

Plant mobility in the Mesozoic: Disseminule dispersal strategies of Chinese and Australian Middle Jurassic to Early Cretaceous plants

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ABSTRACT

Four upper Middle Jurassic to Lower Cretaceous lacustrine Lagerstätten in China and Australia (the Daohugou, Talbragar, Jehol, and Koonwarra biotas) offer glimpses into the representation of plant disseminule strategies during that phase of Earth history in which flowering plants, birds, mammals, and modern insect faunas began to diversify. No seed or foliage species is shared between the Northern and Southern Hemisphere fossil sites and only a few species are shared between the Jurassic and Cretaceous assemblages in the respective regions. Free-sporing plants, including a broad range of bryophytes, are major components of the studied assemblages and attest to similar moist growth habitats adjacent to all four preservational sites. Both simple unadorned seeds and winged seeds constitute significant proportions of the disseminule diversity in each assemblage. Anemochory, evidenced by the development of seed wings or a pappus, remained a key seed dispersal strategy through the studied interval. Despite the rise of feathered birds and fur-covered mammals, evidence for epizoochory is minimal in the studied assemblages. Those Early Cretaceous seeds or detached reproductive structures bearing spines were probably adapted for anchoring to aquatic debris or to soft lacustrine substrates. Several relatively featureless seeds in all assemblages were potentially adapted to barochory or to endozoochory—the latter evidenced especially by the presence of smooth seeds in vertebrate gut contents and regurgitant or coprolitic masses. Hydrochory is inferred for several aquatic plants that notably bear small featureless seeds, particularly aggregated into detachable pods.

1. Introduction

Extensive investigations of Middle Jurassic to Early Cretaceous floras of east Asia and Australia have dealt primarily with the taxonomy of plant groups (see summaries by Douglas, 1969, 1973; White, 1981; Drinnan and Chambers, 1986; Wu, 1999, 2003; Sun et al., 2001; McLoughlin et al., 2002; Wang et al., 2006; X. Wang et al., 2010; Pott et al., 2012a, 2015; Dong et al., 2017; Pott and Jiang, 2017). Relatively few studies of these fossil floras have focused on the palaeobiology or palaeoecology of the plants. Moreover, of those latter studies, most have dealt with growth-ring analysis of fossil woods (Frakes and Francis, 1990; McLoughlin et al., 1995; McLoughlin, 1996; Brison et al., 2001; Ding et al., 2004; Wang et al., 2009), the pollination biology of selected plant groups (Ren et al., 2009) and other aspects of plant–arthropod interactions (Y. Wang et al., 2010, 2012; Pott et al., 2012b; Na et al., 2014, 2017; Ding et al., 2015; McLoughlin et al., 2015; Pott et al., 2015). A few systematic studies have noted distinctive morphological characters of seeds that reflect specialized adaptations to particular environmental vectors (e.g. X. Wang et al., 2010). However, seed types

have not been surveyed systematically to assess the range of dispersal strategies in the Mesozoic vegetation of these regions. This dearth of studies is significant because Eriksson et al. (2000) and Leslie et al. (2017) emphasized that small fleshy fruits in angiosperms and some other seed plants originated prior to the mid-Cretaceous, and this interval was probably important for establishing a broad range of interactions between seed plants and their animal dispersers. One of Tiffney's (1984) primary findings in a review of the interactions between angiosperms and frugivorous seed dispersers was that the significant diversification of fleshy fruits and divergence in angiosperm seed size in general commenced around 80 Ma. However, several groups of potentially granivorous or frugivorous small vertebrates were already present by the Late Jurassic and their influence on seed dispersal strategies has not been assessed in detail.

Most vascular plants grow in fixed positions, obtaining the bulk of their mineral nutrients from rooting structures. Therefore, the dispersal of spores, seeds or other disseminules is clearly advantageous in reducing competition for resources for both the parent plant and the germlings, and for extending the potential range of the taxon, thus

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improving the chances of the species' survival in the event of local disturbance or change in the environment over longer time periods (Howe and Smallwood, 1982; Hughes et al., 1994; Tiffney, 2004). Dispersal of disseminules may also have the benefit of removing offspring from an area that is already the target of intense herbivory or pathogen attack.

Plants have developed an extensive array of dimensional, morphological and anatomical adaptations to enhance disseminule dispersal (van der Pijl, 1982). Such modifications began to appear very early in the history of land plants and developed in sophistication through the entire course of plant evolution. Two broad categories of plant reproduction can be considered: asexual and sexual processes. Asexual reproduction generally involves modifications of the roots, stems or leaves and may include the production of various specialized structures, such as suckers, tubers, bulbils, and gemmae. It may also involve simpler vegetative forking of axes or thalli, budding, production of rhizomes, stolons and other forms of fragmentation whereby the younger portions of the plant develop their own root systems and become segregated from other growing tips by the death of the central or older part of the parent axis, thus creating a clonal colony. Plants employing vegetative reproduction are commonly herbaceous or woody perennials in which cloning facilitates survival between seasons and promotes their expansion in size. Because sexual reproduction can be defined as the fusion of gametes, spore formation in algae and plant sporophytes can be categorized as a form of asexual reproduction (agamogenesis). In seed plants the megaspore is retained on the parent plant as part of the seed-forming process but, in free-sporing plants, dispersal of the spores is an important means of extending the distribution of a species.

Sexual reproduction in higher plants results in the production of seeds, although some arborescent heterosporous lycophytes of the late Palaeozoic also evolved seed-like disseminules (Scott, 1901). The earliest seed-like structures appeared in the Late Devonian (Serbet and Rothwell, 1992), and since that time have been modified into a broad array of architectures to facilitate dispersal.

Modern seeds have evolved a multitude of morphological innovations and their mass ranges through at least 11 orders of magnitude from the dust-sized seeds of orchids to the immense double coconut, *Lodoicea maldivica* (J.F. Gmelin) Persoon, reaching diameters up to 50 cm and weights of 30 kg (Westoby et al., 1992; Moles et al., 2005). The broad spectrum of sizes is commonly interpreted to constitute an evolutionary trade-off between the production of many small seeds, enhancing the odds of dispersal and establishment, and fewer large seeds, provided with greater food reserves favouring seedling survival (Leishman et al., 1995, 2000; Moles and Westoby, 2004). However, seed size probably varies according to an array of more complex relationships involving, among other factors, reproductive output, plant size, plant growth rate and plant longevity—characters that are, nonetheless, influenced by ecological and environmental parameters, such as latitude, altitude, climate, growth form, forest structure, dispersal agents, and genome size (Salisbury, 1974; Lord et al., 1997; Leishman et al., 2000; Moles and Westoby, 2006; Beaulieu et al., 2007; Díaz et al., 2016; Eriksson, 2016).

Seed or fruit dispersal by any physical environmental vector or animal agent is termed allochory. Wind- and water-dispersal (anemochory and hydrochory respectively) have probably been common traits among plant disseminules since the appearance of land plants. Dispersal via ingestion by animals (endozoochory) has probably occurred since the rise of vertebrate herbivores in the late Palaeozoic. Endozoochory is well known in angiosperms but is also widespread among conifers and cycads (van der Pijl, 1972; Givnish, 1980; Leslie et al., 2013, 2017). Leslie et al. (2017) noted that seeds especially modified for animal dispersal occur in 37% of extant conifers across all major clades, thus representing at least eight independent origins of endozoochory in the group. Leslie et al. (2017) also found that extant endozoochorous conifers tend to have larger seeds than anemochorous taxa across a broad spectrum of geographically segregated

communities. Moreover, they noted that this relationship is also evident in Gnetales and Cycadales.

In many angiosperms, but also some conifers (see e.g., Leslie et al., 2017) and potentially some other gymnosperms, expansion of the ovary or cupule surrounding the seed(s) to form a fleshy, colourful and/or aromatic fruit, or modifications of the cone or supporting stalk to form a fleshy receptacle or aril have developed as adaptations to attract vertebrate herbivores that facilitate seed dispersal. Invertebrates, particularly ants, also play an important role in modern seed dispersal. Myrmecochorous plants employ a lipid-rich attachment (the elaiosome) as a food offering to attract ants. The ants carry the seed back to the nest, feed the elaiosome to their larvae, then discard the seed underground in a site that is suitable for germination. Myrmecochorous plants are particularly prominent in mid-latitude Mediterranean-type vegetation belts, where they typically constitute around 30–40% of all plant taxa. Ants appear to have evolved in the mid-Cretaceous (LaPolla et al., 2013), so a myrmecochorous strategy would not be expected among plants of older floras.

In modern plants, dispersal of seeds by animals is not restricted to immediate ingestion or specialized attachment to the body surface. Various rodents, for example, will cache fallen seeds that are otherwise unspecialized for vertebrate dispersal (Vander Wall, 1992, 2003).

The appearance and diversification of terrestrial vertebrates with hairy or feathery indumenta in the mid-Mesozoic offered an additional means of dispersal for seeds. Hooks, barbs, and sticky secretions are employed by many modern angiosperms to attach to the indumenta of mammals and birds (Fahn and Werker, 1972) to facilitate dispersal (epizoochory). Birds and mammals underwent significant radiations in the mid-Mesozoic, hence epizoochory might be expected to increase from that time (Tiffney, 2004). However, it cannot be discounted that other animal groups with longer stratigraphic ranges (e.g., feathered dinosaurs and pterosaurs) were also vectors for epizoochory. Simple adhesion of seeds to animal vectors by mud or other residues is also a common process among modern plants (Ridley, 1930; Figuerola and Green, 2002a, 2002b) and probably plays an important role in long-distance dispersal of aquatic and hydrophilous plants (Raulings et al., 2011).

In a few cases, combinations of asexual fragmentation and retention of seeds on detached vegetative parts (forming a diaspore) facilitates dispersal of the species (e.g. in tumbleweeds). Another strategy is adopted by mangroves, whereby the seed germinates while still attached to the parent plant. The seedling then either grows within, or out through, the fruit to produce a propagule that can be detached and float long distances, but which also commonly has an anchoring device for settling on new substrates. Modifications of the seed coat and surrounding fruit wall to produce various flotation devices [e.g. in *Cocos nucifera* L. and *Barringtonia asiatica* (L.) Kurz] is another means to promote hydrochory and these strategies developed early in the evolution of mire, stream and lake-margin plants (DiMichele, 2014).

Ballochory, the forceful ejection of seeds under turgor pressure is employed by several modern taxa and possibly by plants as early as the Triassic (Bomfleur et al., 2014). This process normally disperses seeds only on the order of a few metres, but in the case of *Hura crepitans* L., ejection of seeds up to a distance of 100 m has been reported (Swain and Beer, 1977; Feldkamp, 2006).

Barochory is the term applied to gravity dispersal of seeds or fruits. This strategy is normally invoked for plants with heavy seeds or fruits, but this category may simply relate to disseminules that have no specializations for other mechanisms of dispersal (Castro et al., 2010). Despite the obvious advantages of dispersal away from the parent plant, some modern species produce seeds that show no obvious structural modifications to facilitate dissemination.

We studied fossil plant disseminules preserved in four well-known Lagerstätten of late Middle Jurassic to Early Cretaceous age from northeastern China and eastern Australia. Both Jurassic floras lack flowering plants, whereas each of the Early Cretaceous floras contains

the earliest records of angiosperms from the respective regions. This interval also witnessed active breakup of the Gondwanan continents, progressive isolation of southeast Australian biotas at middle to high southern latitudes, and significant floristic turnovers in both regions (Vakhrameev, 1991; Anderson et al., 1999; McLoughlin, 2001; Laurie et al., 2012). We aim to compare and contrast the disseminule assemblages to identify any patterns in the representation of plant propagule types through time in each region and on either side of the Neotethys Ocean. We assess whether granivory/frugivory, and potentially endozoochory, were important strategies around the dawn of flowering plant evolution. We investigate the representation of fleshy or featureless disseminules through the upper Middle Jurassic to Lower Cretaceous succession to assess whether dispersal by animal ingestion was increasing during this interval. We seek to identify any morphological modifications of disseminules that might indicate adaptations to transport via the special integumentary structures of animal groups that underwent significant radiations in the middle to late Mesozoic, i.e., by mammals (fur) and birds (feathers). By considering the representation of plant groups and disseminule dispersal strategies, we assess the implications for vegetation structure in the northern middle palaeolatitudes (China) and southern high palaeolatitudes (Australia) on either side of the Neotethys Ocean.

2. Materials and methods

We undertook investigations of fossil collections in several museums from four key Lagerstätten spanning the target interval: the fossil-bearing beds at Daohugou (Jiulongshan or Tiaojishan Formation; Callovian to possibly Oxfordian), Inner Mongolia, China; The Talbragar Fossil Fish Bed (Kimmeridgian–Tithonian), New South Wales, Australia; the Yixian and Jiufotang formations (upper Hauterivian–Aptian), Jehol Group, Liaoning, China; and the Koonwarra Fossil Bed (?Barremian–Aptian), Victoria, Australia. We supplemented these investigations by reconnaissance field excursions to each site, and surveys of past literature documenting fossils from the target assemblages.

The studied specimens are stored in various institutions: the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing; the Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing; the Queensland Museum (QM), Brisbane; the Australian Museum (AM), Sydney; the New South Wales Geological Survey (MMF), Sydney; Museum Victoria (NMV), Melbourne; the Natural History Museum (NHM), London; and the Swedish Museum of Natural History (NRM), Stockholm. Specimens from all localities are preserved as impressions, with no (or minimal) organic material preserved. All relevant plant fossils were photographed using low-angle illumination from the upper left using a Nikon D90 digital camera at IVPP and NIGPAS, and a Canon EOS 40D digital camera at the other institutions. In some cases, a polarizing filter was employed to enhance the image contrast. Authorities to extant plant taxa mentioned in the text can be found at the International Plant Names Index online portal (<http://www.ipni.org/ipni/plantnamesearchpage.do>).

For each deposit we assessed the relative representation of plant groups based on fossil leaves and fertile organs. Seeds and other disseminules were identified to plant groups as far as possible based on physical attachment, similarity in morphology, or correspondence in detachment scars. Seeds were also assigned to a range of morphological categories that were interpreted to reflect similarities in function (e.g., winged seeds—adaptation to wind dispersal; bulbils—adaptation to asexual propagation). We use the term fleshy fruit or fleshy seed in the broadest sense to encompass any reproductive structure with a thickened, edible pulp layer enclosing seeds (Jordano, 2000). Hence, this potentially includes structures that strictly are not parts of the fruit, e.g. the aril of Taxaceae, but which are functionally equivalent.

We undertook a semi-quantitative analysis by documenting the representation of seed types and sizes in the assemblages, but these results must be considered preliminary, since we are aware that all the fossil

assemblages probably experienced some taphonomic sorting and the curated collections likely suffer from considerable sampling biases, thus, they are unlikely to provide a complete picture of the representation of plant types in the original vegetation.

3. Geological settings

We provide brief summaries of the geology of the four studied fossiliferous deposits in order to place the plant assemblages into the context of a geochronological succession, palaeolatitudinal settings, and depositional environments.

3.1. Jiulongshan or Tiaojishan Formation (Daohugou)

There has been considerable controversy surrounding the age and stratigraphic nomenclature applied to strata hosting the ‘Daohugou biota’ (= Yanliao biota of recent studies) exposed in several small intermontane basins around the common boundaries of Inner Mongolia, Liaoning and Hebei provinces, China. Discontinuous outcrops, local faulting and distribution over an uneven predepositional topography means that the thickness of the fossiliferous deposits varies over short distances and individual beds are difficult to trace laterally between isolated exposures. The most productive strata for fossils are exposed around the village of Daohugou itself (Na et al., 2017). There, an approximately 440-m-thick package of greyish to green, very finely laminated tuffaceous silty claystones and tuffs intercalated with cm- to tens of m-thick tuffs rests on Precambrian basement and is overlain by c. 100 m of volcanic and brecciated volcanic rocks. This in turn is overlain by sandstones and conglomerates of the Tuchengzi Formation (Sullivan et al., 2014). Many studies of the invertebrate fauna have attributed the interbedded tuff/claystone package to the Middle Jurassic Jiulongshan Formation (or the coeval Haifanggou Formation) (Ren et al., 2010; Selden and Huang, 2010; Giribet et al., 2012). However, other studies, particularly focusing on the fossil vertebrate fauna have favoured a Late Jurassic age and attribution to the Tiaojishan Formation (Zhang et al., 2008; Wang and Li, 2008; Evans and Wang, 2009). We follow Sullivan et al. (2014) who noted that there is currently insufficient evidence to determine whether the main fossiliferous strata at Daohugou constitute the Jiulongshan Formation as proposed by Gao and Ren (2006) or represent the lower part of the Tiaojishan Formation, as favoured by Y.-Q. Liu et al. (2006, 2012) and Peng et al. (2012). In this study, we simply refer to the plant fossil assemblages from this deposit as the Daohugou flora. Apart from abundant fossils of plants, the Daohugou deposits host a rich fauna of insects, salamanders, pterosaurs, dinosaurs and early mammals (Zhang, 2010; Selden and Huang, 2010; Sullivan et al., 2014; Xu et al., 2016). Strata at Daohugou are typically characterized by normal grading, which together with the fine-grained lithology, thin laminae and composition of the fossil fauna are indicative of deposition in low-energy lacustrine settings.

The precise ages reported for the deposits at Daohugou have also varied according to the technique employed and the beds sampled. Radiometric dating of samples from volcanic rocks overlying the fossiliferous beds at Daohugou has yielded $^{206}\text{Pb}/^{238}\text{U}$ SHRIMP ages of 162 ± 2 Ma and 152 ± 2.3 Ma (Y.X. Liu et al., 2006), an $^{40}\text{Ar}/^{39}\text{Ar}$ age of 159.8 ± 0.8 Ma (He et al., 2004; Y.X. Liu et al., 2006), two further $^{206}\text{Pb}/^{238}\text{U}$ SHRIMP ages of 166 ± 1.5 Ma and 165 ± 2.4 Ma, an additional $^{40}\text{Ar}/^{39}\text{Ar}$ age of 164 ± 2.5 Ma (Chen et al., 2004), and two more $^{206}\text{Pb}/^{238}\text{U}$ SHRIMP ages of 164 ± 1.2 Ma and 165 ± 1.2 Ma (Yang and Li, 2004). A final $^{206}\text{Pb}/^{238}\text{U}$ SHRIMP age of 165.0 ± 1.2 Ma was obtained from samples recovered specifically from the fossiliferous beds (Yang and Li, 2008). Collectively, these data favour a Callovian (latest Middle Jurassic) or possibly Oxfordian age for the fossiliferous beds at Daohugou, and this is consistent with phytos-tratigraphic data (Na et al., 2017). Daohugou was located at around 50° – 60°N during the Middle–Late Jurassic (Scotese, 1997; Fig. 1).

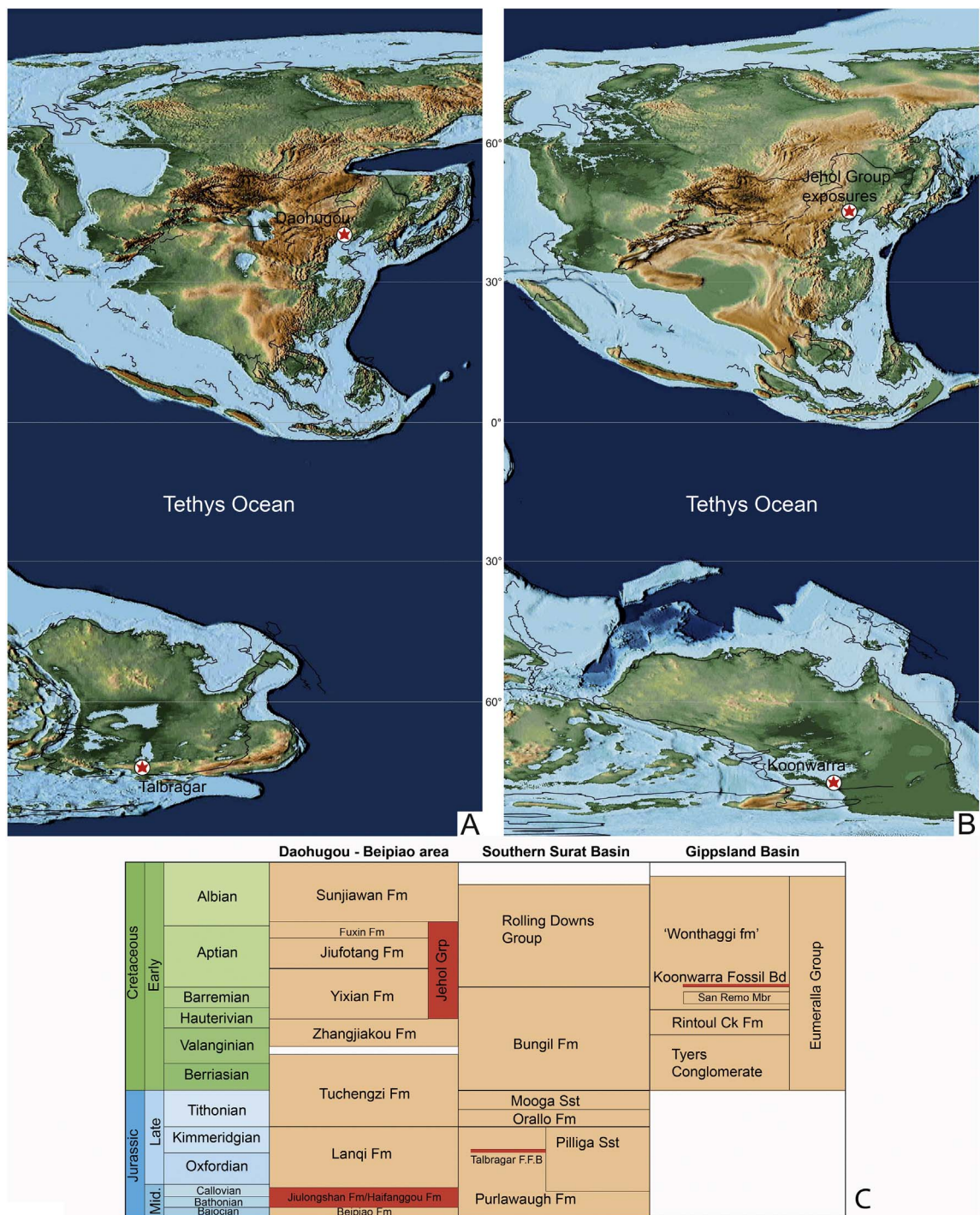


Fig. 1. Palaeogeographic maps for the Late Jurassic (A) and Early Cretaceous (B) showing the locations of the Daohugou (Callovian), Talbragar (Kimmeridgian–Tithonian), Jehol Group (upper Hauterivian to Aptian), and Koonwarra (?Barremian to Aptian) assemblages; and composite stratigraphic correlation chart (C) of the Daohugou–Beipiao region, China, Talbragar district, southern Surat Basin, and Koonwarra district, Gippsland Basin, Australia, with the studied units highlighted in red (after Price, 1997; Sha, 2007; Xu and Li, 2015; Tosolini et al., 2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Yixian and Jiuftotang formations

The Jehol Group (originally ‘Series’ of Grabau, 1923) was established for a succession of richly fossiliferous fine-grained lacustrine and fluvial siliciclastic sedimentary rocks, tuffs and volcanic extrusive rocks deposited in one or more continental fault-bound sedimentary basins in northeast China (Gu, 1962, 1983). Continental strata equivalent to the Jehol Group are widespread across northeast China, Mongolia and the Russian Far East attesting to extensive sedimentation in lake systems at

that time. These basins developed via subsidence associated with the regional Yanshanian Orogeny of the middle to late Mesozoic (Yan et al., 2002). The basal unit of the Jehol Group is designated the Yixian Formation and rests unconformably on Precambrian and Palaeozoic strata. The Yixian Formation consists of fine-grained siliciclastic sedimentary rocks and thin tuffs intercalated with basalts. This unit has been subdivided into several members and beds; the formation as a whole spanning the upper Hauterivian to lower Aptian (Wang et al.,

2016). The Yixian Formation is overlain conformably by the Jiufotang Formation, which comprises mainly lacustrine sandstones, shales and mudstones interbedded with a lesser proportion of tuff beds than for the preceding unit (Chang et al., 2003). The uppermost unit of the Jehol Group is the Fuxin Formation, which consists of coal-bearing siliclastic rocks. Wang et al. (2016) ascribed an Aptian to for the Jiufotang Formation and an Aptian–Albian age to the Fuxin Formation. The Jehol Group is overlain disconformably by the Sunjawan Formation, which is in turn overlain unconformably by the Daxingzhuan Formation, both of Late Cretaceous age (Sha, 2007). The Fuxin–Yixian–Jinzhou Basin in western Liaoning, from which most of the studied Jehol Group plant remains derive, was located at around 50°–60°N during the Early Cretaceous (Scotese, 1997; Fig. 1).

3.3. Talbragar Fossil Fish Bed

The Talbragar Fossil Fish Bed strictly contains several discrete 5–60-cm-thick beds and is exposed in a small southerly outlier of the epicratonic Surat Basin near Gulgong in central New South Wales, Australia. This deposit has poor natural exposures, but has been excavated for the collection of fossil plants and animals on several occasions over the course of more than a century. The beds can be traced laterally for only around 200 m and consist of yellow–brown silicified siltstone and tuff that collectively reach about 1.4 m thick (Beattie and Avery, 2012). Beds near the top of this succession are thinner, more finely laminated and have a richer volcanic ash component than those near the base (Turner et al., 2009). All beds within the unit are richly fossiliferous. A lacustrine depositional environment is interpreted for this unit based on the fine-grained and finely laminated nature of most beds and the abundance of fossil fish (Percival, 1979). There are no indications of desiccation features on bedding planes. The high proportion of volcanogenic grains and euhedral nature of the zircon crystals suggest that deposition of ash from a nearby felsic eruptive centre was responsible for the occurrence of several mass-mortality horizons within the upper part of the unit and the rapid entombment of a range of plants, fish and arthropods (Bean, 2006a, 2017; Turner et al., 2009). Radiometric dating of the youngest zircon population extracted from this deposit has yielded an age of 151.55 ± 4.27 Ma (Bean, 2006b; Turner et al., 2009), or Kimmeridgian–Tithonian in terms of the current International Chronostratigraphic Chart (Cohen et al., 2013). The Talbragar Fossil Fish Bed was deposited at a palaeolatitude of c. 75°S (Veevers, 2000; Fig. 1).

3.4. Koonwarra Fossil Bed (Eumeralla Formation)

The Koonwarra Fossil Bed was discovered in 1961 by Country Roads Board of Victoria workers who were straightening and widening the South Gippsland Highway 3 km east of Koonwarra and 142 km south-east of Melbourne, Australia. Traditionally, the bed has been placed in the informal ‘Wonthaggi formation’ of the Strzelecki or Koonwarra Group, within the Gippsland Basin succession (Drinnan and Chambers, 1986; Holdgate and McNicol, 1992; Chiupka, 1996). However, VandenBerg et al. (2006) proposed extending the application of the name Eumeralla Formation (of the Otway Group), from the adjacent Otway Basin, to the thick feldspathic sandstone succession in the Gippsland Basin encompassing the Koonwarra Fossil Bed. The Koonwarra Fossil Bed represents an 8-m-thick succession of thinly laminated siltstone–sandstone couplets that have been interpreted to represent varved lacustrine deposits (Waldman, 1971). The palaeo-lake sediments are not known to contain volcanic ash deposits but host a rich fossil biota of plants, invertebrates, fish and dispersed feathers. It is assumed that seasonal freeze–thaw cycles contributed to the development of mass-mortality horizons within the deposit. Dettmann (1986) interpreted the spore–pollen assemblage recovered from this deposit to reflect a ?Barremian–Aptian age. The Koonwarra Fossil Bed was deposited at a palaeolatitude of c. 75°S (Veevers, 2000; Fig. 1).

4. Composition of the fossil floras

All four studied fossil floras contain a diverse range of plant groups. Macroalgae and fungi were not positively identified in any of the assemblages in this study. We do not aim to provide a comprehensive review of the floras and we refer readers to previous systematic accounts of the fossil assemblages for detailed descriptions of taxa. We briefly outline the general characteristics of the fossil biota in each deposit.

4.1. Daohugou flora

The thinly laminated siliclastic strata at Daohugou contain a rich fossil biota. Plant fossils are generally scarce, but owing to extensive excavation and sampling efforts by local farmers and researchers, a rich assemblage of plant remains has now been recovered. Na et al. (2017) recorded 49 species of plant macrofossils referable to 32 genera from beds at Daohugou in contrast to Pott and Jiang (2017), who identified 17 genera with 21 species (excluding seeds) in this assemblage. Our current assessment of the collective published diversity within this flora, accounting for synonyms and misidentifications in previous works, is c. 70 species in c. 45 genera, excluding seeds (see Supplementary Table 1). The flora has a strong representation of the groups that dominated mid-Mesozoic floras of the Northern Hemisphere, viz., ferns, caytoniales, bennettitales, ginkgoopsids, leptostrobaeans and conifers (Zhou et al., 2007; Pott et al., 2015; Wei et al., 2015; Dong et al., 2017; Pott and Jiang, 2017). Subsidiary elements in the fossil flora include mosses, lycophytes, sphenophytes and putative cycads. The beds at Daohugou are also renowned for their rich and diverse assemblages of invertebrate and vertebrate fossils (Huang et al., 2006; Ren et al., 2010; Sullivan et al., 2014).

4.2. Yixian and Jiufotang formations (Jehol Group) flora

Wu (1999, 2003) and Sun et al. (2001) have provided extensive accounts of the Jehol Group fossil flora, establishing numerous new taxa. The flora contains over 80 macrofossil-based species and is dominated by conifers, leptostrobaeans and ferns but also incorporates a diverse array of other seed- and spore-bearing plants including ginkgoaleans, bennettitales, nilssonialeans, equisetaleans and lycophytes among other groups (Supplementary Table 2). The flora is notable for the occurrence of several early angiosperm taxa and a relatively diverse array of gnetalean remains (Sun et al., 1998, 2002; Friis et al., 2003; Ji et al., 2004; Rydin et al., 2006; Rydin and Friis, 2010). A diverse array of terrestrial and freshwater invertebrates and vertebrates are co-preserved with the flora (Wang et al., 2006; Ren et al., 2010; Xu and Norell, 2006).

4.3. Talbragar Fossil Fish Bed

The Talbragar Fossil Fish Bed hosts a rich fossil biota of non-marine invertebrates (Beattie and Avery, 2012), fish (Bean, 2006a; Turner and Avery, 2017) and plants (Walkom, 1921; White, 1981; Turner et al., 2009), some of which show damage features that enable reconstruction of trophic interactions in the Late Jurassic ecosystem (McLoughlin et al., 2015). The flora, studied most thoroughly by Walkom (1921) and White (1981), is represented by around 13 species based on leaves and several additional taxa defined on reproductive structures, some of which have not been formally described. The flora includes araucariacean and putative podocarpacean conifers [*Podozamites jurassica* (White, 1981), *?Rissikia talbragarensis* White, 1981, *Brachyphyllum* sp., *Pagiophyllum* sp., *Elatocladus australis* Frenguelli, 1944, *Allocladus cribbii* Townrow, 1967, *Allocladus milneanus* (Tenison Woods) Townrow, 1967], pentoxyleans (*Taeniopteris*, *Carnoconites* and *Sahnia* spp.), *?Cycadales* (*Nilssonia compta* (Phillips) Brongniart, 1828), some enigmatic, possibly umkomasialean seed-ferns (*Rintoulia* sp., *Komlopteris*

sp.), lycophytes (*Isoetes* sp.) and ferns attributable to several families. Many of the fish and most of the plant impressions are coated by white kaolinite and opaline quartz that do not preserve the finer characters of leaf venation or epidermal details.

4.4. Koonwarra Fossil Bed (*Eumeralla* Formation)

The Koonwarra Fossil Bed hosts a rich plant impression flora (44 taxa) that was described thoroughly by Drinnan and Chambers (1986). The flora includes liverworts, mosses, lycophytes, sphenophytes, several families of ferns, pentoxylaleans, possible umkomasialean seed ferns, ginkgoaleans, probable gnetaleans, araucariacean and podocarpaceous conifers, the oldest known angiosperm remains in Australia, and several plant reproductive structures of uncertain affinity. The Koonwarra Fossil Bed is also renowned for its rich fauna of actinopterygian fishes, freshwater molluscs, annelids and arthropods (Talent et al., 1966; Waldman, 1971; Jell and Duncan, 1986; Bean, 2017). The deposit also contains several dispersed bird or theropod feathers (Rich and Rich, 1989). Palynological studies of the bed have also identified a substantial algal component in the palaeolacustrine biota (Dettmann, 1986).

5. Results

5.1. Asexual propagules

5.1.1. Observations

Asexual vegetative reproduction is represented in all four studied floras by several strategies. Examples of branched liverwort thalli (Fig. 2A, B, D–G, I) or forked selaginellalean axes or moss gametophytes (Fig. 2C, H) are well represented in the Daohugou, Jehol and Koonwarra assemblages. No bryophytes have yet been documented from Talbragar. Terminal growth of bryophyte thalli probably left older parts of the plant to decay leaving the daughter tips/stalks isolated from their clonal siblings.

Equisetalean axes are sparsely represented at Daohugou, and we did not detect the presence of any associated tubers. Equisetaleans are not yet known from the Talbragar flora, however, that assemblage contains a slender-stemmed aquatic plant that White (1981, Fig. 53) referred to *Selaginella*. It appears to form tangled masses of profusely branched fragile stems that may have fragmented in the aquatic environment to produce daughter plants. Several equisetalean axes in the Jehol Group assemblages represent rhizomes based on the presence of rootlets departing from nodes and the occurrence of solitary or clustered tubers also located at nodes. Both branching of the rhizomes (Fig. 2L, M) and isolation and development of shoots from tubers (Fig. 2J–M) offered means of vegetative propagation for these plants. Equisetalean rhizomes are present in the Koonwarra assemblage and show both branching and tuber development (Drinnan and Chambers, 1986, Fig. 12E–G).

Ferns are common in all four assemblages but are represented mainly by detached foliar fragments. We cannot be certain whether these fronds were borne on prostrate or erect axes. However, given that some fronds are attributed to typical ground-fern families, such as Dipteridaceae, Osmundaceae, and Polypodiaceae (Sun et al., 2001), it is likely that many were borne on prostrate, rhizomes with branches that had the potential to separate from the parent axes and survive independently.

We have little data on the palaeoecology of the herbaceous angiosperms (*Archaeofructus* and *Sinocarpus*) in the Yixian assemblages. Although most specimens found to date are reproductive, given their slender branched stems and apparently aquatic habitat, it is possible that, apart from reproducing sexually, these plants also underwent dispersal by fragmentation or, especially in the case of *Archaeofructus*, by production of lateral shoots from the rhizome (Qiang et al., 2004).

5.1.2. Remarks

Asexual reproduction was probably widely employed by free-sporing plants in all of the studied assemblages. A substantial representation in both diversity and abundance of fern foliage in all assemblages attests to a significant expression of understorey vegetation. These free-sporing plants were probably effective at reproducing via rhizome division or fragmentation. Equisetaleans with tubers are consistently represented in the Cretaceous assemblages, but we find no evidence of bulbils, gemmae cups or other specialized asexual reproductive features on ferns or liverworts within any of the assemblages. Direct evidence for asexual reproduction among the seed plants is lacking, although McLoughlin et al. (in press) argued on the basis of their scrambling habit and dearth of fossilized ‘flowers’ that Australian high-latitude Mesozoic williamsoniacean bennettitaleans and pentoxylaleans might have supplemented sexual reproduction by suckering where lateral branches touched the ground.

5.2. Free-sporing plants

5.2.1. Observations

A wide range of fertile homosporous ferns is represented in each of the studied floras (Fig. 3A–C, H; Supplementary Online Tables 1–4). Strobili of lycophytes (Fig. 3D) and sporangia of bryophytes (Fig. 3E, F) are also represented in the Jehol and Koonwarra floras. Collectively, such plants represent around 10–30% of the foliar remains in the studied floras. The ferns are attributed to various families including Ophioglossaceae, Osmundaceae, Dipteridaceae, Schizaeaceae, Gleicheniaceae, Dicksoniaceae, Pteridaceae and Polypodiaceae (Walkom, 1921; White, 1981; Drinnan and Chambers, 1986; Sun et al., 2001; Pott and Jiang, 2017). Several families are present across all of the floras, but no species are shared.

5.2.2. Remarks

Together with *Equisetum* and various lycophytes and bryophytes, free-sporing ferns could propagate the gametophyte stage of their life cycle by spore dispersal. Both wind and water play important roles in spore dispersal (Traverse, 1988), and exine modifications, such as the pronounced flange-like equatorial zona on some lycophyte spores may represent particular adaptations to enhance such dispersal.

5.3. Seeds adapted for wind dispersal

5.3.1. Observations

Numerous and diverse seeds in each of the four studied assemblages bear marginal flanges. These include forms with symmetrical narrow marginal wings essentially encircling the seed body (Figs. 4I–K, 5A–D), forms with very broad and seemingly delicate wings of consistent width encircling the seed body (*Gurvanella* sp. Fig. 4X–Z), forms with exaggerated lateral (Fig. 4G), apical (Fig. 4H) or basal? (Fig. 5P) development of a marginal wing, forms with a wing extending along one flank and developing into a prominent apical wing endowing asymmetry on the seed (Fig. 4S–W), and paired (united) seeds with prominent and separated apical wings diverging at acute to obtuse angles (Fig. 4L–Q) or fused laterally (Fig. 4R). In addition, some araucariacean seeds in the Talbragar flora appear to have been retained on, and shed with, the cone scale (Fig. 4AB, AC). In these cases, the cone scale represents a rhombic, more or less flattened wing-like extension around the seed that may have acted as an aerofoil as in some ancient and modern seed-bearing fruits or their appendages (Prevec et al., 2008; De Jaegere et al., 2016). Other araucariaceans in the Koonwarra flora have distinctive scars on the cone scales (Fig. 4AA, AD) that match the chalazal end of detached flattened rhombic seeds (Fig. 4AE) in the same assemblage (Chambers et al., 1998). In these cases, the seeds themselves bear narrow lateral wings, probably derived from the cone scale complex (Contreras et al., 2017).

A second major category of appendage facilitating wind dispersal is

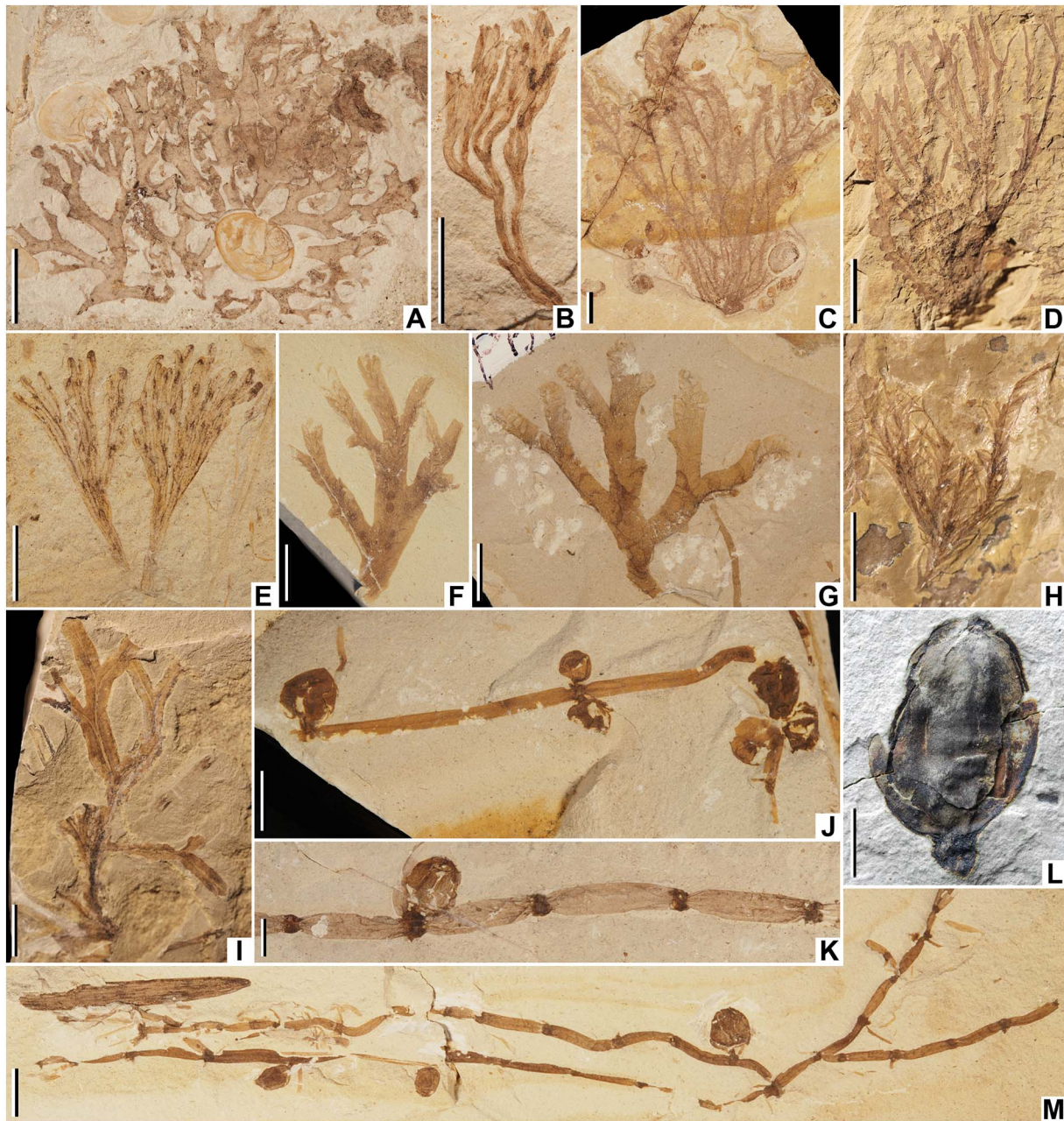


Fig. 2. Examples of vegetative reproduction in plants of late Middle Jurassic to Early Cretaceous age from China and Australia. All scale bars = 5 mm.

A, Thalloid liverwort or lichen with decay of older portion of thallus, Daohugou, B0474.

B, Slender branched thalloid liverwort, Daohugou, B0475.

C, Multi-branched moss, leafy liverwort or seleginellalean, Daohugou, B0456.

D, Leafy liverwort with decay of older portion of thallus, Koonwarra, MVP167325.

E, Slender branched thalloid liverwort (*Thallites riccioides* Wu), Jehol Group, PB18973.

F, Branched thalloid liverwort, Jehol Group, PB18977.

G, Branched thalloid liverwort, Jehol Group, PB18224.

H, Branched moss gametophyte, Koonwarra, MVP230894.

I, Branched thalloid liverwort (*Hepaticites* sp.), Koonwarra, MVP205070.

J, Equisetalean rhizome with tubers at nodes, Jehol Group, PB18983.

K, Equisetalean rhizome with tuber at node, Jehol Group, PB18984.

L, Enlargement of detached Equisetalean tuber, Jehol Group, B0100B.

M, Branched Equisetalean rhizome with tubers at nodes, Jehol Group, PB18985B.

represented by species of the putative bennettitalean seed (*Problematospermum*; Fig. 4A–F) preserved in both the Daohugou and Jehol assemblages, although more common in the latter (Wu, 1999; Sun et al., 2001; X. Wang et al., 2010; Friis et al., 2011; Pott and Jiang, 2017). In this genus, a small, elliptical, microrugulate seed bears a hairy appendix (pappus) around 20 mm long consisting of several dozen

individual filaments. The filaments are < 0.1 mm wide and are commonly arrayed in a fan-like or conical manner.

5.3.2. Remarks

The large taxonomic range (around 29 species in the four studied assemblages) and number (several hundred) of individual seeds with



Fig. 3. Examples of free-sporing plants of late Middle Jurassic to Early Cretaceous age from China and Australia. All scale bars = 5 mm.

- A, *Botrychites reheensis* Wu, fertile frond, Jehol Group, B0157.
 B, *Eboracia lobifolia* (Phill.) Thomas, fertile frond, Jehol Group, PB19017.
 C, *Xiajiaqenia miribila* Sun, Zheng et Mei, fertile frond, Jehol Group, PB19032.
 D, *Selaginellites fausta* (Wu) Sun et Zheng, branched axis with terminal strobili, Jehol Group, PB18979.
 E, F, Bryophyte sporophytes, Jehol Group, INFO037.
 G, *Onychiopsis paradoxus* Bose et Dev, fertile frond, Koonwarra, MVP167462.
 H, *Aculea bifida* Douglas, fertile frond, Koonwarra, MVP167531.

flattened or filamentous appendages indicates that anemochory was an important seed dispersal strategy employed by diverse plant groups in each of the four studied assemblages. The considerable range in morphology of each of the major winged seed categories makes it difficult to accurately demarcate the precise number of natural species represented in the fossil assemblages. Both single- and double-winged forms are well represented.

Double-wings (narrow marginal wings) provided ancient seeds with enhanced aerodynamic properties, reducing descent rates and improving dispersal (Souza and Iannuzzi, 2012; Stevenson et al., 2015).

Similar seeds are produced by modern plants, such as *Betula*—a well-documented anemochorous genus. *Gurvanella* sp., with an extremely broad and apparently delicate (papery) wing, has a morphology very similar to several typical wind-dispersed seeds produced by disparate plant groups, e.g., *Welwitschia*, *Ptelea trifoliata* L. (hop tree) and *Ulmus* (elm).

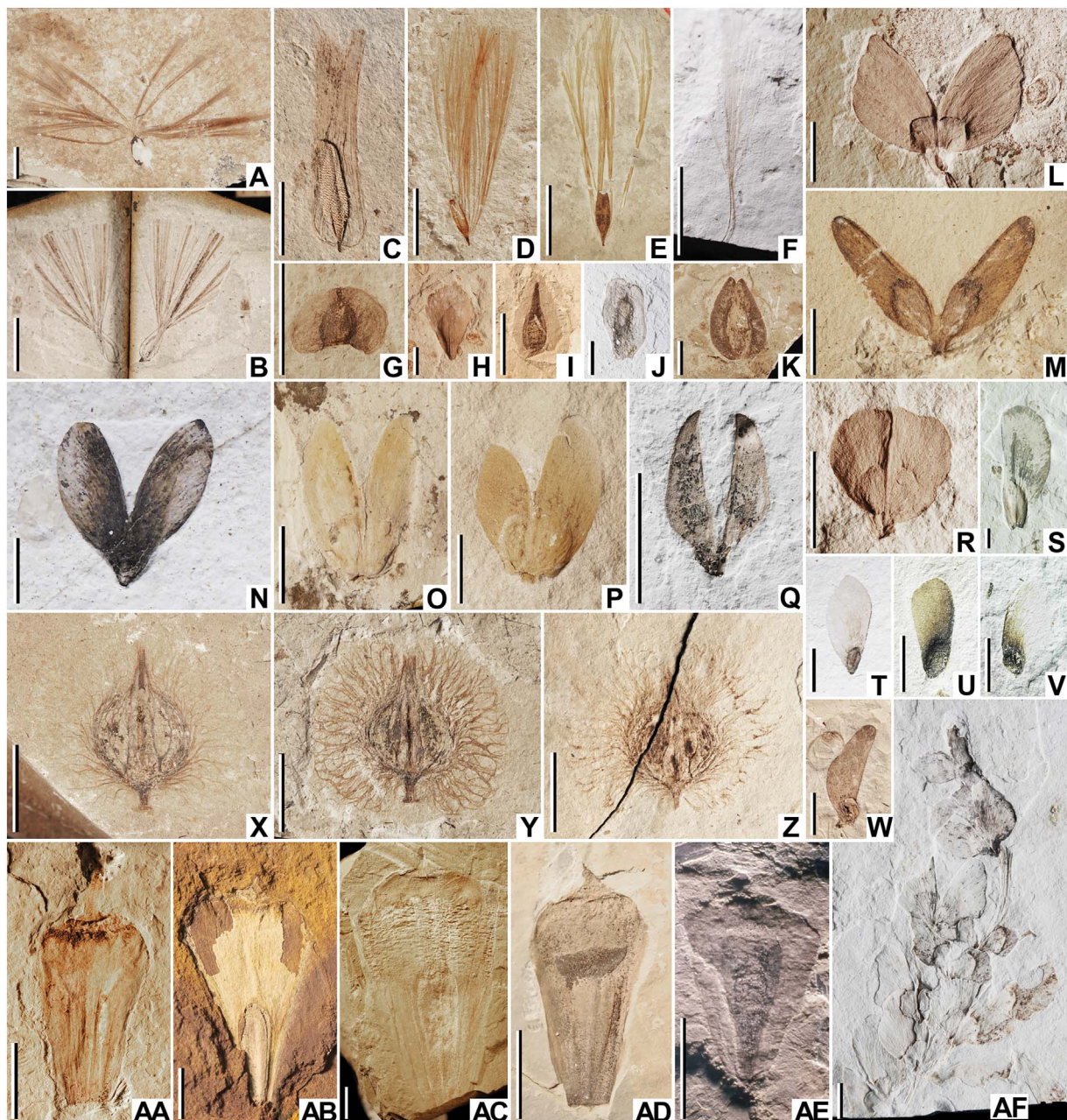
Single-winged forms endowing asymmetry to the seed are morphologically similar to a broad range of modern anemochorous conifer (e.g., *Pinus*) and angiosperm (e.g., *Acer*, *Pterospermum*) seed types. Such seeds developed early in the evolution of conifers (Stevenson et al.,

2015). Asymmetrical single wings, or paired wings of different sizes, induce autorotation in freefall providing a much slower rate of descent, and enhancing the potential for lateral dispersal by wind (Stevenson et al., 2015). Further, Stevenson et al. (2015) noted that the relative efficacy of retardation of descent improves with increase in seed weight. It is, therefore, not surprising that single or asymmetrically winged seeds are among the largest in the four studied assemblages. Winged seeds of all types are particularly prominent in the Jehol Group assemblage. The considerable range within and between seed morphotypes in this assemblage likely produced substantial variation in dispersal capacity among disseminules. A degree of taphonomic sorting in the large lake systems that accumulated the Jehol Group may have differentially favoured representation of some readily dispersed seeds over foliage.

The well-developed pappus of *Prolematospermum beipiaoense* Sun et Zheng (in Sun et al., 2001) and related species is broadly similar to the filamentous structures (pappus or coma) on seeds of many members of

extant Asteraceae and Asclepiadoideae (Apocynaceae) and probably represented a similar adaptation for buoyancy in the air column and dispersal by wind. Krassilov (1973, 1997) favoured a bennettitalean affinity for these fossil seeds—an interpretation supported by subsequent studies (Sun et al., 2001; Friis et al., 2011; Pott and McLoughlin, 2014). Moreover, similar pappus-bearing seeds attributed to *Baisia* from Lower Cretaceous strata of the Lake Baikal area, Russia, also have putative bennettitalean affinities (Krassilov and Bugdaeva, 1982).

Contreras et al. (2017) noted that over half of all extant conifer genera and species have winged seeds and are anemochorous. An even greater percentage of anemochorous taxa might be expected in the mid-Mesozoic before the major diversification pulses of birds and mammals. The current survey seems to bear this out with heavy representation of winged seeds in all assemblages and pappus-bearing seeds prominent in the Jurassic–Cretaceous of China. Most modern wind-dispersed woody plants are canopy trees or vines; relatively few are understorey trees



(caption on next page)

Fig. 4. Seeds adapted for wind dispersal of late Middle Jurassic to Early Cretaceous age from China and Australia. All scale bars = 5 mm.

- A, *Problematospermum beipiaoense* Sun et Zheng, Jehol Group, PB19188.
 B, *Problematospermum ovale* Tur.-Ket., Jehol Group, B0482A,B.
 C, *Problematospermum ovale* Tur.-Ket., Jehol Group?, INFO084.
 D, *Problematospermum ovale* Tur.-Ket., Jehol Group, PB18333.
 E, *Problematospermum ovale* Tur.-Ket., Jehol Group, PB19191.
 F, *Problematospermum* sp., Daohugou, MES-NJU 57004.
 G, Broadly bi-winged seed, Koonwarra, MVP167723.
 H, Apically winged seed or cone scale, Daohugou, B0412A.
 I, Pyriform bi-winged seed, Koonwarra, MVP167689.
 J, Irregularly bi-winged seed, Daohugou, MES-NJU 57071.
 K, Ovate bi-winged seed, Daohugou, B0489.
 L, *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld, Jehol Group, INFO098.
 M, *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld, Jehol Group, PB18304.
 N, *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld, Daohugou, MES-NJU 57025.
 O, *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld, Jehol Group, PB18278.
 P, *Schizolepidopsis moelleri* (Seward) Doweld, Jehol Group, PB19126.
 Q, *Schizolepidopsis* sp., Huajiyi Formation (lateral equivalent of the Yixian Formation), B1073A.
 R, *Schizolepidopsis* sp. cf. *S. chilitica* (Sun et Zheng) Doweld, Jehol Group?, HFSJ-7-3.
 S, *Pityospermum* sp., Daohugou, B0164A.
 T, *Pityospermum* sp., Daohugou, MES-NJU 57073.
 U, *Pityospermum* sp., Huajiyi Formation (lateral equivalent of the Yixian Formation), B1255B.
 V, *Pityospermum* sp., Huajiyi Formation (lateral equivalent of the Yixian Formation), B1229.
 W, *Pityospermum* sp., Daohugou, B0405A.
 X, *Gurvanella exquisita* Sun, Zheng et Dilcher, Jehol Group, PB1918.
 Y, *Gurvanella exquisita* Sun, Zheng et Dilcher, Jehol Group, PB19178.
 Z, *Gurvanella exquisita* Sun, Zheng et Dilcher, Jehol Group, PB19177.
 AA, Spinose araucariacean cone scale with seed detachment scar, Koonwarra, MVP167640.
 AB, Spinose araucariacean cone scale with embedded seed, Talbragar, AMF72404B.
 AC, Spinose araucariacean cone scale with embedded seed, Talbragar, MMF3170.
 AD, Spinose araucariacean cone scale with seed detachment scar, Koonwarra, MVP167635.
 AE, Isolated bi-winged araucariacean seed, Koonwarra, MVP167675.
 AF, Lax cone with *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld seeds, Daohugou, B0191.

and shrubs (Howe and Smallwood, 1982). Thus, we consider that the majority of Jurassic–Cretaceous winged or pappus-bearing seeds were produced by forest canopy plants, or by small trees and shrubs in relatively open vegetation.

5.4. Seeds and fruits with spines and hooks

5.4.1. Observations

The Daohugou and Talbragar floras appear to lack seeds with obvious spinose, hooked or barbed appendages. Seeds or fruits assigned to *Hemitrapa* sp. (Fig. 6J–M) have two or three weakly to strongly divergent spines at one end and are relatively common in the Koonwarra Fossil Bed (Douglas, 1963, 1969; Drinnan and Chambers, 1986). The spines typically have a terminal curvature to form a weak hook. Similar spinose or weakly hooked seeds attributed to *Lappacarpus aristata* Douglas, 1969 also occur in slightly younger beds (upper Eumeralla Formation) in southeastern Australia (Douglas, 1969). The Jehol Group flora contains several sturdy reproductive structures that bear long divergent apical spines (Fig. 6A, D–I). Most have been assigned to *Beipiaoa*—a genus that appears to incorporate at least three forms of both seeds and fruiting bodies. In each case, the structures bear long, generally straight and robust spines that vary from being slightly divergent to arranged at almost 180°. *Beipiaoa* fossils are moderately common (represented by dozens of specimens) and in a few cases have been found in tight clusters on bedding planes (Fig. 6A). Araucariacean cone scales are abundant in the Talbragar and Koonwarra assemblages of Australia (> 30 specimens at each locality) and some may have been shed with seeds retained on the scales as in extant *Araucaria* (Boland et al., 2006). These scales typically bear a single prominent apical spine (Fig. 4AA–AD), in some cases reaching 20 mm long.

5.4.2. Remarks

As Leng et al. (2003) noted, spinose seeds/fruits similar to *Hemitrapa*, *Lappacarpus* and *Beipiaoa* are superficially similar to reproductive structures produced by a range of modern aquatic angiosperms.

However, at least some modern aquatic angiosperms (e.g., *Trapa natans* L.) have spinose fruits/seeds that fall predominantly to the floor of the water body immediately beneath the parent plant (Mikulyuk and Nault, 2009). In these cases, spines might function more for the protection of the seed or for anchoring in soft substrates than for facilitating dispersal (Schneider and Williamson, 1993). The lack of lateral barbs or hooks on most of the Cretaceous fossil seeds makes them unlikely to have functioned as efficient adaptations for epizoochory. Nevertheless, in modern ecosystems, many disseminules can be dispersed by non-standard vectors (Heleno and Vargas, 2015) and it is possible that some morphologically unspecialized seeds in the Jurassic–Cretaceous assemblages were transported via epizoochory through simple adhesion (via clay or organic residues) to body surfaces. Moreover, the strongly divergent spines of some seed species, and especially the curled or hooked termini of *Hemitrapa* spines probably afforded these disseminules some potential to become entangled in floating organic debris and, thus, enhance their dispersal in aquatic environments. Mutual entanglement may explain the close aggregations of some *Beipiaoa* seeds in the Jehol Group (Fig. 6A).

Compact gnetalean cones assigned to *Liaoxia* or *Ephedrites* from the Jehol Group (Sun et al., 2001; Rydin et al., 2006), and possibly *Leon-gathia* from the Koonwarra flora (Krassilov et al., 1998; Fig. 6N) have divergent setose bracts but these are likely to have functioned more for protection of the developing seeds from invertebrate herbivores than for dispersal (Fig. 6B, C). Similarly, the single spines of dispersed araucariacean cone scales, which are common in the Australian Jurassic and Cretaceous assemblages (Fig. 4AA–AD), probably functioned as a defence against herbivory of the developing cones, rather than for assisting zoochory.

5.5. Simple seeds and fruits

5.5.1. Observations

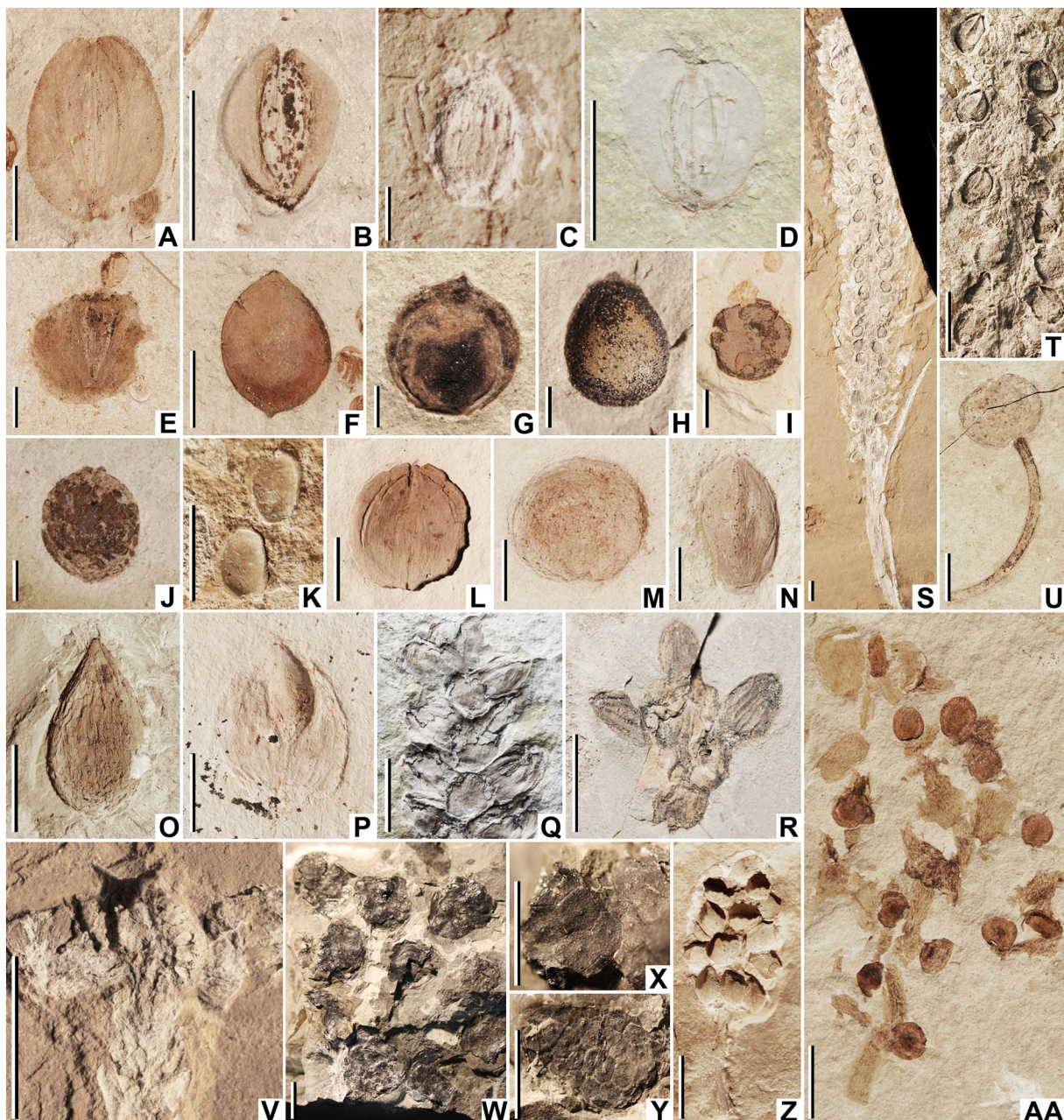
Relatively few obviously fleshy seeds are evident among the many disseminules represented in the four studied assemblages

(Supplementary Tables 1–4). A single example of a solitary globose seed borne on a slender stalk from the Yixian Formation (Fig. 5U) appears to have a slightly wrinkled or dimpled surface that suggests a strong degree of fleshiness. The seed is about 7 mm long, 10 mm wide, supported on a 22 mm long, 1 mm wide stalk. Although the stalk appears to lack a collar, and bears only a single seed, the seed-bearing unit is otherwise similar to those of *Ginkgo*. Ginkgoalean foliage is present in the Daohugou deposits but in the past has been associated with clusters of smooth *Allicospermum*-like seeds (5–12 mm long and 4–10 mm wide) borne on long stalks and attributed to *Yimaia* (Zhou et al., 2007, Figs. 2–4, 5B–F, 6C). Some other smaller (< 9 mm diameter) featureless dispersed seeds (Fig. 5I) in this assemblage might also be ginkgoalean.

In the Southern Hemisphere, *Ginkgo*/*Ginkgoites* leaves are unknown from the Talbragar flora. Ginkgoalean foliage and microsporangiate structures are present at Koonwarra, but their seeds have not been identified with confidence. However, there are several other

reproductive structures from both Talbragar and Koonwarra that are candidates for fleshy seeds/fruits. Among these, the Pentoxylalean cone *Carnoconites* possessed a compact head of seeds (Drinnan and Chambers, 1985; Howe and Cantrill, 2001) that has been interpreted to have been fleshy (Tiffney, 2004). Pentoxylalean seeds typically retain a three-dimensional shape when preserved in these lake deposits (Fig. 5K, V–Y; White, 1981) suggesting that they had a compression-resistant integument, but whether the outer coat was fleshy is unclear.

Examples of cone-borne or isolated, small (Fig. 5G, H, J) and medium-sized (Fig. 5F, I, L–O, Q), relatively smooth, spherical to pyriform, wingless seeds in the Koonwarra, Jehol and Daohugou assemblages may have been hard or fleshy. These seeds lack any obvious architectural modifications for dispersal, but they retain a more three-dimensional form than other impressions in the assemblages suggesting a stony, fleshy or leathery character. Another small seed type attached in clusters to a short cone(?) axis from Koonwarra is characterized by longitudinal ridges that also were resistant to compression (Fig. 5R). In



(caption on next page)

Fig. 5. Seeds adapted for wind dispersal and featureless or fleshy seeds of late Middle Jurassic to Early Cretaceous age from China and Australia. All scale bars = 5 mm for A, B, D–F, I, K–AA; 1 mm for C, G, H, J.

- A, Bi-winged elliptical seed, Daohugou, B0443.
- B, Bi-winged elliptical seed, Jehol Group, B0444A.
- C, Bi-winged elliptical seed, Talbragar, AMF134510.
- D, Obovate bi-winged elliptical seed, Daohugou, MES-NJU 57052.
- E, Araucarian seed with broad lateral wings, Daohugou, B0568B.
- F, Ovate featureless seed, Daohugou, B0464A.
- G, Circular seed with broad rim, Jehol Group, PB19200.
- H, Ovate seed impression with high relief, Koonwarra, MVP167729.
- I, Circular seed with thick, leathery, organic coat, Daohugou, B0371B.
- J, Featureless elliptical seed, Jehol Group, B0374.
- K, Two small, featureless, elliptical seeds, Talbragar, MMF3151.
- L, Circular seed with broad rim, Jehol Group, B0247A.
- M, Circular seed with compression creases, Jehol Group, B0499B.
- N, Elliptical seed or bract, Jehol Group, B0467.
- O, Ovate seed with linear ornament, Koonwarra, MVP167727.
- P, Elliptical seed with basally expanded wing, Jehol Group, B0278.
- Q, Elliptical seeds with weak longitudinal ridging borne in a conifer cone, Daohugou, B0111B.
- R, Longitudinally ribbed ovate seeds attached to cone axis, Koonwarra, MVP230895.
- S, Lax cone bearing carinate seeds, Talbragar, AMF59822.
- T, Enlargement of carinate seeds, Talbragar, AMF59822.
- U, *Ginkgo*-like seed on stalk, Jehol Group, INFO058.
- V, Diminutive seeds in terminal cone of *Allocladus cribbii* Townrow, Talbragar, AMF59988A.
- W, *Carnoconites cranwellii* Harris, compact cone, Koonwarra, MVP167514.
- X, *Carnoconites cranwellii* Harris, details of seeds, Koonwarra, MVP16751.
- Y, *Carnoconites cranwellii* Harris, details of seeds, Koonwarra, MVP167516.
- Z, *Carnoconites* sp., compact cone with compression-resistant seeds, Talbragar, MMF3163.
- AA, Disaggregated cone with circular, featureless seeds, Jehol Group, PB18986.

some cases, small featureless seeds occur clustered on large showy cones (Fig. 5S, T, U, Z) or are tightly packed into composite fruiting structures (Fig. 5V–Y) that might have been attractive to specialist herbivores.

5.5.2. Remarks

Various herbivorous and omnivorous mammals are known to consume extant *Ginkgo biloba* seeds (Singh et al., 2008). van der Pijl (1966, 1982) and Tiffney (1984) suggested that the odoriferous, somewhat fleshy seeds of ginkgoaleans may have attracted reptilian/dinosaurian herbivores in the Mesozoic. The loss of these endozoochorous agents at the end of the Cretaceous has even been invoked as a possible cause for the decline of Ginkgoales in the Cenozoic (Rothwell and Holt, 1997). Del Tredici (1989) alternatively invoked multituberculates as potential consumers/dispersers of ginkgoalean seeds. Other potential mammalian herbivores of the Mesozoic (marsupials and zhelestid eutherians) radiated mainly in the Late Cretaceous (Grossnickle and Newham, 2016). Those radiations are too late for these groups to have been involved in the dispersal of ginkgoalean seeds identified in this study, but multituberculate mammals (ranging from Jurassic to Eocene) might have been involved in early zoochory (Collinson and Hooker, 1991). A contrasting opinion raised by Mack (2000) argued that the foetid pulp of *Ginkgo* seeds is unpalatable to most herbivores and that it is equally plausible that this character originated as a defence against frugivory.

The lack of obvious structural modifications to assist wind or water transport on the diverse range of small featureless seeds suggests that many may have been dispersed by simple barochory or developed simple fleshy coats as a reward for frugivores and promotion of endozoochory.

Yang and Wang (2013) reported fleshy cones of *Ephedra* from the Yixian Formation. Modern *Ephedra* have three main dispersal strategies (Hollander and Wall, 2009; Hollander et al., 2010). Those producing colourful fleshy cones (section *Ephedra*) are mainly dispersed over tens to thousands of metres via ingestion and excretion by birds. Those with dry coriaceous bracts and large, unwinged seeds (Section *Asacara*) are dispersed by rodents that cache seeds in the shallow subsurface up to tens of metres from the source. Those with dry membranous winged cone bracts with small attached seeds (Section *Alatae*) are presumed to be dispersed by wind over variable distances. *Ephedra carnosus* Yang et

Wang, 2013 from the Yixian Formation had an apparently fleshy ovuliferous cone and is interpreted to have been a potential early candidate for bird dispersal (Yang and Wang, 2013). Early angiosperms from the studied localities also produced relatively simple unornamented seeds (Fig. 7A, F) that may also fall into this broad category but there is reason to suspect that hydrochory was an important dispersal mechanism in their lifecycles as outlined below.

5.6. Vertebrate-ingested seeds

5.6.1. Observations

We did not examine vertebrate fossils for the presence of preserved seeds in the alimentary tract or in coprolites. Nevertheless, we surveyed the literature for examples of fossil vertebrate gut contents from the four studied units. Two occurrences are notable: seeds in the gut of *Jeholornis prima* (Zhou and Zhang, 2002); and a dense mass of irregularly orientated reticulate-ornamented seeds identified as *Carpolithes pachythelis* Sun et Zheng (in Sun et al., 2001; Fig. 8J).

5.6.2. Remarks

To date, no terrestrial vertebrates have been recorded from the Talbragar Fossil Fish Bed, and the only terrestrial vertebrate remains in the Koonwarra fossil bed are dispersed feathers. Much richer terrestrial vertebrate assemblages occur in the two Chinese fossil biotas.

Zhou and Zhang (2002) identified over 50 conspecific seeds preserved in the stomach of a specimen of *Jeholornis prima* from the Jiufotang Formation (Jehol Group). The seeds are roughly circular (possibly spherical before compression), 8–10 mm in diameter and bear only indistinct longitudinal grooves and ridges. The seeds were initially referred to the form genus *Carpolithes* but Zhou and Wu (2006) suggested that they were of ginkgoalean affinity. *Jeholornis prima* was a large (> 70 cm long) archaic arboreal bird with a long tail and a few reduced conical teeth. The combination of a large number of intact seeds and reduced dentition suggests that the seeds were ingested whole, to be broken down (or at least their fleshy coats removed) in a large crop. Zhou and Zhang (2003), Zhou (2006) and Zheng et al. (2011) also noted that several Early Cretaceous birds (e.g. *Sapeornis*) had well-developed digestive systems with preserved gizzard stones in a crop—a feature characteristic of modern herbivorous birds. Although

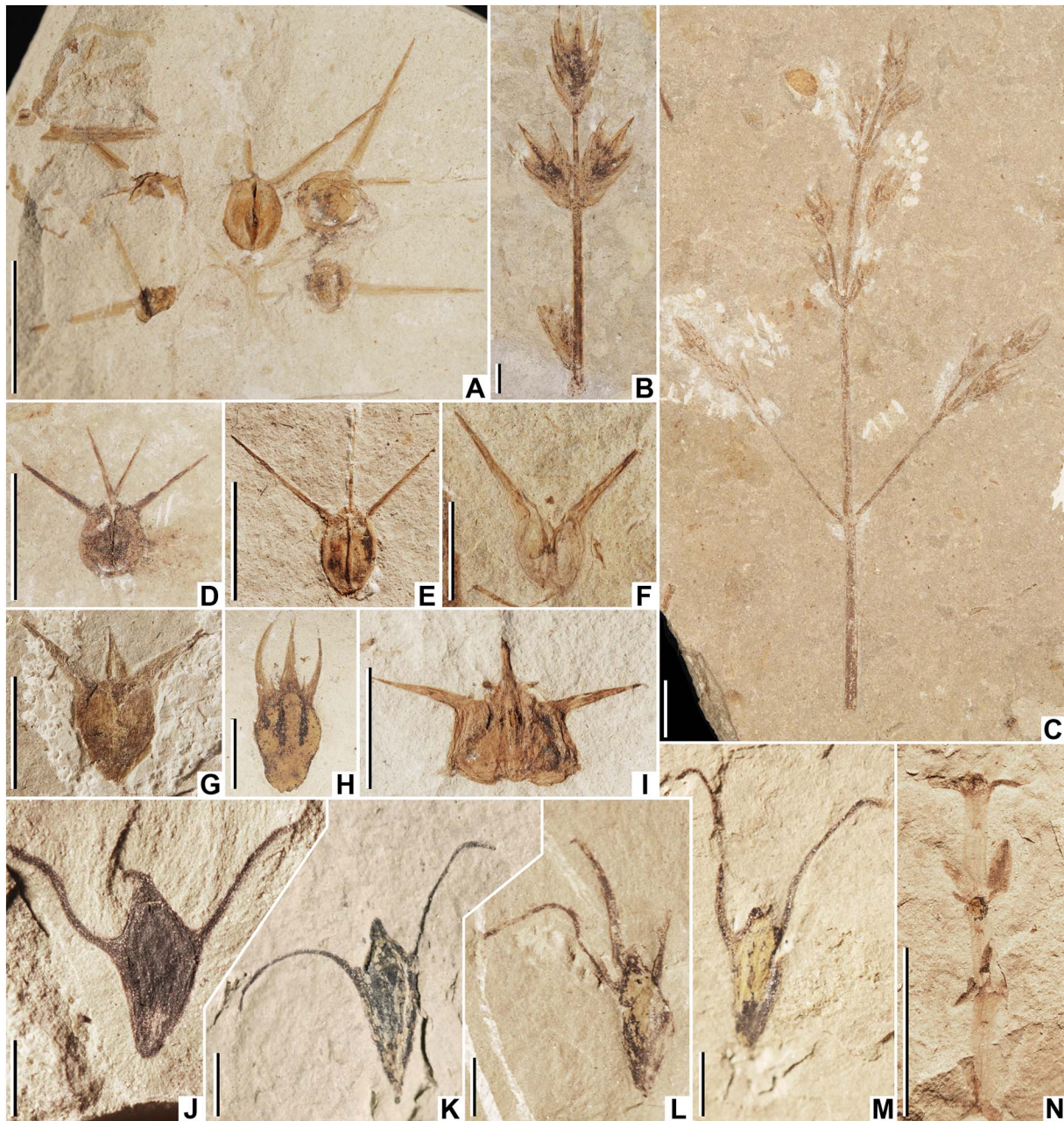


Fig. 6. Seeds with spines and hooks of late Middle Jurassic to Early Cretaceous age from China and Australia. All scale bars = 5 mm.

- A, *Beipiaoa rotunda* Dilcher, Sun et Zheng, Jehol Group, PB18958.
 B, *Ephedrites chenii* (Cao et Wu) Guo et Wu X.W., Jehol Group, PB19168.
 C, *Ephedrites chenii* (Cao et Wu) Guo et Wu X.W., Jehol Group, PB18313.
 D, *Beipiaoa parva* Dilcher, Sun et Zheng, Jehol Group, PB18953.
 E, *Beipiaoa parva* Dilcher, Sun et Zheng, Jehol Group, A20-a-xxx.
 F, *Beipiaoa parva* Dilcher, Sun et Zheng, Jehol Group, PB18957.
 G, *Beipiaoa spinosa* Dilcher, Sun et Zheng, Jehol Group, PB18314.
 H, *Beipiaoa spinosa* Dilcher, Sun et Zheng, Jehol Group, PB18959.
 I, *Beipiaoa spinosa* Dilcher, Sun et Zheng, Jehol Group, PB18960.
 J, *Hemitrappa* sp., Koonwarra, MVP167749.
 K, *Hemitrappa* sp., Koonwarra, MVP3526B.
 L, *Hemitrappa* sp. Two overlapping seeds, Koonwarra, MVP167760.
 M, *Hemitrappa* sp., Koonwarra, MVP3520.
 N, *Leongathia elegans* Krassilov, Dilcher, Douglas, Koonwarra, MVP205117.

nothing can be determined about the viability of the seeds passing through the digestive tract of these animals, the large monospecific assemblage of seeds in the gut of *J. prima* indicates specific targeting of a single seed type for food. Seeds provide high-energy nutrition in small, easily manipulated packages, and were clearly an important food

item for birds very early in their evolutionary history. It is likely that plants rapidly took advantage of this relationship to enhance seed dispersal.

Several pterosaur fossils have been described from the Daohugou and Jehol biotas but no published examples have yet revealed evidence

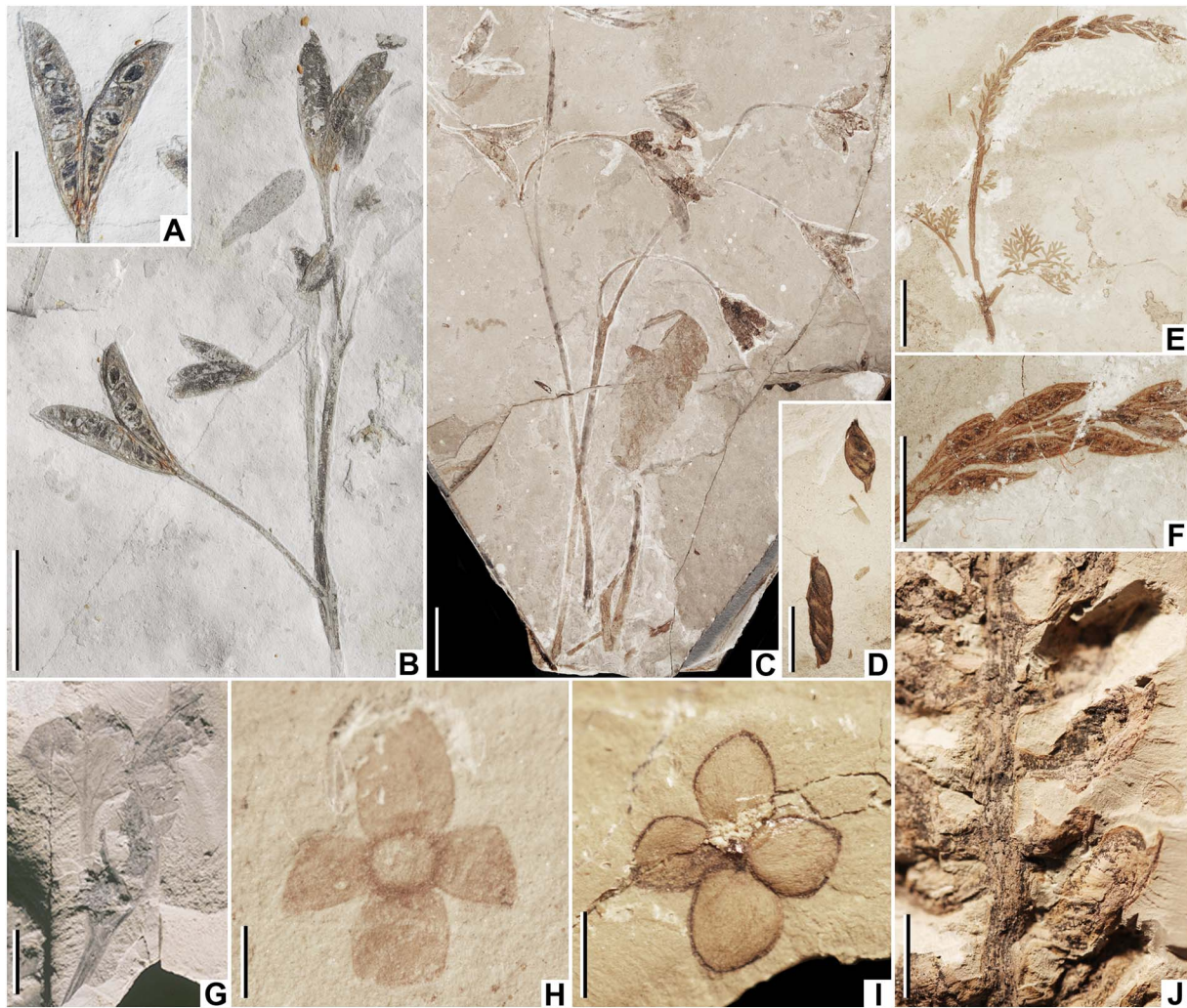


Fig. 7. Early angiosperms and flower-like structures of Early Cretaceous age from China and Australia.

- A, *Sinocarpus decussatus* Leng et Friis, Jehol Group, B0162A.
 B, *Sinocarpus decussatus* Leng et Friis, Jehol Group, B0162A.
 C, *Sinocarpus decussatus* Leng et Friis, Jehol Group, B0168A.
 D, *Archaeofructus liaoningensis* Sun, Dilcher, Zheng et Zhou, Jehol Group, PB18939-40.
 E, *Archaeofructus liaoningensis* Sun, Dilcher, Zheng et Zhou, Jehol Group, PB19283.
 F, *Archaeofructus liaoningensis* Sun, Dilcher, Zheng et Zhou, Jehol Group, PB19283.
 G, Angiosperm twig with attached leaves and flower, Koonwarra, MVP167565.
 H, Cruciform structure 1, Koonwarra, MVP167763.
 I, Cruciform structure 2, Koonwarra, MVP167762A.
 J, *Palissya* sp., Koonwarra, MVP167742.

of feeding on seeds by way of dentition characters, gut contents or coprolites. Nevertheless, [Fleming and Lips \(1991\)](#) presented an argument that this was a morphologically and behaviourally diverse animal group that ought to have developed frugivorous/granivorous habits like ecologically similar extant groups (birds and bats). They argued that upland fruit/seed-feeding pterosaurs would have had much lower chances of fossilization compared to their coastal or lowland relatives and their remains may simply have not been discovered yet. [Wang and Zhou \(2006\)](#) also noted that, although most Jehol Group pterosaurs were piscivorous, some have adaptations for other feeding styles including filtration, insectivory, frugivory or omnivory.

The dense mass of *Carpolithes pachythesis* Sun et Zheng documented by [Sun et al. \(2001\)](#) from the Yixian Formation and re-illustrated herein ([Fig. 8J](#)) may represent a regurgitant mass or coprolite containing numerous undigested woody seed coats. The seeds are small (slightly over 4 mm long) and apparently woody but possibly enveloped by a fleshy coat during life, and they are densely aggregated on the bedding plane. They are collectively surrounded by dark, amorphous organic debris.

Several other irregular aggregations of simple seeds surrounded by amorphous material from the same formation may represent similar coprolites or regurgitant masses ([Fig. 8E, I](#)). Which, if any, vertebrate consumed these seeds is unknown but we assume it was a small animal of selective diet—possibly an early bird.

Few other avenues of research linking Mesozoic macroherbivores and seed/fruit food are available. However, an analysis of microwear patterns on teeth might provide additional insights into the feeding habits of terrestrial vertebrates in the two Chinese fossil biotas. [Brocklehurst \(2017\)](#) noted that among both mammals and dinosaurs, herbivores tended to develop a greater range of morphological innovations (e.g., varied tooth morphologies, horns, antlers, trunks, long necks, great size, frills and duckbills) compared with the more morphologically conservative lineages of Carnivora and Theropoda. Thus, even in the absence of preserved gut contents, coprolites, or specialized fleshy seeds or fruits, it might be possible to infer endozoochory or at least frugivory by analysis of fossil vertebrate dentition.

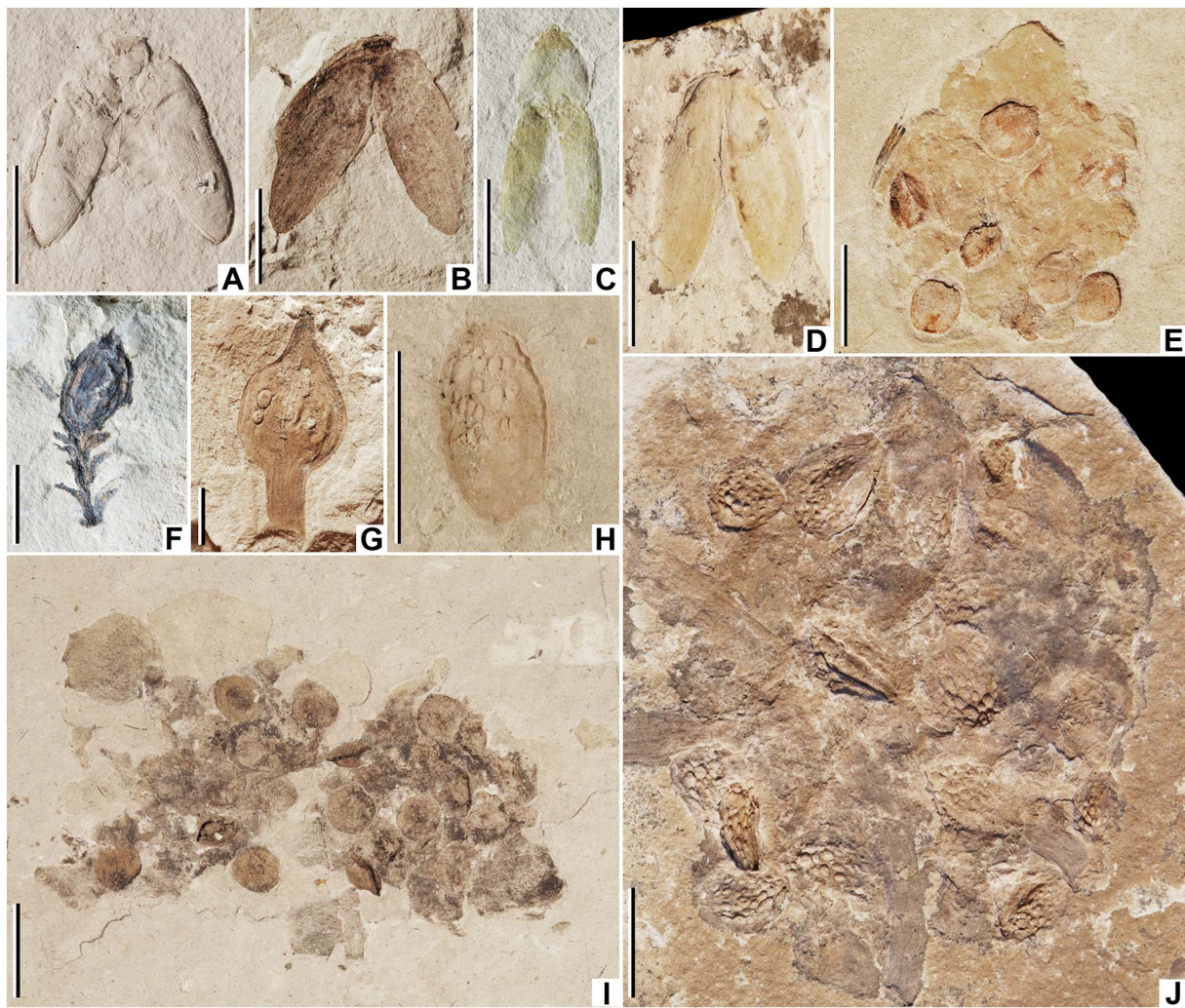


Fig. 8. Examples of animal interactions with plants of late Middle Jurassic to Early Cretaceous age from China and Australia.

A, C, Coleopteran body impressions, Jehol Group, B0394A and B0218 respectively.

B, D, *Schizolepidopsis jeholensis* (Yabe et Endo) Doweld illustrated with wings to the bottom and matching the morphology and size of co-preserved coleopterans, Jehol Group, PB19133 and PB18278 respectively.

E, Featureless circular seeds preserved within an amorphous mass possibly representing a coprolite, Jehol Group, PB19199.

F, Seed- or fruit-like apical gall on a conifer twig (*Pagiophyllum beipiaoense* Sun et Zheng), Jehol Group, B0063.

G, Probable apical gall on ?gnetalean stem apex, Jehol Group, A20-103.

H, Elliptical seed with elliptical scars, Lushanfeng, Fangshen (Haifanggou Formation, lateral equivalent of fossiliferous beds at Daohugou), unregistered specimen 193 IVPP.

I, Featureless circular seeds preserved within a field of amorphous organic material possibly representing a coprolite or regurgitant mass, Jehol Group, PB19001.

J, Punctate seeds (*Carpolithes pachythelisi*) preserved with leaf/stem fragments within a field of amorphous organic material possibly representing a coprolite or regurgitant mass, PB19152.

5.7. Aquatic dispersal

5.7.1. Observations

Fully aquatic vascular plants are scarce in the studied Jurassic and Cretaceous assemblages. The slender-stemmed vascular plant from the Talbragar Fossil Fish Bed that White (1981, Fig. 53) referred to *Selaginella* might have been fully aquatic, producing water-borne seeds, but disseminules have not yet been identified for this plant. The Koonwarra Fossil Bed hosts some diminutive seeds unspecialized for wind or animal transport (Fig. 5H) but these also lack features definitive for aquatic dispersal. The Jehol Group has yielded several seed plants that may have been fully or partly aquatic. *Archaeofructus* (Fig. 7D–F), considered partly or fully aquatic by Friis et al. (2003) has seeds that are more or less featureless, ellipsoidal and 1–2 mm long. In *Sinocarpus* (Fig. 7A–C), an early angiosperm from the same unit, the seeds/ovules are also 1–2 mm long, somewhat flattened and faintly ribbed (Leng and Friis, 2003). An early angiosperm from the Koonwarra Fossil Bed

(Fig. 7G) has very small flowers, and presumably produced diminutive seeds, but their manner of dispersal is uncertain. The Daohugou flora contains few plants that could be considered fully aquatic, although equisetaleans and some bryophytes from that site may have been partially aquatic. Aquatic fern megaspores referable to *Arcellites* are common in strata equivalent to the Jehol Group in northeastern China (Li and Batten, 1986) and in strata equivalent to or slightly younger than the Koonwarra Fossil Bed in southeastern Australia (Tosolini et al., 2002).

5.7.2. Remarks

The absence of specialized flotation characters (e.g., aerenchyma or bladders) on any of the disseminules suggests that none of the plants in the four studied assemblages was adapted to long-distance aquatic dispersal of seeds or other propagules. Nevertheless, comparisons with extant aquatic taxa in Cabombaceae, Zannichelliaceae and Alismatales led Friis et al. (2003, 2006) to suggest a fully aquatic habit for

Archaeofructus, although others have suggested an emergent state for the reproductive parts (Sun et al., 2002). In either case, being surrounded by water, transport of the seeds of this plant in an aquatic environment (either by flotation and movement by winds or transport in the water column by currents) seems likely. Although *Sinocarpus* has broader leaves that are more typical of a terrestrial plant, the pod-like simple fruits, small unspecialized seeds, and slender, gracile axes are similar to those of *Archaeofructus* and, together with their recovery from equivalent lacustrine deposits, suggest a broadly similar—perhaps semi-aquatic—growth habit in a lake-margin environment. Since several detached seed pods are represented in the Jehol Group assemblage (Fig. 7E), the pod may have been the main dispersal unit in *Archaeofructus* and *Sinocarpus*, as it is for some modern legumes (Beresford-Jones, 2011).

Diminutive size is a common trait among modern water-dispersed diaspores (Howe and Smallwood, 1982) and it is possible that some small featureless seeds in the Koonwarra Fossil Bed were produced by aquatic plants and dispersed in water but definitive evidence is lacking. Several diminutive, cruciform, flower-like structures have been illustrated from the lacustrine Koonwarra Fossil Bed (Fig. 7H–J), but no seeds have been associated with these fossils and they may alternatively represent dehiscent bryophyte sporangia or even some vegetative organ (Drinnan and Chambers, 1986). Dispersed megaspores referable to *Arceclites* have elaborate proximal acrolamellae that may represent an adaptation to flotation and were probably produced by semi-aquatic ferns (Batten, 2009). Their occurrences in roughly coeval strata in northeastern China and southeastern Australia (Li and Batten, 1986; Tosolini et al., 2002) are among the earliest examples of this group and suggest that heterosporous ferns rapidly dispersed throughout the world in the Early Cretaceous contemporaneously with angiosperms.

5.8. Cryptic seeds

5.8.1. Observations

All of the studied assemblages contain some pteridosperm or conifer groups that, based on the size of their reproductive structures, presumably bore very small (< 2 mm diameter) seeds. Among these groups are Caytoniales, putative Peltaspermales (*Scytophyllum*) and Leptostrobales (= Czekanowskiales) from Daohugou, Leptostrobales from the Yixian Formation, and Palissayaceae from Talbragar and Koonwarra. Some conifers with scale-like foliage attributed to *Brachyphyllum*, *Allocladus* or *Cyparissidium* species in all of the studied assemblages appear to be linked to small cones that could only have produced minute seeds. In a few cases, diminutive seeds (< 1 mm in diameter) are preserved in situ within such cones (Fig. 2G).

5.8.2. Remarks

The dispersal mechanism for this category of seeds is unclear, however, their small size and protection within cupules or spiny cones would probably have made them unfavourable targets for mammalian, avian or reptilian herbivores, hence, dispersal by endochory was unlikely unless the herbivore consumed the whole cone/cupule (Pott and McLoughlin, 2014). The diminutive size of such seeds means that they were probably readily moved by wind, hence, anemochory is the most likely dispersal syndrome even in the absence of specialized wing structures. Simple barochory is also possible, especially in more closed-forest communities.

5.9. Arthropod interactions with seeds

5.9.1. Observations

We did not detect any evidence of invertebrate-mediated propagule dispersal but we identified several features related to interactions with seeds or axis apices that are noteworthy. One seed from the Haifanggou Formation (equivalent to the Jiulongshan Formation at Daohugou) bears elliptical scars on the distal half that may represent predation features (Fig. 8H), although such features may alternatively represent

simple ornamentation (Ricardi-Branco et al., 2013). Several axis apices in the Daohugou and Jehol assemblages have superficial similarities to seeds or fruiting structures (Fig. 8F, G), but we identify them as galls. Paired seeds with apical wings attributed to *Schizolepidopsis* (Fig. 8B, D) bear remarkable resemblances in size and shape to certain coleopterans (Fig. 8A, C), which are widely represented in the same assemblages (Ren et al., 2010).

5.9.2. Remarks

Arthropod damage to foliage is common and diverse in all of the studied assemblages but evidence for animalian interactions with the seeds is scarce—with just a single example of possible seed predation (Fig. 8H).

Dispersed *Schizolepidopsis* seeds are among the most distinctive and common seeds in the Jehol Group deposits. Mimesis of dispersed *Schizolepidopsis* by ground-dwelling coleopterans may have been an effective strategy for avoiding predators in forest floor litter communities (Fig. 8A–D).

The swollen stem apices in the Daohugou and Jehol Group assemblages that superficially resemble seeds or fruiting structures lack diagnostic characters, such as wings, micropyle and associated bracts, or they have features typical of an expanded stem, i.e., possession of reduced lateral leaves. We interpret these ‘pseudo-fruits’ as apical galls on stems (Fig. 8F, G), probably induced by arthropods.

6. Discussion

6.1. Taphonomic influences

All four studied fossil assemblages are preserved in thinly laminated claystones and siltstones typical of quiet, shallow-water lacustrine conditions. Three of the four deposits contain abundant thin ash beds, the rapid deposition of which may have facilitated fossilization of the biota. Only the Koonwarra deposit lacks obvious ash layers. The thin claystone–siltstone/sandstone laminae couplets of that deposit may represent seasonal varves in a cold-climate, high-latitude setting (Waldman, 1971), since coeval deposits in the region host ice-rafted dropstones, glendonites and other cold-water sedimentary indices (Frakes and Francis, 1990; Frakes and Krassay, 1992; Frakes et al., 1995; Constantine et al., 1998). Apart from several feathers preserved at Koonwarra (Talent et al., 1966), the Australian fossil assemblages differ from their Chinese counterparts by lacking terrestrial vertebrates. However, in representation of sedimentary facies and general fossil content, the four Lagerstätten constitute similar depositional systems and host similar biotas. They are all rich in fish, insects, aquatic invertebrates and plant foliage. On this basis, the assemblages ought to be broadly comparable in terms of the representation of plants from the surrounding vegetation and the range of disseminule strategies that these plants employed.

All four assemblages host a broad spectrum of free-sporing and seed-producing plants. In each assemblage, foliage is well preserved, suggesting minimal or non-turbulent transport and deposition in low-energy conditions. The assemblages typically lack any common alignment of fossils on bedding planes indicating an absence of strong currents. All of the assemblages preserve diverse plant reproductive structures, but the Talbragar flora has notably fewer isolated seeds than the other deposits. Several seeds at Talbragar are retained on larger reproductive structures, such as cones or cone scales. This might indicate nearshore accumulation of plants at Talbragar. Otherwise disseminules show no obvious signs of winnowing or sorting in the assemblages.

6.2. Vegetation composition and structure

The vegetation contributing to each fossil assemblage appears to have consisted of a similar mix of broad- and scale-leaved canopy and mid-storey seed plants, and a wide range of understorey free-sporing

plants, although the representation of specific plant groups varies between the assemblages (Supplementary Data Tables 1–4). In some cases, these differences may reflect sampling biases, but broadly, the variance can be interpreted as genuine geographic differentiation of the floras or temporal (evolutionary) shifts in plant-group representation.

The main differences between the Jurassic and Cretaceous assemblages are the greater representations of gnetaleans and angiosperms

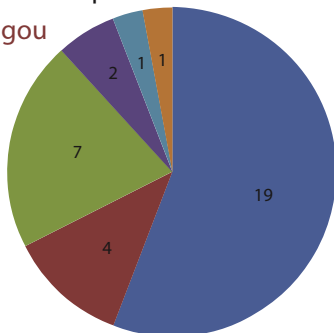
and reduction in seed ferns in the latter. Only the Koonwarra and Jehol floras contain plants confidently attributable to angiosperms.

The collective northern (Chinese) floras contain a richer representation of Gnetales than their southern (Australian) counterparts. Moreover, Pinales and Leptostrobales are restricted to the Northern Hemisphere assemblages. In contrast, Pentoxylales and Palissyaceae are exclusive to the Southern Hemisphere floras, and araucariacean

Relative diversity of spore-bearing plants and dispersed seeds

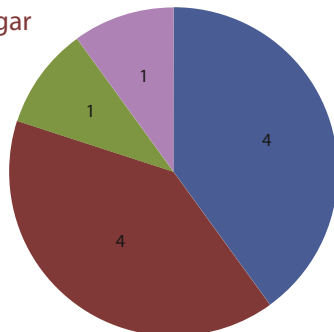
Daohugou

N = 34



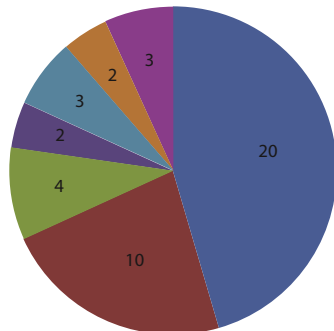
Talbragar

N = 10



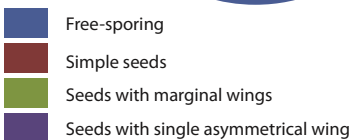
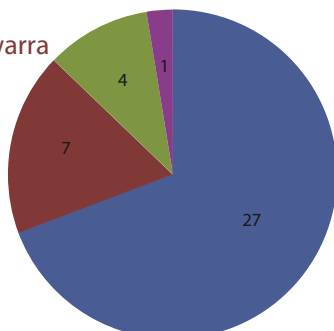
Jehol

N = 44



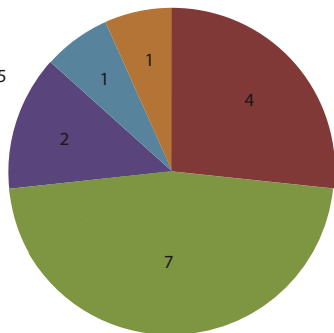
Koonwarra

N = 39

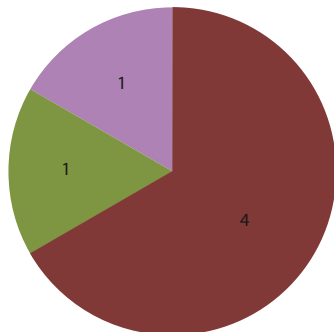


Relative diversity of seeds

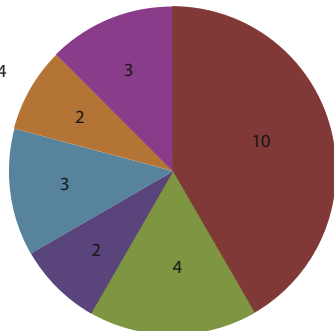
N = 15



N = 6



N = 24



N = 12

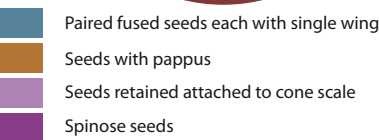
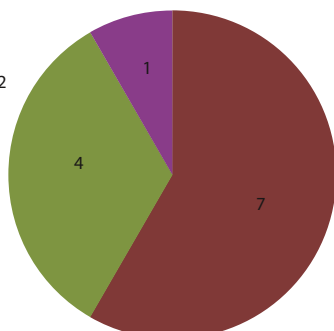


Fig. 9. Pie charts of the diversity of disseminule strategies in the four studied assemblages of late Middle Jurassic to Early Cretaceous age from China and Australia. The first column incorporates free-sporing plants and dispersed seed types; the second column compares dispersal syndromes based on seeds alone.

conifers and putative Umkomasiales are substantially more abundant in that region. Bennettitales are well represented in the Chinese floras but are sparse or absent from the two studied Australian assemblages, although this group is known to occur in low to moderate numbers and diversity in coeval deposits elsewhere on that continent (Hill et al., 1999; McLoughlin et al., 2000; McLoughlin and Pott, 2009).

The Jehol Group flora has a particularly high diversity of foliage types (at least 52 species: Wu, 1999, 2003; Sun et al., 2001) but this may be a function of sampling intensity. By contrast, the single small outcrop hosting the Talbragar flora has yielded just 13 foliage-based species. The Koonwarra flora is particularly rich in free sporing plants (about 11 bryophyte gametophyte types and 16 lycophytes, sphenophytes and ferns). This may reflect vegetation adapted to cooler and wetter conditions experienced at southern high latitudes during the Aptian compared to the other sites. All of the floras except that from Koonwarra contain multi-veined, broad-leafed conifers. All of the floras contain a strong representation of Ginkgoales, except the Late Jurassic Talbragar flora. This appears to be part of a general dearth of Ginkgoales from Australian Jurassic floras (Turner et al., 2009). Aquatic plants have a patchy or equivocal expression during the Jurassic but appear to be represented by at least one angiosperm species by the Early Cretaceous (preserved in the Jehol Group). Plants with very broad leaves do not noticeably dominate any of the studied assemblages. Rather, gymnosperms with scale-, needle- and strap-like leaves are relatively common. On this basis, we interpret the canopies of the parent vegetation for all four assemblages to have been relatively open (i.e. woodland-type communities).

6.3. Cathaysian versus Gondwanan disseminule strategies through time and space

Around 56 seed types attributable to seven broad morphological categories in addition to numerous spore and vegetative propagation strategies were identified in the four studied assemblages (Supplementary Data Tables 1–4). The representation (species richness) of each seed category varies between the four assemblages (Fig. 9).

Free-sporing plants are well represented in all assemblages (Fig. 9). This is to be expected for fossil accumulations derived from vegetation growing in relatively moist, lake-margin settings. In addition to liberating spores, most of the bryophytes, lycophytes, sphenophytes and ferns representing this category probably also underwent vegetative reproduction via the production of tubers, rhizome division or suckering.

Simple wingless seeds markedly increase in number of taxa from the Jurassic to Cretaceous floras of both hemispheres, although there is no significant change in this group as a proportion of the seed flora diversity (Fig. 9). The increase in number of simple seeds may correspond to the persistence of Pentoxylales, Ginkgoales into the Cretaceous, together with the rise of new angiosperms and taxacean and podocarp conifers producing equivalent seed types.

Platyspermic seeds with marginal wings, i.e., those with symmetrical wings flanking the seed margins, are more or less common throughout all the studied assemblages. These may have been produced by a broad range of seed fern, conifer and gnetalean groups. Seeds in this category were probably produced by different families/orders of these groups on either side of the Tethys Ocean. For example, Umkomasiales and araucarian conifers probably produced seeds of this type in southeastern Gondwana, but Gnetales, cupressacean and podozamitacean conifers and possibly Caytoniales were more important producers of this seed type in China.

Seeds with single asymmetrical wings, and those with paired, fused seeds with apical wings are restricted to the Chinese assemblages. This probably reflects the restriction of the inferred parent plants (Pinaceae) to the Northern Hemisphere. Seeds with a pappus are similarly restricted to China. That is, they occur in assemblages where bennettitalean foliage is relatively common. The strong representation of

pappus-bearing and winged seeds of all types suggests that each assemblage was characterized by relatively open vegetation in which anemochory was a viable dispersal mechanism for plants of a range of statures.

Seeds retained in attachment to cone scales were recorded only in the Talbragar assemblage. This is a feature characteristic of some araucarian conifers. Araucariaceae foliage (assigned to '*Agathis*' *jurassica* by White, 1981) is very commonly associated with such seed-bearing scales in the Talbragar assemblage. Araucariacean foliage is also common in the Koonwarra assemblage but the affiliated seeds at that site were shed separately from the cone scales in a manner similar to the strategy of *Wollemia* (Chambers et al., 1998). Araucariacean foliage and seeds are scarce in the Chinese floras (Fig. 5Q).

Spinose seeds/fruits are represented only in the Cretaceous assemblages of both China and Australia. Although it might be argued that spiny seeds appeared as an adaptation to take advantage of new animal groups with fur and feather indumenta, this type of seed may simply reflect the invasion of freshwater habitats by several vascular plant groups and the development of spines to facilitate entanglement in floating debris for dispersal or as anchoring devices in soft substrates. The specific architecture of spinose seeds differs between the Chinese and Australian examples and probably reflects independent development of such appendages on landmasses either side of the Tethys Ocean.

There are no strong differences in seed dimensions between the studied assemblages except for a weak trend in the Chinese floras of reduction in size between the Daohugou and Jehol floras (Fig. 10). Ten species (66%) of the seeds documented in the Daohugou flora are > 10 mm long. In the Jehol flora, only four species (16%) of the seeds exceed 10 mm in length. The Australian floras do not show any clear change in seed dimensions through time—perhaps owing to the lesser general representation of seeds in those assemblages. The reduction in seed size between the Middle Jurassic and Early Cretaceous of China might be a function of several biological pressures. Seed size in modern plants has a complex relationship to both biotic and physical environmental parameters. Large seeds can develop in regions with drier, low-nutrient soils to provide improved chances of seedling survival. In turn, larger seeds may then become a more attractive food source for herbivores (Leslie et al., 2017). Ruderal plants, with rapid growth rates and short lifespans tend to have smaller and relatively more abundant seeds compared to K-strategist plants, which invest more energy in providing a food resource for the germling (Gibson and Gibson, 2006). However, pressure from herbivores can also induce a reduction in seed size; smaller seeds being more difficult to detect and providing less nutrition for granivorous animals (Thompson, 1987). Herbivory pressure is not restricted to vertebrates. In this respect, it is pertinent to note that seed size reduction from the Jurassic to Early Cretaceous of China corresponds to the transition between Labandeira's (2006) terrestrial arthropod herbivore expansion phases 3 and 4 after which modern insect herbivory patterns developed.

Lacustrine assemblages have a special role to play in understanding biotic community relationships through time. Lakes commonly accumulate biotic remains from a broad hinterland source area providing an excellent representation of the local biota, they preserve both animals and plants, and the quality of fossil preservation is commonly exquisite. Increasing numbers of lacustrine Lagerstätten of various ages are now being investigated globally (Lee et al., 2016). Since seeds are commonly well represented in such deposits, lacustrine assemblages have the potential to enable researchers to track the patterns of plant disseminule representation throughout the 370 million years of seed-plant history.

6.4. Plant-animal co-evolution

Despite the increase in birds and/or feathered dinosaurs and mammals through Middle Jurassic to Early Cretaceous times, we find no clear indication of plants utilizing vertebrate indumenta for seed

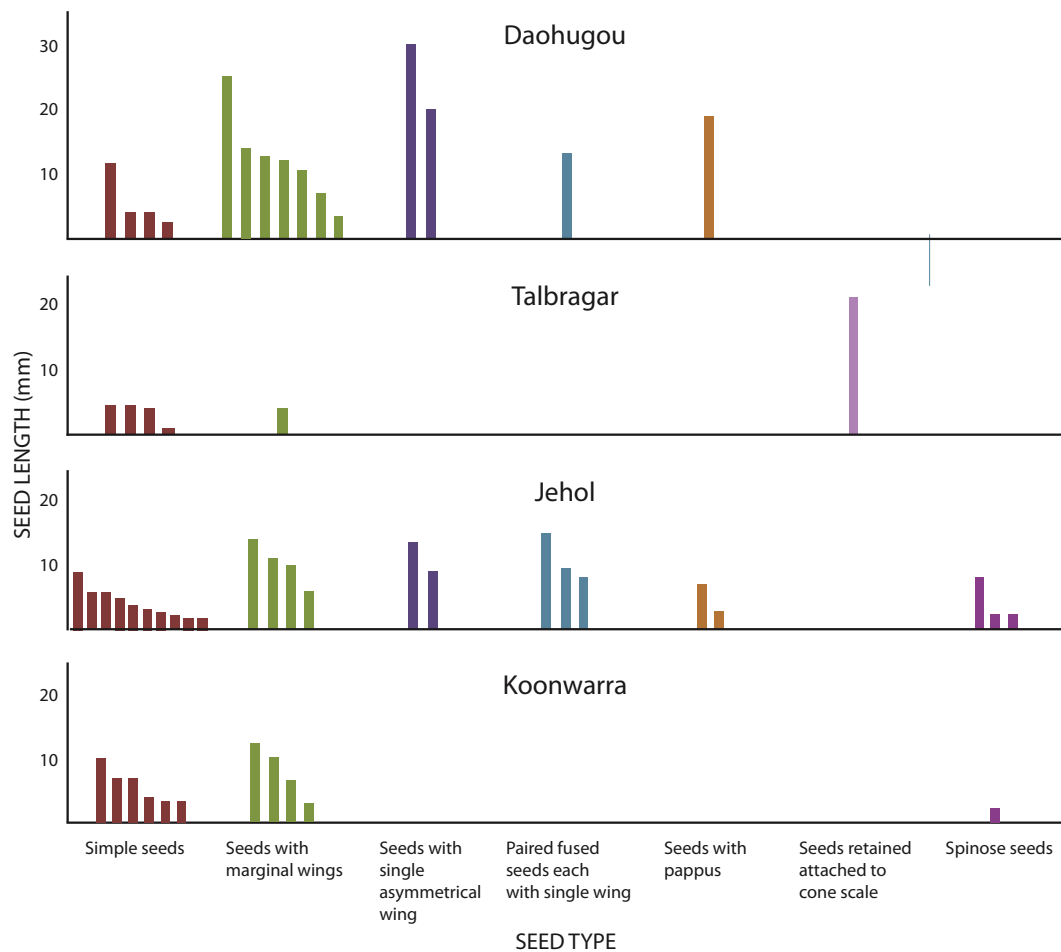


Fig. 10. Histograms of seed length for seven categories of dispersal syndromes in plants of late Middle Jurassic to Early Cretaceous age from China and Australia: simple seeds; seeds with marginal wings; seeds with single asymmetrical wing; paired fused seeds each with single wing; seeds with pappus (pappus length not included); seeds retained attached to a cone scale; spinose seeds (spine length not included).

dispersal (epizoochory) in the four studied assemblages. The development of spinose projections on disseminules in the four studied floras probably represents adaptations for defence or for anchoring seeds in soft substrates.

Endozoochory was likely for some seeds (especially simple, unadorned types) in each of the assemblages. The presence of simple seeds in the gut content of early birds in the Jehol biota (Zhou and Zhang, 2002) clearly indicates that birds were targeting such seeds as rich nutritional packages. Further, the occurrence of some seeds with apparent woody integuments occurring in irregular clusters of organic debris suggests emplacement as the regurgitant masses or coprolites of some vertebrate. Our data indicate that unadorned stony or fleshy seeds (or fruits) were present in moderate numbers and diversity during the late Middle Jurassic to Early Cretaceous at middle to high latitudes. Apparently, such seeds were an increasingly important resource for herbivores into the late Mesozoic, developing interactions with animals through the plant's provision of a food source traded for enhanced seed dispersal as outlined in several studies. For example, fleshy diaspores of both Podocarpaceae and Ephedraceae appear to have been present globally by the Early Cretaceous (Archangelsky, 1966; Rydin et al., 2004; Yang and Wang, 2013). In Patagonia, an example of the Toarcian–Bajocian neornithischian dinosaur *Isaberrysaura mollensis* Salgado, Canudo, Garrido, Moreno-Azanza, Martínez, Coria et Gasca, 2017 was preserved with gut contents including large (up to 35 mm diameter) cycadalean seeds and smaller (< 10 mm diameter) platyspermic seeds (Salgado et al., 2017). Even some Cretaceous crocodylomorphs, such as *Chimaerasuchus paradoxus* from China and *Hylaeochampsidae* from

Europe developed heterodont dentition interpreted to reflect adaptation to herbivory and particularly to a diet of fruits/seeds (Wu et al., 1995; Ósi and Weishampel, 2009). The fossil record has not yet revealed convincing evidence that pterosaurs were significant dispersers of seeds.

Inference of plant fitness and success based on interactions with animals is difficult even in modern ecosystems. The past four decades of research has revealed that the influences on plants of a particular frugivore are generally weak and vice versa (Herrera, 1987, 1998, 2002; Jordano, 1995a, 1995b, 2000; Jordano et al., 2007). Instead, plant-frugivore interactions are important at the group level, whereby multiple animals typically feed on any one fruit/seed type and any one animal generally feeds on a broad selection of fruits/seeds at a given time. In most cases, fitness is not tied to the success a single interacting producer-consumer couplet (Eriksson, 2016).

Wing and Tiffney (1987) argued that large herbivorous dinosaurs may have consumed angiosperm fruits, but only incidentally as part of a generalist 'vacuum-cleaner' browsing strategy, rather than targeting them as preferred food items. Although Weishampel (1984) assumed that various bennettite fruits were targeted by Mesozoic vertebrates, Pott and McLoughlin (2014) and McLoughlin et al. (in press) argued that there is little direct evidence of vertebrate herbivory on bennettite reproductive structures.

Large seeds and showy fruits with rich quantities of fleshy endosperm appear to have arisen among angiosperms only in the Late Cretaceous. Their development may have been associated with the diversification of omnivorous mammals, birds and small feathered

dinosaurs. However, Herrera (1989) disputed the significance of endozoochory in the success of angiosperms noting that a greater proportion of gymnosperm than angiosperm families are endozoochorous and that in both groups, families that employ endozoochory are not more species rich than families utilizing other dispersal strategies.

In a survey of published Cretaceous and Cenozoic floras, Eriksson et al. (2000) and Eriksson (2016) found that seeds remained predominantly small through the Cretaceous, only increasing in size towards the end of the period (at around 80 Ma). They found that inferred zoochory was more frequent than determined in previous studies for the full extent of angiosperm history. They also noted that although seed mass may be related to levels of endozoochory, the general pattern of seed size through the last 125 million years is more closely related to climate in terms of the prevalence of open vegetation during the Cretaceous, the establishment of closed multi-stratal forests in the Paleogene, and the development of more open vegetation in the Neogene.

The role of invertebrates in seed set and dispersal in the studied assemblages is ambiguous. Although several gall-like structures are represented in the assemblages (Fig. 8F, G), and elliptical scars are present near the apex of some seeds (Fig. 8H), clear evidence of direct seed predation by invertebrates is minimal. However, we cannot exclude that some entrance and exit boring holes were cryptic on seeds, especially those preserved as impressions. The potential example of mimesis between coleopterans and dispersed *Schizolepidopsis* seeds (Fig. 8A–D) adds to a growing record of such interactions in the Chinese Mesozoic assemblages (Y. Wang et al., 2010, 2012).

7. Conclusions

Although the studied assemblages represent some of the finest lacustrine Lagerstätten in the world, seeds remain slightly under-represented in collections compared with foliage, possibly as a consequence of both taphonomic and collecting biases. Future work specifically targeting disseminules might offer greater insights into the full representation of dispersal strategies and interactions with animals. The increasing numbers of lacustrine Lagerstätten of various ages being investigated globally offer opportunities to track the patterns of plant disseminule representation throughout the course of seed-plant history.

No seed species are shared between the Northern and Southern Hemisphere assemblages. Very few species are shared between the Jurassic and Cretaceous assemblages in the respective regions.

Anemochory, via development of wings or a pappus, remained a key strategy for seed dispersal from the late Middle Jurassic to Early Cretaceous. Evidence for epizoochory is minimal. Those seeds that developed spines in the Cretaceous appear to have been adapted to anchoring to aquatic debris or to soft substrates. Several, relatively featureless seeds in all assemblages are potential candidates for endozoochory, especially based on the presence of such seeds in vertebrate gut contents and regurgitant or coprolitic masses. Future studies of tooth morphology and dental microwear studies of vertebrate herbivores might offer supplementary information on seeds as a portion of the diet. Disseminules show few clear changes in size or representation of dispersal categories apart from a slight reduction in seed length between the Daohugou and Jehol assemblages. Free-sporing plants are major components of the four studied assemblages. Both featureless and winged seeds also represent significant proportions of the disseminule diversity in each of the studied assemblages. The representation of specific seed-form categories is controlled largely by north–south phylogeographic differences in the family-level composition of the floras.

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