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 species-rich, 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 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 present-day 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 *Clathropteris* 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 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 pinnately 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.

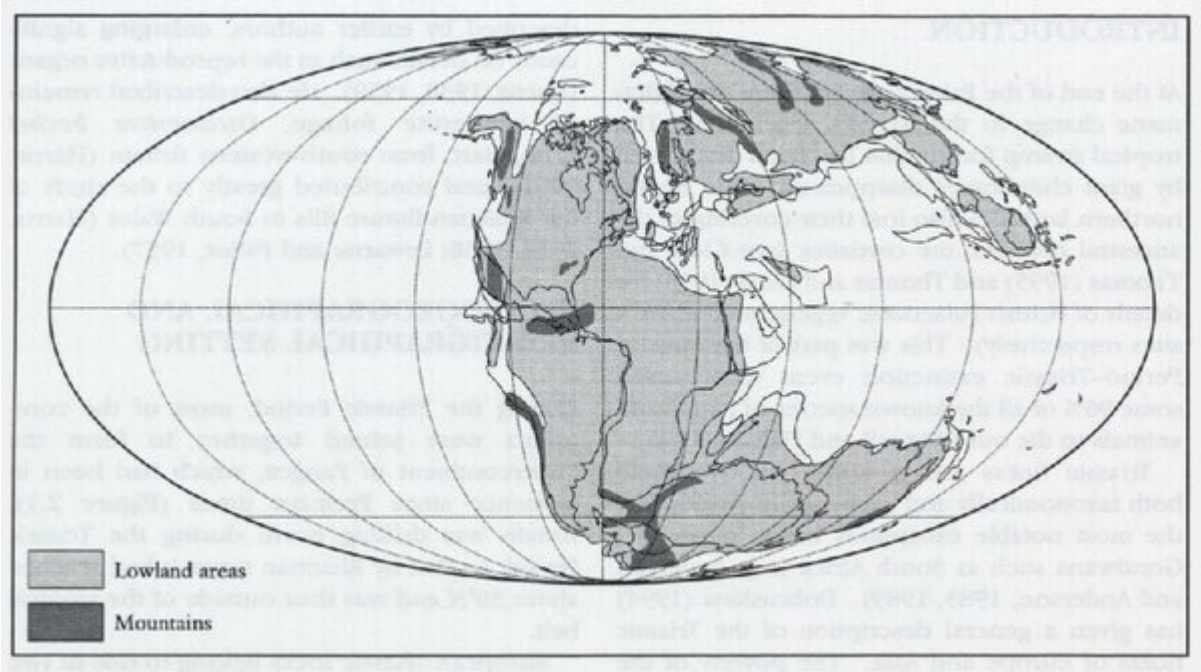
Triassic palaeobotanical sites in Britain

Although there are few British Triassic plant-bearing 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 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.

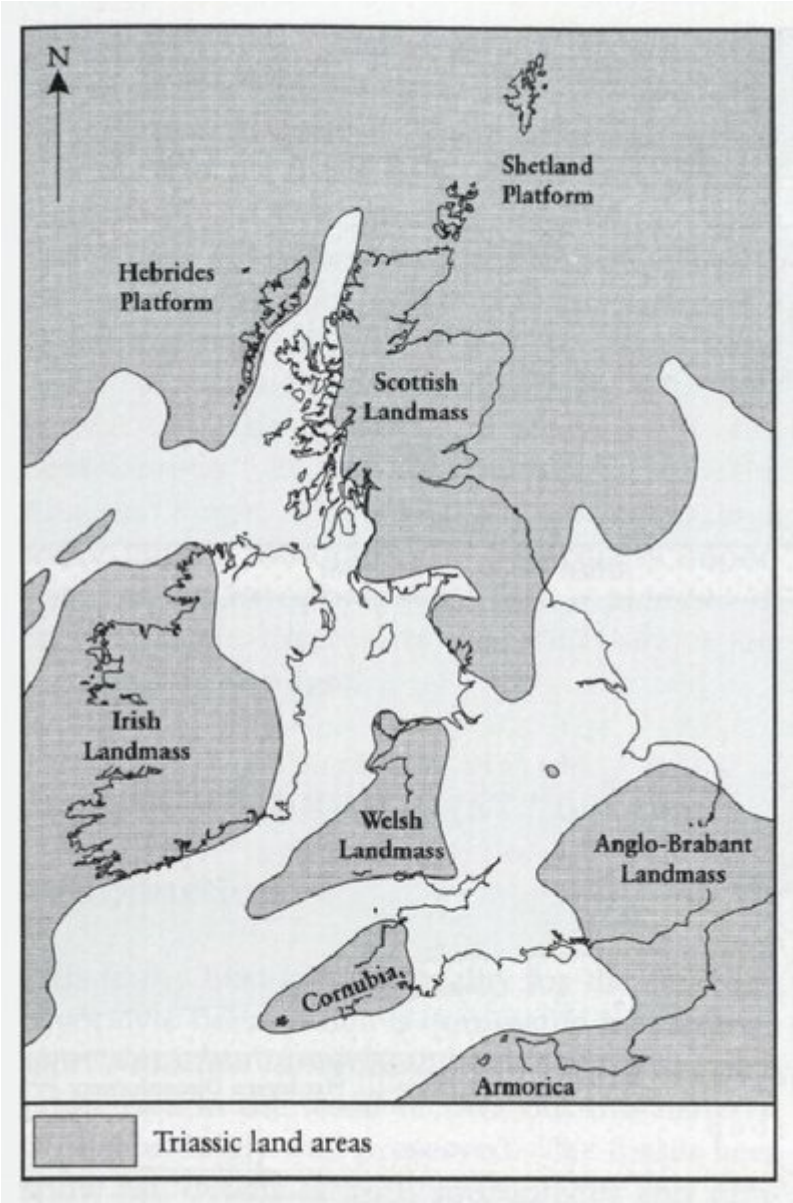
The main genera from these areas are *Cordaites, Schizoneura, Equisetites* and a male cone, which may belong to the conifer *Voltzia.* In comparison with the continental rocks of Germany and France, the British floras relate most closely to those of the Voltziensandstein, which immediately underlies 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 non-marine 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 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).

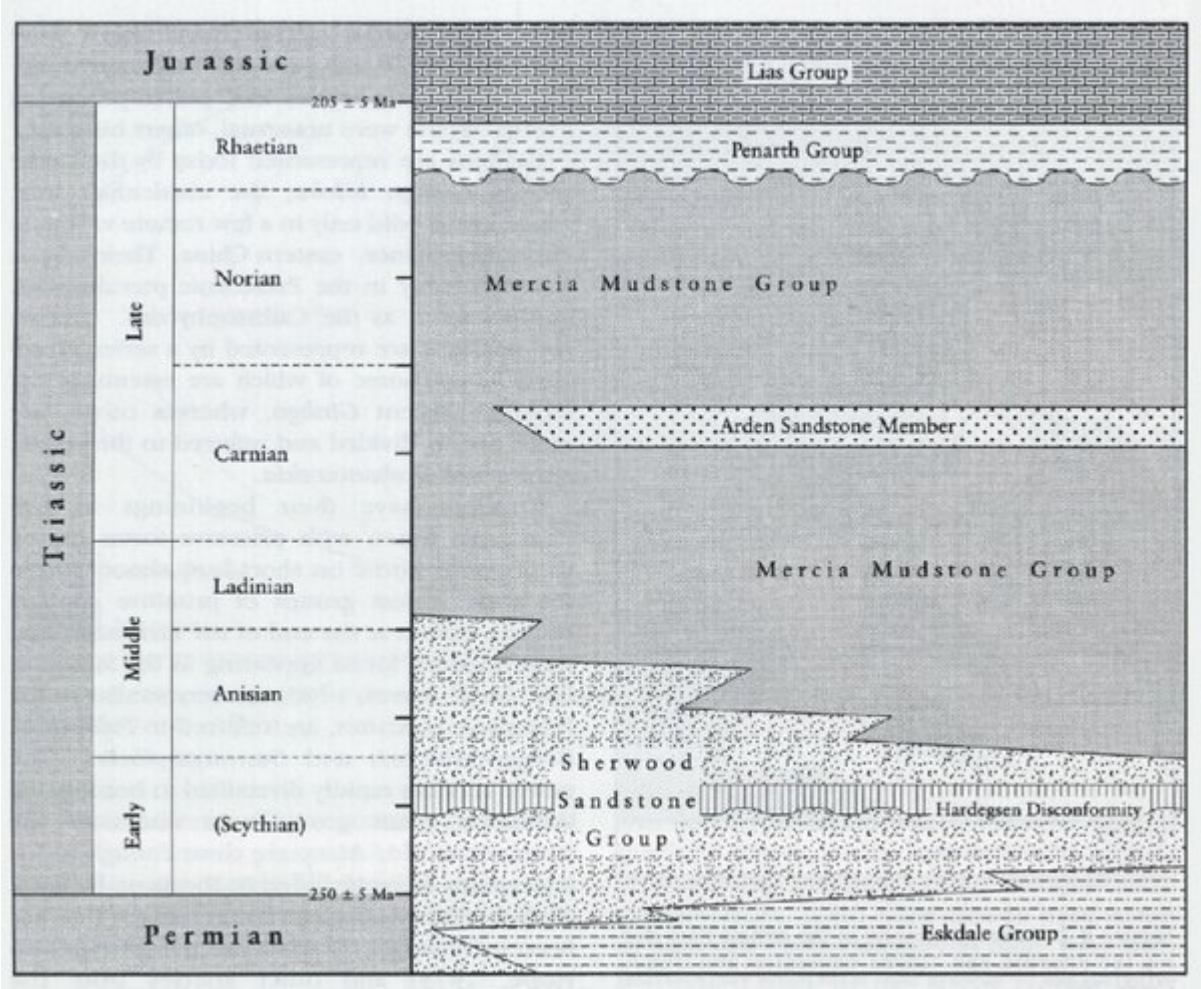
References



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



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



(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.)