cyclomeia and Taktajanodoxa. In Middle and Upper Triassic rocks there are remains of many other plant groups, including ferns and conifers belonging to families that are still present today, and representatives of now-extinct groups such as the gymnosperm bennettitaleans. A spurt of evolutionary change occurred in the Triassic Period to give the range of plants that were to dominate the vegetation for much of the Mesozoic Era. The oldest fossil evidence of typical Mesozoic vegetation is Late Triassic in age and coincides closely with the first appearance of the dinosaurs (Thomas and Cleal, 1998). The equatorial floras, such as those in Germany and the south-western USA, were the most speciesrich, with a range of ferns, horsetails, pteridosperms, cycads, bennettites, leptostobaleans, ginkgos and conifers. There is, however, little evidence for latitudinal variation in lowland Triassic vegetation, although this may be more apparent than real because of insufficient data.

For most of the Triassic Period, Britain was mainly above sea level, but during Rhaetian times shallow marine conditions spread over southern and central parts (Figure 2.2), leading to the accumulation of sediments that comprise

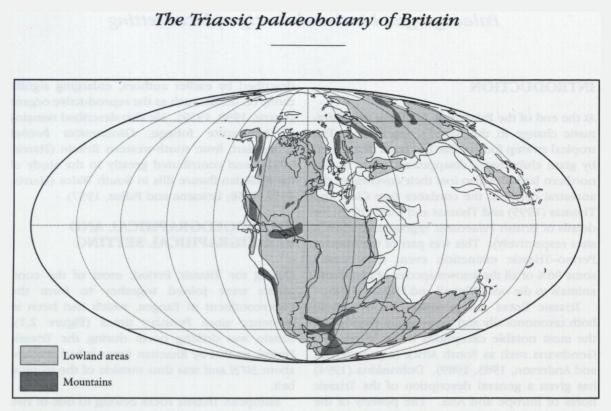


Figure 2.1 Palaeogeography of the Late Triassic (Rhaetian) world showing main areas of land and mountains. (After Smith *et al.*, 1994.)

the Penarth Group. This succession has yielded most of the Triassic plant fossils in this country other than the fissure-fill deposits such as at Cnap Twt. British Triassic chrono- and lithostratigraphy is summarized in Figure 2.3.

TRIASSIC VEGETATION

Triassic plant fossil assemblages are not very common, with the best ones being in presentday Germany (Mader, 1970), France (Grauvogel-Stamm, 1978), and south-western and eastern USA (Ash (1972) and Delevoryas (1970) respectively). The rather different Southern Hemisphere floras in present-day South America, southern Africa, Australasia, India and Antarctica were dominated by the corystosperm (gymnosperm) Dicroidium (Anderson and Anderson, 1983). In the south-west Pacific the Dictyophyllum-Clathropteris assemblage ranged from Ladinian-Carnian to Rhaetian times (Vozenin-Serra and de Franceschi, 1999).

The dominance of the spore-bearing plants that covered much of the land in Palaeozoic times ended in the early part of the Mesozoic Era. Nevertheless, there is evidence that much smaller Triassic lycopsids, such as the unbranched *Pleuromeia* (Neuburg, 1960) which was up to two metres tall, dominated most of the Early Triassic lowland habitats. Other smaller, *Isoetes*-like lycophytes called *Taktajanodoxa* (Snigirevskaya, 1980) often grew in pure stands in waterside environments and there were truly herbaceous lycopsids that appear to be indistinguishable from extant *Selaginella* (Ash, 1972). The sphenopsids, such as the Early Triassic *Schizoneura* and the later *Neocalamites* (Boureau, 1964), were also much smaller than their Palaeozoic counterparts.

Many Palaeozoic fern species became extinct although the survivors rapidly diversified to become the dominant herb throughout the Mesozoic world. Some Triassic ferns were still relatively simple, having only some of the characters of modern families. *Cynepteris*, for example, is similar to living members of the Schizaeaceae, but does not have all the characters necessary to be included in the family. In contrast, *Wingatea* can be included in the Gleicheniaceae, *Phlebopteris* in the Matoniaceae, and *Dictyophyllum* and *Clatbropteris* in the Dipteridaceae (Ash, 1969; Ash *et al.*, 1982).

Gymnosperm seed plants became dominant in nearly all early Mesozoic habitats. Cycads today are relatively rare tropical plants that include the genera *Cycas*, *Zamia*, *Macrozamia* and *Encephalartos*. These have trunks that are



Figure 2.2 Palaeogeography of the British Isles during the Rhaetian Age. (After Warrington and Ivimey-Cook, 1992.)

usually unbranched and above ground, with a crown of large divided leaves giving them the appearance of small palm trees. The first cycads appeared in the Permian of China (Gao and Thomas, 1989a,b) where there is evidence of seed-bearing structures that are very similar to those of modern *Cycas*. They spread westwards and became common throughout the Northern Hemisphere during the Mesozoic Era. One of the earliest Mesozoic cycad leaves is the pinnate-ly divided *Aricycas* Ash 1991 from the Upper Triassic Chinle Formation in Arizona.

Other, quite different, Mesozoic plants had cycad-like foliage. For many years they were believed to come from cycads. It is now known that they belong to an extinct order of gymnosperms, the Bennettitales. These plants either had slender, branching stems that bore their fructifications in the axils of branches, or shorter unbranched stems that bore them directly on their surface. The fructifications were often flower-like with petal-like bracts surrounding seed-bearing ovules and pollen-producing organs. Some were unisexual, others bisexual.

Ginkgos are represented today by the single species *Ginkgo biloba*, the maidenhair tree, which grows wild only in a few remote valleys in Zhejiang Province, eastern China. Their origins were probably in the Palaeozoic pteridosperm group known as the Callistophytales. Triassic ginkgoaleans are represented by a series of isolated leaves, some of which are essentially the same as Recent *Ginkgo*, whereas others are more deeply divided and referred to the genera *Baiera* and *Czekanowskia*.

Conifers have their beginnings in late Palaeozoic times, with primitive forms having their ovules borne on short leafy shoots within the cone. Most groups of primitive conifers became extinct at the end of the Palaeozoic Era, more modern forms appearing in the Mesozoic Era. Some leaves, which are very similar to the Palaeozoic cordaites, are referred to Pelourdea, Noeggerathiopsis and Desmiophyllum. The newer conifers rapidly diversified to become the dominant plant group over much of the Mesozoic world. Many are close enough to living species to be included in the same families. Thus the Triassic Comostrobus from the USA has been included in the Pinaceae (Delevoryas and Hope, 1973) and other species from the Southern Hemisphere have been referred to the Podocarpaceae (Miller, 1982). In addition to these there were, however, a number of important families extant in the Mesozoic Era that are now extinct, the most important and successful being the Cheirolepidiaceae (Watson, 1988). The foliage of representatives of this family is similar to that of living cypresses, but their reproductive cones are more like those of the living monkey puzzles such as Araucaria, although much smaller. It is these conifers that are found in British Upper Triassic deposits.

TRIASSIC PALAEOBOTANICAL SITES IN BRITAIN

Although there are few British Triassic plantbearing deposits, they are nevertheless important. The lower Sherwood Sandstone Group (which includes the Bunter deposits of previous 'classic' terminology) contains very few plant remains, all of which are facies-related and completely inadequate for correlation and

The Triassic palaeobotany of Britain

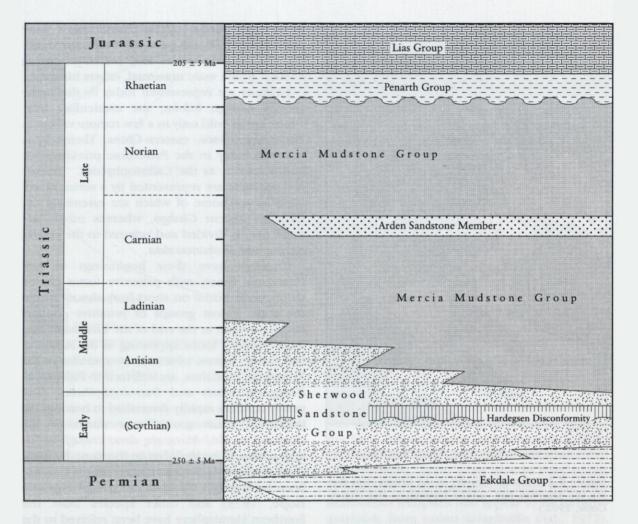


Figure 2.3 The Triassic stratigraphy of Britain, showing the internationally recognized chronostratigraphy on the left and the main lithostratigraphical units (groups) on the right. (After Warrington and Ivimey-Cook, 1992.)

stratigraphical purposes (Warrington, 1976). The remainder of the Sherwood Sandstone Group and the overlying Mercia Mudstone Group (formerly the 'Keuper Sandstone' and 'Keuper Marl') also contain few plant remains. Triassic plants have been described mostly from the upper 'Keuper' of Worcestershire and Warwickshire, and the Rhaetian deposits of the Bristol area.

The main genera from these areas are *Cordaites*, *Schizoneura*, *Equisetites* and a male cone, which may belong to the conifer *Voltzia*. In comparison with the continental rocks of Germany and France, the British floras relate most closely to those of the Voltziensandstein, which immediately underlies the Muschelkalk and is, therefore, of Early–Middle Triassic age. The presence of ripple marks, sun cracks and

rain prints in evaporites in the Mercia Mudstone Group suggests salt-lake conditions, which would explain the rarity of plants. The few fossils that have been found probably represent plants that grew on slopes near the lakes. Even though conditions were still arid and desert-like, the 'continental' assemblages are richer and more diverse.

The Rhaetian deposits of Northern Europe are typically a passage succession between the nonmarine Triassic and the marine Liassic strata. The Rhaetian Age was probably of only brief duration; Rhaetian deposits have been described previously as the uppermost part of the Keuper, a separate formation, and the basal unit of the Jurassic System. However, it is now generally accepted as the uppermost part of the Triassic System, incorporating the uppermost Mercian

Hapsford Bridge

Mudstone Group (Blue Anchor Formation) and the overlying Westbury and Lilstock Formations of the Penarth Group. The standard floras for comparison are those of Germany, Sweden and Greenland. In Germany and Sweden two main zones have been identified: the Thaumatopteris (Filicales) Zone and the Lepidopteris (Pteridosperm) Zone. The Thaumatopteris Zone corresponds to the Hettangian Stage (the lowest of the Jurassic System) and the Lepidopteris Zone approximately to the Rhaetian Stage. The Rhaetian flora in Britain is more limited although it is particularly important for the bryophyte Naiadita, a member of the Hepaticae (liverworts; see GCR site report for Hapsford Bridge).

HAPSFORD BRIDGE (ST 760 495)

Introduction

This is the best-known locality for the Rhaetian bryophyte flora, which is dominated by the liverwort *Naiadita lanceolata*. Bryophytes are generally rare in the fossil record, but this material is outstandingly well preserved. The fossils here show full details of both sporophytes and gametophytes, including the reproductive organs.

Fossils here have been known for about 160 years from a layer of rock approximately 10 cm thick in the upper part of the Rhaetian strata that occurs extensively in the West Country and the Midlands of England. It is not, however, a homogenous unit but consists of thin layers with different fossils, of which *Naiadita* is the principal plant found. This is now known to be a liverwort and is perhaps the best example of a bryophyte preserved in British deposits.

Many of the older sites described in the literature are no longer accessible, so the Hapsford Bridge site is particularly important. This locality falls within the Vallis Vale Site of Special Scientific Interest near Frome in Somerset.

Description

Stratigraphy

Rhaetian deposits in the British Isles are limited to the principal outcrop stretching from Dorset to North Yorkshire and other small outcrops in Wales, Northern Ireland and Scotland. The main outcrop, which is about 30 m thick at its maximum development, includes a number of horizons that contain the remains of mostly marine animals. However, because these are mainly fish, bivalves and ammonites being absent, they cannot be accurately correlated with the typical marine Rhaetian rocks of the Alps (Warrington, 1976).

Fossil plants are scarce and, with the exception of the fissure fills in places such as Cnap Twt, they are limited to a thin, but remarkably persistent bed – the *Naiadita* bed. This is known to extend about 145 km from east of the Mendip Hills to south Worcestershire and Warwickshire. Wilson (1891) called this deposit 'Bed K', and Richardson (1911) described some sections in the region of this GCR site.

The plant-bearing layers are part of the Cotham Member, which is the lower unit of the Lilstock Formation (Warrington and Ivimey-Cook, 1992). This member consists of finegrained, micaceous grey-green mudstones and fine white siltstones, which are over 9 m thick in eastern Lincolnshire but thin to less than a metre in Somerset. These lagoonal deposits in the Vallis Vale area were some distance from the sea and do not contain the coarser conglomerates found elsewhere. Rather they are largely composed of pale marls and limestones containing *Euestheria*, ostracods, fish scales and plants.

Palaeobotany

The main plant fossil of the British Rhaetian flora is *Naiadita lanceolata* Buckman emend. Harris. The species was first discovered near Bristol and named by P.B. Brodie in 1845 who thought they were monocotyledonous plants. Unfortunately he published it as a *nomen nudum* and it was left to Buckman (1850) to publish the name validly. Sollas (1901) examined some new material from the Bristol area and came to the conclusion that it was a member of the Lycopodiaceae. It is now accepted that Gardner (1886b) interpreted the fossils correctly when he referred them to the bryophytes.

Naiadita has simple, single-cell-thick leaves borne spirally on a slender stem from which unicellular rhizoids emerge (Figure 2.4). The naked female reproductive organs, archegonia, are borne laterally on short stalks that later elongate. They also become enveloped in scales that resemble foliage leaves. After fertilization the sporophyte grows into a spherical capsule and a minute foot. Ripe capsules are full of spore-

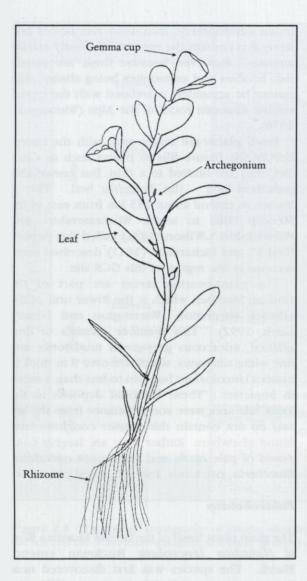


Figure 2.4 Reconstruction of Niaidita.

tetrads with no sterile cells of any kind. Conical asexual gemma cups are formed on branches. *Naiadita*, as described by Harris (1938), is evidently a liverwort with a most unusual combination of characters. It is most similar to *Riella* in the Sphaerocarpales but is sufficiently different for Harris to have suggested that it cannot really be closely related to any living genus.

The alga *Botryococcus braunii* Kützing was described from the site by Harris (1938), as were some branched filaments resembling moss rhizoids. Another leafy liverwort, *Hepaticites solenotus* Harris, has been described from other localities of the *Naiadita* bed but not yet from Hapsford Bridge.

Interpretation

The flora consists almost entirely of *Naiadita longifolia*, which has made its reconstruction considerably easier and more secure. Harris (1938) suggested that it grew as a submerged plant covering the bottom of the shallow parts of large lakes. Sedimentation in the lake preserved the adult plants and the large numbers of embryos that were starting to grow in the unconsolidated sediments before their food reserves were exhausted. Temporary marine incursions would have killed the *Naiadita* and its animal associates to form a fossil-rich bed. Regression of the sea would have been followed by the reestablishment of freshwater communities.

Conclusion

Hapsford Bridge is an outstanding locality for the Rhaetian bryophyte *Naiadita* and a key site for understanding bryophyte evolution.

CNAP TWT (SS 911 753)

Introduction

A number of Mesozoic fissure deposits in the Carboniferous outcrop of the Bristol channel have yielded animal and plant remains (Figure 2.5). Owen (1871) and then Simpson (1928) first described the vertebrate remains. Detailed work recommenced in the 1940s and has continued up to the present day. Robinson (1957) described the geology and reviewed previous work on all the fissures and their vertebrate faunas in South Wales and Somerset. Much of the work has been on the vertebrate remains. Kühne (1949) and Kermack et al. (1968) described early mammals from South Wales fissures, and Benton and Spencer (1995) included details of all the fissure faunas in their GCR volume on fossil reptiles.

Plant fossils were first described from deposits in the Vale of Glamorgan by two students of Harris (Lewarne and Pallot, 1957) and then by Harris himself (1957). Since then no further work has been published on the plants, except for Harris' (1958) use of the fusainized (charcoalified) preservation state of the plant remains as evidence of forest fire. There is clearly great potential for additional palaeobotanical studies of these deposits.

The most productive fissures for plant

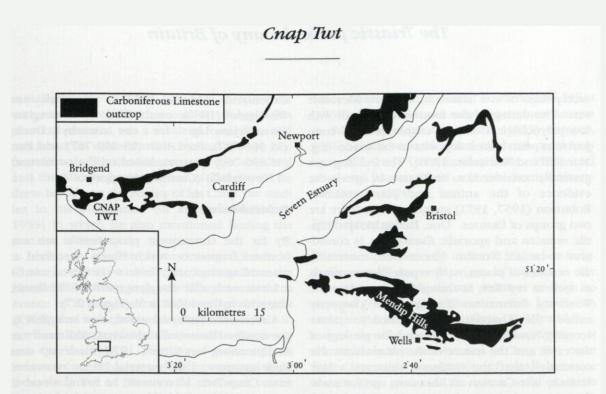


Figure 2.5 Distribution of Carboniferous Limestone deposits with fissure fills in eastern South Wales and southwest England, showing the position of the Cnap Twt GCR site. (From the *Fossil Mammals and Birds of Great Britain* GCR Volume, in preparation.)

remains are at Cnap Twt (Figure 2.6). Harris described two of these in the year the quarry closed, as follows:

'Here there are two fissures which changed their appearance greatly as the section was cut back. When I saw them, the south fissure was an oblique crack up to 50 cm wide, running obliquely up the limestone face from the quarry entrance to the hillside 50 ft [15 m] above. There was another fissure, looking like a cave, but narrowing above and partly occupied by great blocks of limestone. The north fissure was poorly exposed.'

The face has since weathered and deteriorated although fissures can still be identified.

Description

Stratigraphy

The Lower Carboniferous Limestone of the Mendip Hills and parts of South Wales formed an

Figure 2.6 Cnap Twt. The Rhaetian fissure deposits within the Carboniferous Limestone, such as the one visible here, have yielded charcoalified remains and pollen of cheirolepidiacean conifers, which are believed to be the precursors of all living conifers. Fragments of bennettites and other conifers have also been reported from here. (Photo: B.A. Thomas.)



archipelago of low islands in the early Mesozoic sea. The dating of the fissures is difficult with few palynological data to enable detailed comparisons with other deposits to be made (e.g. Marshall and Whiteside, 1980). The infillings are generally considered to be Triassic in age on the evidence of the animal and plant remains. Robinson (1957, 1971) suggested that there are two groups of fissures. One, having yielded reptile remains and sporadic Euestheria, is considered to be late Norian. The second, containing the remains of plants, early reptile-like mammals as well as reptiles, is thought to post-date the Westbury Formation transgression (formerly called 'the Rhaetian transgression'). More recently, Simms (1990) reviewed the geology of the caves and the nature of the palaeokarst. He concluded that the evidence suggests a Late Triassic, late Carnian to Rhaetian, age for some fissures, and an Early Jurassic, Hettangian-Sinemurian, age for others.

The plant remains from the Vale of Glamorgan fissures can be compared with those in the basal Lias of Germany and the Rhaetian deposits of Greenland (Harris, 1957). Marshall and Whiteside (1980) established a Hettangian– Sinemurian age for the nearby Duchy (SS 906 757), Pont Alun (SS 899 767) and Pant (SS 896 760) quarries, based on the occurrence of *Hirmeriella (Cheirolepis*) spores.

Palaeobotany

By far the commonest plant fossils are carbonized fragments, which Harris described as resembling charcoal. These were sieved out on a 1 mm mesh after disaggregration of the fissure clay with hydrochloric acid (Figure 2.7).

Carbonized bark and wood, now referable to the conifer *Hirmeriella airelensis* Muir and van Konijnenburg-van Cittert, 1970, made up over three-quarters of the material Harris recovered from Cnap Twt. In contrast, he found wood to comprise 98% of the plant material recovered from a fissure in the nearby working Ewenny Quarry. Microsporophylls and seeds referred to the conifer were also recovered from Cnap Twt. Harris interpreted all of these carbonized

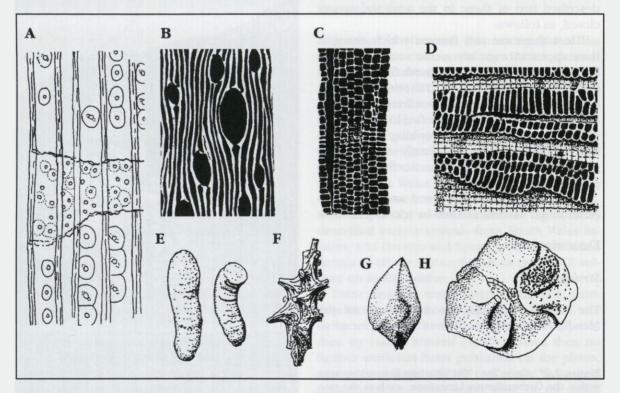


Figure 2.7 Examples of some of the types of fossil found in the Rhaetian fissure-fill deposits at Cnap Twt. (A–D) *Cheirolepis* wood. (A) Macerated tracheids close to protoxylem, \times 500. (B) Charcoal fragment, tangential surface showing distorted rays, \times 500. (C) Charcoal fragment, showing growth rings, \times 200. (D) Charcoal fragment, in oblique radial section, \times 100. (E) Two pollen masses, \times 10. (F) Male cone axis, \times 10. (G) Seed showing hilum, \times 8. (H) Base of male cone showing a mass of pollen grains, \times 10. (After Harris, 1957.)

remains as true charcoal, based on comparisons with modern conifer charcoal. He thought this charcoal material was a result of forest fires and remarked on other similar charcoal that he had found in the Rhaeto-Liassic rocks of Greenland and the Middle Jurassic strata of Yorkshire. He drew heavily on the results of his Cnap Twt studies in his publication on forest fires (Harris, 1958) in which he also mentioned finding the remains of beetles.

Identical conifer leaves were found by Chaloner (1962) in Rhaetian deposits from the Henfield borehole, in fissure fillings in northern France by Briche et al. (1963) and Levet-Carette (1964), and in lacustrine deposits at Airel, also in northern France, by Muir and van Konijnenburgvan Cittert (1970). The last of these authors referred their fragments of male cones and those from Cnap Twt to Hirmeriella airelensis on the basis of association and their consistent structure (two pollen sacs on each microsporophyll). Harris had originally referred the Cnap Twt conifer to Cheirolepis (= Hirmeriella) muensteri but Muir and van Konijnenburg-van Cittert (1970) distinguished it from this species, which has up to 12 pollen sacs on each microsporophyll.

Harris recovered numerous pollen grains of *Cheirolepis*. The age range of such grains, called *Classopollis*, extends from the Late Triassic Epoch through the remainder of the Mesozoic Era. Those from Cnap Twt and identical forms from Airel were named *Classopollis harrisii* by Muir and van Konijnenburg-van Cittert (1970).

Harris also recovered small cuticle fragments of *Dolerophyllum*, *Ctenis*, *Pterophyllum*, an unidentified conifer, *Cycadolepis*, and two forms of small seed. Lycophyte microspores were referred to *Heliosporites reissingeri* (Harris, 1957) by Chaloner (1969), and Harris referred other miospores to *Pityosporites* type, *Leiotriletes* spp., *Entylissa* spp. and about eight other unidentified species. Lewarne and Pallot (1957) described some megaspores, now known as *Bacutriletes tylotus* (Harris, 1935) Potonié, 1956, which were identical to those previously recorded from Greenland (Harris, 1935) and northern France (Muir and van Konijnenburgvan Cittert, 1970).

Interpretation

The limestone outcrop in South Wales was originally part of an archipelago of islands in the Rhaetian sea. The climate was wet enough to support *Hirmeriella*. These conifers have been interpreted as both trees (Alvin, 1983) and succulent shrubby xerophytes (Watson, 1988). It seems likely that the remains at Cnap Twt came from a scrubby vegetation of small trees or shrubs that grew in the poor soils of these islands.

Fires, presumably started by lightning strikes that swept through the scrub, burnt and charcoalified the twigs and their reproductive organs. Subsequent storms would have washed these remains, together with mud and sand, into the drainage fissures that ran through the limestone. Anaerobic conditions in these waterlogged sediments preserved them in exquisite detail, with the best twigs and male cones showing every cell equally well preserved.

Conclusion

Cnap Twt is the best Rhaetian fissure-fill deposit in Britain to yield a good plant fossil assemblage. The charcoalified remains give a unique insight into the plants that lived in southern Britain at this time. It is a site of outstanding palaeobotanical significance and an exceptional locality for Rhaetian plant fossils, most notably those of primitive conifers.