

Palynostratigraphy of dinosaur footprint-bearing deposits from the Triassic–Jurassic boundary interval of Sweden

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Abstract: The Triassic–Jurassic boundary (c. 200 Ma) marks one of the five largest Phanerozoic mass extinction events and is characterized by a major turnover in biotas. A palynological study of sedimentary rock slabs bearing dinosaur footprints from Rhaeto–Hettangian strata of Skåne, Sweden was carried out. The theropod dinosaur footprints (*Kayentapus soltykovensis*) derive from the southern part of the abandoned Vallåkra quarry (Höganäs Formation) and were originally dated as earliest Jurassic (Hettangian) based on lithostratigraphy. Our results reveal that two of the footprints are correlative with the latest Triassic (latest Rhaetian) disaster zone typified by a high abundance of the enigmatic gymnosperm pollen *Ricciisporites tuberculatus* and *Perinopollenites elatoides* together with the key taxon *Limbosporites lundbladii* and fern spores. Two footprints are dated to correlate with the Transitional Spore-spike Interval. One footprint is interpreted as Hettangian in age based on the relatively high abundance of *Pinuspollenites* spp. together with the presence of the key taxa *Retitriletes semimuris* and *Zebbrasporites intercriptus*. Our new palynological study suggests that the *Kayentapus* ichnogenus already appeared in the end of Triassic, and our study highlights the use of palynology as a powerful tool to date historical collections of fossils in museums, universities and elsewhere. The Hettangian footprint reflects a marine influence while all other studied ichnofossil specimens occur in non-marine (floodplain and delta interdistributary) sediments. The sediments associated with the Hettangian footprint include a significant proportion of charcoal transported from land after wildfires. The Rhaeto–Hettangian vegetation was otherwise characterized by multi-storey gymnosperm–pteridophyte communities.

Keywords: Triassic–Jurassic; dinosaur footprints; ecological crisis; palynology; Sweden.

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Introduction

The Triassic–Jurassic (Tr–J) boundary, dated by U–Pb at 201.6 ± 0.3 Ma (Schaltegger et al. 2008), is marked by a mass extinction of biota in both marine and terrestrial ecosystems (Raup & Sepkoski 1982; Hallam 2002; Hesselbo et al. 2002, 2007; Andréasson 2006; Ruhl et al. 2009; Akikuni et al. 2010; Deenen et al. 2010; Sha et al. 2011). The causal mechanisms behind this mass extinction remain strongly disputed as its duration, magnitude and geographic signal are not resolved.

Although the signature of extinction in the marine realm is fairly well understood, at least for the northern Hemisphere Tr–J successions (Hesselbo et al. 2002, 2007; Götz et al. 2009; Deenen et al. 2010), the magnitude of the extinction and the pattern of recovery in the continental realm are highly ambiguous (Akikuni et al. 2010; Sha et al. 2011; Pieńkowski et al. 2012). Severe changes in the vegetation record across the Tr–J boundary have been documented from several parts of the northern Hemisphere, i.e. North America and Greenland (Fowell & Olsen 1993; Olsen et al. 2002; McElwain et al. 2009; Larsson

2009; van de Schootbrugge et al. 2009; Steinthorsdottir et al. 2011). In the northern European pollen and spore record, this is expressed as a pronounced increase in relative abundance, the so-called spike, of the enigmatic gymnosperm pollen *Ricciisporites tuberculatus* in uppermost Triassic strata, making this pollen a species of key stratigraphic importance (Pedersen & Lund 1980; Mander et al. 2013). The species ranges from the Norian to the Sinemurian but has a pronounced acme in the Rhaetian in NW Europe (Pedersen & Lund 1980; see also Pieńkowski et al. 2012). The botanical affinity of this pollen is not known as it has not been recovered from fossilized reproductive structures (Mander et al. 2012).

The *Ricciisporites* spike is followed by a fern spore-spike across the boundary interval (Bonis et al. 2009; Götz et al. 2009; Larsson et al. 2009) that has been defined as the Transitional Spore-spike Interval (TSI) based on assemblages from southern Sweden (Larsson 2009) and was recently identified in the latest Rhaetian of Poland (Pieńkowski et al. 2012). The spore-spike is

generally followed by a *Classopollis* (Cheirolepidiaceae)-dominated flora marking the beginning of the Jurassic, as is the case in Clarence-Moreton and Surat basins of Australia (Jansson et al. 2008a,b; Turner et al. 2009), the Newark Basin, USA (Fowell & Olsen 1993) and Scandinavia (Guy-Ohlson 1981; Dybkjær 1991). Kuerschner et al. (2007) suggested that the first appearance of *Cerebropollenites thiergarti* together with a spore-spike marks the Tr–J boundary in Austria.

Rhaetian–earliest Jurassic macrofloras of Skåne have been studied for nearly two centuries and are collectively represented by a broad range of bryophytes, lycophytes, sphenophytes, ferns (especially Matoniaceae, Dipteridaceae, Gleicheniaceae, Dicksoniaceae and Osmundaceae), pteridosperms, Bennettitales, Ginkgoales and conifers (Nathorst 1878, 1879; Halle 1908; Johansson 1922; Lundblad 1949, 1950, 1959a; Pott & McLoughlin 2009, 2011; McLoughlin & Vajda 2013). Harris (1931) noted a significant disjunction in the composition of the floras across the Tr–J boundary in Jameson Land, Greenland, erecting the “*Lepidopteris* flora” and “*Thaumatopteris* flora” for what were essentially macrofloral assemblage zones of the Rhaetian and Hettangian, respectively. Lundblad (1959b) applied these concepts to the Skåne Tr–J floras and noted a similar stratigraphic disjunction, with key taxa of *Lepidopteris*, *Ptilozamites*, *Sphenobaiera*, *Ginkgoites*, *Pterophyllum* and *Anomozamites* restricted to the Rhaetian, and *Thaumatopteris schenkii* restricted to the Jurassic. These floristic differences provide a ready means of differentiating Tr–J continental strata in Skåne and signify a major disruption to plant communities at the close of the Triassic that can be recognized globally (Zhou 1995; Anderson et al. 1999).

Large predators were represented in the Late Triassic of Central Europe, contributing to a rich community that included dicynodonts and small dinosauromorphs (Gorzalak et al. 2010; Niedźwiedzki et al. 2012), but only the tracks remain of these in the Tr–J strata in Sweden (Vajda & Wigforss-Lange 2009). Dinosaur tracks have long been recognized as important sources of palaeontological information in Mesozoic sedimentary deposits globally (e.g. Gierliński & Ahlberg 1994; Meyer et al. 2001; Turner et al. 2009; Niedźwiedzki 2011; Thulborn 2013). The extinction of non-avian dinosaurs at the Cretaceous–Paleogene boundary has been the subject of intense debate (Ocampo et al. 2006; Wigforss-Lange et al. 2007; Schulte et al. 2010a,b), but relatively little attention has been given to the dinosaurian response to environmental changes during the end-Triassic extinction event (Brusatte et al. 2010). Interestingly, Olsen et al. (2002) noted that non-dinosaurian footprint diversity drops at the Tr–J boundary, whereas dinosaurian ichnogenetic diversity increases to a maximum in the overlying Jurassic sediments of the Newark Basin, USA. This coincides with a 20% increase in theropod dinosaur track size and with the first appearance of *Eubrontes giganteus* (Olsen et al. 2002). More recent studies have confirmed that the records of theropod and ornithischian dinosaurs markedly increase over the Tr–J boundary, indicating a radiation rather than major extinction within these groups (Brusatte et al. 2010).

The Department of Geology, Lund University, Sweden, hosts several dinosaur footprints preserved in clastic sedimentary rock slabs collected primarily during coal and clay exploration in the 20th century (Norin 1949; Gierliński & Ahlberg 1994). Previous dating of these ichnofossils was based on lithostratigraphical data only; thus, the detailed stratigraphical positions of these ichnofossils are in many cases uncertain. Palynology

is a powerful tool for palaeoenvironmental analysis in Mesozoic deposits when applied as changes in relative abundance of different pollen and spore taxa coupled with the presence of key species (Vajda & Wigforss-Lange 2006; Mehlqvist et al. 2009). Palynology is further useful when dating transported, fossil-bearing concretions and museum specimens of unknown age or provenance (Vajda & Raine 2010). We use this technique to date the collection of dinosaurian footprints and to reconstruct the vegetation and palaeoenvironment in which these animals lived about 200 million years ago.

Geological setting and stratigraphy

The Late Triassic–Early Jurassic sedimentary successions in southern Sweden (Skåne) were deposited in areas separated by structural highs, each area reflecting its own depositional and tectonic conditions. These Mesozoic sediments rest disconformably mainly on Palaeozoic strata. In general, tectonic movements along the Fennoscandian Border Zone (Fig. 1) influenced deposition and erosion, leaving unique sedimentary successions and hiatuses in different tectonic blocks (see review by Ahlberg et al. 2003a). Tr–J sediments are extensively distributed in the subsurface of the marginal parts of the Danish Basin (south-western parts of Skåne; Larsson et al. 2000; Vajda 2001, 2008; Fig. 1), whereas outcrops occur mainly in the northwestern and central parts of Skåne. The Norian part of the succession is characterized by barren semi-arid continental redbeds. The onset of regional maritime humidity in the Rhaetian led to deep basement weathering and the development of extensive peat-forming mires in fluvio-deltaic and marginal marine settings. The thick accumulations of Rhaetian siliciclastic strata are rich in plant and animal body and trace fossils (Ahlberg et al. 2002, 2003b).

Exposures of strata spanning the Tr–J boundary are located mainly in the north-western Skåne and, in the central parts, along the north-eastern fault zone of the Vomb Trough (Norling 1990; Norling et al. 1993). Palynostratigraphy is the main tool applied for the dating and correlation of these strata. The Tr–J boundary beds, of interest here, form part of the Höganäs Formation and are relatively well documented (e.g. Hermelin 1773; Troedsson 1943, 1951; Sivhed 1984; Pieńkowski 1991a,b; Ahlberg et al. 2003a,b; Lindström & Erlström 2006; Larsson 2009; Vajda & Wigforss-Lange 2009). The Höganäs Formation comprises mainly alluvial and deltaic sediments and is approximately 250 m thick. It is subdivided into the Vallåkra, Bjuv and Helsingborg Members (Ahlberg et al. 2003a; Fig. 2). The basal Vallåkra Member consists mainly of mudstones and siltstones, reaching a maximum thickness of 30 m. The overlying heterolithic Bjuv Member incorporates coal seams, palaeosols and crevasse splay sands representing mostly low-energy floodplain deposits. The two major coals are regionally important markers and are designated the B (lower) and A (upper) seams: the upper surface of the latter has been proposed to mark the Tr–J boundary (Sivhed 1984; Ahlberg et al. 2003b). The uppermost member, the Helsingborg Member, forms the bulk of the Höganäs Formation and constitutes basal Jurassic heterolites, arenites and mudstones with thin coal seams (Ahlberg et al. 2003a). These strata reflect a marginal marine setting and signal the onset of an extended transgression across the Höganäs Basin.

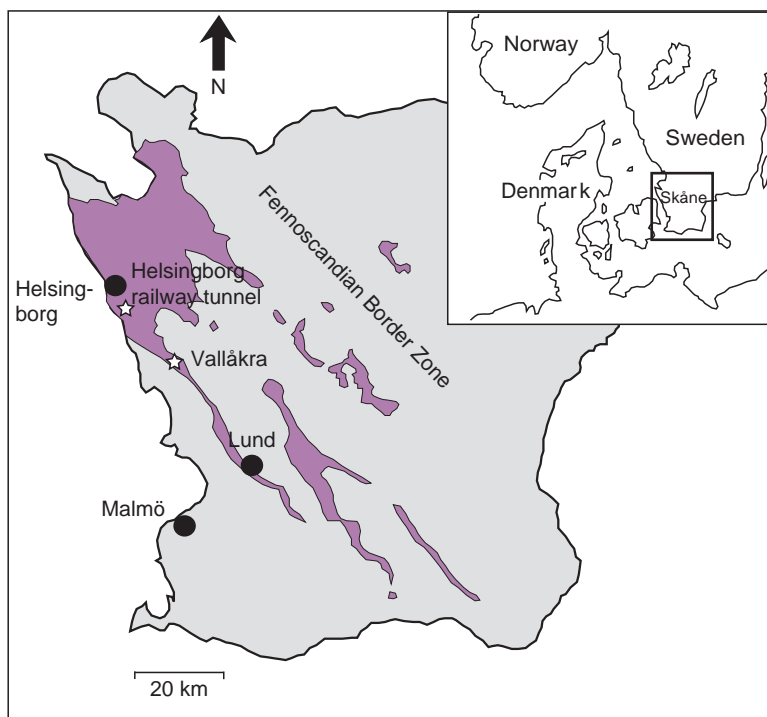


Fig. 1. Geological map of the study area with Sweden inset. Fossil dinosaur track localities marked with star.

Occurrence of dinosaur footprints in Skåne

Findings of dinosaur footprints in Sweden are rare and restricted to the Höganäs Formation from which four track sites have been described (Gierliński & Ahlberg 1994). The first footprints were discovered in the early 1950s as the regionally important B-coal seam in the Bjuv Member was excavated in the now inaccessible Gustaf Adolf mine at Höganäs and in the Haberga mine at Billesholm (Böläu 1952; Fig. 1). The numerous tracks, no less than 170 in 45 m² at one place, were discovered in the roof of the mines as the coal was quarried. Individual tracks measured up to 38 cm in length and were designated simply as theropod tracks (Böläu 1952). A few of the specimens from the Gustaf Adolf mine were subsequently identified as *Eubrontes* sp. by Haubold (1986) and as *Grallator* (*Eubrontes*) sp. (most specimens) or *Grallator* (*Eubrontes*) cf. *giganteus* (single well-preserved footprint) by Gierliński & Ahlberg (1994).

The next important finding of dinosaur footprints dates to the mid-1970s, this time in the southern quarry at Vallåkra (“Vallåkra Södra”; Figs. 3 and 4). The strata at this locality were assigned to the early Hettangian Boserup Beds by Sivhed (1984), although its heterolithic facies differ from exposed facies of the fluvial Boserup Beds (Ahlberg et al. 2003a). The ichnofossils at Vallåkra were discovered by members of the Geological Survey of Sweden and named as “Theropodian footprints” by Pleijel (1975). The footprints range in length from 15 to 35 cm and were found in several beds in the lowermost metre of a 6.4-m thick succession of wavy and lenticularly bedded heteroliths (starved mud-draped sandy ripples) with abundant rootlets and desiccation mud cracks, interpreted as formed in marginal marine, brackish or even freshwater (lake) environments. There is a size variation within the footprint assemblage at Vallåkra that has been interpreted reflecting ontogenetic stages (a pack or herd) (Gierliński &

System	Stage	Formation	Member	Miospore Zone
Jurassic	Toarcian	Rya Formation	Rydebäck Member (70)	<i>Spheripollenites-Leptolepidites</i>
	Pliensbachian		Katslösa Member (40)	<i>Chasmatosporites</i>
	Sinemurian		Pankarp Member (70)	<i>C. macroverrucosus</i>
			Döshult Member (80)	
201.6	Hettangian	Höganäs Formation	Helsingborg Mb	<i>Pinuspollenites-Trachysporites</i>
Triassic	Rhaetian		Bjuv Member	Transitional Spore-spike Interval
			Vallåkra Member	<i>Corollina - Ricciisporites</i>
	Norian	Kågeröd Formation		Undefined

Fig. 2. Stratigraphic column of the Tr–J units of Skåne correlated with local pollen zones (from Koppelhus & Nielsen 1994; Larsson 2009).



Fig. 3. The southern wall of the Vallåkra “Södra” quarry south-east of Helsingborg, showing mudstone with thin sand partings (heterolithic facies). This locality is the origin for several dinosaur footprints (G) that in this study are dated as latest Rhaetian–earliest Hettangian.

Ahlberg 1994). All specimens from this locality have subsequently been assigned to one single ichnotaxon, namely *Grallator* (*Eubrontes*) *soltykovensis* = *Kayentapus soltykovensis* (Gierliński & Ahlberg 1994; see Gierliński 1996).

The most recent find of dinosaur footprints from the Höganäs Formation derives from the early Hettangian strata that were excavated during the construction of the Helsingborg railway tunnel in the late 1980s. The two specimens described there were both assigned to *Grallator* (*Eubrontes*) sp. but could not be collected due to construction safety (Ahlberg & Siverson 1991).

Olsen (1980) argued that most of the Triassic and Lower Jurassic theropod track morphologies represent members of a *Grallator*–*Anchisauripus*–*Eubrontes* plexus, and that ichnologists could use the double-barreled “ichnogenus” labels *Grallator* (*Grallator*), *Grallator* (*Anchisauripus*) and *Grallator* (*Eubrontes*). This ichnosystematic scheme has been accepted by some authors (e.g. Gierliński 1991; Gierliński & Ahlberg 1994). Finally, Olsen et al. (1998) subsequently abandoned this nomenclature when re-describing the type material of the three theropod dinosaur ichnogenera *Grallator*, *Anchisauripus* and *Eubrontes* as distinct morphotypes. In the Lower Jurassic deposits, the *Kayentapus* ichnogenus has been identified also in numerous sites in North America and Europe, and has quite consistently been regarded as a distinct ichnogenus (Lockley et al. 2011). Although some dinosaur ichnologists have suggested that *Kayentapus* might be a synonym of *Eubrontes* (see Rainforth 2005; Lucas et al. 2006). *Kayentapus* is the

ichnogenus name applied to relatively large (pes length ~25–35 cm) tridactyl tracks of a bipedal theropod dinosaur, originally described by Samuel Welles, in 1971, based on a short trackway from the Lower Jurassic Kayenta Formation of Arizona.

Materials and methods

Five dinosaur ichnofossils from the collection of the Department of Geology in Lund were selected for palynological analysis. Small chips of rock were carefully removed from the specimens without damaging the footprints. The samples were processed according to standard palynological procedures at Global Geolab Limited, Canada. About 30 g of sediment was first treated with dilute hydrochloric acid to remove calcium carbonate, and further macerated in 45% hydrofluoric acid. The organic residue was sieved using a 10- μ m mesh and mounted in epoxy resin on two microscopic slides. Three hundred pollen and spores were identified per sample and the percentage of each palynomorph taxa was calculated (Appendix A). Palynofacies analysis involved counting the relative abundance of organic particles based on 500 counts per slide. Classification of palynological matter was based on the scheme developed by Batten (1996). The following palynofacies groupings were distinguished: (I) palynomorphs (pollen, spores, acritarchs), (II) wood, (III) charcoal, (IV) plant cuticle and (V) amorphous organic matter (AOM; Fig. 5). The slides and residues are deposited at the Department of Geology at Lund University and illustrated specimens are identified by LO numbers.

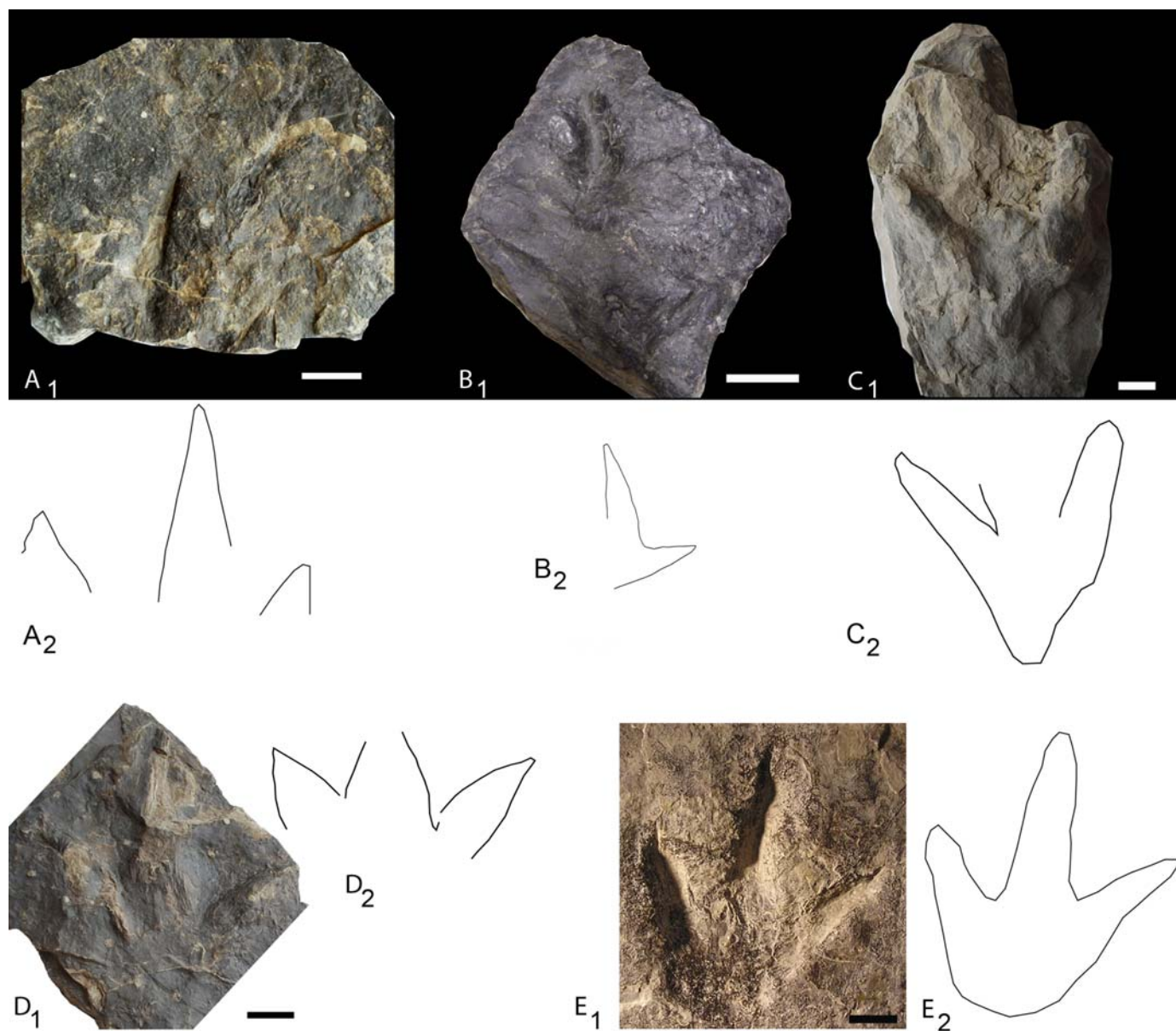


Fig. 4. The five-sampled Tridactyl tracks (pes prints) of *G. (E.) soltykovensis* Gierliński 1991 (= *K. soltykovensis*) (Rhaetian–Hettangian), Sweden. **A.** Hettangian (LO11768t), **B.** Rhaetian (LO11769t), **C.** Rhaetian (11770t), **D.** Transitional Tr–J boundary (LO11771t), **E.** Transitional Tr–J boundary (LO5463t). Specimens are deposited in the Department of Geology at Lund University. Photographs (A1–E1) and drawings (A2–E2). Scale bars 5 cm.

Results

Sample 1 (LO11768t)

Ichnofossil *G. (E.) soltykovensis* (= *K. soltykovensis*) belonging to a theropod dinosaur set in a light grey siltstone with dark carbonaceous lamina. The footprint was collected from the abandoned Vallåkra quarry (Höganäs Formation). The ichnofossil is preserved as a negative imprint, an epichnia observable as a concave feature on the uppermost bedding plane of the siltstone block. The palynological assemblage recovered from the sediments hosting the ichnofossil is dated to earliest Jurassic (Hettangian).

Palynofacies. – The microscopic organic matter is in this sample dominated by wood remains (51%) and charcoaled matter

(26%). Pollen and spores together attain a relative abundance of 20% (Fig. 5A; Table 1).

Palynology. – Within the palynological assemblage of Sample 1, 25 species of pollen and spores were identified (Appendix A). The spores attain 51% of the assemblage and gymnosperm pollen grains attain 47.5%. In addition, two marine acritarch species were identified, making up 2% of this otherwise terrestrial assemblage. The spores are dominated by fern spores which in turn are strongly dominated by the trilete spore *Cyathidites minor* (36%), followed by the spores produced by the ground fern *Gleicheniidites senonicus*. Lycophyte spores reach a relative abundance of 5%, whereas bryophytes spores represent 2%. The gymnosperms are dominated by the enigmatic gymnosperm pollen *Ricciisporites* with unresolved affinity. Other important

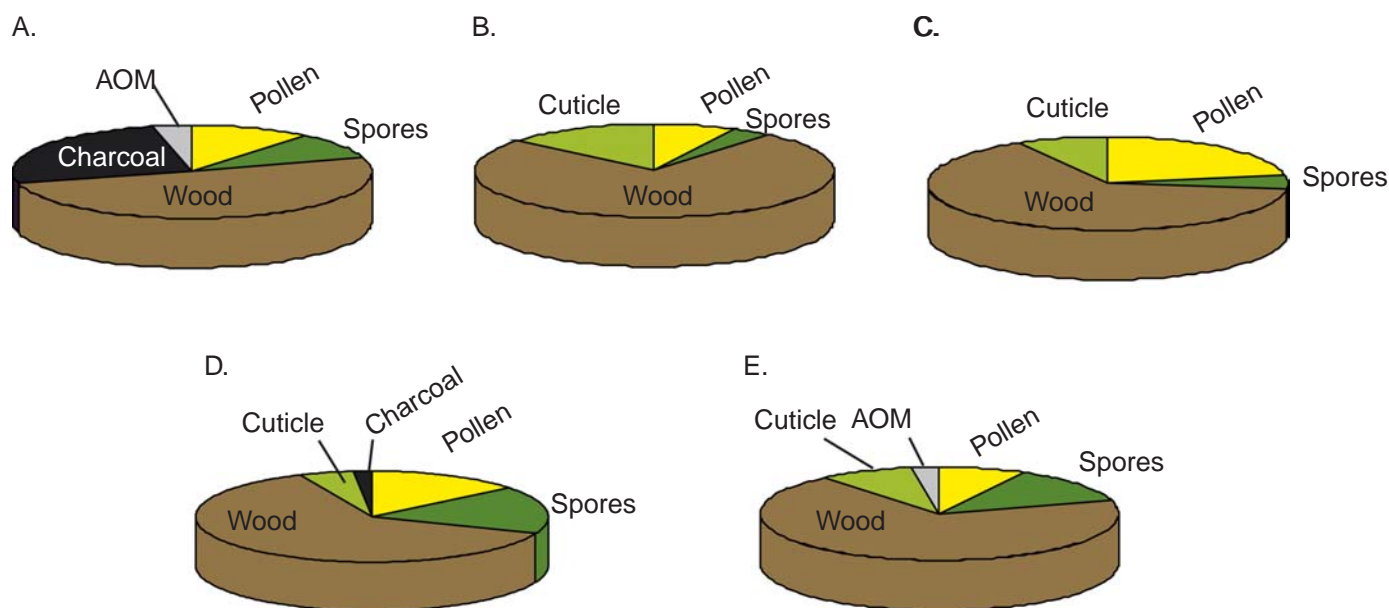


Fig. 5. Graphical representation of the percentages for each palynofacies category for the different samples. **A.** Footprint 1 (LO11768t), Early Jurassic, Hettangian. **B.** Footprint 2 (LO11769t), latest Triassic Rhaetian. **C.** Footprint 3 (LO 11770t), latest Triassic Rhaetian. **D.** Footprint 4 (LO11771t), transitional Tr–J boundary interval. **E.** Footprint 5 (LO5463t), transitional Tr–J boundary interval.

gymnosperms include *Pinuspollenites* (10%), *Perinopollenites elatoides*, *Alisporites*, *Classopollis* and *Quadraeculina anellaeformis* (Figs. 6 and 7).

Age. – Important key species occurring in low numbers include *Acanthotriletes varius*, *Striatella seebergensis*, *Retitriletes semimuris*, *Zebrasporites intercriptus* and *Cibotiumspora juriensis*, and for the dating, most importantly, *Pinuspollenites* makes up 10% of the palynoflora. Based on these characteristics, the age of this footprint is interpreted as earliest Jurassic, Hettangian.

Sample 2 (LO11769t)

Ichnofossil *G. (E.) soltykovensis* (= *K. soltykovensis*) belonging to a theropod dinosaur occurring in a carbonaceous mudstone. The footprint was collected from Vallåkra abandoned quarry (Fig. 3) from the Höganäs Formation. Based on the palynological results of this study, these sediments are dated as late Rhaetian.

Palynofacies. – The organic matter in Sample 2 is dominated by wood particles which, together with cuticle remains, represent 89% of the organic particles; pollen and spores together comprise the remaining 11% (Fig. 5B; Table 1).

Palynology. – The species diversity is relatively poor and only 12 miospore species were identified in Sample 2 (Appendix A).

The assemblage is entirely terrestrial with no marine palynomorphs identified. Spores comprise 35% of the assemblage and gymnosperm pollen grains comprise 65%. The gymnosperm pollen grains are dominated by *P. elatoides* (35%) followed by *Ricciisporites* (19%). Other important gymnosperm pollen includes *Classopollis* and *Podocarpidites* (Fig. 6; Appendix A). The spores are dominated by ferns (19%), lycophytes (14%) and bryophytes (2%; Appendix A).

Age. – A late Rhaetian age is inferred for this sample based on the relative abundance data showing high portions of *R. tuberculatus* and *P. elatoides*, together with the presence of the typical Rhaetian key species *Limbosporites lundbladii*.

Sample 3 (11770t)

Ichnofossil *G. (E.) soltykovensis* (= *K. soltykovensis*) belonging to a theropod dinosaur preserved as a positive-relief hypichnia, observable as a convex feature on the uppermost bedding plane of the light siltstone block. Collected at Vallåkra, southern side of the quarry, Höganäs Formation. Dated to Rhaetian based on the palynological results of this study.

Palynofacies. – The organic residue in Sample 3 is dominated by wood particles (65%) and cuticles (8%). Pollen and spores reach 26% together (Fig. 5C; Table 1).

Table 1. Percentages of the each palynofacies category representing the different ichnofossil Samples 1–5.

Ichnofossil Age	1 (LO11768t) Hettangian	2 (LO11769t) Rhaetian	3 (LO11770t) Rhaetian	4 (LO11771t) Transitional	5 (LO5463t) Transitional
Palynofacies category (%)					
Pollen	11	7	22	14	8
Spores	9	4	4	17	13
Wood	51	75	65	62	68
Cuticles	0	14	8	5	9
Charcoal	26	0	0	2	0
AOM	4	0	0	0	3

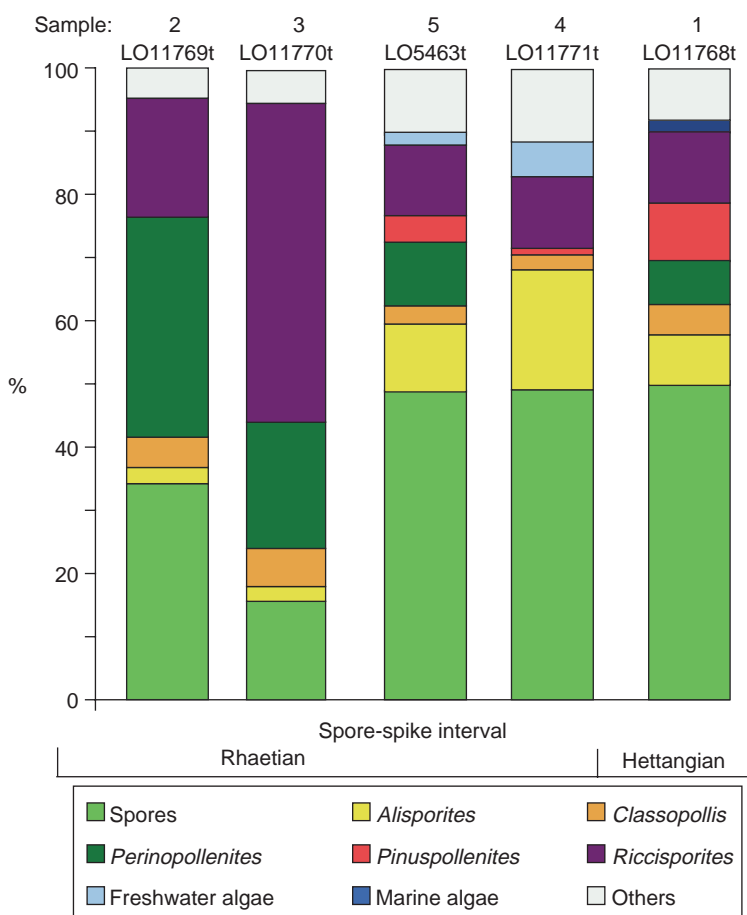


Fig. 6. Relative abundance (%) of spores, freshwater taxa, marine taxa and selected pollen taxa in palynological assemblages from sedimentary rocks hosting *G. (E.) soltykovensis* (= *K. soltykovensis* sensu Gierlinski 1996) tracks in Skåne. The samples are arranged stratigraphically.

Palynology. – Fourteen taxa were identified in Sample 3 (Appendix A). Gymnosperm pollen grains overwhelmingly dominate (84% of total relative abundance) mainly due to the very high counts of *Riccisporites* spp. (51%) and *P. elatoides* (20%).

Age. – The sample was dated to Rhaetian based on the anomalously high proportions of *Riccisporites* and *Perinopollenites*, together with the presence of the typical Rhaetian key species *L. lundbladii* (Fig. 7).

Sample 4 (LO11771t)

Ichnofossil *G. (E.) soltykovensis* belonging to a theropod dinosaur, set in heterolithic siltstone. The footprint is preserved as a positive-relief hypichnia on the uppermost bedding plane of the siltstone block. Dated to latest Rhaetian based on palynology in this study.

Palynofacies. – Despite the fact that the organic residue in Sample 4 is dominated by wood particles (62%), pollen and spores collectively make up a relatively high proportion of the sample (31%). Charcoal particles were also detected in this sample (2%; Fig. 5D).

Palynology. – Nineteen palynomorph taxa were identified in Sample 4, all of them are non-marine (Appendix A). Spores dominate, with a relative abundance of 53%, and the main portion is made up by the fern-spore genus *Cyathidites* (30%).

Gymnosperm pollen grains constitute 41%, dominated by taxa belonging to *Alisporites* (20%) followed by *Riccisporites* (13%). This sample also contains freshwater algae including *Botryococcus braunii* (6%).

Age. – The dating of this sample was somewhat difficult. It differs from the other samples in lacking the gymnosperm pollen *P. elatoides* and also in having a number of freshwater algae. Definite marker species are lacking. *Riccisporites* attains 11% and spores reach a high relative abundance of 53%. Based on the palynological assemblage, this sample is tentatively dated as latest Rhaetian – earliest Hettangian correlative with the “Topmost upper Rhaetian” of Lund (1977). This interval is also described in Larsson (2009) from Laröd and Vallåkra in Skåne, and part of the TSI of Larsson (2009).

Sample 5 (LO5463t)

Ichnofossil *G. (E.) soltykovensis* (Fig. 4) belonging to a theropod dinosaur set in a flaser-bedded siltstone with dark carbonaceous lamina from the Vallåkra quarry (Fig. 3). This ichnofossil was originally described by Gierliński & Ahlberg (1994) and dated to latest Rhaetian to earliest Hettangian and part of the TSI of Larsson (2009).

Palynofacies. – The microscopic organic matter in this sample is dominated by wood remains (68%) followed by miospores (21%; Fig. 5E, Table 1). AOM is present (3%) but no marine components were identified.

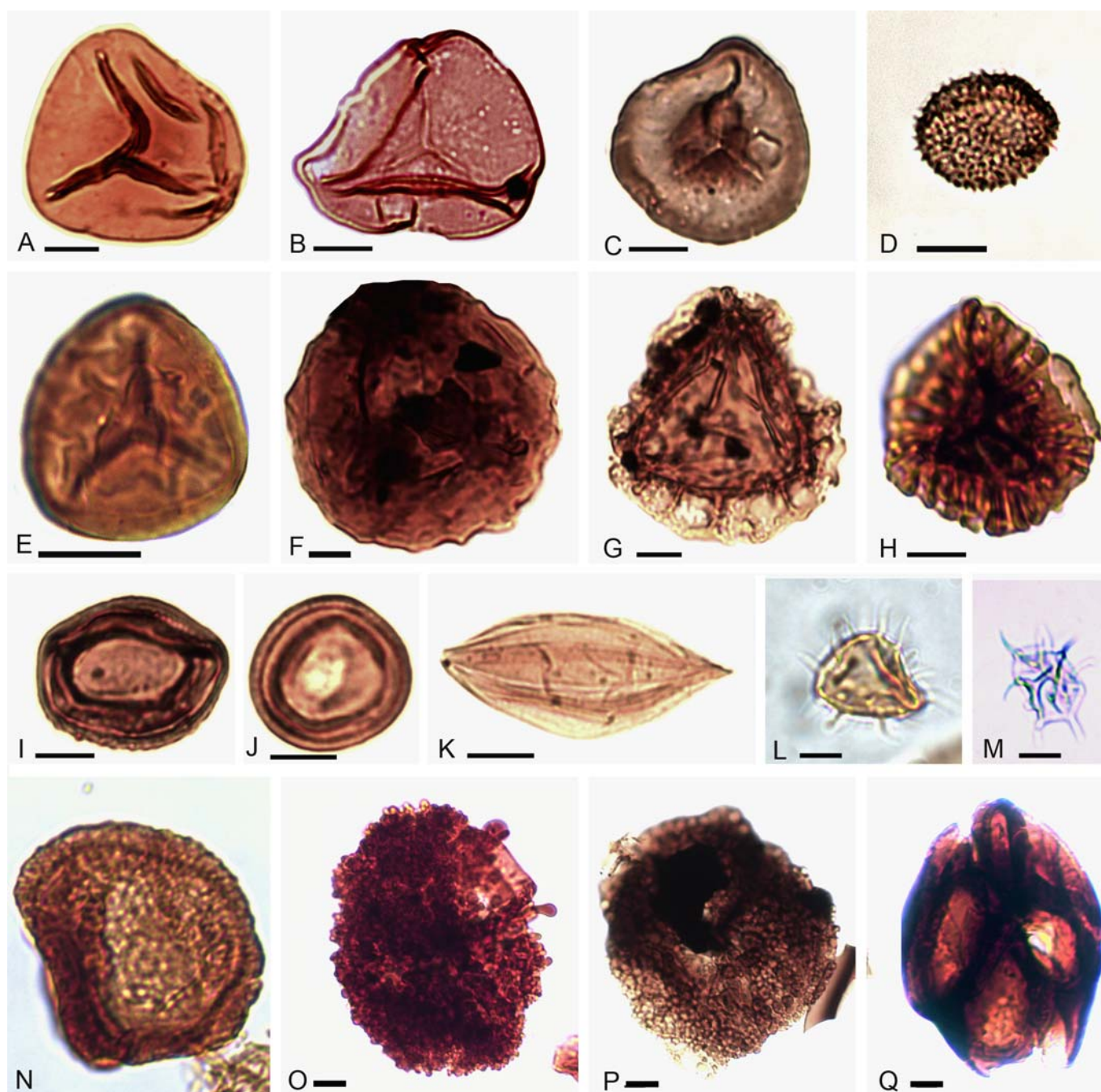


Fig. 7. Light micrographs of representative pollen and spores from the investigated samples, scale bars = 10 μ m. Taxa, sample number and England Finder Reference (EFR) and LO numbers A. *C. minor*, 1, EFR: P26-2 (LO11710t); B. *C. minor*, 5, EFR-L28 (LO11711t); C. *Annulispora folliculosa*, 1, EFR: N36-2 (LO11712t); D. *Echinosporis*, 2, EFR: U35-2 (LO11713t); E. *Z. intercriptus*, 1, EFR: R22 (LO11714t); F. *Camarozonosporites rudis*, 3, EFR: N28-1 (LO11715t); G. *L. lundbladii*, 1, EFR: J26-1 (LO11716t); H. *Limbosporites* sp. 3, EFR: M27 (LO11717t); I. *Classopollis* spp., 2, EFR: H20-3 (LO11718t); J. *Classopollis* spp., 2, EFR: H31-1 (LO11719t); K. *P. elatoides*, 2, EFR: P31 (LO11720t); L. *Michrystidium* sp., 1, EFR: N35-3 (LO11721t); M. *Michrystidium* sp. 1, EFR: M33-2, (LO11722t); N. *Q. anellaeformis*, 3, EFR: N31-3 (LO11723t); O–P. *R. tuberculatus*, 3, EFR: U46-4 (LO11724t); Q. *Ricciisporites* sp. 1, 3, EFR: L30 (LO11725t).

Palynology. – In this palynological assemblage, 17 species of pollen and spores and one freshwater alga were identified (Appendix A). Spores represent 48% of the assemblage, whereas gymnosperm pollen grains comprise 50% (Appendix A). This assemblage is non-marine. The spores are dominated by fern spores which in turn are strongly dominated by the spore genera *Cyathidites* (27%) and *Deltoidospora* (10%). Lycophyte spores

reach a relative abundance of 2% and bryophytes spores reach 3%. The gymnosperms are dominated by *Ricciisporites* together with *Alisporites* and *P. elatoides* (Figs. 6 and 7; Appendix A).

Age. – Important key species include *L. lundbladii* and, based on the abundance of *Ricciisporites*, *P. elatoides* and *Pinuspollenites minimus*, Sample 5 is interpreted to be spanning the Tr–J

boundary. The palynological composition of this transitional zone agrees very well with the TSI of Larsson (2009).

Discussion and conclusions

Five theropod dinosaur ichnofossils attributed to *G. (E.) soltykovensis* (= *K. soltykovensis*) by Gierliński & Ahlberg (1994) were investigated by sampling the host sediments for palynological assemblages.

The ichnofossils were all dated to an interval spanning the Tr–J boundary (Table 1, Fig. 6). Of these, two were attributed to the late Rhaetian, and two to the Tr–J boundary interval, the so-called TSI of Larsson (2009; Fig. 6). Specimen (LO11768t) was dated as earliest Hettangian based on the presence of key Jurassic spore–pollen taxa and high portions of *P. minimus* in the host sediments. The extremely high relative abundance of the pollen *R. tuberculatus* in Sample 3 (LO11770t) may partly reflect taphonomic sorting as this footprint is a hypichnia, a sediment sheet infilling the trace. These sediments were possibly deposited under higher energy environments during more rapid sedimentation than the finer grained sediments constituting the other specimens. Under these circumstances, more buoyant pollen, such as *R. tuberculatus*, may have been transported longer distances and winnowed into greater concentrations.

Our new biostratigraphical data thus resolve the age of these sediments previously dated to the earliest Jurassic based on lithostratigraphy, and show that the heterolithic mudstone in the southern wall of the Vallåkra quarry is positioned stratigraphically below the Boserup beds. Since first described by Welles (1971), *Kayentapus (Grallator (Eubrontes) sp. sensu Gierliński 1991; see Gierliński 1996)* has become one of the most widely recognized Early Jurassic theropod track ichnogenera. According to new palynological studies present in this paper, it may occur also in the uppermost Triassic deposits.

The palynofacies analysis reveals an organic content dominated by phytoclasts (wood remains and plant cuticles; Fig. 5). The sediment bearing the basal Jurassic ichnofossil shows evidence of marine elements and a high proportion of AOM (Fig. 5A) that attests to deposition within a paralic, probably tidal, environment. These sediments further include significant proportions of charcoal particles transported from hinterland areas.

On the basis of this palynological study, we conclude that the vegetation was primarily composed of a range of ground ferns with a canopy of Cupressaceae (cypress), seed ferns and minor portions of Podocarpaceae, Araucariaceae and, in the younger sediments, also Pinaceae. The conifer producing the “disaster taxon” *R. tuberculatus* was abundant in the late Rhaetian ecosystem signalling abnormal environmental conditions. The volcanic activity in the Central Atlantic Magmatic Province (CAMP) has been proposed as one of the major causes behind the Tr–J extinction (e.g. Wignall 2001; Marzoli et al. 2004; Hesselbo et al. 2007; Schaltegger et al. 2008; van de Schootbrugge et al. 2009) with rapid global warming (Wignall 2005) and increased fire activity (Belcher et al. 2010). The CAMP flood basalts were most probably the main factor influencing the European floras, providing conditions that in some way were advantageous for the plants producing *Ricciisporites*. However, as its systematic affinities are as yet unresolved, we can only speculate which specific factors connected to CAMP that made it possible for the “*Ricciisporites* plants” to proliferate and the species warrants further study.

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Appendix A: Quantitative palynological data.

Dinosaur footprint	1 (LO11768t)	2 (LO11769t)	3 (LO11770t)	4 (LO11771t)	5 (LO5463t)
Number of taxa	25	12	14	19	18
Filicophyta (ferns)					
<i>Acanthotriletes varius</i>	1		1		
<i>Baculatisporites comamensis</i>	1		2		2
<i>Cibotiumspora juriensis</i>	1				
<i>Cyathidites australis</i>		7		2	6
<i>Cyathidites minor</i>	36	5	6	28	21
<i>Deltoidospora</i> sp.				14	10
<i>Gleicheniidites senonicus</i>	4	5			5
<i>Peromonolites densus</i>		2	1		
<i>Sriatella seebergensis</i>	1			1	
<i>Todisporites major</i>	1				
<i>Todisporites minor</i>	1				
Total ferns (%)	44	19	11	45	44
Lycophyta (club mosses)					
<i>Camarozonosporites rudis</i>			1	1	0.5
<i>Klukisporites neovariegatus</i>	1				
<i>Limbosporites lundbladi</i>		12	2		0.5
<i>Lycopodiumsporites</i> sp.	1				1
<i>Lycopodiumsporites clavatooides</i>				1	
<i>Retitriteles austroclavatidites</i>	1	2			
<i>Retitriteles semimuris</i>	1				
<i>Zebbrasporites intercriptus</i>	1			1	
Total club mosses (%)	5	14	4	3	2
Bryophyta (mosses)					
<i>Annulispora folliculosa</i>	1				1
<i>Cingutriteles clavus</i>	1			1	
<i>Densoisporites psilatus</i>		2			
<i>Stereisporites antiquasporis</i>	1		2	4	2
Total mosses (%)	2	2	2	5	3
Total spores (%)	51	35	16	53	49
Gymnosperma					
<i>Alisporites parvus</i>	8	2	2	20	11
<i>Araucariacites australis</i>	2			1	6
<i>Classopollis</i> spp.	5	5	6	2	3
<i>Cycadopites</i> sp.			1		
<i>Perinopollenites elatoides</i>	7	35	20		10
<i>Pinuspollenites</i> sp.	10			1	4
<i>Podocarpidites</i> sp.	1	5	1	1	3
<i>Quadraeculina annelaeformis</i>	5		2	2	
<i>Ricciisporites</i> spp.	11	19	51	13	13
<i>Vitreisporites bjuvensis</i>				1	
Total pollen (%)	47	65	84	41	50
Others					
<i>Michrystidium</i> spp.	2				
Freshwater algae				4	1
<i>Botryococcus braunii</i>				2	
Total marine/freshwater taxa (%)	2			6	1
All palynomorphs	100	100	100	100	100

Note: Numbers represent the relative abundance in percentages for each taxon.