The Flora of the Insect Limestone (latest Eocene) from the Isle of Wight, southern England

Peta Angela Hayes[1] and Margaret Elizabeth Collinson[1,2]

[1]Department of Earth Sciences, the Natural History Museum, Cromwell Road, London, SW7 5BD, UK.
Email: p.hayes@nhm.ac.uk.
[2]Department of Earth Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK.
Email: M.Collinson@es.rhul.ac.uk.

ABSTRACT: Latest Eocene fossil plant remains occur in concentrations within blue-grey micrite known as Insect Limestone near the base of the Bembridge Marls Member (Bouldnor Formation, Solent Group), Isle of Wight, southern England. Some of the previously reported taxa (collections in the Natural History Museum, London) are not preserved within the Insect Limestone. These (e.g., all Arecaceae (palms)) are excluded from the floral list. New non-destructive techniques have yielded additional taxonomic information. Leaves previously assigned to *Ficus* and *Fagus* are now *incertae sedis*. Wetland elements are abundant, particularly *Typha*, but also *Acrostichum*, *Azolla*, *Potamogeton*, *Sparganium* and others. Non-wetland elements are rare. Trees and shrubs included representatives of Betulaceae, Caprifoliaceae, Juglandaceae, Lauraceae, Rhamnaceae (the sclerophyllous *Zizyphus*), other flowering plants and several genera of conifers. There are rare specimens of possible herbaceous plants and propagules with plumes or awns, the latter possibly an early fossil record of *Clematis*. The common plant remains were probably derived from vegetation near a freshwater body, sometimes with slight brackish influence, whilst rarer elements were probably blown in from a greater distance. There is little evidence of plant–insect interaction; one leaf with small galls, a stem containing an insect larva and a possible association between stratiomyid flies and *Typha*.

KEY WORDS: Fossil angiosperm leaves, fossil fruits and seeds, plant–insect interaction, wetland flora.

Fossil plants from the late Eocene–early Oligocene of southern England provide important evidence for understanding changes in vegetation and climate during this period of differentiation of the British flora and global cooling. This study focuses on the fossil flora of the latest Eocene Insect Limestone exposed on the Isle of Wight. The Insect Limestone is famous for the insect fauna (see papers in both Insect Limestone volumes) but the diverse flora, with many species unique to this bed, is also of great significance. In addition, insects and plants are preserved in association, allowing the consideration of plant–insect interaction and the use of both sources of information in palaeoenvironmental reconstruction.

The Insect Limestone flora is one of a series of Paleogene floras in the southeastern UK which form a global benchmark for studies of Paleogene vegetation (Mai 1995; Collinson & Hooker 2003) and it is a European benchmark for the Bembridge–Spechbach floral assemblage (Kvaček 2010). The UK floras were reviewed and summarised by Collinson & Cleal (2001a, b, c). A detailed comparison of the Bembridge Marls and underlying Bembridge Limestone floras was presented in Collinson *et al.* (1993). Apart from making a significant contribution to this floristic series, the Insect Limestone flora is important because it lies close to the Eocene–Oligocene transition, a time of major global change associated with the build up of the first major ice sheet on Antarctica (Hooker *et al.* 2004, 2007, 2009; Grimes *et al.* 2005; Sheldon *et al.* 2009). In addition, the Insect Limestone flora contains wetland elements typical of the Solent Group floras; along with fruits, seeds and leaves representing non-wetland elements including trees, shrubs, one climber and putative herbs (Collinson & Cleal 2001b). In combination, these provide a unique window on vegetation of this time interval. Exceptional preservational conditions have also led to the survival of delicate structures such as wings and plumes on fruits and seeds.

The aim of this paper is to provide a revised list of the Insect Limestone flora which can be used to interpret the vegetational context of the insects. Within this remit, we have paid special attention to taxa of significance for understanding plant–insect interactions.

1. Geological context

The plants are preserved in tabular to lenticular bands of very fine-grained micrite known as Insect Limestone. This unit lies close to the base of the Bembridge Marls Member (e.g., within the basal 1.5 m at Gurnard) of the Bouldnor Formation in the Solent Group (Fig. 1). On the basis of labels in the collections of the Natural History Museum, London, the Dinosaur Isle Museum, Isle of Wight, and published information in Reid and Chandler (1926) most, if not all, of the plant specimens come from exposures in Gurnard and Thorness Bays (Fig. 1).

Hooker *et al.* (2007) re-identify the Eocene–Oligocene transitional interval magnetochrons in Gale *et al.* (2006) such that at least the lowest 4.5 m of the Bembridge Marls Member are latest Eocene in age, belonging in subchron 1 of Chron C13r and not in Chron C13n. The biostratigraphy indicates that the position of Chron C13n should lie higher in the sequence in the hiatus below the Nematura bed of the overlying Hamstead Member (Hooker *et al.* 2004, 2007). Further refined
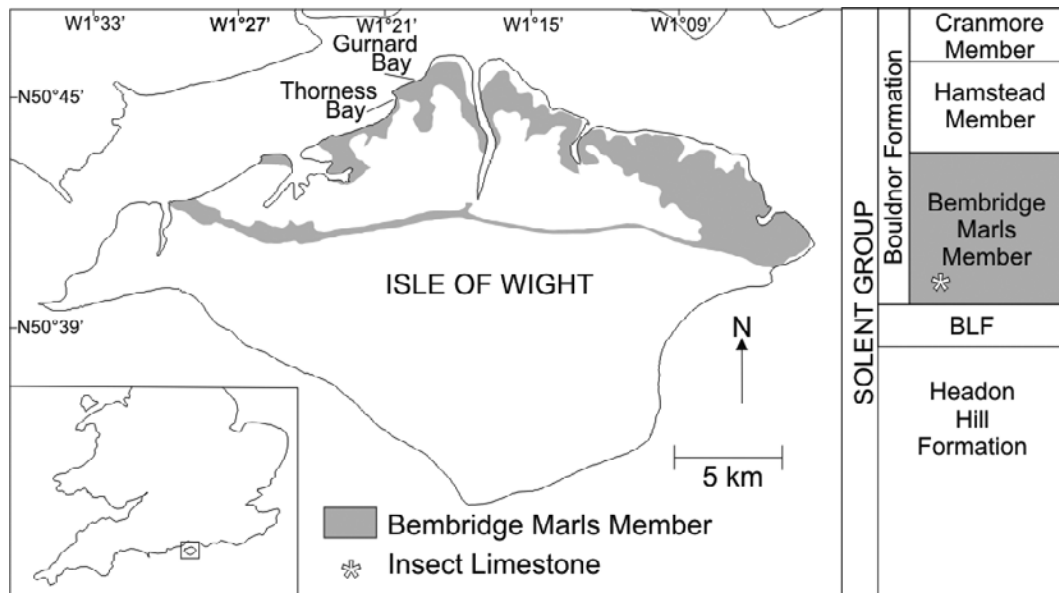
Figure 1 Extent of the outcrop of the Bembridge Marls Member which contains the Insect Limestone at the stratigraphic position shown by the asterisk. BLF = Bembridge Limestone Formation.

correlation of the UK succession to the global timescale was presented in Hooker *et al.* (2009). The Insect Limestone is therefore latest Eocene in age.

2. Previous work on the flora

Much of our knowledge of this flora is based on the collections of Joseph Edwin Ely A'Court Smith (1813–1900), a retired chief officer with the Merchant Service and a keen amateur geologist. Early reports on the plant fossils were made by Gardner in the 1880s (Gardner 1883, 1884, 1885, 1886, 1888). Most of A'Court Smith's collection was eventually deposited in the Natural History Museum, London. This collection was the focus of the first comprehensive publication on the Insect Limestone flora, comprising over 100 taxa, by Reid & Chandler (1926). Collinson & Cleal (2001b) reviewed and summarised the flora, but their work did not involve any new collecting and did not attempt to apply new techniques to gain additional information from the existing fossils.

3. Revision of the floral list

3.1. Identifying specimens from the Insect Limestone lithology

The Insect Limestone is a micrite which is light olive grey/ light greenish grey/light bluish grey in colour when fresh and weathers at extremes to a very pale orange/greyish orange (according to the Geological Society of America (1984) Rock-Color Chart). It fractures conchoidally and is well-cemented.

The collections in the Natural History Museum, London, were found to contain specimens preserved in light-dark moderate brown (5 YR 4/4 to 5 YR 3/4) to dark reddish brown ironstone concretions quite distinct from the Insect Limestone lithology (although they were labelled as Insect Limestone). Ironstone concretions and bands do occur within the Bembridge Marls Member, including one in the cliffs in Gurnard Bay at a slightly higher level than the Insect Limestone. All plant fossils preserved only in the ironstone lithology have here been excluded from the Insect Limestone floral list. Where this has resulted in removal of a taxon from the floral list, the specific

examples are stated in the text. This has resulted in the exclusion of all Charophyta, all Arecaceae (palms), the genus *Aldrovanda* (Droseraceae) and the fern genus *Anemia*. For further details see later sections of text.

3.2. Field collecting

During the course of this project, three week-long collecting trips were undertaken by one of us (Hayes). Insect Limestone was examined at sites ranging from Gurnard Point to Burnt Wood, including Sticelet Ledge, Saltmead Ledge and Gurnard Bay. Collinson has periodically studied Insect Limestone at Gurnard Point over many years of field excavations in the Solent Group. In addition, we have had access to material collected by Dr E.A. Jarzembowski on Geologists' Association field trips. Some of the most important specimens have been found by dedicated enthusiastic amateur collectors, especially Andy Yule. Information from all of these collections is incorporated into our understanding of the relative frequency of different elements in the Insect Limestone flora.

3.3. Taxonomic revision and new techniques

The descriptions provided by Reid & Chandler (1926) have proven to be comprehensive and accurate. Some taxonomic revisions have already been undertaken by other authors (reviewed in Collinson & Cleal 2001b), and these are incorporated in the revised floral list. Our aim has been to apply new nondestructive techniques involving minimal risk, to try to gain additional information that might help to confirm or refute taxonomic assignments.

Many of the specimens have deteriorated since originally described. A number of important taxa, including fruits, seeds and leaves, are represented by single specimens. For fruits and seeds, many of the key specimens now consist of fragmentary organic material more or less loose within a limestone external mould. We have attempted to produce improved images of selected specimens using the Alicona infinite focusing microscope and low-vacuum scanning electron microscopy (VP SEM) (Leo 1455VP SEM with Oxford Instruments INCA analysis system, 19Pa, 15–20 kV). The former has proved unsuccessful so far, due to lack of experience with this new technology,
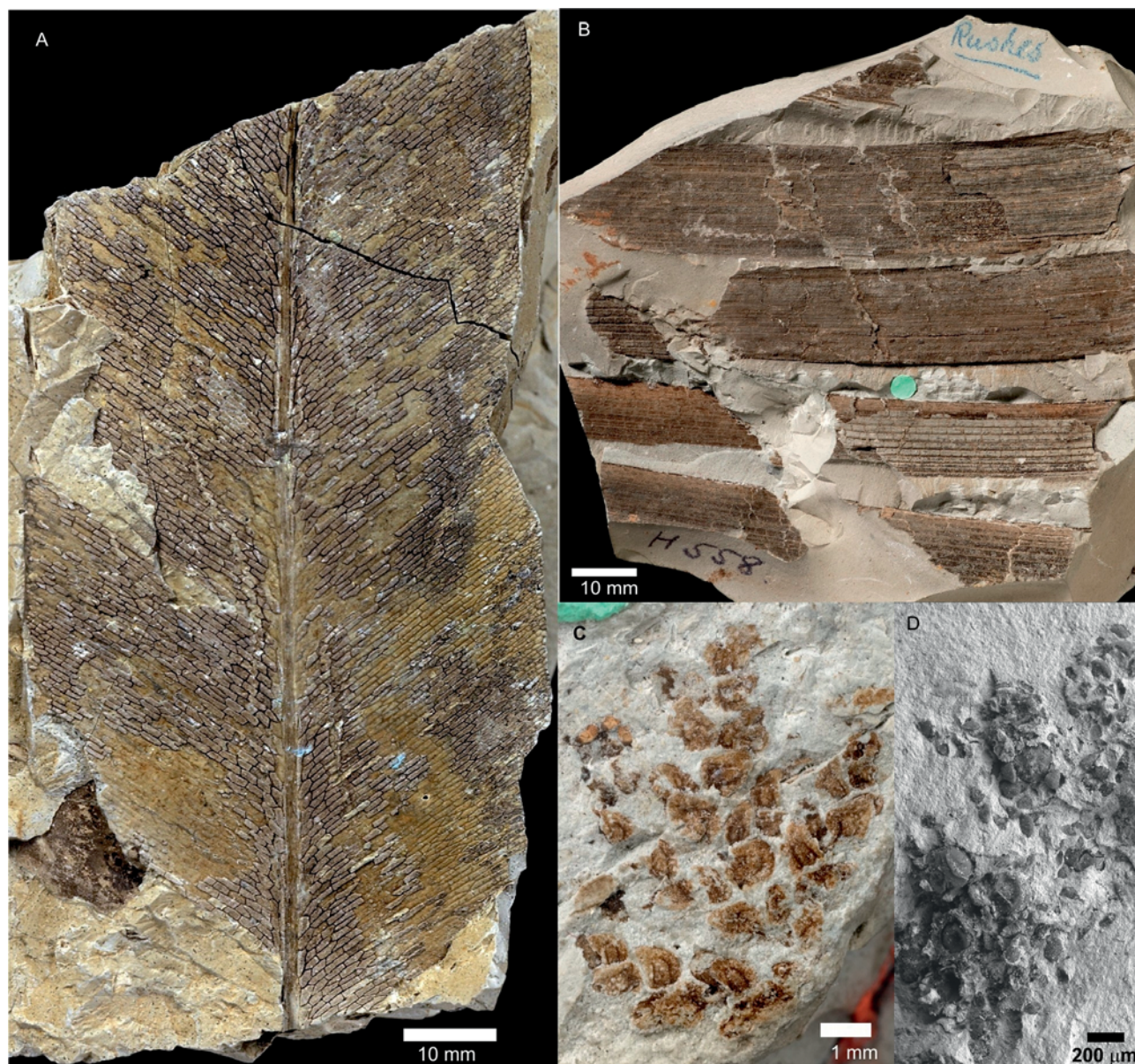
Figure 2 Typical wetland elements from the Insect Limestone: (A) *Acrostichum*, NHMUK V 68469; (B) *Typha* leaves, NHMUK V 17521; (C–D) *Azolla*: (C) a partial plant with megaspore apparatuses near top left, NHMUK V 17002, same specimen as line figure by Reid & Chandler (1926, fig. 2); (D) a clump of dispersed megaspore apparatuses with entwined microspore massulae, VP SEM, Collinson, personal collection.

but does have potential for application to this material. The VP SEM has proven useful in some cases (see plumed seeds).

Most of the leaf specimens have been covered in varnish at some point in the past. Cross-polarised light has been used to reduce glare and increase contrast to enable venation detail to be studied and illustrated. The use of this technique for plant fossils was developed by Cedric Shute (Crabb 2001).

4. Discussion of the revised floral list

4.1. Wetland floral elements
The nearest living relatives of many of the Insect Limestone plant fossils are wetland herbaceous plants (Fig. 2A–D). There are free-floating plants, such as *Azolla* (a small fern) and *Stratiotes* (a monocot) and one submerged plant, *Ottelia* (another monocot), which is a rare element in the middle and late Eocene of Europe (Mai & Walther 1978). Rooted plants with floating leaves are represented by *Potamogeton* (monocot) and *Sabrenia* (dicot). The monocots *Typha* and *Sparganium*

and the fern *Acrostichum* are marginal emergent plants, and the Cyperaceae may also have been marginal emergents. Modern leaves of *Typha* and *Sparganium* are similar. However, details of the leaf venation and the net-like diaphragms in the internal aerenchymatous chambers confirm that the Insect Limestone leaves are *Typha* (Smith *et al.* 2010). Fossil *Typha* is represented not only by leaves but also by fruits and seeds in the Insect Limestone. *Najas* (known only from two specimens) may be a member of this community, but the identification has not been confirmed as the specimens have not been located. There are no charophytes in the Insect Limestone, although charophytes occur elsewhere in the Bembridge Marls Member (Collinson 1983) in association with the other wetland plants listed above. *Aldrovanda intermedia* Reid & Chandler is not preserved in Insect Limestone and has been removed from the floral list.

Acrostichum is one of few ferns able to tolerate mangrove habitats today. However, specimens from the Eocene and Oligocene of the USA, Germany, the Czech Republic and elsewhere in the UK are all preserved in freshwater deposits (Collinson
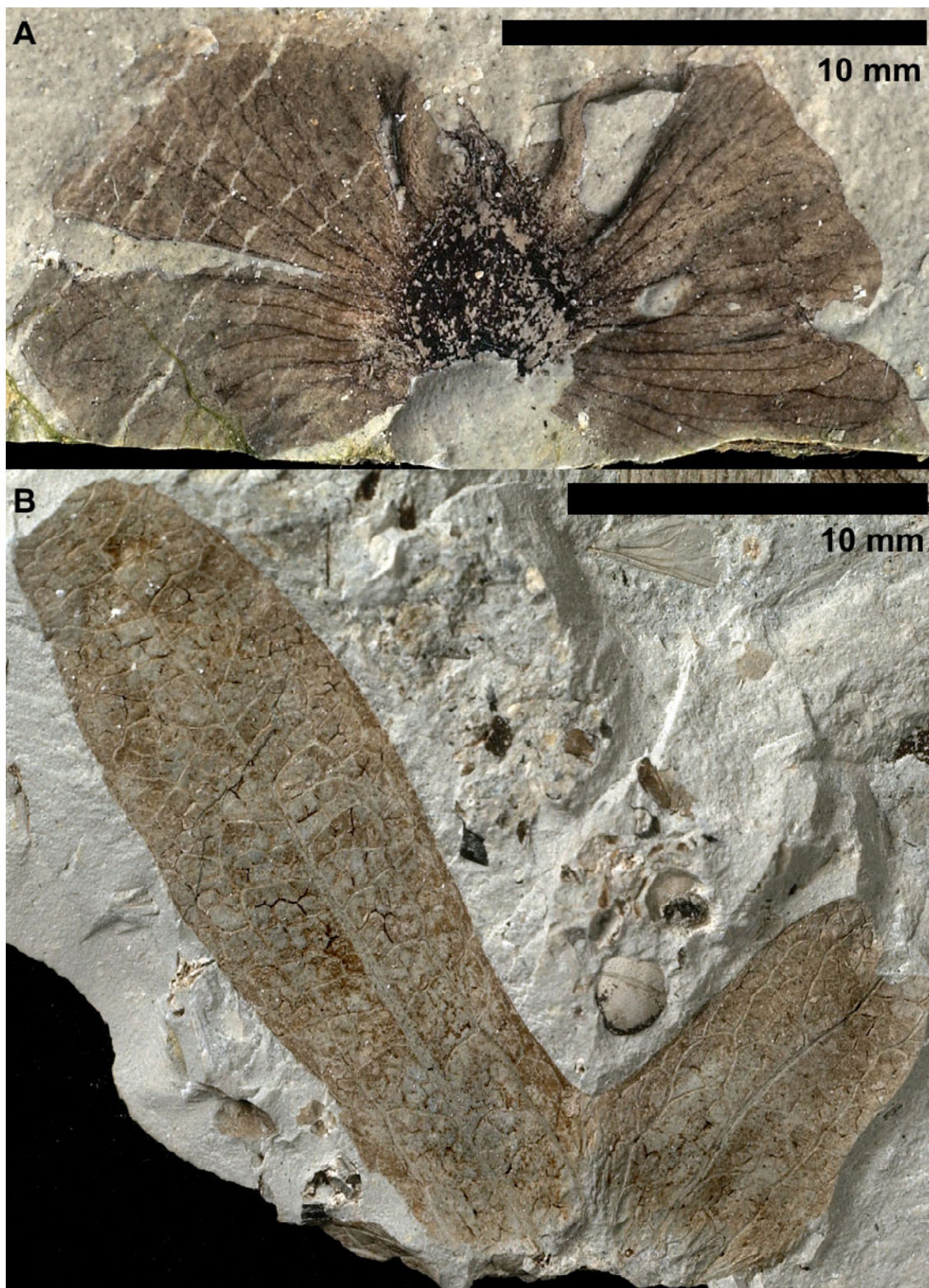
Figure 3 Recently collected Juglandaceae winged fruits: (A) *Hooleya*, NHMUK V 68470; (B) *Palaeocarya*, NHMUK V 68471. Note in (B): insect wing top centre and other plant debris on same slab.

2002). Therefore, the presence of *Acrostichum* need not imply a brackish palaeoenvironment.

The presence of *Limnocarpus* as a fairly common element is similar to other occurrences in the lower part of the Bembridge Marls Member (Collinson 1983). There, this genus is associated with other freshwater wetland elements, but also with brackish elements such as organic walled linings of foraminiferans. The Insect Limestone wetland plant habitat may therefore range from fully freshwater to slightly brackish conditions at times

(at maximum <3.5 ppt). Halite crystal cavities may suggest occasions of hypersalinity (A. Ross pers. comm., 2012), although these cavities have not been noted on the plant-bearing surfaces that we have studied.

The wetland elements are the most abundant plant fossils in the Insect Limestone. During recent collecting trips, specimens of *Typha* foliage were the most frequent plant fossil encountered. *Typha* seeds, *Potamogeton* and *Sparganium* fruits, *Acrostichum* foliage and clusters of *Azolla* megaspores and massulae have

Figure 4 (A) Photograph of *incertae sedis* dicotyledonous leaf (formerly *Ficus* sp. *sensu* Reid & Chandler (1926)), NHMUK V 17576. (B) Line interpretation of venation pattern which reveals more information than Reid & Chandler (1926, fig. 6) through use of cross-polarised light, and demonstrates that the specimen cannot be included in the genus *Ficus*.

also been collected recently. In contrast, non-wetland elements are rarely encountered. Only two specimens of Juglandaceae fruit and a couple of fragmentary dicotyledonous leaves have been found on recent trips.

4.2. Non-wetland floral elements

4.2.1. Juglandaceae trees. Juglandaceae (walnut, hickory and wingnut family) are represented in the Insect Limestone flora by two species, *Palaeocarya macroptera* (Brongniart) Jähnichen, Friedrich & Takáč (1984) (Fig. 3B) and *Hooleya hermis* (Heer) Reid & Chandler (1926) (Fig. 3A). Both of these are well understood fossil members of the family, the former being represented by co-occurring fruits and leaves at various sites (Manchester 1987). One new specimen of each of these species has been collected recently, indicating that they were regular components of the source vegetation of the Insect Limestone flora. Collinson and Cleal (2001b) erroneously listed *Engelhardtia* sp., from the Insect Limestone but this specimen (*E.* sp. 2 in Reid & Chandler 1926) had been included in *P. macroptera* by Manchester (1987).

4.2.2. Putative *Ficus* leaf: rejected. (Fig. 4A, B) There is a very specialised relationship between members of the genus *Ficus* (figs) and fig wasps. Fig wasp larvae can only develop within fig sarconia, unique enclosed inflorescences, and fig wasps are the only pollen vectors for figs. Rønsted *et al.* (2005) have provided molecular phylogenies calibrated using fossil records, and suggest that there is evidence for long-term codivergence of this association going back 60 million years. Three fig wasp specimens have been found in the Insect Limestone and, in combination with their *in situ* pollen, these prove that the fig wasp–fig tree mutualism has existed for at least 34 million years (Compton *et al.* 2010).

A single leaf specimen had been marked "*Ficus*" by Gardner in the late nineteenth century. Reid & Chandler (1926) agreed that it showed the general characteristics of *Ficus* (fig) and drew comparisons with herbarium material at Kew. The identification of this leaf specimen is important because of the fig wasps newly discovered in the Insect Limestone (Compton *et al.* 2010). However, there is just one incomplete specimen, with detail obscured by a coating of varnish applied in the past. Using cross-polarised light to increase contrast and reduce
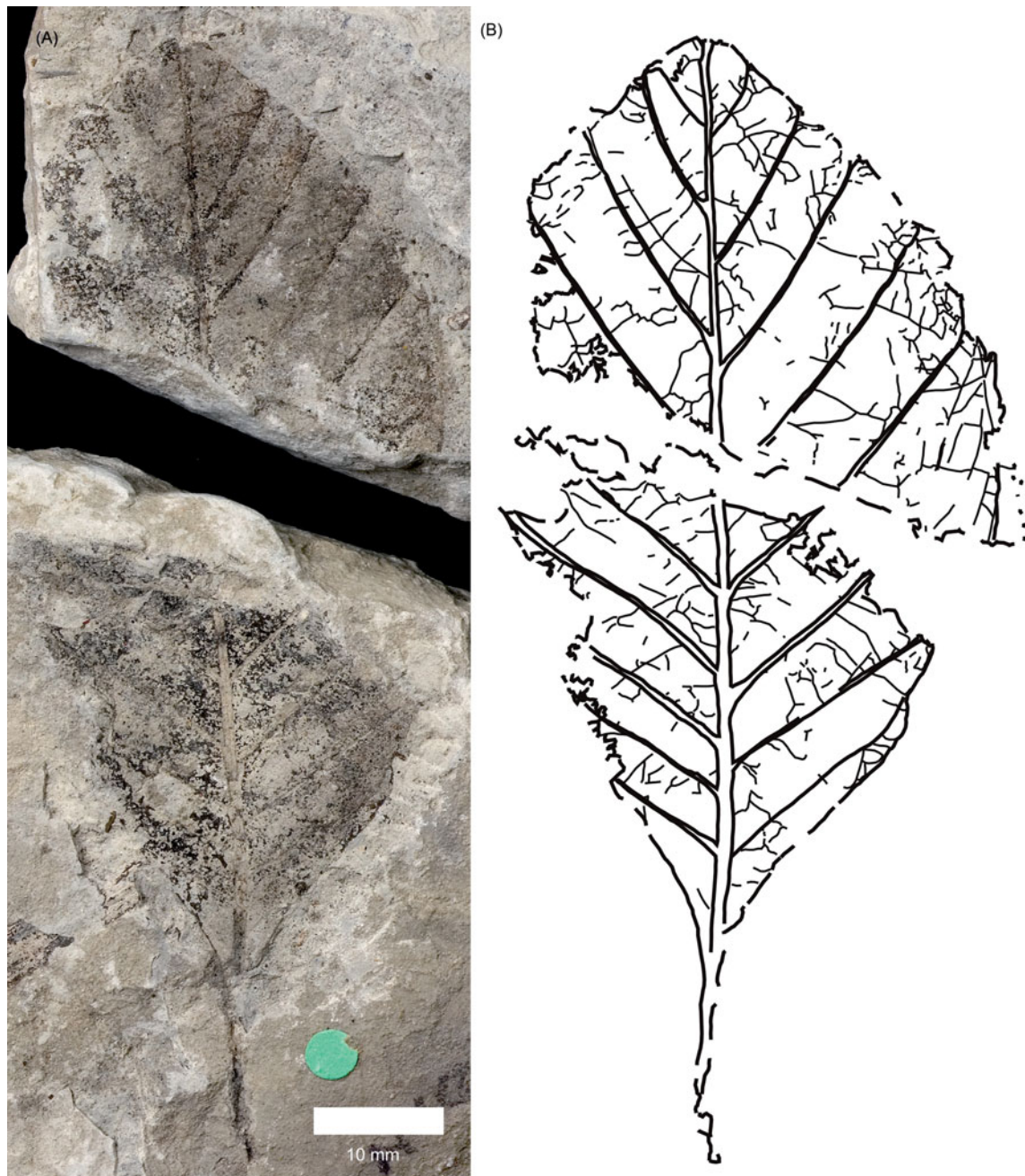
Figure 5 (A) Photograph of *incertae sedis* dicotyledonous leaf (formerly *Fagus* sp. ? *sensu* Reid & Chandler (1926)), NHMUK V 17574. (B) Line interpretation of venation pattern showing features of a variety of fagalean groups.

glare, it has been possible to study, draw and describe the fine detail of the leaf architecture (Fig. 4B).

Many of the features are consistent with those seen in some fig species: asymmetrical lamina; obovate leaf form; acute cuneate base; entire margin; presence of a petiole; pinnate brochidodromous venation, with abruptly curved loop-forming branches enclosed by secondary, tertiary and quaternary arches; moderate acute angle of divergence of secondary veins from midvein, with lowest pair of secondary veins more acute than those above; reticulate pattern of tertiary veins; distinct higher order venation; and looped marginal ultimate venation.

However, further comparative study is required because there are some inconsistencies, particularly in the angle of divergence of the tertiary and higher order veins. It is, therefore, not possible to confirm the identification of this specimen as *Ficus*.

4.2.3. Other trees and shrubs. Reid & Chandler (1926) assigned two specimens to the Fagaceae (the oak and beech family). Collinson & Cleal (2001b) considered the nut tentatively assigned to *Quercus* sp.? as indeterminate. The leaf tentatively assigned to *Fagus* sp.? (Fig. 5A, B) is broken, abraded and poorly preserved. Attempts to study the detail of this leaf have not revealed diagnostic characters. Although much of the primary and secondary vein pattern can be illustrated (Fig. 5B), the higher order venation and the leaf margin are not clear. The pinnate simple craspedodromous venation and possibly toothed margin are typical of the Fagaceae, but these features are also characteristic of many other Fagalean forms and other groups, such as the Urticales and Betulales (Hamamelidae) and families within the Dilleniidae and Rosidae. It is therefore concluded that this specimen should not be assigned to *Fagus*.

Figure 6   *Zizyphus paradisiacus* (Unger) Heer, NHMUK V 17018, representing the rare sclerophyllous elements.

Reid & Chandler (1926) assigned one specimen to *Carpinus* sp. in the Betulaceae (the birch family). Manchester & Donoghue (1995, p.721) assigned this specimen and a single specimen of *Abelia* sp. 4 to the genus *Asterocarpinus*, an extinct genus of Betulaceae. The other species of "*Abelia*" described by Reid & Chandler (1926) (see Appendix) were all regarded as *incertae sedis* by Manchester & Donoghue (1995), though one was revised and placed in the genus *Raskya* (of unknown affinity) by Manchester & Hably (1997). The remaining record of Caprifoliaceae, *Dipelta*, a deciduous tree, was critically reappraised and accepted by Manchester & Donoghue (1995).

Three genera of Bignoniaceae (the trumpet creeper family), two of which could be trees, were described from the Insect Limestone by Reid & Chandler (1926), each based on a single specimen. The winged seed attributed to *Catalpa* is similar to a fossil assigned to this genus from the Oligocene of Oregon (Meyer & Manchester 1997). Reid & Chandler (1926) had

"no doubt" about the affinity of the winged seed of *Radermachera*. There seems to be no reason to doubt these taxonomic assignments. The Rutaceae are represented by Zanthoxylae, *Zanthoxylum*, a single specimen of a characteristic seed.

One single leaf specimen (Fig. 6) was assigned to *Zizyphus* (Rhamnaceae) by Reid & Chandler (1926). *Zizyphus*, a genus of shrubs to small trees, has been recognised as a sclerophyllous element in European late Eocene and early Oligocene floras (see Collinson & Hooker 2003 and references therein). The winged fruit of *Raskya* (affinity unknown, formerly *Abelia*) is an associated but rarer element. A few additional dicotyledon leaf morphotypes are not identifiable to family and some of these specimens are small, relatively coriaceous leaves which, like *Zizyphus*, may be considered to be sclerophyllous elements. *Dicotylophyllum pinnatifidum* Reid & Chandler (which is *Palibinia*-like, Collinson & Hooker 2003) is another sclerophyllous element. Conifers are represented by several genera

Table 1 Possible herbaceous (likely non-aquatic) flowering plants listed in the Insect Limestone flora. Those where the lithology is unknown may not be from the Insect Limestone. Generic and family affinities are not confirmed unless revisions are cited. Families are from APG (2003).

Family	Genus	Number of specimens	Comment
Acanthaceae	*Acanthus*	1	
Apocynaceae	*Cypselites*	14	See section 4.3.2 and Collinson *et al.* 2012a)
Araceae	*Epipremnites*	1	Revised by Gregor & Bogner (1984)
Apocynaceae	*Phyllanthera*	5	
Apocynaceae	*Tylophora*	1	
Bignoniaceae	*Incarvillea*	1	
Lamiaceae	*Melissa*	1	Lithological context unknown
Lamiaceae	*Ajuginucula*	1	Lithological context unknown
Papavaraceae	*Papaver*	1	Lithological context unknown
Ranunculaceae	*Ranunculus*	6	
Ranunculaceae	*Myosurus*	22	Revised by Mai & Walther (1978)

with scale-like or needle leaves, although only one (*Araucarites gurnardi* Florin leafy shoots) is represented by more than one or two specimens. These leafy shoots may have been produced by the same plant that produced the *Doliostrobus* Marion cone scales and may belong in the Taxodiaceae, Araucariaceae or the extinct family Doliostrobaceae (see discussion and references in Collinson 1996; Kunzmann 1999; Kvaček 2002; Kvaček & Teodoridis 2011; Collinson *et al.* 2012a). Other conifers include rare Pinaceae (*Pinus* is represented by one seed and one group of needles and there is one seed assigned to *Pityospermum*) and Cupressaceae (*Quasisequoia*, one twig assigned to ?*Libocedrus* sp. and one cone to *Cupressus* sp.).

Reid & Chandler (1926) identified three palm taxa: the fan-palm *Sabal major* (Unger) Heer; an unnamed species of *Palmophyllum* Conwentz; and *Palaeothrinax mantelli* Reid & Chandler, later reidentified as *Palmacites* Brongniart (Read & Hickey 1972). None of these palms are preserved within the Insect Limestone and they have therefore been removed from the floral list.

The Lauraceae are represented by three species: *Daphnogene lanceolatum* Unger; *Daphnogene cinnamomifolia* (Brongniart) Unger; and an unnamed species of *Neolitsea* Bentham. *Daphnogene lanceolatum* is a widespread species in the European Paleogene (e.g. Mai & Walther 1978, 1985; Kvaček & Teodoridis 2011).

In summary, trees and shrubs are represented by members of the flowering plant families Juglandaceae (*Palaeocarya* and *Hooleya*); Betulacaeae (*Asterocarpinus*); Caprifoliaceae (*Dipelta*); Bignoniaceae (*Catalpa*, *Radermacher*a); Rhamnaceae (*Zizyphus*); Rutaceae (*Zanthoxylum*); and Lauraceae (*Daphnogene* and *Neolitsea*); and by several conifers. This list includes both mesophytic and sclerophyllous elements and deciduous and evergreen taxa. With the exception of the Juglandaceae, all of these named taxa are represented by very few specimens (many by only a single specimen) and they have not been encountered in any recent collecting efforts. Therefore, they are unlikely to have been common elements in the local vegetation.

4.3. Habitats uncertain

4.3.1. Putative herbs.
A number of flowering plant genera recognised in the Insect Limestone include herbaceous plants amongst their nearest living relatives (Table 1). The majority of these are represented by very few specimens, in several cases only a single specimen. Apart from their potential herbaceous affinity, these records are also important because they represent very early examples of the taxa in the fossil record. Unfortunately, no new specimens of any of these taxa have been discovered during recent collecting and the specimens in the collections are represented by fragmentary organic material within limestone moulds which have deteriorated since they were originally studied. Therefore, it has not been possible to confirm or refute these identifications; see Table 1. In addition there are six specimens of undeterminable sterile fern pinnules and one specimen of an *Equisetum* (horsetail) node with nodal plate.

4.3.2. Taxa with plumed propagules.
Plumed propagules are rare in the Paleogene fossil record, with the modern diversity being a relatively recent evolutionary innovation (Collinson & van Bergen 2004). The Insect Limestone contains two genera of plumed seed. *Phyllanthera* (Apocynaceae) is represented by six specimens, but it has not been possible to confirm the identification. The generic name *Cypselites* (Apocynaceae) has nomenclatural priority (Collinson *et al.* 2012a) over *Apocynospermum* (used by Reid & Chandler 1926). The genus is represented by four species (total 14 specimens) in the Insect Limestone (Fig. 7A) and is rare but widespread in the Eocene and Oligocene (Wilde & Frankenhäuser 1998; Manchester 1999; Collinson *et al.* 2012a). The mode of attachment of the hair tuft, confirmed here by VP SEM, is consistent with some modern representatives of Apocynaceae, but consideration of generic affinity would require an extensive survey of all modern seeds in the family.

4.3.3. Possible climbers, including *Clematis*-like awned fruits.
There are 34 specimens of awned fruit (Fig. 7B) assigned to the species *Clematis vectensis* Reid & Chandler (1926) (Ranunculaceae). The modern genus *Clematis* includes both lianas and herbs. Re-examination of several of the Insect Limestone specimens by VP SEM has not yielded any new information, nor has SRXTM (synchrotron radiation x-ray tomographic microscopy) on very similar fruits (*Carpolithus* sp. 2) from the Eocene Messel oil shales (Collinson *et al.* 2012b). *Carpolithus* sp. 2 from Messel (Collinson *et al.* 2012a) has a similar morphology to the Insect Limestone specimens attributed to *Clematis*; however, key features of the latter are not evident on the former. Fruits with a long persistent style (awn) are very rare in Paleogene floras and both these occurrences are linked to exceptional preservation conditions. The Insect Limestone and Messel oil shale specimens may be early records of the genus *Clematis*, but they both lack the long hairs which typically occur on the fruit body and style of modern members of the genus (Collinson *et al.* 2012a). Therefore, this generic determination remains

Figure 7 (A) *Apocynospermum striatum* Reid & Chandler (1926), NHMUK V 17598 (generic name *Cypselites* has nomenclatural priority see text). (B) *Clematis vectensis* Reid & Chandler (1926), NHMUK V 17584, plumed and awned propagules.

unconfirmed. Becker (1969) included a leaflet identified as *Clematis ellensburgensis* as a component of the Beaverhead Basins fossil flora of SW Montana, USA, now considered early Oligocene (or less likely latest Eocene) (Leilke *et al.* 2012). However, Leilke *et al.* (2012) also assert that the taxonomic assignments provided by Becker (1969) are in need of a thorough taxonomic revision. Recent molecular phylogeny suggests that *Clematis* was an ancient genus with an origin in the Oligocene (Xie *et al.* 2011), a result which would be consistent with presence of *Clematis*-like fossils in the middle and late Eocene. However, Xie *et al.* (2011, p. 917) stated "the stem age is consistent with the earliest reliable fossilized fruits in western Europe" and they cited the Insect Limestone fossils as an example. We are not aware of any verified pre-Quaternary records of *Clematis* and this may call into question the divergence times estimated by Xie *et al.* (2011).

Three seeds have been tentatively assigned to ?*Actinidia* sp. (Chandler 1963, p. 329), a genus which includes climbers such as the kiwi fruit today, but also includes shrubs and trees. As there is doubt about the generic determinations and a range of habits within the modern genera, neither of these taxa can be taken as evidence for climbers or lianas in the Insect Limestone flora.

4.4. Comparison with other mid-latitude northern hemisphere fossil floras

There are a number of fossil floras of late Eocene and early Oligocene age that can be compared with the flora from the Insect Limestone. These include North American floras (reviewed in Devore & Pigg 2010), the late Eocene Zeitz floristic complex from the Weisselster Basin in Germany (Mai &

Figure 8 Galls on an indeterminable non-dicotyledonous leaf or stem fragment (Sedgwick Museum, CAMSMX.50195).

Walther 1985), the Haselbach flora (probably early Oligocene) from the same Basin in Germany (Mai and Walther 1978; Kunzmann & Walther 2012) and other late Eocene to early Oligocene floras from far east Russia and central Europe discussed in Akhmetiev *et al.* (2009).

The only one of these floras showing a noteworthy similarity with the Insect Limestone flora is the Kučlín flora from North Bohemia, Czech Republic, (Akhmetiev *et al.* 2009; Kvaček & Teodoridis 2011) that is probably slightly older than the Insect Limestone (Kvaček & Teodoridis 2011). In the Insect Limestone flora, the aquatic elements dominate and the surrounding vegetation is poorly represented, in terms of both specimen number and diversity. Nevertheless, elements in common between the two floras include *Cypselites, Daphnogene, Doliostrobus, Hooleya, Palaeocarya, Quasisequoia, Raskya* and *Zizyphus*. Taking account of the wider floristic diversity at Kučlín, Kvaček (2010) interpreted the zonal vegetation as mid-latitude notophyllous broad-leaved evergreen forest, whilst Kvaček & Teodoridis (2011), after fully revising the Kučlín flora, recognised that notophyllous elements were not so significant and interpreted the vegetation as broad-leaved evergreen forest.

Despite the above similarities, the Kučlín flora differs from the Insect Limestone flora in having far greater diversity, including some thermophilic elements (e.g. Icacinaceae) that last appear in the UK sequence earlier in the late Eocene (Collinson & Cleal 2001b; Collinson & Hooker 2003). The rare winged bignoniaceous seeds, the possible herbs of the Acanthaceae, Lamiaceae and Apocynaceae (except *Cypselites*) and the distinctive, abundant *Clematis*-like awned fruit from the Insect Limestone are all missing from the Kučlín flora. The small

seeds of the possible herbs (Table 1) might not have been recognised in the leaf-dominated Kučlín fossil assemblage, but the winged seeds and awned fruit would most likely have been collected had they been present.

5. Insect–plant interactions

In spite of the highly diverse and abundant insect fauna, we have found very little evidence of insect–plant interaction. One indeterminable leaf fragment shows evidence of insect damage in the form of several small galls (Fig. 8). Gall wasps are recorded in the insect fauna (Antropov *et al.* 2014, this volume). Jarzembowski (1980) figured an insect larva in a plant stem. None of the seeds show any evidence of borings such as those made by weevils, but this is not unexpected in view of the relatively recent earliest occurrences and rarity of evidence of this interaction in the Paleogene record (Collinson & van Bergen 2004). Weevils are, however, a diverse and abundant group of beetles from the Insect Limestone. Although three fig wasps, with fig pollen, are recorded amongst the insects (Compton *et al.* 2010) the putative *Ficus* leaf must be considered as *incertae sedis*.

Adults and larvae of stratiomyid flies occur in the Insect Limestone. Two important specimens recently collected by Andy Yule show these larvae together with plant debris, including fragments of *Typha* leaves and with lymnaeid gastropods. Adults and larvae of some modern stratiomyid flies are commonly associated with plant debris and with vegetation, including Cyperaceae and *Typha* (James 1981; Stubbs & Drake

Figure 9 A block of Insect Limestone, NHMUK V 17503, showing a typical plant debris accumulation which includes a *Myosurus* fruit, fragments of monocotyledonous leaves (*Typha*) and fragments of *Azolla*. In addition there are insect wings and wing-cases.

2001). Unfortunately, we cannot undertake a wider survey to test this association evidence, as the museum collections of stratiomyids are mostly on small pieces of Insect Limestone that have been trimmed after collection and do not show the original facies context of the specimens.

6. Taphonomy

Large portions of the Insect Limestone are totally barren of any fossils. Plant fossils typically occur in concentrations of mixed plant debris along laminations (Fig. 9) and more rarely as larger separate fossils (Fig. 2A). The plant debris concentrates are poorly sorted. Elongate leaf fragments in random orientation co-occur with round seeds, whilst thin cuticular fossils (leaves, *Typha* seeds) co-occur with thick sclerotic seed coats. This suggests a lack of current winnowing or sorting, such as might occur during flow or in varying depositional energy regimes. The plant fossils often occur in concentrates and sometimes these also contain rare planorbid and lymnaeid freshwater gastropods, with rare thin and smooth ostracods and also insect wings. The plant debris sometimes includes fine rootlets and rooted rhizome fragments, but these are not common and are unlikely to indicate rip-up of living rooted vegetation.

Elsewhere in the Bembridge Marls Member, laminated mudrocks contain similar plant debris with a wide variety of wetland floral elements in association with freshwater faunas, including ostracods and gastropods (Collinson 1983). However,

the plant occurrences in these horizons are mostly laterally (100 m–several km) and vertically (up to 20 cm) extensive and continuous, not patchy (Collinson 1983), in strong contrast to the Insect Limestone occurrences. Some other mudrock horizons in the Bembridge Marls Member, and elsewhere in the Solent Group, contain large almost monotypic concentrates of one particular wetland fruit or seed type, such as *Stratiotes* or *Sabrenia* or *Potamogeton* or *Limnocarpus*, which may have resulted from current sorting or winnowing. These are absent in the Insect Limestone.

The most plausible scenario for the accumulation of the Insect Limestone plant fossils seems to be that they represent plant debris concentrated by minor wind movements and water turbulence at the surface or margins of a water body. Subsequent deposition could have resulted from waterlogging, or from short term stranding during minor water level fluctuations. We see no evidence that the plant remains dried out (such as might occur during a long interval of shoreline stranding) prior to deposition. The more common plant remains were probably derived from plants living in, or close to, the water body, whilst rarer elements were probably blown in from a greater distance, especially in the case of the winged and plumed seeds and also possibly most of the dicotyledonous leaves.

The association of a variety of freshwater wetland plants as the most frequent plant fossils occasionally associated with freshwater gastropods and ostracods suggests that freshwater conditions existed locally, at least in some places or at certain intervals, during deposition of the Insect Limestone. However,

the laterally and vertically discontinuous occurrence of plant debris rules out the existence of an extensive, persistent freshwater marsh and wetland comparable to that which has been reconstructed for other parts of the Bembridge Marls Member (Collinson 1983), the lower Hamstead Member (Hooker *et al.* 2004) and other parts of the Solent Group (Collinson 1990; Collinson *et al.* 1993). The presence of *Limnocarpus* probably indicates slight brackish water influence at times, as has been suggested elsewhere in the lower part of the Bembridge Marls Member (Collinson 1983).

7. Conclusions

This revision provides new information on the composition of the Insect Limestone flora. Study of the collections upon which previous work was based has shown that the three palm genera (*Sabal*, *Palmophyllum*, *Palmacites*), the one taxon representing the Droseraceae (*Aldrovanda*), two species of fern (*Anemia* sp. ?*A. colwellensis* Chandler and one indeterminable species), one species of conifer (indeterminable) and the charophytes are not preserved within the Insect Limestone and have been excluded from the floral list. Detailed analysis of the architecture of fragmentary dicotyledonous angiosperm leaf specimens under cross-polarised light has shown that there is insufficient evidence to include *Ficus* and *Fagus* within the macroflora. These results, along with the conclusion that the nut assigned to *Quercus* sp. ? is indeterminate (Collinson & Cleal 2001b), have removed the Moraceae and Fagaceae from the flora. The revised floral list is presented in Appendix 1. A small number of the taxa are represented by specimens with no surrounding matrix and therefore may not be from the Insect Limestone. In addition, many of the taxa are represented by only one or very few specimens, and some of this material is not well preserved, so it has not been possible to confirm or refute all of the existing identifications.

Low-vacuum scanning electron microscopy (VP SEM) has confirmed some important taxonomic features, e.g. hair tuft attachment in *Cypselites*, but has not yielded any new diagnostic characters. The mode of attachment of the hair tuft in *Cypselites* is consistent with some modern representatives of Apocynaceae. Unfortunately, synchrotron radiation X-ray tomographic microscopy (SRXTM) of specimens from the Messel oil shales did not reveal any new diagnostic characters (Collinson *et al.* 2012b). Placing *Cypselites* within a phylogenetic context would require an extensive survey of all modern seeds in the family. It is disappointing that some possible herbaceous flowering plants (Acanthaceae, Apocynaceae, Lamiaceae), the two winged seeds (attributed to *Catalpa* and *Incarvillea* of the Bignoniaceae) and the awned fruit (attributed to *Clematis*) cannot be firmly identified to those taxa and that no close living relative has been recognised for the extinct plumed seed *Cypselites* (Apocynaceae). The putative Bignoniaceae and herbs are poorly preserved, with very few specimens. The plumed seeds and awned fruit failed to reveal new diagnostic characters, even when studied from two floras using two different new approaches (VP SEM and SRXTM) known to be capable of delivering important new data from fossils.

Recent collecting has provided new insights on the relative frequencies of the different types of plant fossils and it has been possible to build up a picture of the local vegetation. Fragments of *Typha* foliage are the most abundant fossils and, along with other wetland elements, dominate the flora. The abundance and varying sizes of leaves, together with fruits and seeds, strongly suggests that *Typha* plants were a very important element in the marginal emergent vegetation. The non-wetland plants most frequently represented are trees of the Juglandaceae. Remains of other flowering plant trees and shrubs and conifers are very rare. There are also specimens of possible herbaceous plants and plants bearing plumed and awned propagules, but the closest modern genus for many of the taxa is unconfirmed and the nearest living relatives of the families listed show a variety of habits. Comparison with other fossil occurrences and nearest living relatives suggests that the local wetland vegetation grew in, or close to, a freshwater body which may sometimes have experienced a slight brackish influence. Since the plant debris is only preserved in concentrations, it is unlikely that there was an extensive, persistent marsh. Trees, shrubs and herbs probably grew in patches a greater distance from the water. There is little evidence of plant–insect interaction, but galls and a possible association between stratiomyid flies and *Typha* have been observed. The patchy and sporadic nature of the plant occurrences means that further collecting is particularly important to improve our understanding of this flora.

8. Acknowledgements

9. Appendix 1. Revised floral list from the Insect Limestone

Current classification follows Smith *et al.* 2006 for pteridophytes, Farjon 2001 for gymnosperms and (based on APG2) Judd *et al.* 2002 and Bremer *et al.* 2003 for angiosperms. Refer to text for comments on specific taxa, especially the reliability of determinations to modern genera.

In all these cases, confirmation of the generic attribution would require extensive comparative surveys of the fruits/seeds of all modern genera in the respective families and close sister taxa. This has not been possible during the current project and, in some cases, the preservation of the fossil will no longer permit such detailed comparisons.

Taxon			Comments
Pteridophytes:	Family/Order (Reid & Chandler 1926)	Family (following Smith *et al.* 2006)	
Equisetum lombardianum Saporta (1886) ?	Equisetales	Equisetaceae	
Lygodium sp. [?]	Schizaeaceae	Lygodiaceae	
Acrostichum lanzaeanum (Visiani) Chandler (1925)	Polypodiaceae	Pteridaceae	
Azolla prisca Reid & Chandler (1926) emend Fowler (1975)	Salviniaceae	Salviniaceae	
Filix *incertae sedis* sp.1, 2, 4 & 6			Six specimens of unidentified fern pinnule.
Gymnosperms:	Family (Reid & Chandler 1926)	Family (following Farjon 2001)	
Cupressus sp.	Cupressineae	Cupressaceae	
? *Libocedrus* sp.	Cupressineae	Cupressaceae	
Quasisequoia couttsiae (Heer) Kunzmann (1999) (?)	Taxodineae	Cupressaceae	See Collinson & Cleal (2001a) table 8.2, footnote 2. Kunzmann (1999) determined that this species represented an extinct member of the Taxodiaceae, here merged with Cupressaceae following Farjon (2001).
Doliostrobus taxiformis (Sternberg) Kvaček (1971) emend Kunzmann (1999) and *Araucarites gurnardi* Florin (in Reid & Chandler 1926)	Araucarineae	? Cupressaceae/ ? Araucariaceae/ ? Doliostrobaceae	Reid & Chandler (1926) suggested that *Araucarites gurnardi* Florin in Reid & Chandler (1926) leafy shoots might belong to the same plant as the *Doliostrobus* cone scales. See Kunzmann (1999), where *Doliostrobus* is included within the Taxodiaceae, here merged with Cupressaceae following Farjon (2001). See also comments in text.
? *Pinus dixoni* (Bowerbank) Gardner (1884)	Abietineae	Pinaceae	Missing, not traced by Reid & Chandler; believed pyritised and completely decayed.
Pinus vectensis Gardner (1888)	Abietineae	Pinaceae	Missing, not traced by Reid & Chandler; believed pyritised and completely decayed.
Pinus sp. 1 & 2	Abietineae	Pinaceae	
Pityospermum ambiguum Reid & Chandler (1926)	Abietineae	Pinaceae	This genus was assigned to Abietineae by Reid & Chandler (1926). Following Farjon (2001), the Abietaceae are here united with the Pinaceae (see Reveal & Hoogland 1992).
Angiosperms:	Family (Reid & Chandler 1926)	Family (following Angiosperm Phylogeny Group 2003)	
Acanthus rugatus Reid & Chandler (1926) [*Generic attribution not confirmed]	Acanthaceae	Acanthaceae	
? *Actinidia* sp.	Dilleniaceae	Actinidiaceae	Listed in Chandler (1963), presumably revised from *Carpolithus actinidiformis* Reid & Chandler (1926), not listed in Chandler (1964).
Apocynospermum dubium Reid & Chandler (1926)	Apocynaceae	Apocynaceae	The generic name *Cypselites* has nomenclatural priority for seeds with this morphology (Collinson *et al.* 2012a).
Apocynospermum elegans Reid & Chandler (1926)	Apocynaceae	Apocynaceae	The generic name *Cypselites* has nomenclatural priority for seeds with this morphology (Collinson *et al.* 2012a).
Apocynospermum rostratum Reid & Chandler (1926)	Apocynaceae	Apocynaceae	The generic name *Cypselites* has nomenclatural priority for seeds with this morphology (Collinson *et al.* 2012a).
Apocynospermum striatum Reid & Chandler (1926)	Apocynaceae	Apocynaceae	The generic name *Cypselites* has nomenclatural priority for seeds with this morphology (Collinson *et al.* 2012a).
Apocynospermum ?	Apocynaceae	Apocynaceae	The generic name *Cypselites* has nomenclatural priority for seeds with this morphology (Collinson *et al.* 2012a)
Phyllanthera vectensis Reid & Chandler (1926) [*Generic attribution not confirmed]	Asclepiadaceae	Apocynaceae	The Asclepiadaceae have now been included within the Apocynaceae (see Endress & Bruyns 2000).

Taxon			Comments
Tylophora antiqua Reid & Chandler (1926) [*Generic attribution not confirmed]	Asclepiadaceae	Apocynaceae	The Asclepiadaceae have now been included within the Apocynaceae.
Asterocarpinus sp.	Betulaceae	Betulaceae	Described by Reid & Chandler (1926) as *Carpinus* sp. and *Abelia* sp. 4, each from a single specimen. They were transferred to *Asterocarpinus* by Manchester & Donoghue (1995, p 721).
Catalpa rugosa Reid & Chandler (1926) [*Generic attribution not confirmed]	Bignoniaceae	Bignoniaceae	
Incarvillea pristina Reid & Chandler (1926) [*Generic attribution not confirmed]	Bignoniaceae	Bignoniaceae	
Radermachera pulchra Reid & Chandler (1926) [*Generic attribution not confirmed]	Bignoniaceae	Bignoniaceae	
Dipelta europaea Reid & Chandler (1926)	Caprifoliaceae	Caprifoliaceae	*Dipelta* was critically reappraised and accepted by Manchester and Donoghue (1995).
Palaeocarya macroptera (Brongniart) Jähnichen, Friedrich & Takáč (1984)	Juglandaceae	Juglandaceae	Formerly *Engelhardtia macroptera* (Brongniart) Unger, see Manchester (1987).
Hooleya hermis (Unger) Reid & Chandler (1926)	Juglandaceae	Juglandaceae	
Ajuginucula smithii Reid & Chandler (1926) [*Generic attribution not confirmed]	Labiatae	Lamiaceae	Unknown if this single specimen is from the Insect Limestone because it was removed from the matrix.
Melissa parva Reid & Chandler (1926) [*Generic attribution not confirmed]	Labiatae	Lamiaceae	Unknown if this single specimen is from the Insect Limestone because it was removed from the matrix.
Daphnogene cinnamomifolia (Brongniart) Unger (1850)	Lauraceae	Lauraceae	Reid & Chandler (1926) used the name *Cinnamomum scheuchzeri* Heer (1856) for this material. The species was not listed by Chandler (1963) and hence was erroneously omitted by Collinson & Cleal (2001b) although it appears in the Chandler (1964) list of lower Tertiary macrofossils and was discussed in Chandler (1957) as it is represented at Bovey Tracey. This Insect Limestone fossil is included within *D. cinnamomifolia* according to Z. Kvaček (pers. comm., 2013).
Daphnogene lanceolata Unger (1851)	Lauraceae	Lauraceae	Reid and Chandler (1926) referred to this as *Cinnamomum lanceolatum* (Unger) Heer (see Mai & Walther 1978, 1985).
Neolitsea sp.	Lauraceae	Lauraceae	Following McNeill *et al.* (2006) (ICBN Vienna Code), *Neolitsea* conserved against *Litsea* sect *Neolitsea*.
Papaver pictum Reid & Chandler (1926) [*Generic attribution not confirmed]	Papaveraceae	Papaveraceae	Unknown if this single specimen is from the Insect Limestone because it was removed from the matrix.
Sabrenia chandlerae Collinson (1980)	Nymphaeaceae	Nymphaeaceae	Formerly *Brasenia ovula* (Brongniart) Reid & Chandler (1926), see Collinson 1980.
Clematis vectensis Reid & Chandler (1926) [*Generic attribution not confirmed]	Ranunculaceae	Ranunculaceae	
Myosurus heterostylus (Reid & Chandler) Mai in Mai & Walther (1978).	Ranunculaceae	Ranunculaceae	Formerly *Ranunculus heterostylus* Reid & Chandler (1926), see Mai & Walther (1978).
Ranunculus ovaliformis (Reid & Chandler) Chandler (1963)	Ranunculaceae	Ranunculaceae	
Zizyphus paradisiacus (Unger) Heer (1859)	Rhamnaceae	Rhamnaceae	
Zanthoxylum(?) *costatum* Reid & Chandler (1926)	Rutaceae	Rutaceae	
Epipremnites ornatus (Reid & Chandler) Gregor & Bogner (1984)	Araceae	Araceae	Formerly listed as *Epipremnum ? ornata* Reid & Chandler (1926) by Chandler (1963). Gregor & Bogner (1984) erected the new organ genus *Epipremnites* for Araceae seeds with these characteristics and published the new combination.

Taxon			Comments
? Costus sp.	Zingiberaceae	Costaceae	
Carex gurnardi Reid & Chandler (1926)	Cyperaceae	Cyperaceae	
Carex sp.	Cyperaceae	Cyperaceae	
Cladiocarya foveolata Reid & Chandler (1926)	Cyperaceae	Cyperaceae	
Najas oligocenica Reid & Chandler (1926)	Najadaceae	Hydrocharitaceae	Missing.
Ottelia britannica Reid & Chandler (1926)	Hydrocharitaceae	Hydrocharitaceae	
Stratiotes neglectus Chandler (1923)	Hydrocharitaceae	Hydrocharitaceae	
Limnocarpus forbesi (Heer) Chandler (1961) emend Collinson (1982)	Potamogetonaceae	Potamogetonaceae/Ruppiaceae	Formerly *Limnocarpus headonensis* (Gardner) Reid, see Chandler (1961, p28–29).
Limnocarpus spinosus Reid & Chandler (1926)	Potamogetonaceae	Potamogetonaceae/Ruppiaceae	See Collinson (1982) for discussion of *Limnocarpus*. This species was doubtfully referred to genus *Limnocarpus* as the diagnostic character of bicarpelate fruits is not proven.
Potamogeton pygmaeus Chandler (1925)	Potamogetonaceae	Potamogetonaceae	See Collinson (1983) for distinction of *P. tenuicarpus* Reid & Chandler emend Collinson (1983).
Potamogeton ? spp.	Potamogetonaceae	Potamogetonaceae	Leaves of doubtful affinity. Three species.
Sparganium multiloculare Reid & Chandler (1926)	Sparganiaceae	Sparganiaceae	
Typha latissima Al. Braun (1851) emend Reid & Chandler (1926) emend Collinson (1983)	Typhaceae	Typhaceae	See Collinson (1983) for seed diagnosis and Reid & Chandler (1926) for emended diagnosis to include both fruits and leaves.
? Spirematospermum wetzleri (Heer) Chandler 1925 emend Koch & Friedrich (1971)	Zingiberaceae	Zingiberaceae / Musaceae	See Collinson & Cleal (2001b) for discussion of *Spirematospermum*.
Incertae sedis:	Original identification (Reid & Chandler 1926)	Revised identification	
'*Abelia*' *quinquealata* Reid & Chandler (1926)	Caprifoliaceae	*Incertae sedis*	This is regarded as *incertae sedis* by Manchester & Donoghue (1995). Note: All specimens of '*Abelia*' *quinquealata* Reid & Chandler (1926) were redetermined as '*Abelia*' *quadrialata* by Crane (1987). However, Manchester & Hably (1997) did not include specimens of *A. quinquealata* when they synonymised *A. quadrialata* with *Raskya vetusta*.
'*Abelia*' *trialata* Reid & Chandler (1926)	*Incertae sedis*	*Incertae sedis*	These are regarded as *incertae sedis* by Manchester & Donoghue (1995).
Carpolithus spp. *Dicotylophyllum* spp. *Dicotylophyllum* spp *Dicotylophyllum pinnatifidum* Reid & Chandler (1926)	*Incertae sedis* *Incertae sedis* *Incertae sedis*	*Incertae sedis* *Incertae sedis* *Incertae sedis*	
Fagus sp. ?	Fagaceae	*Incertae sedis*	See text.
Ficus sp.	Urticaceae	*Incertae sedis*	See text.
Flabellicula anglica Reid & Chandler (1926)	*Incertae sedis*	*Incertae sedis*	
Monocotylophyllum sp.	Monocot – *incertae sedis*	Monocot / Commelinid – *incertae sedis*	
Raskya vetusta (Ettingshausen) Manchester & Hably (1997)	*Incertae sedis*	*Incertae sedis*	*Abelia quadrialata* Reid & Chandler (1926) was included in this species by Manchester & Hably (1997).
Rhamnospermum bilobatum Chandler (1925)	Rhamnaceae ?	*Incertae sedis*	The modern affinities of these fossil seeds are not known although they occur throughout the UK Paleogene (Collinson 1983).
Genus ?	Cruciferae ?	*Incertae sedis*	
Genus ? sp. 1, sp. 2 & sp. 3; Gramineae ?	Gramineae ?	*Incertae sedis*	Fragments (including leaves) of uncertain affinity.

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