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Fossil oak galls preserve ancient multitrophic interactions

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Trace fossils of insect feeding have contributed substantially to our understanding of the evolution of insect–plant interactions. The most complex phenotypes of herbivory are galls, whose diagnostic morphologies often allow the identification of the gall inducer. Although fossil insect-induced galls over 300 Myr old are known, most are two-dimensional impressions lacking adequate morphological detail either for the precise identification of the causer or for detection of the communities of specialist parasitoids and inquilines inhabiting modern plant galls. Here, we describe the first evidence for such multitrophic associations in Pleistocene fossil galls from the Eemian interglacial (130 000–115 000 years ago) of The Netherlands. The exceptionally well-preserved fossils can be attributed to extant species of *Andricus* gallwasps (Hymenoptera: Cynipidae) galling oaks (*Quercus*), and provide the first fossil evidence of gall attack by herbivorous inquiline gallwasps. Furthermore, phylogenetic placement of one fossil in a lineage showing obligate host plant alternation implies the presence of a second oak species, *Quercus cerris*, currently unknown from Eemian fossils in northwestern Europe. This contrasts with the southern European native range of *Q. cerris* in the current interglacial and suggests that gallwasp invasions following human planting of *Q. cerris* in northern Europe may represent a return to preglacial distribution limits.

Keywords: cynipid; fossil; Pleistocene; multitrophic; gall; oak

1. INTRODUCTION

Trace fossils made by feeding insects have played a major role in our understanding of the evolution of insect–plant interactions (Labandeira & Phillips 1996; Wilf *et al.* 2001, 2006; Currano *et al.* 2008). The most structurally complex signs of insect activity in plant tissues are galls, plant tissues whose development is controlled by the gall-inducing organism (the galler) and which provide the galler with nutrition and protection (Cornell 1983; Price *et al.* 1987; Stone & Schönrogge 2003). The insect control of gall morphology is such that galls are the extended phenotypes of galler genes (Crespi & Worobey 1998; Stone & Cook 1998), and many gallers can be identified to species on the basis of gall morphology alone (Raman *et al.* 2005). Although three-dimensionally preserved insect-induced galls, dated at *ca* 305 Myr, are known, most are two-dimensional impressions whose lack of morphological characters precludes more specific identification of the causer (e.g. Scott *et al.* 1994; Labandeira & Phillips 1996). However, the inducers of well-preserved and structurally complex galls can sometimes be identified with high taxonomic resolution (e.g. Dieguez *et al.* 1996; Waggoner 1999; Erwin & Schick 2007).

In addition to the causer, many galls support communities of specialist herbivorous inquilines and natural enemies. The herbivorous inquilines are obligate inhabitants of galls induced by specific host galler species, and though they do not feed on the galler, their activities can cause its death either directly or indirectly (Shorthouse 1980; Washburn & Cornell 1981; Askew 1984;

Wiebes-Rijks & Shorthouse 1992; Ronquist 1994). The inquilines are often closely related to the gall inducers whose galls they attack (Ronquist 1994; Crespi & Abbot 1999; Miller & Crespi 2003), and this association (termed agastoparasitism by Ronquist 1994), closely parallels true parasitism. Both gall inducers and inquilines are attacked by natural enemies, particularly parasitoid wasps, and all three trophic groups commonly leave characteristic signatures in gall tissues (Stone *et al.* 2002; Raman *et al.* 2005). Fossil galls thus have the potential to provide direct evidence of within-gall multispecies associations. Here, we describe the first evidence for such associations, in Pleistocene fossil galls from the Eemian interglacial (130 000–115 000 years ago) whose excellent three-dimensional preservation not only allows precise identification of the causers but also provides the first fossil evidence of gall attack by specialist inquilines. Furthermore, phylogenetic placement of one of the Eemian gall causers in a lineage showing highly conserved host plant associations allows new palaeobotanical inferences for northwestern Europe that provide a striking contrast with the current interglacial.

2. FOSSIL MATERIAL STUDIED

The fossil galls (figures 1 and 2) were discovered in a gravel pit near Raalte, Overijssel Province, The Netherlands (see van der Ham *et al.* (2008) for a description of the site and associated biological material). They were preserved in Late Eemian (*ca* 125 000 BP) sediments of the Kreftenheye Formation (de Mulder *et al.* 2003) laid down by the ancient Rhine in the valley of the present river IJssel (van der Ham *et al.* 2008). Eemian vegetation at the site comprised temperate woodland including wetland

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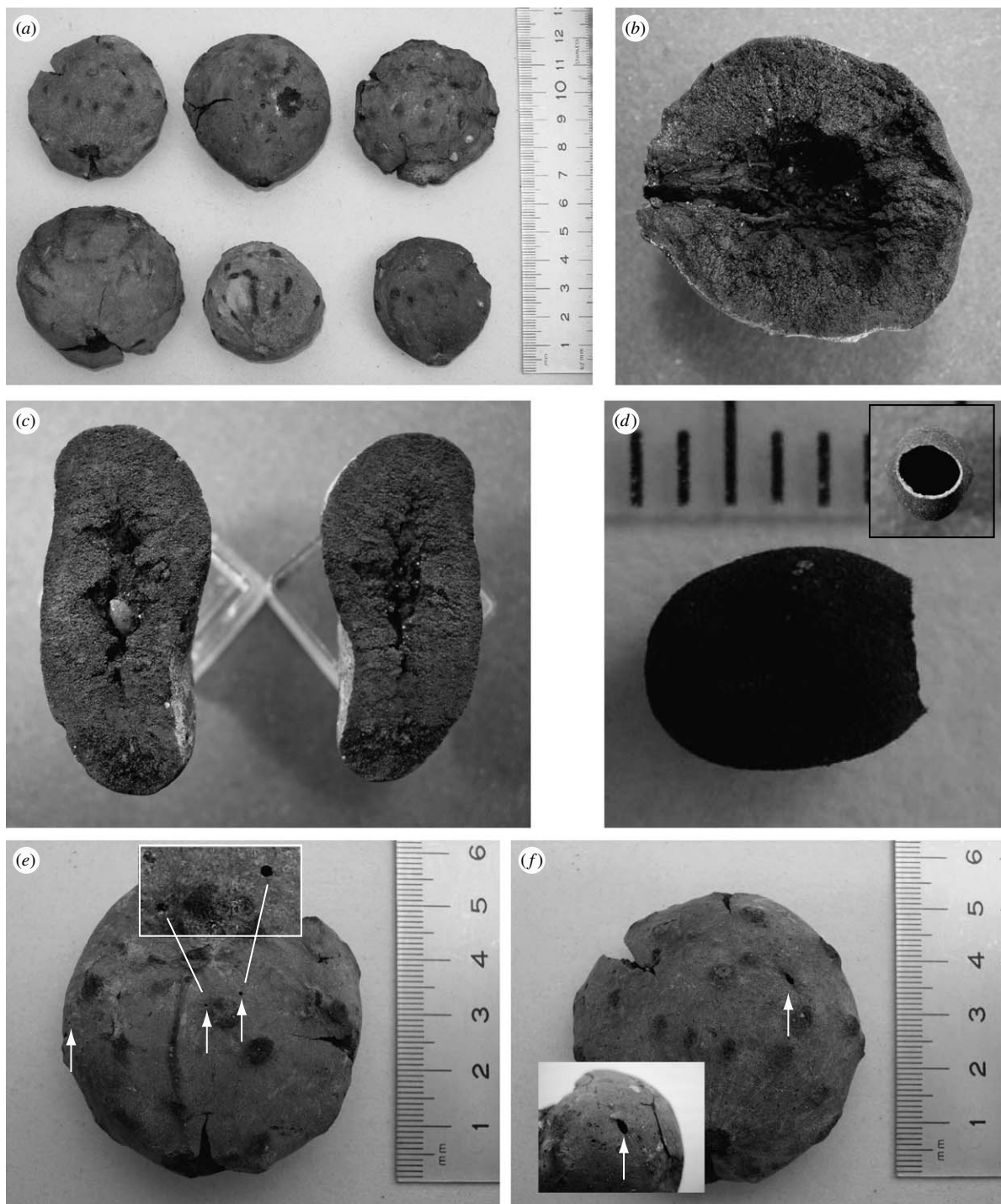


Figure 1. Type 1 gall fossils. (a) External views (scale in cm). (b) Longitudinal section showing internal airspace, with inner larval chamber missing. The gall's point of attachment is to the left. (c) Two halves of a sectioned compressed gall, showing the larval chamber in the left of the section. (d) A larval chamber, with the adult emergence hole to the right and (inset) in end-on view (scale in mm). (e, f) Two views of the same fossil gall, showing multiple emergence holes (arrowed). In (e), two of the small emergence holes are shown in enlarged view (boxed).

trees (e.g. *Alnus*, *Populus* and *Salix*) and upland forest species (e.g. *Abies alba*, *Acer*, *Carpinus betulus*, *Ilex aquifolium* and *Quercus*). The fossils are of two types.

- (i) *Type 1*. The most abundant type ($n=47$; figure 1) is preserved as a slightly (figure 1b) to moderately (figure 1c) compressed structure, originally approximately spherical and 37–57 mm in diameter. The original outer gall surface is exceptionally well preserved and marked with small regularly spaced tubercles or parallel ridges (figure 1a). The fossils have

a hollow interior (figure 1b,c) and, when complete, contain a single thin-walled chamber 5–6 mm long (figure 1d) that in some cases is attached to the interior wall on each side of its long axis (figure 1c). In all cases, this chamber has a smooth-edged hole 2 mm in diameter at one end. Three fossils have holes in the exterior (arrowed in figure 1e,f); each has a single larger slightly lenticular hole (figure 1f; dimensions 1.9×0.8 mm, 3×1.2 mm and 1.9×1.0 mm), while two galls have 1–3 smaller circular holes 0.6–0.8 mm in diameter (figure 1e,f).

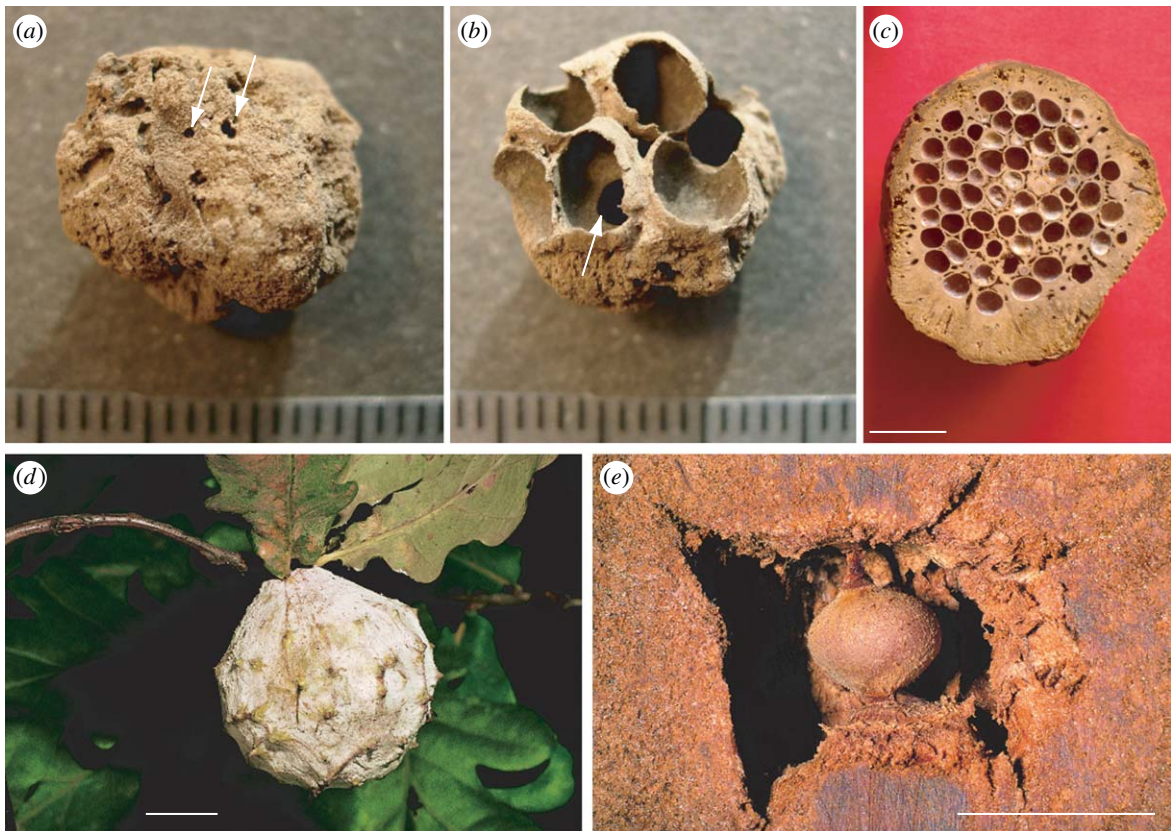


Figure 2. (a) Type 2 fossil external view, showing small emergence holes (arrowed, scale bar in mm). (b) Internal view of the same specimen, showing aggregated larval chambers (scale bar in mm). (c) A sectioned asexual generation gall of the modern oak gallwasp *A. quercusradicis* (scale bar, 1 cm). (d) Mature asexual generation gall of the modern oak gallwasp *Andricus hungaricus*. (e) The same in cross-section, showing the suspended inner larval chamber (c–e, courtesy of Dr György Csóka).

- (ii) *Type 2*. A single example (figure 2a,b) was found of a second type. One surface lacks obvious structure but bears several small holes approximately 1 mm in diameter (arrowed, figure 2a). The opposite surface comprises an aggregation of thin-walled chambers (figure 2b) approximately 5 mm long, joined in one case by a smoothly rounded hole 2 mm in diameter (arrowed, figure 2b).

3. DIAGNOSIS

Both fossil types can be unambiguously identified as galls induced by oak gallwasps (Hymenoptera: Cynipidae) on the basis of striking similarity to modern forms. No other gall inducers produce galls of this size and complexity in the Western Palaeartic (Docters van Leeuwen 1957; Buhr 1964–1965). Oak cynipid galls are diagnostic not only of the gallwasp species but also of alternating sexual and asexual generations in a parthenogenetic life cycle (Stone & Cook 1998; Stone *et al.* 2002, 2008). Phylogenetic relationships, oak host associations and associated gall communities of the Western Palaeartic gallwasp fauna have been studied in depth (Stone & Cook 1998; Cook *et al.* 2002; Rokas *et al.* 2003b), allowing extensive inference of biology and associated communities from gall structures. Studies of within-species genetic diversity show that all modern Western Palaeartic oak gallwasp species so far studied are at least 1–2 Myr old, and so long predate the Eemian (Rokas *et al.* 2001, 2003a; Stone *et al.* 2002, 2007; Challis *et al.* 2007). The Raalte fossils are thus certainly young enough to be attributable in principle to extant species.

- (i) *Type 1*. Only oak cynipid gallwasps induce galls of this size and complexity and the presence of a single larval chamber within an internal airspace places the galler with certainty within the *quercuscalicis* clade of the genus *Andricus* (figure 3). More significantly, these fossils are identical in size, external structure (figure 2d) and the suspension of the larval chamber within an internal airspace (figure 2e) to the asexual generation galls of extant *Andricus hungaricus* (Hartig 1843). These are the first fossil galls ever to be so clearly attributable to an extant gall inducer. The asexual generation galls of *A. hungaricus* are among the largest in the Western Palaeartic, and develop on shoot buds only of *Quercus robur*. They comprise up to 20% tannin dry weight (Ambrus 1974) and are resistant enough to decay that gallwasps diapause up to 6 years (Stone *et al.* 2002)—properties that may predispose these galls to fossilization.
- (ii) *Type 2*. The clustered cells in this fossil most closely resemble the asexual generation galls of *Andricus quercusradicis* (figure 2c). These galls comprise multiple aggregated larval chambers within a woody outer layer lacking distinctive surface sculpture, reaching a total diameter of 80 mm (Docters van Leeuwen 1957; Ambrus 1974). We interpret the type 2 fossil as a fragment of such a gall, whose exterior bears the small holes in figure 2a. The quality of preservation of the type 1 galls suggests that remnants at least of any more distinctive surface structures would be visible. Other woody, multichambered Western Palaeartic cynipid galls

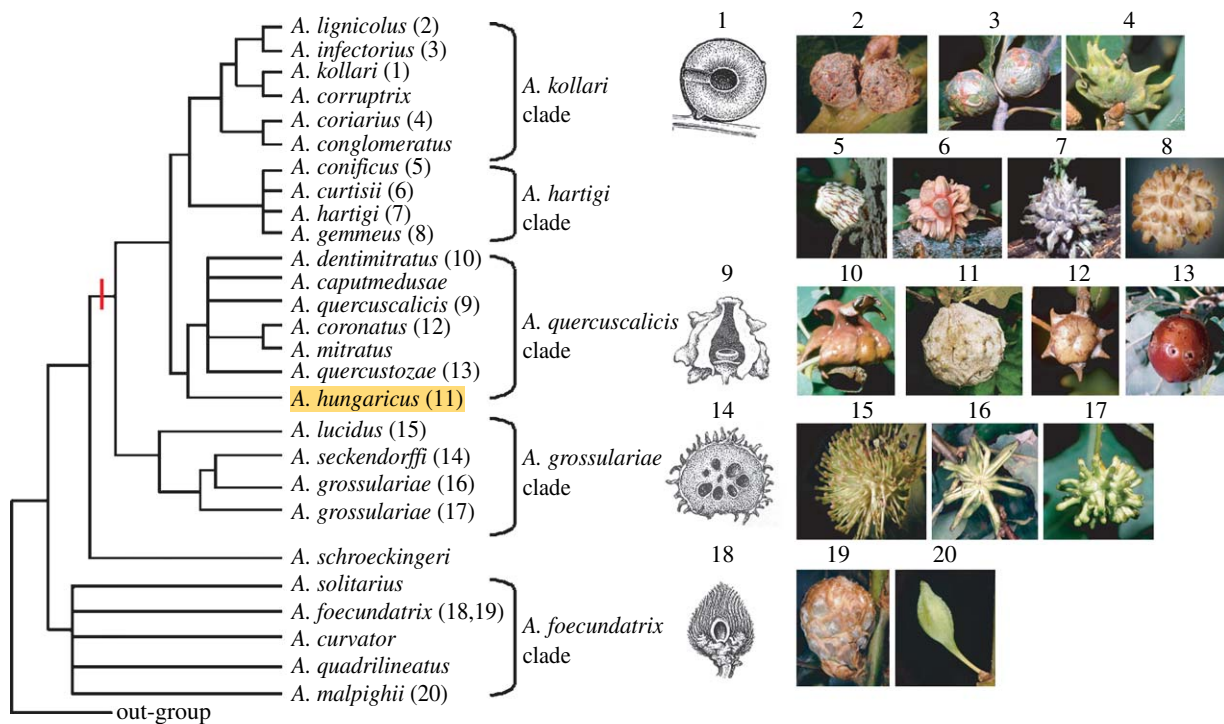


Figure 3. A phylogeny of the oak gallwasp genus *Andricus*, generated from DNA sequence data and showing the main species groups found in the Western Palaearctic. The gall structures illustrated are for the asexual generation. The only group to contain a separate larval chamber within an internal airspace is the *Andricus quercuscalicis* clade. The red bar shows the common ancestor of the host-alternating *Andricus* clade. Phylogeny from Stone & Cook (1998) and Cook *et al.* (2002). 1, *Andricus kollari*; 2, *Andricus lignicolus*; 3, *Andricus infectorius*; 4, *Andricus coriarius*; 5, *Andricus conficus*; 6, *Andricus curtisii*; 7, *Andricus hartigi*; 8, *Andricus gemmeus*; 9, *A. quercuscalicis* (shown in cross-section); 10, *Andricus dentimitratus*; 11, *A. hungaricus*; 12, *Andricus coronatus*; 13, *Andricus quercustozae*; 14, *Andricus seckendorffi*; 15, *Andricus lucidus*; 16, 17, *Andricus grossulariae*; 18, 19, *Andricus foecundatrix*; 20, *Andricus malpighii*.

contain smaller larval chambers (approx. 2 mm long: some *Plagiotrochus* and *Pseudoneuroterus*), comprise larval chambers with no surrounding woody material (*Callirhytis* asexual generation galls in acorns) or have an outer surface ornamented with spines (the *Andricus grossulariae* clade in *Andricus*; figure 3; Docters van Leeuwen 1957; Ambrus 1974; Stone & Cook 1998; Melika *et al.* 2000; Nieves-Aldrey 2001).

(a) Multispecies interactions

Both gall types show holes in the gall surface and, for the type 2 fossil, between internal larval chambers. These holes are characteristic of those made by emerging adult members of the gall community. The single larger surface holes on type 1 galls match the diameter of the aperture in the single inner larval chamber (figure 1d), and were chewed by an emerging gallwasp. Gallwasps emerging from multichambered galls commonly chew their way through vacated surrounding chambers, explaining the larger internal hole in the type 2 fossil. The smaller surface openings are too small to have been made by the galler in either case. Oak cynipid galls are commonly occupied by inquiline cynipids (Cynipidae: Synergini) that cannot induce their own galls but inhabit those induced by other causers, predominantly gallwasps (Stone *et al.* 2002). The inquilines are always smaller than the gall inducer and induce their larval chambers either within the host larval chamber (in which case the galler is always killed) or in the outer gall tissues (Washburn & Cornell 1981; Askew 1984; Wiebes-Rijks & Shorthouse 1992; Ronquist 1994; Stone

et al. 2002). The presence of both large and small emergence holes in a single type 1 gall can only be attributed to attack by outer gall inquilines. All outer gall inquilines in modern oak cynipid galls are species in the genus *Synergus*, and the small emergence holes must lead to chambers induced by Eemian *Synergus*. *Synergus* inquilines are themselves attacked by chalcid parasitoids (Askew 1961, 1984; Schönrogge *et al.* 1995, 1996a,b) and the smaller emergence holes could thus have been made either by emerging adult inquilines or parasitoids. Both of these trophic groups are associated with modern *A. hungaricus* galls (Melika *et al.* 1997). The many-chambered structure of the type 2 fossil makes the identification of causers of the smaller surface emergence holes less certain: though too small to have been made by the galler, they could have been made by emerging inquilines or by parasitoids of either inquilines or gallers.

4. DISCUSSION

(a) Multispecies interactions

To our knowledge, this is the first concrete evidence for multiple trophic groups in a fossil gall. Though fossil inquiline cynipids are known as far back as the Middle Eocene (45 Myr ago; Ronquist 1999), this is the first direct fossil evidence of their presence in cynipid gall tissues. Inquilines in the outer tissues of cynipid galls support rich communities of chalcid parasitoids that are often distinct from those attacking the inducer in the same gall (Askew 1961, 1984; Schönrogge *et al.* 1995, 1996a,b). Though we cannot distinguish emergence holes made by these two trophic groups, it is highly probable that some of the

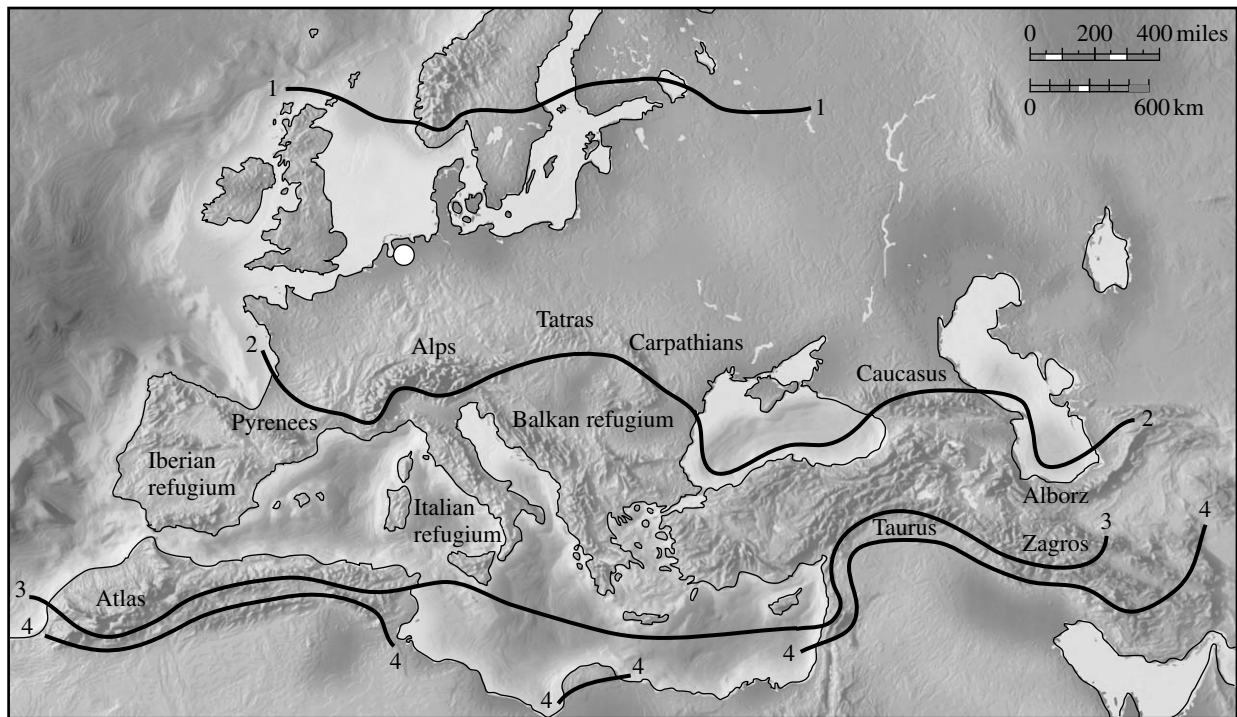


Figure 4. Location of the Raalte sampling location (white circle) relative to modern natural distributions of the oak sections *Quercus sensu stricto* and *Cerris*. Line 1 represents the northern limit of oaks in the section *Quercus* and of all oaks in the Western Palaearctic. Only section *Quercus* oaks are native between lines 1 and 2. Line 2 represents the northern limit of the natural distribution of section *Cerris* oaks. Oaks in sections *Quercus* and *Cerris* are naturally found together between lines 2 and 3. Line 3 represents the southern limit of oaks in the section *Quercus*. Only section *Cerris* oaks are found between lines 3 and 4. Line 4 represents the southern limit of section *Cerris* oaks. Distributions are based on regional floras as explained in Stone et al. (2007).

emergence holes in the Raalte fossils were made by chalcid parasitoids. The precise identification of the gall inducer from the gall phenotype, and hence a prior expectation of the relative sizes of the gall inducer and other gall inhabitants, was central to our interpretation of the trace fossils. It is possible that other fossil galls showing apparent emergence holes that are small relative to the size of the gall may represent evidence of inquiline or parasitoid attack: candidates include galls DT83 and DT84 in the web-based Guide to Insect (and Other) Damage Types on Compressed Plant Fossils at <http://paleobiology.si.edu/insects/index.html> (Dr C. Labandeira 2008, personal communication). However, many large galls house multiple small gall inducers (see Raman et al. (2005) for examples in many arthropod groups), and the relative size of galls and emergence holes may be an unreliable guide to the presence of non-galling inhabitants. Nevertheless, we expect that the examination of other fossil galls attributable to extant galler taxa, whose associated communities are well known, will yield further evidence of dependent trophic interactions.

(b) Oak gallwasps as indicators of past floras

Andricus hungaricus lies within a clade of *Andricus* species whose lifecycles require obligate alternation between two different taxonomic sections of the genus *Quercus* (Cook et al. 2002; Stone et al. 2008). The asexual generation always galls section *Quercus sensu stricto* oaks (such as *Q. robur* and *Quercus petraea*), while the sexual generation always galls section *Cerris* oaks (particularly Turkey oak, *Quercus cerris*). The most recent common ancestor of this host-alternating clade long predates the Pleistocene (Cook et al. 2002), implying that the Eemian causer of gall type 1 was also a host alternator. This allows a novel

palaeobotanical inference, because while the presence of section *Quercus* oaks at the Raalte site is confirmed by pollen and macrofossils (van der Ham et al. 2008), there is no direct evidence for section *Cerris* oaks. The type 1 fossils imply that during the relatively short (*ca* 15 000 years) Eemian interglacial, both oak sections and their associated insects escaped their southern European glacial refugia (Petit et al. 2002) to colonize northern Europe. The identification of the type 2 fossil provides additional (though weaker) support for this conclusion, for although both generations of *A. quercusradicis* can be found on section *Cerris* and section *Quercus*, the sexual generation is most commonly associated with section *Cerris* (Ambrus 1974; Melika et al. 2000).

(c) Implications for modern gallwasp distributions

The presence of section *Cerris* oaks inferred from the Raalte fossils contrasts with the oak flora native to the same region in the current interglacial. Only two section *Quercus* oaks, *Q. robur* and *Q. petraea*, are native to northern Europe, while section *Cerris* oaks (and hence associated gallwasps) are restricted to southern Europe and predominantly to regions south of the Pyrenees, Alps and Carpathians (figure 4). More specifically, *A. hungaricus* is now restricted to a region far to the south and east of its Eemian distribution, in Hungary and the Balkan refugium (figure 4; Ambrus 1974; Melika et al. 2000). However, over the last 500 years, human planting has extended the distribution of *Q. cerris* far beyond its natural distribution, and it is now naturalized as far north and west as Ireland and Scotland (Walker et al. 2002). Northwards range expansion by *Q. cerris* was thus prevented not by physiological limitations, but by inability to escape its Pleistocene glacial

refugia (Svenning & Skov 2004). The introduction of *Q. cerris* has in turn triggered invasion of northern Europe by multiple host-alternating gallwasps and their natural enemies (Stone *et al.* 2002; Hayward & Stone 2006), with potential for major direct (competition, parasitoid attack) and indirect (apparent competition mediated by shared enemies) impacts on native communities (Schönrogge *et al.* 1995, 1996a,b, 1999, 2000; Stone *et al.* 1995; Atkinson *et al.* 2002). At least four host-alternating species are now established in The Netherlands (*Andricus corruptrix*, *Andricus kollari* (figure 3, gall 1), *Andricus lignicolus* (figure 3, gall 2), *Andricus quercuscalicis* (figure 3, gall 9): Docters van Leeuwen 1957; Stone & Sunnucks 1993; Stone *et al.* 2007). The Raalte fossils imply that these gallwasps, though anthropogenic invaders in the current interglacial, were native to northwestern Europe in the previous interglacial. Their current range expansion should thus perhaps be considered as a return to preglacial distribution limits and ecology.

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