Delineating climate and palaeoecological changes from miospores of the Upper Jurassic Helmsdale

Boulder Beds Formation, Sutherland, Scotland

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Abstract

A study of the palynomorphs of the Upper Jurassic Helmsdale Boulder Beds Formation, of the Inner Moray

Firth Basin has been conducted to determine if cooling of the marine environment was experienced on the

Scottish landmass. Thirty samples contain assemblages dominated by trilete spores and alete pollen grains. The

composition of the palynofloras was analysed by reference to their botanical affinity and using correspondence

and C-means Fuzzy Cluster statistical analysis for their ecological setting. Assemblages are observed to vary

through the Upper Jurassic; those in the Kimmeridgian being dominated by spores from ferns and fern allies,

whilst the Tithonian deposits show a progressive change to pollen dominated by coniferous gymnosperms.

Analysis of the miospores has revealed a distinct bi-modal distribution, interpreted to represent a climatic shift

from a warm humid-temperate in the Kimmeridgian to a cool semi-arid climate, in the wheatlevensis Zone of

the Upper Tithonian, correlating well with IMF sea-temperature change and climate change previously

identified at lower latitudes. This climate change is associated with a phase of cooling at the Jurassic –

Cretaceous boundary.

Keywords: Upper Jurassic, Inner Moray Firth, palynology, palaeoclimate change

1. Introduction

Studies of Late Jurassic (Oxfordian – Tithonian, 161.2 – 145.5 Ma (Ogg et al. 2008)) climate are numerous (e.g. Hallam 1984; Moore et al. 1992a; Moore et al. 1992b; Hallam 1994; Valdes et al. 1995; Hubbard & Boulter 1997; Ridding & Hubbard 1999; Price 1999; Sellwood et al. 2000; Bartolini et al. 2003; Gröcke et al. 2003; Pross et al. 2006; Husinec & Read 2007; Sellwood & Valdes 2008; Hesselbo et al. 2009), identifying western Europe as a region with a warm, stable climate (Lécuyer et al. 2003), however detailed studies have largely been limited to southern regions e.g. the southern North Sea (Abbink et al. 2001; Abbink et al. 2004a; Abbink et al. 2004b), southern England (Pearson et al. 2004) and France (Brigaud et al. 2008; Carcel et al. 2010) and detailed analysis from more northerly localities has so far been limited (e.g. Ditchfield 1997; Nunn & Price 2010). Evidence for a climatic shift from a warm-temperate to semi-arid climate has been documented from southerly localities (Wignall & Ruffell 1990; Hallam 1993; Ruffell & Rawson 1994; Abbink et al. 2001, Hesselbo et al. 2009), with distinct reductions in precipitation noted during the Early Tithonian (Abbink 1998) and a drop in sea-temperature recorded in the IMF from the Helmsdale Boulder Beds by Nunn & Price (2010).

Here, we present analysis of a palynological data set, from marine Upper Jurassic sediments of the Inner Moray Firth (IMF) Basin (Fig. 1). High resolution biostratigraphy (Barron 1989) has enabled calibration of samples with the standard sub-boreal ammonite biozonation, which allows accurate timing of the ecosystem change. Given the stratigraphical precision available for study of the IMF sequences it is now possible to assess the impact of the Early Tithonian sea surface temperature drop (Nunn & Price, 2010) in the higher latitude NE Scottish sections. Using palynofloras derived from the Scottish landmass, we have assessed the record of the Early Tithonian drop in marine surface temperature, and investigated its impact on land surface temperature.

2. Regional setting

The IMF Basin has been subject to multiple phases of rifting, initially in the Permo-Triassic and a subsequent phase in the Late Jurassic (Thompson & Underhill 1993). The main phase of IMF rifting occurred in the Late Jurassic, from the Oxfordian to the Tithonian (Rattey & Hayward 1993), associated with the regional phase of extension in the North Sea. This Late Jurassic extension led to the development of a series of half graben structures across the basin and with relatively high sea-level during this epoch (Hallam 2001), the basin was filled with a succession of deep marine sediments (Hudson & Trewin 2002) that form the basis of this research. Thermal subsidence prevailed across the Moray Firth and northern North Sea basins during the Cretaceous (Harker 2002). Thermal uplift associated with emplacement of the North Atlantic Igneous Province affected much of the Scottish landmass in the early Cenozoic resulting in erosion and exposure of the Mesozoic basin-fill succession on the northern margin of the IMF Basin (Argent et al. 2002).

The Upper Jurassic sediments are exposed along 18 km of shoreline (GR 923 074 to GR 062 175) in the vicinity of Helmsdale (Fig. 2) comprising a near continuous 970 m thick section of strata adjacent to the Helmsdale Fault (McArthur et al. 2012). These sediments belong to the Allt na Cuile Sandstone and the Helmsdale Boulder Beds formations. These sediments have been studied in detail (e.g. Bailey & Weir 1932; Crowell 1961; Pickering 1984; MacDonald 1985; Davies & Pickering 1999; Hudson & Trewin 2002) and consist of a series of siltstones and sandstones interspersed with "boulder beds"; debris flow deposits that are inferred to have been derived from the Helmsdale Fault scarp in the Late Jurassic (Pickering 1984; MacDonald & Trewin 1993; Hudson & Trewin 2002).

The footwall region to the Helmsdale Fault was situated on the margin of the Scottish landmass (Fig. 1) and though the immediate hangingwall was submerged in the Late Jurassic (Hudson & Trewin 2002), it was very proximal to exposed land, with only a narrow shelf (<5 km) separating the deep marine setting from the landmass (Bradshaw et al. 1992; Hudson & Trewin 2002). This proximity is confirmed by the large amounts of terrestrial material present in the Helmsdale Boulder Beds Fm., which contain abundant well preserved fossil plant material (van Konijnenburg van Cittert & van der Burgh 1996). The marine sediments from which the

palynomorphs have been extracted for this study were deposited in a location proximal to the source of this vegetation.

Over a century of palaeoentological work has allowed an excellent biostratigraphic control initially from ammonites (Bailey & Weir 1932; Brookfield 1976) and more recently from dinoflagellate cysts (Barron 1989) with sub-boreal ammonite biozones (Fig. 2) constraining the age of deposition. The biozones demonstrate a complete stratigraphic section, spanning 12 ammonite zones and 8 Ma, ranging from the basal Kimmeridgian *Pictonia baylei* Zone (155.7 Ma) to the Upper Tithonian *Progalbanites albani* Zone (147.7 Ma) (Barron 1989). Detailed work has been conducted on both the marine (Bailey & Weir 1932; Brookfield 1976; Wignall & Pickering 1993) and terrestrial (Seward 1911; van der Burgh & van Konijnenburg-van Cittert 1984; van Konijnenburg-van Cittert & van der Burgh 1989; van Konijnenburg van Cittert & van der Burgh 1996; van Konijnenburg van Cittert 2008) macrofossils and microfossils (Lam & Porter 1977; Riley 1980; Barron 1989; Gregory 1989; Hesketh & Underhill 2002), which has contributed to the understanding of the palaeoecology of this region in the Late Jurassic. The most recent miospore studies were conducted by Lam & Porter (1977) and Riley (1980) comprising taxonomic assessments of the palynomorph associations.

In the Late Jurassic the study area lay on a palaeolatitude of 39° N (Hudson & Trewin 2002; Fig. 1), with winter temperatures of approximately 5 - 15° C and summer temperatures of 15 – 30° C (Rees et al. 2000). An abundance of plant remains associated with warm climates (van Konijnenburg van Cittert & van der Burgh 1996) and remains of reptiles have been used to infer a warm temperate palaeoclimate and a heavily vegetated Scottish landmass, with rivers and deltas feeding the marine sediments, which were entering a largely anoxic marine environment (Wignall & Pickering 1993) via a rocky shallow marine shelf (Hudson & Trewin 2002). However recent work by Nunn & Price (2010) analyzing stable isotopes (δ^{18} O and δ^{13} C) and Mg/Ca ratios from belemnites recovered from the Helmsdale section, has provided evidence of a significant change in IMF seawater temperatures during the latest *scitulus* Zone of the Lower Tithonian, indicative of the onset of a distinctive cooling episode.

3. Material & Methods

Thirty samples were taken from key stratigraphic intervals (Fig. 3) to represent the Allt na Cuile and Helmsdale Boulder Beds formations. Good exposure allowed regular sampling, which was restricted to siltstone intervals. Samples were processed using standard palynological techniques (Wood et al. 1996), with the addition of overnight treatment with Schulze solution to remove the high density of amorphous organic material. All samples were analysed qualitatively and quantitatively and a minimum count of 200 palynomorphs per sample was conducted to provide data for statistical analysis; palynomorph preservation is moderate to good. All rock samples, organic residues, microscope slides, primary data and figured material are housed in the collections of the University of Aberdeen's Micropalaeontology Research Laboratory.

The impact of transportation and preservation of the palynomorphs in this marginal marine setting is not considered to be a factor, with palynomorph assemblages from proximal settings considered to be directly reflecting changes in the terrestrial vegetation (Heusser 1979; Tyson 1995; Batten 1996; Traverse 2007). Importantly empirical studies demonstrate that relative abundances of miospores are directly related to the distribution of plant communities (Suc 1984; van der Kaars 1991; van der Kaars & Dam 1995; Abbink et al. 2001; Twitchett et al. 2001; Crouch & Visscher 2003; Moss et al. 2005; Umetsu & Sato 2007).

4. Results

4.1 Palynoflora association observations and variations in biodiversity

The palynomorph assemblages of the Helmsdale Boulder Beds Frest typical of the Upper Jurassic marine deposits of NW Europe, samples being dominated by alete pollen, trilete spores, dinoflagellate cysts and acritarchs, totalling representatives of 95 genera. The dinoflagellate cysts are the basis for the high resolution biostratigraphic calibration of the section (Barron 1989). The samples contain many long ranging Mesozoic palynomorph taxa and an abundance of woody debris. This study is principally focussed on the terrestrial palynomorphs (Fig. 4), with dinoflagellate cysts only being utilized to confirm the age of samples. The ratio of

sporomorphs to dinoflagellate cysts and acritarchs remains relatively constant throughout the section, with terrestrial palynomorphs accounting for no less than 62% and no more than 81% of the total counts.

The oldest terrestrial palynomorph assemblages were dominated by bryophyte (e.g. *Antulsporites* sp.), lycopodiopsida (e.g. *Lycopodiumsporites* sp., *Foveosporites* sp.) and pteridophyte spores (e.g. *Deltoidospora* spp., *Gleicheniidites* spp. and *Verrucosisporites* sp.), cycad pollen (*Cycadopites* sp.), and equisetales spores (*Calamospora mesozoica*) (Fig. 4). Gymnosperm pollen (e.g. *Alisporites* spp., *Perinopollenites elatoides*) was present but only in very low numbers (Fig. 4).

This domination of the assemblages by ferns and fern allied spores continued up to the *eudoxus* Zone (151.2 Ma), with increasing numbers of Lycopodiopsida spores, particularly *Lycopodiumsporites* sp. and *Staplinisporites* sp. (Fig. 4), which became particularly prevalent in the interval from the *cymodoce* to the *eudoxus* Zone deposits (155-152.4 Ma). These ferns and fern allied palynomorphs peaked at the top of the *eudoxus* Zone (151.2 Ma) in the Upper Kimmeridgian deposits, where they account for over 75% of the assemblage.

From the end of the *eudoxus* Zone to the *scitulus* Zone (151.2 – 150.3 Ma), the palynoflora assemblages remained dominated by ferns and fern allied spores (Fig. 4). Gymnosperm pollen continued to represent only a minor constituent, except *Cycadopites*, however even this initially abundant pollen is observed to decrease after a peak at the end of the *eudoxus* Zone (Fig. 4).

By the Lower Tithonian *wheatleyensis* Zone (150 Ma) the early dominance of fern and fern allied spores began a sharp decline, with the majority of species being severely reduced in their representation by the end of this biozone (149.8 Ma; Fig. 4). Conversely a sharp increase in gymnosperm pollen, particularly *Alisporites* spp., *Araucariacites australis* and *Inaperturopollenites* spp. is observed (Fig. 4). This trend, of reducing fern spores and increasing gymnosperm pollen continued from the top of the *wheatleyensis* Zone through to the

pallasioides Zone (149.8 – 148.6 Ma), where the gymnosperm pollen peaked at 65% of the palynomorph assemblage.

Following this peak in gymnosperm pollen in the *pallasioides* Zone (~149.3 Ma), a sharp reduction in most gymnosperm related pollen is observed (Fig. 4). Fern spores increased in number through the Upper Tithonian *rotunda* Zone deposits (~148.6 Ma). However from the *fittoni* Zone the ferns and fern allies declined once more and gymnosperm pollen returned to dominate into the *albani* Zone of the Upper Tithonian, at the top of the succession (Fig. 4).

4.2 Ecological association of palynofloras

The changes observed in the miospore association reflected changes in the ecosystem, mainly in response to variation in temperature, disturbance and moisture availability. By determining the various botanical affinities of the palynomorphs, by the use of the Nearest Living Relative (NLR) technique (Mosbrugger & Utescher 1997 and references within), it is possible to identify the principle ecological controls behind these changes. This then provides the basis from which to constrain palaeoclimate change and determine the key ecological factors of temperature and moisture availability. Although there are constraints with NLR analysis, particularly in the accuracy of pre-Cenozoic relationships (Chaloner & McElwain 1997), it remains a robust and commonly utilised method for investigating ancient ecosystems (e.g. Filatoff 1975; Vakhrameev 1991; Boulter & Windle 1993; Duane 1996; Abbink 1998; Hubbard & Boulter 2000; Abbink et al. 2001; Abbink et al. 2004a; 2004b; Wang et al. 2005; Utescher & Mosbrugger 2007; Bozukov et al. 2009). Based upon NLR analysis it is possible to delineate palynomorph taxa which required relatively wet conditions and those that were resistant to arid conditions (Table 1); the botanical affinities and climatic inferences of the palynomorphs broadly follow the Sporomorph Ecogroup Model of Abbink et al. (2004a).

4.3 Ecological statistical analysis

In order to corroborate the ecological interpretations from NLR analysis, multivariate statistical analysis is appropriate. Using Correspondence Analysis (CA), the data shows a high degree of confidence and separation into six principle groupings (Fig. 5). Eigenvalues for the first two axes (Eigenvalues Axis 1: 0.338 and Axis 2: 0.053) of the dataset show that axis one is exerting the principle control on the distribution. Axis one is interpreted as the principle control and is a function of water availability. This observation is based upon the distribution of taxa along this axis, with miospores possessing the lowest values (left hand side), e.g. Monosulcites, Araucariacites and Perinopollenites being derived from vegetation known to be the most drought resistant, whilst those with the highest values, e.g. Antulsporites, Uvaesporites and Verrucosisporites are produced by vegetation which requires high levels of moisture (Table 1). Axis two is less well defined but would appear to be a function of ecosystem disturbance, rather than succession, with variable pioneer communities arranged along this axis. Again this is based upon an observation of taxa distribution, with palynomorphs associated with vegetation most tolerant of disturbance demonstrating the lowest values, whereas those that require a stable environment with the least disturbance have the highest values, found at the top of the chart. Because the composition of these associations clearly relates to their botanical affinity and all samples were taken from marine siltstones that are independent of lithological restrictions, confidence can be assured in their ecological interpretation.

The main constituents of grouping one are products of mesophytic vegetation, comprising of monoaperatureate and inaperaturate pollen grains combined with saccate and bisaccate pollen. The grouping is numerically dominated by bisaccate pollen grains, produced by Pinaceae and Podocarpaceae type trees. Although derived from pollen over producers, saccate and bisaccate pollen was included in this statistical study because of their abundance in the later assemblages (Fig. 6). They also display a frequency trend comparable to the non-saccate gymnosperm pollen (Fig. 6). The remainder of the grouping is comprised of non-saccate pollen grains derived from Araucariaceae, Cheirolepidiaceae and Cupressaceae plants with lower frequencies of Bennettitales and Marattiaceae Pteridosperms. The conifers and Cheirolepidiaceae which dominate this grouping are associated with low moisture availability (Vakhrameev 1991) and are interpreted here to be derived from a mixed dry

forest. The very low frequencies of ferns and fern allies in this mixed dry forest community support this interpretation, also suggesting a cooler climate. This grouping was initially rare in the Kimmeridgian, coming to prominence in the Tithonian (Fig.6).

Grouping two is dominated by miospores from cycads and ferns of the Cyatheaceae and Gleicheniaceae. These taxa are recorded as being associated with wet margin riparian zones in the Jurassic (Vakhrameev 1991) and this ecological grouping is interpreted as a riverbank ecosystem. Though not dependent on a humid climate, the mesophytic to hygro-mesophytic vegetation comprising this plant ecosystem would have favoured increased moisture availability of river margins. The long term stability of this niche resulted in distribution peaks in the Early Kimmeridgian and Early Tithonian (Fig. 6).

Grouping three is dominated by hygrophytic "fern allies", principally the horsetail *Calamospora* but also by Lycopodiaceae spores; these are indicative of a marsh ecosystem (Abbink et al. 2004a). The presence of *Densoisporites* spp. may indicate raised levels of salinity (Raine et al. 1998), with the possibility of this having been a brackish marsh. This ecosystem would have developed in wet lowland areas and would have required high levels of moisture to sustain. It was most abundant during the Kimmeridgian and earliest Tithonian (Fig. 6).

Grouping four is comprised of a collection of fern families, dominated by Osmundaceae and Schizaeacea families, but also with representation by lycopsids and *Selaginella*. This diverse group of ferns and fern allies comprised a hygrophytic lowland grouping. This grouping is interpreted as a fern prairie ecosystem (e.g. Boulter & Windle 1993). This lush lowland setting represents a humid climate with warm temperatures (Abbink et al. 2004a). This was the dominant ecological grouping in the Helmsdale region for the duration of the Kimmeridgian and earliest Tithonian (Fig. 6).

Grouping five is dominated by representatives of Dicksoniaceae and Pteridaceae fern families and bryophyte mosses. These represent a mixture of both hygro-mesophytic and mesophytic plants, which would have been early colonizers of a disturbed environment and are indicative of an emergent swamp type ecosystem (e.g. Lapasha & Miller 1985). This disturbed, lowland ecosystem would have required a warm and very wet climate (Abbink et al. 2004a) and is most abundant during the Early Kimmeridgian and Early Tithonian (Fig. 6).

Grouping six is represented by hygrophytic Osmundaceae ferns and lycopsids. This grouping of early colonizing ferns and fern allies, comprises the least populous ecosystem (Fig. 6), representing a low diversity grouping of early successional plants associated with high degrees of ecosystem disturbance. This assemblage is indicative of a mud flats type ecosystem, which indicates high levels of moisture were available to support the palaeoflora.

The representatives of the marsh, mud flats and emergent swamp vegetation possess hygrophytic forms encompassing the bryophytes, lycopsids and sphenopsids. Whilst the most abundant constituents of the fern prairie and river bank are mesophytic (e.g. Cyatheceae ferns and cycads) other members of those groupings demonstrate a hygrophytic relationship (lycopsids and Dipteridaceae, Gleicheniaceae, Schizeceae ferns). These groupings therefore imply warm wet conditions.

This contrasts with the dry forest grouping, which is principally represented by mesophytic plants. Whilst certain miospores in the dry forest grouping have xerophytic connections, particularly the Cheirolepidiaceae (Vakhrameev 1991), the remainder were drought resistant conifers (e.g. Araucariaceae, Pinaceae and Podocarpaceae). This implies an ecosystem well adapted to a semi-arid climate, though the conifers were also adapted to withstand relatively cold conditions (Vakhrameev 1991). The comparison of these ecological groupings with the lithostratigraphy yields a clear bimodal trend (Fig. 6).

CA has been tested by the use of C-means Fuzzy Cluster (FCM) analysis (Gary et al. 2009). Three main clusters were derived from this analysis (Fig. 7), with a fuzzy exponent value of 1.5 being used. Fuzzy Cluster (FC) 1 is dominated by *Deltoidospora* (cluster centroid value of 11.3), with strong representation from *Gleicheniidites*, *Antulsporites* and *Lycopodiumsporites*. FC 2 corresponds to the conifer type pollen and is dominated by *Araucariacites* (cluster centroid value of 10.5) with *Alisporites*, *Cerebropollenites* and *Inaperturopollenites* all strongly represented in this grouping. FC 3 is dominated by *Calamospora* (cluster centroid value of 12.0), with sub dominant *Cycadopites*, *Deltoidospora*, *Staplinisporites* and *Verrucosisporites*.

This FCM analysis exhibits a bimodal trend, with initial samples being dominated by FCs 1 and 3, representing the fern and fern ally groupings and a low frequency of FC 2, which represents conifer type vegetation. In the oldest samples from the *cymodoce* Zone, the fern ally FC 3 grouping is dominant, with FC 1 being subdued until a small peak in the *autissiodorensis* Zone. After this event FC 3 again dominates until the *scitulus* Zone, where FC 1 became the dominant grouping. The short dominance by FC 1 is ended in the *wheatleyensis* Zone, when FC 2 became the dominant grouping, a position held to the top of the section. This trend, initially dominated by the fern and fern ally groupings, but with a sharp change to dominance by conifers is identical to the results of the CA analysis (Fig. 6), with these two methods of determining the dominant ecologies in the Late Jurassic of the Helmsdale region corresponding well.

5. Discussion

Three factors may be hypothesized in controlling the major change in the miospore association observed in the Lower Tithonian deposits (Fig. 6). A tectonic control, with significant uplift of the Scottish landmass may have been responsible for the change from a predominantly lowland collection of hygrophytic ecologies to a dry upland dominance. However there is no evidence for substantial uplift of Scotland at this time (Hudson & Trewin 2002). Secondly, edaphic factors and in particular a large rise in sea-level could have been responsible, by drowning low-lying areas, leaving upland vegetation as the dominant ecological grouping. A large sea-level rise in the Early Tithonian (Hesselbo et al. 2008; Fig. 3) may be suspected as causing significant ecosystem

disruption and removing suitable areas for lowland vegetation. Although a decrease in the lowland fern prairie grouping is observed, correlating with a sea-level rise at ~150 Ma (Fig. 6), this grouping recovers before the later major decline of the hygrophytic lowland groupings and sea-level is interpreted to have fallen substantially into the Late Tithonian (Hesselbo 2008), without recovery of the hygrophytic lowland vegetation (Fig. 6). Climate change is the third hypothesized control, with long term climate changes being directly related to variations in temperature and as consequence moisture availability in an ecosystem (Hubbard & Boulter 1997). Changes in temperature and moisture availability will be reflected by the local vegetation and hence palynomorph association (Abbink et al. 2001), with the plants most susceptible to climate change being those from lowland, coastal & river areas (Abbink 1998). As such we will discuss how the changing miospore association may be reflecting climatic change at the time of deposition.

5.1 Kimmeridgian climate

The oldest samples are dominated by taxa with bryophyte, fern and lycopsid affinities (Fig. 8). These have been identified as belonging to hygrophytic ecological groupings principally of the marsh, emergent swamp and mud flat ecologies associated with a warm humid climate (Abbink et al. 2004a), but also with representatives of the fern prairie and river bank ecosystems. The absence of Cheirolepidiaceae, a drought resistant family of conifer, is further indication of wet and warm conditions in the Early Kimmeridgian (e.g. Vakhrameev 1991).

Though there are fluctuations within the ecological groupings (Fig. 6) throughout the Kimmeridgian, the data implies a generally stable ecosystem, with a warm humid climate persisting over ~5 Ma. When examined in greater detail some key fluctuations in the palynomorph assemblages detail minor variations, which may be ascribed to change in the Kimmeridgian climate. Initially high levels of vegetation associated with humid conditions, recorded in the *cymodoce* and into the early *mutabilis* Zone, was followed by a minor decline of wetland ecosystems (Fig. 6). However wetland ecosystems peaked in the *eudoxus* Zone, after which they gradually declined, corresponding to an increase in the fern prairie grouping. The decreasing numbers of mud flats and emergent swamp representatives is interpreted as a gradual drying of the climate that began in the Late

Kimmeridgian. This reduction in hygrophytic groupings is interpreted to reflect reduced moisture availability, which continued up to a second peak in the wetlands ecologies that is observed in Lower Tithonian *scitulus*Zone samples.

5.2 Tithonian climate

A distinct change in the miospore association is apparent from the latest *scitulus* Zone, and is increasingly evident in the *wheatleyensis* Zone of the Early Tithonian (Fig. 4; Fig. 6). The initially dominant fern prairie, swamp and mud flats ecosystems declined, being replaced by taxa from the dry forest ecological grouping (Fig. 6). In the Early Tithonian coniferous gymnosperm pollen produced by plants tolerant of arid conditions (e.g. Cheirolepidiaceae, Cupressaceae and Araucariaceae) became the prevailing representatives of the vegetation (Fig. 9), indicative of drier, semi-arid conditions (Vakhrameev 1991).

It is noteworthy that the onset of aridity was not associated with climate warming. Vegetation associated with warmer climates (e.g. Cycadales and Cyatheaceae ferns) was reducing, particularly the constituents of the fern prairie and river bank ecologies, which were the most reliant on higher temperatures (Vakhrameev 1991), whilst the conifers, tolerant of cold conditions began to flourish during this period.

5.3 Land surface - sea surface palaeoclimate correlation

The palaeoclimate variation observed from the terrestrial miospores displays a distinct switch from wet, warm-temperate to cool, semi-arid. When the total percentage of palynomorphs associated with a relatively wet climate (mosses, lycopsids and most fern families) is compared with the total percentage of those associated with a relatively dry climate (the gymnosperm families), these climatic shifts become more apparent (Fig. 10). The trend of the miospore water dependency, derived from the CA variables corresponding to axis one of the CA analysis (Fig. 5) may also be extracted and demonstrates high water dependence through the Kimmeridgian and Lower Tithonian section, with a decline from the uppermost *scitulus* Zone onwards (Fig. 10).

The data presented here demonstrates a climate change reflected from the terrestrial domain; documented in recent work by Nunn & Price (2010) on stable isotopes (δ^{18} O, δ^{13} C) and Mg/Ca ratios records a temperature change in the IMF seawater. These authors interpreted the change in isotopes to represent a significant cooling of seawater in the Helmsdale vicinity initiating in the latest scitulus Zone (Nunn & Price 2010) and building through the Tithonian (Fig. 10). Comparison of the curves generated from the terrestrial miospores with the seatemperature curve exhibits a strong correlation (Fig. 10), with the sea-temperature decline and the change in the miospore assemblages, both demonstrating a change in climate to a cooler system from the scitulus Zone onwards (Fig. 10). The miospore association implies this drop in temperature was coincidental with a decrease in precipitation. Previous work from southern localities identified a change from a temperate to an arid climate took place across NW Europe as part of a major drying event in the northern hemisphere (Wignall & Ruffle 1991; Valdes & Sellwood 1992; Abbink et al. 2001; Pross et al. 2006; Pienkowski et al. 2008; Hesselbo et al. 2009). Studies from southern England and northern France have variably pointed towards drying occurring in the hudlestoni Zone (Wignall & Ruffell 1991) or marginally earlier in the wheatleyensis Zone (Abbink et al. 2001; Hesselbo et al. 2009). These southerly records correlate with the change that initiated in the latest scitulus Zone (Fig. 10) in this study (Fig. 10).

The changing flora represents a slow drying event, which occurred through the *wheatleyensis* and *hudlestoni* Zones to reach a maximum level of aridity in the *pectinatus* Zone of the Tithonian (Fig. 10). A rejuvenation of fern prairie and marsh associated palynomorphs is observed in the *pallasioides* and *rotunda* Zones (Fig. 10), as the dry forest palynomorphs reduced and representatives of the emergent swamp ecology returned. This compares well with the clay mineralogy study of Hesselbo *et al.* (2009), which described a return of wetter conditions over the same interval (Fig. 10), but does not correspond to any warming of seawater recorded by Nunn & Price (2010). However this return of humid conditions was short lived with reduction of the wetland miospores in the *fittoni* Zone, where those associated with drier conditions peaked (Fig. 10).

5.3 Climate driver

From the Helmsdale locality alone little can be determined regarding the mechanism driving of this drying and cooling event observed in the Early Tithonian. To date the leading hypothesis for this climate change is the formation of polar ice (Hesselbo et al. 2009) postulated at the Jurassic / Cretaceous boundary (Ditchfield 1997; Price 1999; Pucéat et al. 2003; Price & Mutterlose 2004; Steuber et al. 2005). Given recent clay mineralogy data from Russia indicates a similar climatic trend (Hesselbo et al. 2009); the main driving force for this climatic shift is likely to have been more than a localized tectonic effect. However integration of data from around the globe is required to determine if this climate change trend was local to Europe or a more global effect and only further research of Late Jurassic and Early Cretaceous strata in northerly latitudes will help to resolve this issue.

6. Conclusions

The palynomorph association of the Upper Jurassic Helmsdale Boulder Beds Fm. has been critically assessed in order to determine if a cooling trend observed in the marine environment was reflected in land surface temperature. Samples taken from marine siltstones ranged over 8 Ma from the basal Kimmeridgian to the Late Tithonian. A wide variety of terrestrial palynomorphs have been examined and the population was observed to vary through time.

The botanical affinity of the palynomorphs was assessed to provide indications of the palaeoclimatic setting.

CA ecological analysis yielded six groupings: dry forest, river banks, marsh, fern prairie, emergent swamp and mud flats. These associations were charted through time and a bimodal distribution is observed, with the dry forest ecological grouping dominating in the Tithonian, whilst the other ecological groups combine to dominate the Kimmeridgian deposits.

Combined with the interpretation of the botanical affinities, the changes in the ecological groupings through time have been interpreted to record changing climate through the Late Jurassic. Initially in the Early Kimmeridgian the vegetation was composed of ferns and fern allies indicating a warm, humid climate. A slight decline in palynomorphs associated with high levels of humidity occurred over the late Kimmeridgian and Early Tithonian, but peaked again in the *scitulus* Zone.

A distinct change is observed during the *wheatleyensis* Zone to gymnosperm dominated assemblages indicative of a dry forest ecosystem and an onset of aridity and a semi-arid climate is interpreted for the remainder of the Tithonian. The dominance of vegetation associated with aridity continued up to a peak in the *pectinatus* Zone, after which as slight return of humid vegetation occurred in the *pallasioides* Zone, however the semi-arid vegetation returns and increased up to a maximum at the end of the succession in the Upper Tithonian. These climatic findings are consistent with climatic data from across the Northern Hemisphere and the fact that the aridity is combined with an apparent cooling of the climate also recognised in the IMF seawater from geochemistry (Nunn & Price 2010) adds weight to the interpretation that the drying is associated with development of polar ice at the Jurassic – Cretaceous boundary.

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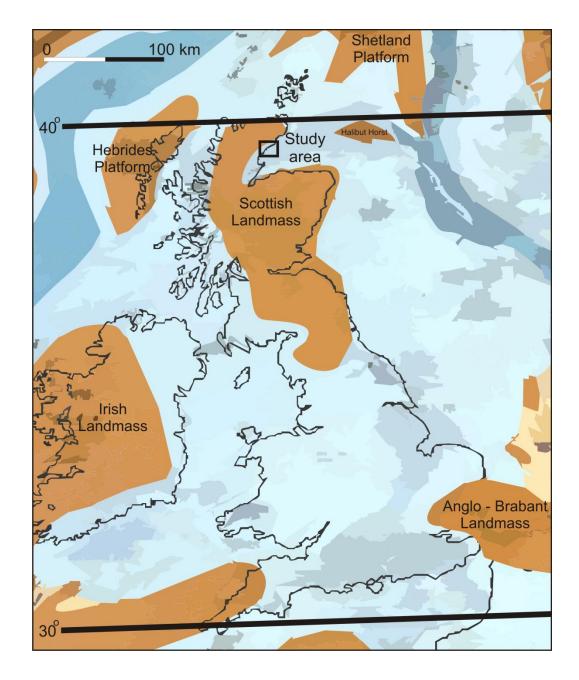


Fig. 1. Palaeogeography of the UK during the *wheatleyensis* Zone of the Early Tithonian after Bradshaw *et al.* (1992), dark shaded areas = land, light = shallow sea and white = deep water.

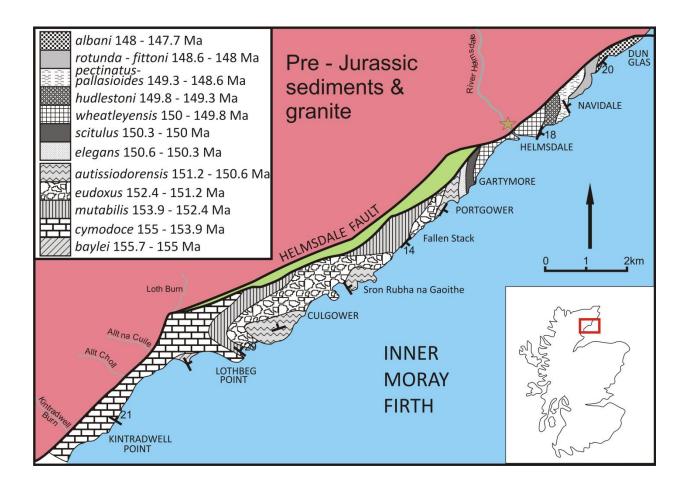
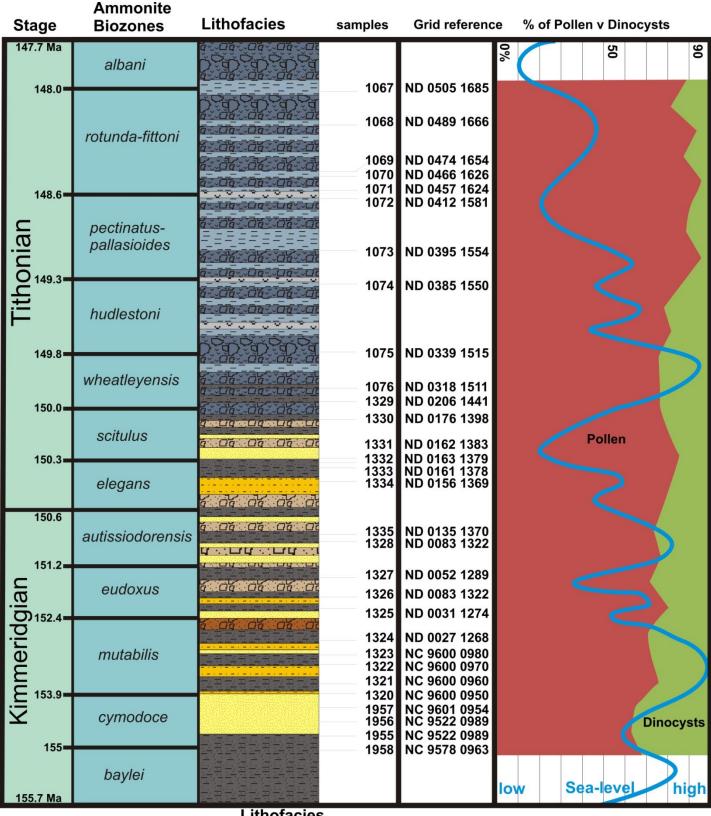
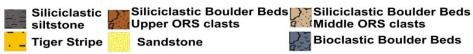


Fig. 2. Study area of the Helmsdale Boulder Beds Fm. With ammonite biozones marked after Barron (1989).



Lithofacies





Relative sea-level curve from Hesselbo 2008

Fig. 3. Kimmeridgian to Tithonian ammonite biozones (Ogg *et al.* 2008) of the sub-boreal region with generalised lithofacies of the Helmsdale Boulder Beds Fm., position of sample collection and percentage of pollen and spores per sample compared to dinoflagellate cysts.

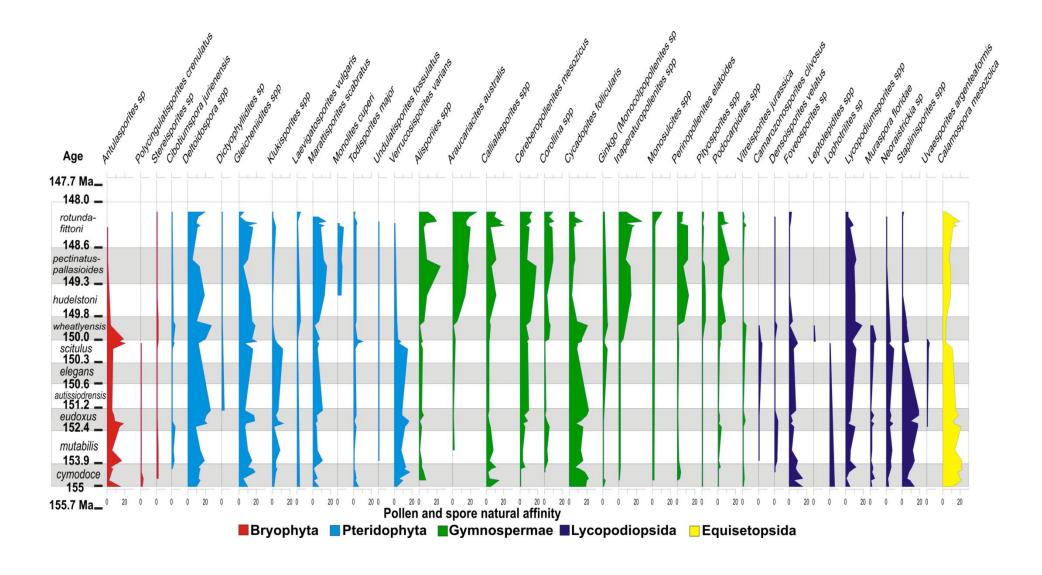


Fig. 4. Range of terrestrial palynomorphs recovered from the Helmsdale Boulder Beds Fm., arranged in stratigraphic order and grouped by botanical affinity.

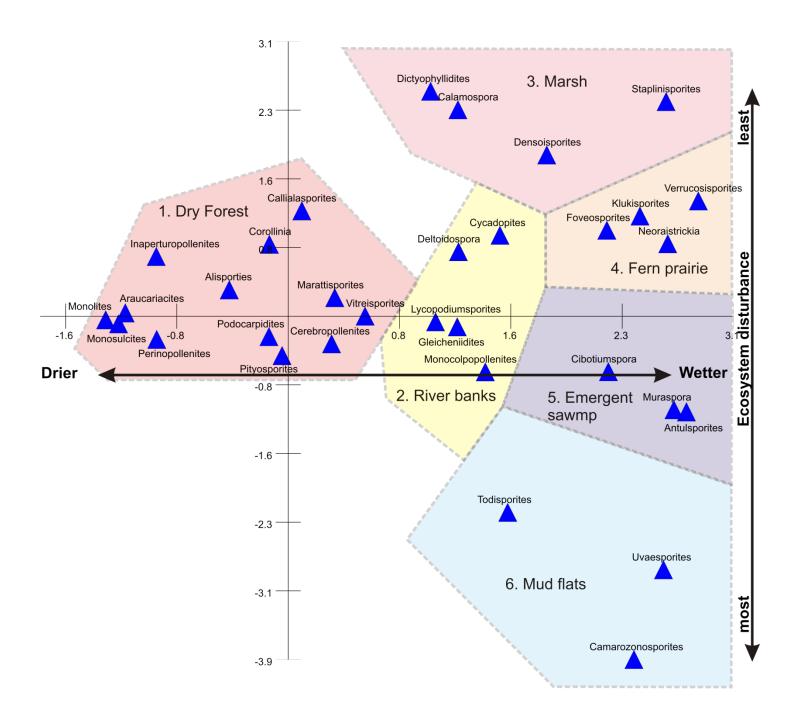
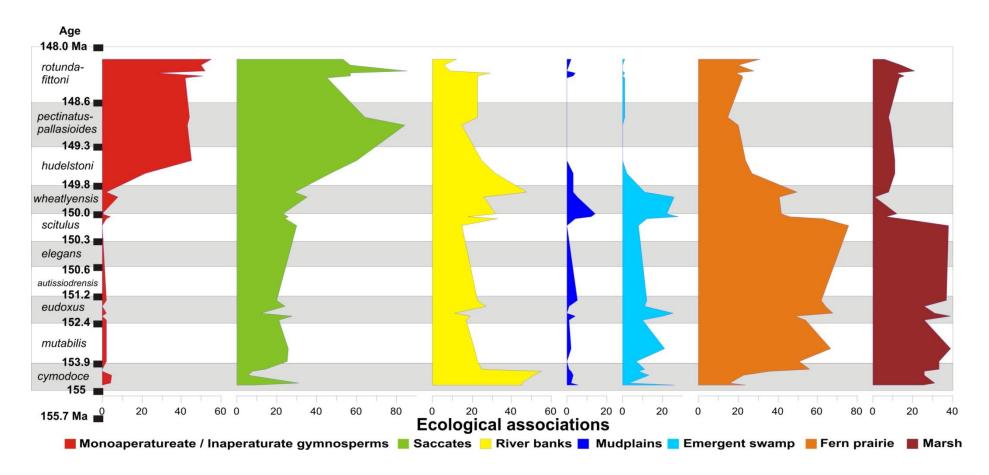


Fig. 5. CA analysis cross plot of the Helmsdale palynoflora dataset.

Fig 6. Abundance of palynomorphs grouped by their ecological association. Note the Dry forest components have been divided to separate saccate pollen taxa, which are often excluded from studies of this kind, from the remainder of the gymnosperm palynofacies.



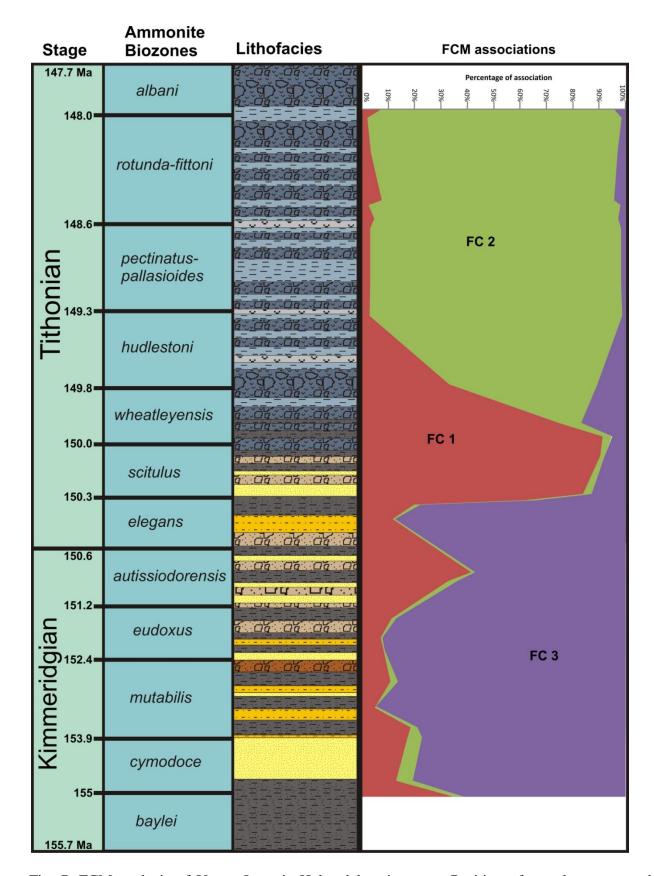


Fig. 7. FCM analysis of Upper Jurassic Helmsdale miospores. Position of sample corresponds to the height below the top of the section, which totals 970 m.

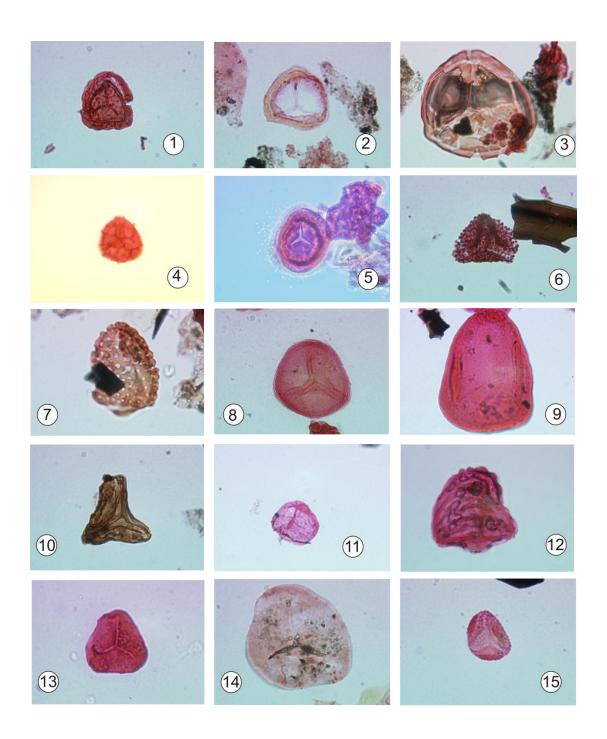


Fig. 8. Constituents of the wet groupings, all specimens at x1000 magnification. 1: *Antulsporites baculatus* 1326, S26-2 2: *Stereisporites antiquasporites* 1332, U29-1. 3: *Polycingulatisporites crenulatus* 1333, U37-2. 4: *Lycopodiumsporites reticulumsporites* 1955, Q33-3. 5: *Staplinisporites caminus* 1069, X51- 2. 6: *Neoraistrickia taylori* 1325, U26-3. 7: *Camarozonosporites clivosus* 1322, U26-3. 8: *Densoisporites velatus* 1328, T39-4. 9:

Deltoidospora sp. 1069, D38-1. 10: Gleicheniidites senonicus 1320, R20-4. 11: Foveosporites labiosus 1069, V32-3. 12: Klukisporites sp. 1074, V38-2. 13: Dictyophyllidites harrisii 1067, X48-1. 14: Todisporites major 1327, V27-1. 15: Verrucosisporites varians 1326, S24-4.

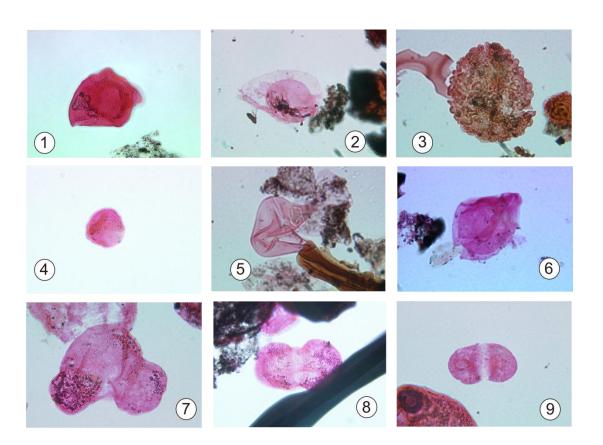


Fig. 9. Constituents of the dry forest grouping, all specimens at x1000 magnification. 1: *Araucariacites australis* 1069, U38-2. 2: *Callialasporites dampieri* 1324, U22-4. 3: *Cerebropollenites mesozoicus* 1324, T26-3. 4: *Corollina cf. chateaunovi* 1069, Q36-2. 5: *Inaperturopollenites hiatus* 1329, W20-4. 6: *Perinopollenites elatoides* 1069, V44-2. 7: *Pityosporites constrictus* 1069, X36-1. 8: *Podocarpidites canadensis* 1069, D37-3. 9: *Vitreisporites jurassicus* 1069, H47-2.

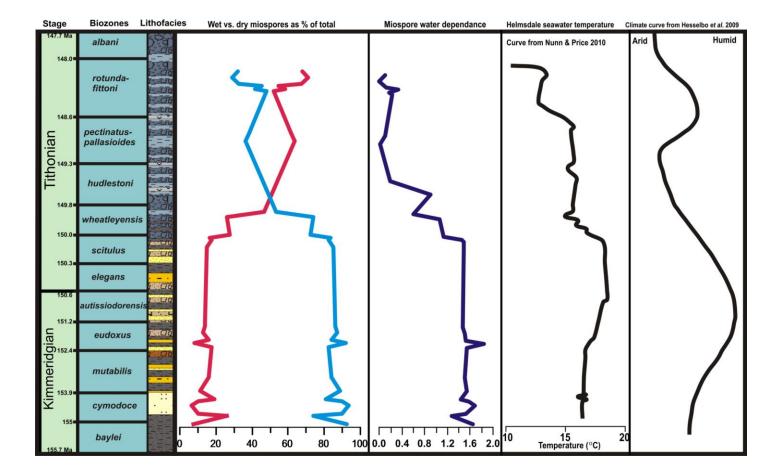


Fig. 10. Curves for the Upper Jurassic of Helmsdale demonstrating the ratio of wet to dry palynomorph types and water dependency compared to climatic curve produced by Hesselbo *et al.* (2009) and IMF seawater temperature curve produced by Nunn & Price (2010).

Miospore	Botanical affinity	Environment	Climatic inference	Authority
Antulsporites spp.	Bryophytes	bogs & marshes	wet	Hubbard & Boulter 1997
Polycingulatisporites spp.	Bryophytes		wet	Schrank 2010
Stereisporites spp.	Bryophytes		wet	Filatoff 1975
Calamospora spp.	Equisetales	riverbanks & marshes	wet & warm	Balme 1995
Monocolpopollenites spp.	Ginkgoale		wet	Royer 2003
Cycadopites follicularis	Cycadale	riverbanks	dry & warm	Filatoff 1975
Monosulcites spp.	Bennettitales		warm	Boulter & Windle 1993
Camarozonosporites spp.	Lycopodiopsida	diverse but wet	wet	Hubbard & Boulter 1997
Densoisporites spp.	Lycopodiopsida, Selaginellales	coastal	wet	Raine <i>et al.</i> 1988
Foveosporites spp.	Lycopodiopsida, Selaginellales	coastal	wet	Balme 1995
Lophotrilites spp.	Lycopodiopsida	diverse but wet	wet	Hubbard & Boulter 1997
Lycopodiumsporites spp.	Lycopodiopsida	diverse but wet	wet	Hubbard & Boulter 1997
Neoraistrickia spp.	Lycopodiopsida	diverse but wet	wet	Hubbard & Boulter 1997
Staplinisporites spp.	Lycopodiopsida	diverse but wet	wet	
Uvaesporites spp.	Lycopodiopsida, Selaginellales	diverse but wet	wet	Balme 1995
Araucariacites spp.	Pinales, Araucariaceae	dry coastal	cool & dry	van Konijnenburgh- van Cittert 1971
Callialasporites spp.	Pinales, Araucariaceae	dry coastal	cool & dry	Boulter & Windle 1993
Inaperturopollenites spp.	Pinales, Araucariaceae	dry coastal	cool & dry	Balme 1995
Corollina spp.	Pinales, Cheirolepidiaceae	dry coastal	warm	Balme 1995
Perinopollenites spp.	Pinales, Cupressaceae	widespread but dry	dry	Gadek et al. 2000
Alisporites spp.	Pinales, Pinaceae	upland forest	cool & dry	Balme 1995
Pityosporites spp.	Pinales, Pinaceae	upland forest	cool & dry	Nichols et al.2006
Podocarpidites spp.	Pinales, Podocarpaceae	upland forest	cool & dry	Hubbard & Boulter 1997
Cerebropollenites spp.	Pinales, Pinaceae	upland forest	cool & dry	Shang & Zavada 2003
Cibotiumspora spp.	Pteridophyta, Pteridaceae	lowland	wet & warm	Wang & Zhang 2010
Dictyophyllidites sp.	Pteridophyta, Dipteridaceae / Matoniaceae	lowland	wet & warm	Balme 1995
Deltoidospora spp.	Pteridophyta, Cyatheaceae	lowland	dry & warm	Abbink 1998
Gleicheniidites spp.	Pteridophyta,	lowland	dry & warm	Potonié 1967
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	Gleicheniaceae			
Klukisporites spp.	Pteridophyta,	lowland	wet & warm	Hubbard & Boulter
	Schizaeaceae			1997
Marattisporites spp.	Pteridophyta,	lowland	wet & warm	Balme 1995
	Marattiaceae			
Murospora florida	Pteridophyta ,	lowland	wet & warm	Hubbard & Boulter
	Dicksoniaceae			1997
Todisporites spp.	Pteridophyta,	lowland	wet & warm	Abbink 1998
	Osmundaceae			
Verrucosisporites spp.	Pteridophyta,	lowland	wet & warm	Balme 1995
	Osmundaceae			
Vitreisporites pallidus	Pteridosperms	mangrove?	dry & warm	van Konijnenburgh-
				van Cittert 1971
Alisporites thomasii	Pteridosperms	mangrove?	dry & warm	Balme 1995

Table 1. Upper Jurassic palynomorphs of the Helmsdale Boulder Beds, their botanical affinity and climatic inference.