A provisional key to eriophyoid mite erinea on *Acer* in Britain

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Introduction

Of the many messes in the naming of eriophyoid mites (Acari: Eriophyoidea), the one associated with *Acer*, and especially with erineum galls (felty patches of hairs, also known as filz galls) on this host, must surely be one of the most extreme. The situation is plagued by a number of issues, including:

- the naming of gall-causers based on examination of galls rather than the causers;
- vague descriptions of gall features associated with a given mite name;
- huge numbers of synonyms, some of which may be illegitimate (not helped by the fact that some names are very similar despite describing different species);
- treating deutogynes (specialised overwintering females) and protogynes (normal females) of one species as two distinct species;
- some gall-causers acting as inquilines elsewhere;
- one mite species potentially causing multiple distinct types of gall, such as both erinea and pouches, and the gall form potentially varying with mite density (Patankar et al. 2012);
- possible 'chimera' galls caused by the overlapping gall-induction of multiple species (Nalepa 1922);

- contradictions between different authors;
- vanishingly few acarologists with the expertise needed to identify eriophyoids based on mite examination. In any case, suitable acarologists tend to dedicate their time to pests of major crop plants.

It is a daunting, almost overwhelmingly confusing rabbit hole to crawl down. But in so doing, I have found it an absorbing piece of detective work, not without its enjoyable moments as pieces of the puzzle seem to fit together. In this article, I present a provisional key to eriophyoid mite erinea on *Acer* in Britain, drawing on a wide range of literature from Britain and beyond, along with the key's implications for record verification (e.g. on iRecord). I begin with a brief discussion of eriophyoid ecology and what it tells us about the way we (should) record eriophyoid galls and their causers.

Miniature savannahs? Eriophyoid ecology and its implications for *Acer* erinea

Eriophyoid mites are minuscule, often gall-causing plant feeders typically less than 200 µm in length, with an elongate worm-like shape and only two pairs of legs at their anterior end (Lindquist 1996). Various aspects of their life cycle and ecology are relevant to the way we record eriophyoids and their galls on *Acer*.

Life cycle

There are two main life cycle types in eriophyoids (both involving development from eggs, through larval/nymphal stages to adults): a 'simple' cycle with one form of female (effectively equivalent to a protogyne), and a 'complex' cycle with protogynes and deutogynes (Lindquist et al. 1996). Focusing on eriophyoids galling the leaves of deciduous trees such as *Acer* in temperate regions, the mites typically overwinter as eggs (in the simple life cycle) or diapausing deutogynes (in the complex cycle) in bark crevices and buds of their host tree (Jeppson et al. 1975; Lindquist et al. 1996; Ueckermann 2010). In spring, emerging deutogynes typically lay eggs on buds (Lindquist et al. 1996). In their case study of the Maple Spindle Gall Mite *Vasates aceriscrumena* (Riley & Vasey 1870), Patankar et al. (2012) found that deutogynes induced galls in primordial leaves by feeding before laying eggs inside them, a behaviour considered by the authors 'typical' of eriophyoids on temperate deciduous hosts. Most deutogynes will have been inseminated the previous year; their fertilised eggs develop into females (mostly protogynes), whilst unfertilised eggs develop into males, in a female-dominated ratio controlled by the founding deutogyne: a reproductive strategy known as arrhenotokous parthenogenesis (Helle & Wysoki 1996). One or more generations of protogynes and males may occur during the spring and summer, with any deutogynes produced (mainly in later summer generations) finding shelter in preparation for winter (Lindquist et al. 1996). In the simple life cycle, reproduction can potentially continue throughout the year, depending on winter conditions (Lindquist et al. 1996).

Dispersal

Whilst some mites remain on their natal tree, others try to disperse to other trees (or potentially elsewhere on their own tree?) in late summer or autumn by adopting 'take-off postures', apparently to catch the wind or attach to a passing animal, including by 'standing up' on their anal lobes on a leaf or other tree parts and waving their legs in the air (a behaviour captured on film in Britain by Chris Leach, e.g. in *Aceria campestricola* (Frauenfeld 1865)), standing on their front legs and raising

their behind in the air, and forming chains of several attached individuals (Patankar et al. 2012; Kiedrowicz et al. 2017). There is limited evidence for phoresy (i.e. adaptive dispersal via animals) in eriophyoids (Michalska et al. 2010), although it has been demonstrated, e.g. in *A. pallida* Keifer 1964, which shows obligate phoresy via a psyllid (Liu et al. 2016); most dispersal via animals, which seems to be frequent in eriophyoids at least on long-lived hosts, is probably accidental (Liu et al. 2016; Kiedrowicz et al. 2017). Dispersal via wind also occurs (Majer et al. 2021), and eriophyoids may even disperse actively (i.e. by walking) for short distances, although this mode's usefulness is probably extremely limited (Majer et al. 2021), perhaps especially on large hosts such as trees. Deutogynes are probably the principal dispersers in eriophyoids with complex life cycles. Dispersal preparation behaviour may also occur when a mite finds itself on an unsuitable host (Skoracka et al. 2007). Dispersal is risky, although it can bring benefits when successful (Kiedrowicz et al. 2017; Majer et al. 2021), such as lower competition or pathogen load. Indeed, Chris Leach (pers. comm.) suspects that high competition for crevices in bark and buds may encourage some mites to disperse further afield. Especially via wind or accidental phoresy, dispersal has no guarantee of landing a mite on its desired host. The trade-offs associated with remaining on a natal tree or dispersing presumably result in a proportion of mites in a population adopting each tactic; perhaps we should assume that most mites stay put.

Host specificity

Host ranges vary in eriophyoids; they are often highly specialised, although existing data are biased by small, observational (rather than experimental) samples that do not differentiate between typical and accidental hosts (Skoracka et al. 2010; Marini et al. 2021), so our knowledge is sketchy. Does host specificity vary depending on whether we are considering gall induction or simply feeding on pre-existing gall structures (e.g. nutrient-rich erineum hairs)? The latter might be accessible to more mite species, as they are designed to be edible (unless there are chemical deterrents to other mite species in gall structures?), whilst the former might require more specialisation, because it involves the triggering of complex physiological pathways in the host, presumably by mite saliva (de Lillo et al. 2018). Although a single mite species could potentially induce galls on multiple host species, e.g. within the genus *Acer*, this largely seems not to be the case based on Nalepa's observations (Nalepa 1922). Some mites have been reported from multiple *Acer* species: for example, Willem Ellis' website Bladmineerders (https://bladmineerders.nl/) reports *Aceria macrocheluserinea* (Trotter 1902) from Field Maple *A. campestre* L., L'Obel's Maple *A. lobelii* Ten., Montpellier Maple *A. monspessulanum* L., Norway Maple *A. platanoides* L., Sycamore *A. pseudoplatanus* L., Italian Maple *A. opalus* Mill. 1768 and Red Maple *A. rubrum* L. However, this does not mean that gall induction occurs on each host.

Implications for recording erineum mites

Eriophyoid mites present in an erineum on an *Acer* leaf might therefore include:

a) the original gall-causer population from nearby overwintering deutogynes/eggs;
b) inquilines from a nearby overwintering population on that host;
c) 'migrant' mites dispersed into the erineum in that year from another host, or perhaps from elsewhere on the same host tree, or from a different erineum on the same leaf (either the gall-causer species or a different species).

For a) and b), a substantial population and evidence of breeding would usually be expected. New dispersed arrivals might be more rarely encountered; they would be more frequent later in the year, and if they are deutogynes, they may quickly move to overwintering locations away from the erineum. Depending on how late they arrive in an erineum, and how suitable the host is, it might even be possible for migrants to breed before winter, but perhaps we should expect migrants to typically consist of a few isolated individuals, without evidence of breeding. If they remain sheltering in an erineum after arrival, they are effectively acting as an inquiline. There may be a spectrum of inquilines from obligate to facultative, from specialist to generalist, and from those that can survive to breed to those that find the host too unsuitable to survive on.

The presence of an erineum indicates that at least one gall-causing eriophyoid species has been present at some point. Although an erineum would probably be expected to correspond most frequently to a single gall-causer, it is possible that 'chimera' erinea could be produced from the overlapping gall-induction of two or more eriophyoid species, e.g. on Sycamore (Nalepa 1922). Nalepa (1922) also observed pustule galls induced in amongst erinea.

The earlier in the year, the more likely it is to find an original gall-causing species in the erineum. Later in the year, the erineum community could become more complex as migrants arrive, inquilines colonise and breed, the original causers disperse, and ecological interactions occur, such as fatal infection by fungal pathogens (McCoy 1996) or predation by tarsonemid mites (Patankar et al. 2012), or competition between different plant-feeders. Indeed, such is the impact of infection and predation that Patankar et al. (2012) speculated that there could be a selective trade-off acting on the mites – *V. aceriscrumena* in their case – to develop more closed galls to reduce access to predators, but more open galls to avoid high humidity and the fungal infection that accompanies it. A confusing situation could even arise whereby the original gall-causing species is absent from an erineum due to any of the reasons mentioned above, but other eriophyoid species are still present. Indeed, if the gall-causer population is removed, perhaps it is then easier for the erineum to be invaded by inquilines from elsewhere; Chris Leach (pers. comm.) has noticed apparently vagrant mites inspecting vacated *A. campestricola* galls.

The possibility of multiple eriophyoid species in a given erineum begs the question of how they interact with each other. Is there high competition and even plant-mediated chemical warfare between gall-causers and inquilines? Or is there safety in numbers from predation, such that large and diverse erineum communities are tolerated? There is clearly much more to investigate here. In any case, we could consider erinea like a miniature Serengeti, with herds of various herbivores (eriophyoids) as well as stalking predators. Indeed, Chris Leach (pers. comm.) has likened the movements of eriophyoids in *A. campestricola* erinea in early autumn to the migration of herds of wildebeest *Connochaetes*.

As an illustration, consider the following observations by the Hungarian acarologist Grazyna Soika (which I have adapted stylistically) from Danish specimens collected by Hans Henrik Bruun and Simon Haarder in 2014 (pers. comm.):

- In erineum on Field Maple, no month given: *Aculops aceris* (Nal. 1894) (2 protogynes, 1 deutogyne) and *Aceria vermicularis* (Nal. 1902) (2 ♀s)

- In erineum on Field Maple, August: *A. aceris* (3 protogynes, 5 larvae)
- In erineum on Field Maple, August: *A. aceris* (15 protogynes, 1 deutogyne, 1 ♀, 4 larvae)
- In erineum on Norway Maple, 10 August: *Aceria eriobia* (Nal. 1922) (26 ♀, 2 protogynes, 4 deutogynes)
- In erineum on Norway Maple, August: *A. aceris* (1 protogyne, 24 deutogynes, 1 ♀, 2 larvae)
- In bud galls on Sycamore, June: *A. vermicularis* (13 ♀s, 3 ♂ s, larvae)

Conclusions from these observations are limited by the fact that no detailed descriptions of the erinea were provided, but the records are nonetheless interesting (sadly, Soika is apparently no longer actively studying eriophyoids, at least on *Acer*). It is especially notable that in all but the last record, Soika found no individuals of the species that we would probably expect to be the gall-causers: i.e. *Aceria lophophyes* (Nal. 1922), *A. macrocheluserinea* (Trotter 1902) or *Cecidophyes gymnaspis* (Nal. 1891) Ripka 2007 for the first three erinea, and *A. platanoidea* (Nal. 1922) or *Rhynchaphytoptus magnificus* (Hodgkiss 1913) for the fourth and fifth erinea (see key below). But perhaps we should not be too surprised, given that most of these records were from high summer, when erinea communities may have been altered by months of ecological changes, such that they might even become dominated by inquilines.

Aculops aceris (≡ *Phyllocoptes aceris* Nal. 1894, = *Vasates aceris* (Nal. 1894)) seems to be consistently associated with the Field Maple erinea, and with breeding evidence. This would be consistent with Nalepa's observations of *P. aceris* as an inquiline in erinea of *Phyllocoptes gymnaspis* Nal. 1891 (= *Cecidophyes gymnaspis*) and *Eriophyes macrochelus eriobius* Nal. 1922 (= *Aceria macrocheluserinea* (Trotter 1902)) on Field Maple (Nalepa 1922). Soika also found *A. aceris* in a Norway Maple erineum in substantial numbers, with breeding evidence. I do not know whether Soika is following Nalepa (1922) or Jeppson et al. (1975) in her concept of *A. aceris*; Nalepa (1922) synonymised his own two species of *A. aceris* on Field Maple and *P. acericola* Nal. 1894 (= *A. acericola* (Nal. 1894)) on Sycamore, but Jeppson et al. (1975) interpret them as separate species; there is inconsistency in the interpretation in the wider literature (see footnotes of the key below). It is unclear whether Soika uses *A. aceris* in the sense of *A. aceris* or *A. acericola* when it is on Norway Maple. In any case, I presume it is an inquiline here too. *Aceria vermicularis* is known from various *Acer* species, typically associated with swollen buds that do not open (see Bladmineerders); but it can clearly also be found elsewhere, such as in small numbers (with no evidence of breeding) in an erineum on Field Maple with *A. aceris*. *Aceria vermicularis* might even be a 'migrant' here. *Aceria eriobia* (= *A. macrocheluserinea*) was found in substantial numbers in a Norway Maple erineum; it is presumably a breeding inquiline here. The June record of *A. vermicularis* seems to match the traditional concept of this species' ecology; it is presumably a gall-causer here.

Background to the key

Only two eriophyoid mites associated with *Acer* erinea are keyed out in Redfern & Shirley (2011): *Aceria pseudoplatani* (Corti 1905) on Sycamore and *A. eriobia* (Nal. 1922) (the accepted name now being *A. macrocheluserinea*) on Field Maple. The forthcoming third edition of this key (Redfern & Shirley 2022 in press) adds *A. platanoidea* galls on Norway Maple and also notes that *A. macrocheluserinea* may be found on Sycamore. In both keys, the possibility of other erineum forms and their causers is noted. Below, I provide a key that incorporates more of these different erinea known on *Acer* in the British literature, as a companion to the main book of keys; the advanced stage

of publication of the third edition precludes all but minor edits. The key presented here lists four distinct erinea on Field Maple, two on Norway Maple, and three on Sycamore. There are several other forms noted by British authors, especially by the late John Robbins, that I do not give separate key entries because they are typically based on limited specimens (so assessing the consistency of the gall features is difficult) and I am wary that they may represent variation in the erinea of other species already known.

A range of literature and online databases have informed the key (Table 1). As far as I am aware, none of these sources other than mites' original discoverers (e.g. Corti and Nalepa), Connold (1901) and perhaps Massee (1965) actually examined mites. Despite not having a concept of protogynes and deutogynes, which confused some of his taxonomy, Nalepa seems peerless in the quality of his observations, with detailed descriptions of both the erinea and mites, and determinations of whether a given mite was a gall-causer or an inquiline.

Table 1. Literature and databases informing the key presented in this article.

References	**Purpose**
Connold (1901); Swanton (1912); Bagnall & Harrison (1928); Massee (1965); Darlington (1968); Winter (1983); Stubbs (1986); Robbins (1994, 2000); Leach (2005); Biggs (2007); Redfern & Shirley (2011, 2022 in press); Roper (2011); Maidstone (2013, 2021); Spooner (2019); Database of Insects and their Food Plants (DBIF, http://www.brc.ac.uk/dbif/homepage.aspx)	Examples of British literature and databases containing information on *Acer* erinea. I draw on a draft of the third edition *British Plant Galls* (Redfern & Shirley 2022, in press) for the description of *A. platanoidea* galls on Norway Maple.
Buhr (1964); Jeppson et al. (1975); Davis et al. (1982); Bernini et al. (2002); Alford (2018, see https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/eriophyes or Google Books); Roskam (2019 – see also the versions of Roskam's *Acer* galls key provided on Bladmineerders at https://bladmineerders.nl/backgrounds/specials/gallers-on-acer/); Bladmineerders; Naturbasen (https://www.naturbasen.dk/); Pflanzengallen (https://pflanzengallen.de/); the Vienna Natural History Museum list of Nalepa's mite species (see https://www.nhm-wien.ac.at/jart/prj3/nhm/system/project-docs/Nalepa/list_Nalepa_species.pdf, hereafter referred to as 'NHMW list')	Geographically wider-ranging literature and databases, with a particular European focus, providing context and seminal texts on European gall-causers.
Corti (1905); Nalepa (1922)	Original descriptions of many of the mites mentioned in the key.

Scope, caveats, and use of the key

The key, which focuses on erinea that are substantially exposed on the leaf surface, rather than pustule-shaped galls that may have erinea contained within them (e.g. the gall of *Aceria macrochela* (Nalepa 1891)), should be treated as a provocation rather than a finished product. Much more study is needed, which I hope this key stimulates, including of the consistency of different erineum forms and taxonomy of the mites. Although we would like to think that human knowledge improves over time, in the case of *Acer* erinea, the older texts are in a way more useful because they have not yet been obfuscated by decades of Chinese whispers. Unfortunately, these historic works are often difficult to get hold of (e.g. the journal *Marcellia*, in which Nalepa published some of his seminal

works), which can disincentivise their examination. In essence, the key attempts to synthesise pre-existing information on British *Acer* erinea in the most accurate manner possible, generating hypotheses for further investigation. Through my research, I am led to believe that we have not even been treating pre-existing information accurately.

Although the key is to erineum forms rather than their causers, I have assigned to all erinea the name of a mite gall-causer species. Names preceded by 'cf.' are placeholders for the causers of erinea known in Britain but not yet in the UK Species Inventory (UKSI), i.e. their causers should ideally be checked by an expert before the 'cf.' is removed; names without 'cf.' are already in the UKSI. Exceptions are *Aceria carinifex* (Kieffer 1901), which has the 'cf.' omitted because even though it is absent from the UKSI, it was noted as British by Bagnall & Harrison (1928), and if the gall is found in Britain it can be confidently matched to the mite name without mite examination; and cf. *Cecidophyes pseudoplatani* (Nal. 1922), which – although it has been noted as British by Massee (1965) – is a relatively controversial name whose host and erineum associations are conflicted, so I would recommend that the mites are examined before they can be confirmed for the UKSI (where the name is currently absent).

As well as *A. carinifex* and *C. pseudoplatani*, species names involved are cf. *A. lophophyes*, *A. macrocheluserinea*, cf. *A. platanoidea*, cf. *A. pseudoplatanea* (Nal. 1922), *A. pseudoplatani*, cf. *C. gymnaspis*, and cf. *Rhynchaphytoptus magnificus*. *Aceria carinifex*, *A. lophophyes*, *A. platanoidea*, *A. pseudoplatanea*, *C. pseudoplatani*, *C. gymnaspis* and *R. magnificus* are all absent from the UKSI at the time of writing (although an aggregate name *A. platanoidea* agg. is present to describe erinea on Norway Maple generally). Four of the inquilines listed by Nalepa (1922) are also absent from the UKSI, including *Aculops aceris* sensu Jeppson et al. (1975), *Phyllocoptes dorsalis* (Nal. 1922), *Rhinophytoptus stylotrichus* (Nal. 1920) and *Shevtchenkella serrata* (Nal. 1892), and should be looked out for. The inquilines *Aculops acericola* (Nal. 1894) (≡ *Phyllocoptes acericola* Nal. 1894, distinct from the American *Vasates aceriscrumena*, ≡ *Acarus aceriscrumena* Riley & Vasey 1870, = *Eriophyes acericola* Garman 1883, = *Phytoptus acericola* Garman 1883) and *Neotegonotus fastigatus* (Nal. 1892) are already on the UKSI. *Aculops acericola* may well have been applied to mites in Britain that are in fact *A. aceris* sensu Jeppson et al. (1975).

Although some of the British erineum forms have an uncertain causer, the situation is occasionally reversed: i.e. a mite name has been noted in the British literature but without description of the associated gall, so I have included both the name and gall description based on European literature even though the presence of the gall in Britain is uncertain.

On all three *Acer* species included here, Roskam (2019) notes the possibility of various other unnamed mite species; I do not aim to incorporate these. Erinea on other *Acer* species may be caused by mites mentioned in the key below or additional mite species; these are also outside the scope of the key (I am not aware of erinea on any other exotic *Acer* species in Britain, although would be delighted to be shown otherwise).

Maidstone (2013, 2021) provides excellent diagrams of many of the galls described in the key; although they are based on Norfolk specimens, they are likely to be relevant for other areas of Britain. Indeed, they agree well with observations of others, e.g. Leach (2005) and my and Jane

Thomas' observations from York. I provide photos to illustrate the key, some of which are of Continental European specimens due to a lack of good photos of British material.

A code is given for each erineum type (before the causer name) for ease of reference. The code is 'E' for 'erineum', then 'Ac', 'Apl' or 'Aps' for the host tree, and finally a unique number. Footnotes to each key entry are provided in a separate subsequent section, including lists of all synonyms that I am aware of. Many synonyms may be slight typos used by authors other than the original namers (especially variation in '-*us*' or '-*a*' endings).

Provisional key to eriophyoid mite erinea on *Acer* in Britain

READ ALL THREE OPTIONS

1. On Field Maple *Acer campestre* → **2**

- On Norway Maple *A. platanoides* → **5**

- On Sycamore *A. pseudoplatanus* → **6**

2. Mostly on leaf upperside, typically along a major vein; bulge or raised keel on the opposite side → **EAc1 *Aceria carinifex*** (Kieffer 1901)

Field Maple leaves with galls of *Aceria carinifex*, Berlin, Germany. Left: leaf upperside, 19/06/2020. Right: leaf underside, 11/09/2020. Photos: Alexis Orion.

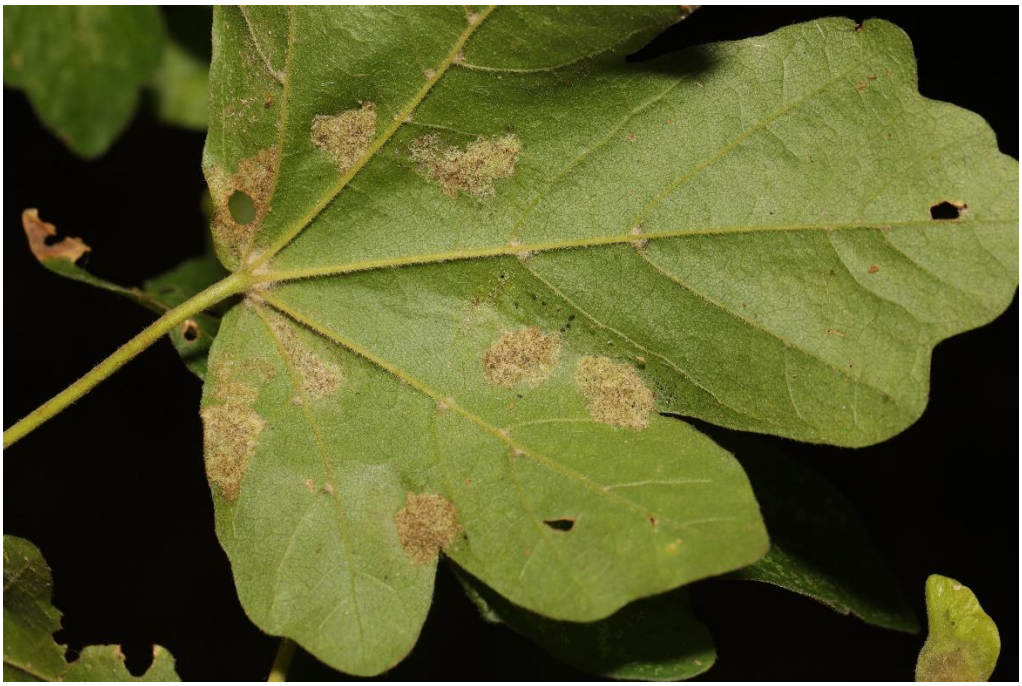
- Gall otherwise; mostly on leaf underside → **3**

3. Abnormal whitish hairs along the veins (never growing on the lamina) and tufts of hair in vein angles at the leaf base and in angles of secondary veins (but still arising from the veins); the hairs start from the leaf base and, in severe infections, also extend to the petiole and smaller side veins, when the hairs can look like irregular, pale islands between main and secondary veins, appearing to be on the lamina when in fact they are still growing from veins; hairs little modified, mostly very elongated, cylindrical, pointed; heavily infected leaves remain small, their leaf surface slightly

sunken along the main veins and yellowish in colour, the leaf margins curved downwards, and the leaf stalks hairy before entering the leaf surface → **EAc2 cf. *Cecidophyes gymnaspis*** (Nal. 1891) Ripka 2007

- Erineum not restricted to veins → **4**

4. Patches scattered over blade, sometimes covering the entire underside (or even extending onto upperside, spreading here from the main veins) in severe infections, often directly adjacent to, and delimited by, major veins; first whitish, then pink (especially in sunny locations) and finally brown; hairs markedly swollen apically, e.g. appearing cap-, funnel- or cup-shaped, later 'deflating'; leaf bulging over the erinea only slight if present at all (heavily galled leaves may curl) → **EAc3 *Aceria macrocheluserinea*** (Trotter 1902)

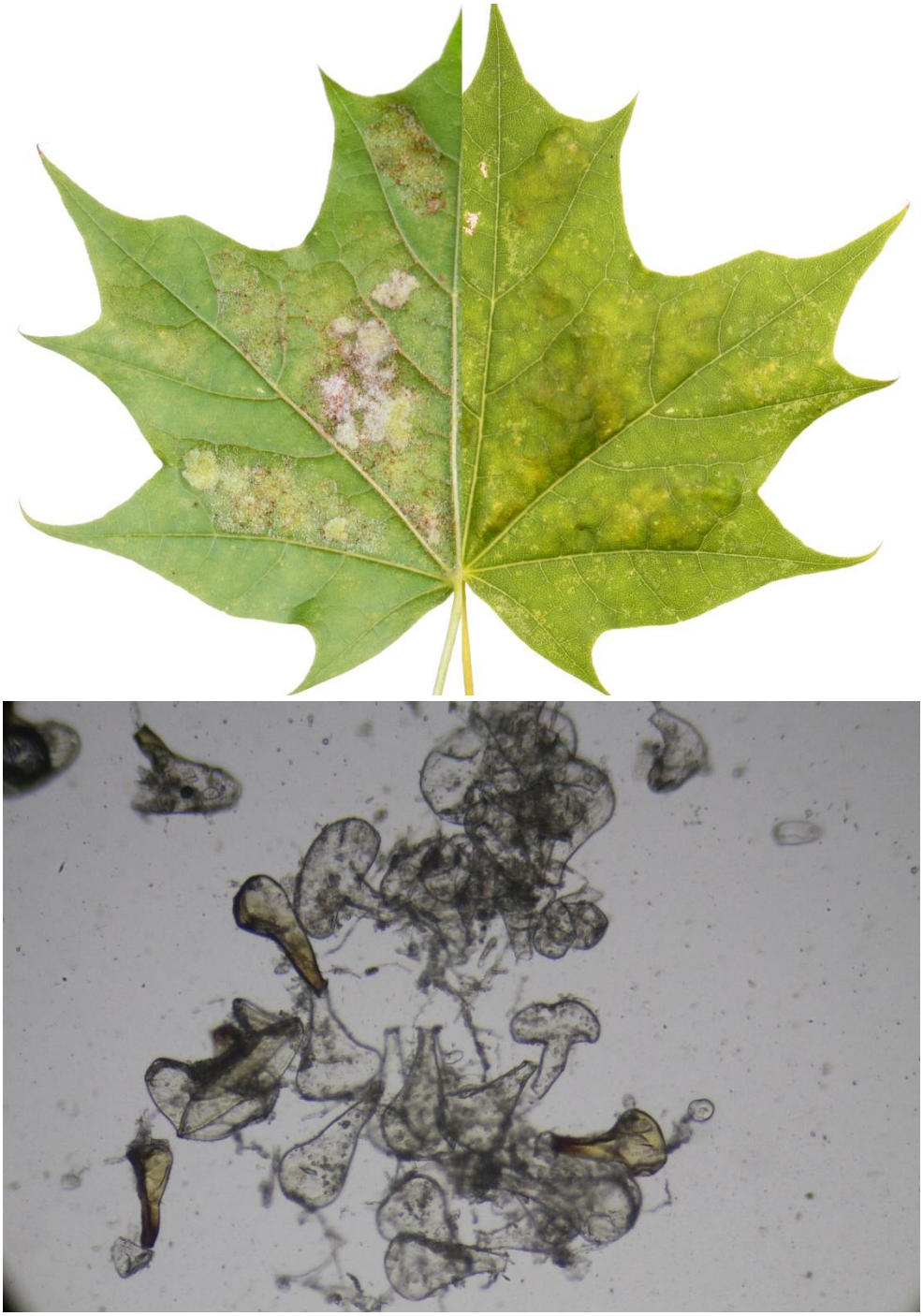


Erinea of *Aceria macrocheluserinea* on Field Maple, Pickerings Pasture, Widnes, 24/09/2021. Photo: Steve J. McWilliam.

- In vein angles, especially near petiole; causes upward bulging of the leaf where erinea located; hairs curled → **EAc4 cf. *Aceria lophophyes*** (Nal. 1922)

Field Maple leaves showing erinea caused by cf. *Aceria lophophyes*. From St Nicholas Fields, York, 29/09/2020. Top: leaf underside. Bottom: leaf upperside, showing bulges corresponding to the erinea. Photos: Sam Buckton.

5. Small patches or more extensive development usually on leaf underside, mainly on lamella away from veins; whitish to pale yellow at first, later brown or reddish brown; hairs markedly swollen apically, such that they look mushroom-, button- or top-shaped, later goblet- or cup-shaped; upperside usually without bulges but with brown, discoloured areas above the erinea → **EApl1 cf. *Aceria platanoidea*** (Nal. 1922)



Erinea of *Aceria platanoidea* on Norway Maple, Minsk, Belarus. Top left: leaf underside. Top right: leaf upperside. Bottom: high-magnification image of the erineum hairs. Photos: Maksim Kazakov (top collage created by Sam Buckton).

- In vein angles on leaf underside, especially near petiole; hairs straight; causes upward bulging of the leaf where erinea located → **EApl2 cf. *Rhynchaphytoptus magnificus*** (Hodgkiss 1913)

READ ALL THREE OPTIONS

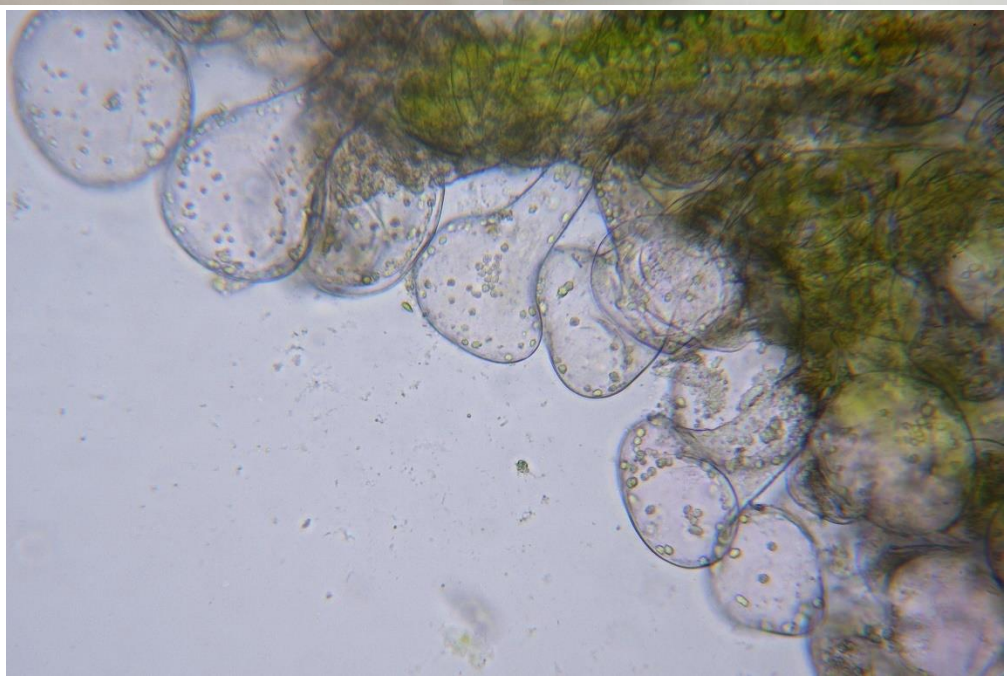
6. Tending to be on lamella between major veins (leaf underside) rather than directly adjacent to them; erineum turns from whitish-cream to pale tan brown as it matures (may be pink on purple-

leaved trees); hairs long and tubular, curled, not substantially broadened apically; causes upward bulging and yellowing or browning of the leaf where erinea located → **EAps1 *Aceria pseudoplatani*** (Corti 1905)

Top: erineum of *Aceria pseudoplatani* on Sycamore (circled) from St Nicholas Fields, York, 13/05/2021, with an erineum of cf. *A. pseudoplatanea* on the same leaf (left: leaf underside; right: leaf upperside). It was confirmed microscopically that the former has sausage-shaped hairs, shown in the bottom photo (05/05/2021). Photos: Jane Thomas.

- In dense patches or scattered, tending to be adjacent to, and delimited by, major leaf veins (including alongside the midrib) such that patches look angular, usually on leaf underside but rarely on upperside; erineum turns from whitish-cream to pink to reddish chocolate brown as it matures; hairs squat and markedly broadened apically, such that they look bead-headed/mushroom-shaped, losing turgor with age; leaf bulging over the erinea only slight if present at all, and rarely any

yellowing of the leaf (the green colour may be intensified above the erinea) → **EAps2 cf. *Aceria pseudoplatanea*** (Nal. 1922)



Top: erineum of cf. *Aceria pseudoplatanea* on Sycamore (circled) from St Nicholas Fields, York, 13/05/2021, with an erineum of *A. pseudoplatani* on the same leaf (left: leaf underside; right: leaf upperside). It was confirmed microscopically that the former has apically swollen hairs, shown in the bottom photo (05/05/2021). Photos: Jane Thomas.

- Abnormal whitish hairs on the veins and hair tufts in the vein angles on the leaf underside, frequently together with EAps1 and EAps2 → **EAps3 cf. *Cecidophyes pseudoplatani*** (Nal. 1922)

Footnotes

All quotes from Nalepa (1922) are translated from the original German using Google Translate and then sense-checked by the author.

EAc1 *Aceria carinifex* (Kieffer 1901)
≡ *Phytoptus carinifex* Kieffer 1901 (most online sources have the year as 1902, but this seems to be erroneous – see Nalepa (1922))
= *Eriophyes macrochelus* var. *carinifex* (Kieffer 1901?) (see Bagnall & Harrison 1928; Bladmineerders)
= *Eriophyes macrochelus carinifex* (Kieffer 1901?) (see Bagnall & Harrison 1928)
= *Eriophyes macrochelus crassipunctatus* Nal. 1909
= *Aceria macrochela crassipunctata* (Nal. 1909)
= *Eriophyes crassipunctata* (Nal. 1909) (GBIF gives this as the root of the *crassipunctatus* names, but the root should presumably be *E. m. crassipunctatus*)
= *Eriophyes crassipunctatus* (Nal. 1909)
= *Aceria crassipunctata* (Nal. 1909)
= *Aceria crassipunctatus* (Nal. 1909)

The gall description is based on Bladmineerders and Nalepa (1922). Bagnall & Harrison (1928) include '*Eriophyes macrochelus carinifex* [sic], Kieff.' on Field Maple in their catalogue of British Eriophyoidea. Description of *A. carinifex* gall characteristics from Britain is unknown. Bagnall & Harrison (1928) also list '*Eriophyes macrochelus crassipunctatus*, Nal.' on Field Maple. Why these names are entered separately is odd, as they are synonyms. Nalepa (1922) describes the gall of *E. macrochelus crassipunctatus* on Field Maple as 'boat-shaped protuberances of the leaf blade downwards, rarely upwards, along veins, lined internally with whitish hairy felt'. However, the erineum can be quite exposed on the leaf upperside, which is why it is included in this key. If the gall is still present in Britain, it must surely be rare (or even extinct?), since it is visually striking.

EAc2 cf. *Cecidophyes gymnaspis* (Nal. 1891) Ripka 2007
≡ *Phyllocoptes gymnaspis* Nal. 1891 (various incorrect years have been attached to this name; e.g. Fauna Europaea and GBIF have 1892, and Davis et al. (1982) has 1894 – see Nalepa (1922) for the correct year. Moreover, GBIF perhaps erroneously gives the basionym as *Phytocoptes gymnaspis*)
= *Coptophylla gymnaspis* (Nal. 1891) Rovainen 1951

We know little about what this erineum looks like in Britain; the gall description is based on the detailed description by Nalepa (1922), and possibly has an affinity to gall no. 70 in Buhr (1964). The 'only authenticated listing' in Britain of *C. gymnaspis* (under its older name *Phyllocoptes gymnaspis*) that Robbins (2000) was aware of was in Bagnall & Harrison (1928) on Field Maple, although *C. gymnaspis* and its synonyms are absent from the UKSI. Bagnall & Harrison (1928) did not describe the erineum features, but they presumably correspond to Nalepa's. Nalepa (1922) emphasises the difference between this erineum and that of *A. lophophyes* (see below), and notes that *Aculops aceris* (using the name *Phyllocoptes aceris*) is an inquiline.

EAc3 *Aceria macrocheluserinea* (Trotter 1902)
≡ *Eriophyes macrocheluserineus* Trotter 1902
= *Phytoptus erinea* Trotter 1902
= *Eriophyes macrochelus* var. *erinea* Trotter & Cecconi 1902 (Bladmineerders gives Nalepa as the namer, which is apparently an error)
= *Eriophyes moniezi* subsp. *erinea* (Trotter 1902)

= *Eriophyes macrochelus eriobius* Nal. 1922
= *Eriophyes eriobius* (Nal. 1922)
= *Eriophyes eriobia* (Nal. 1922)
= *Aceria macrochela eriobia* (Nal. 1922)
= *Aceria eriobia* (Nal. 1922)
= *Aceria eriobius* (Nal. 1922)
= *Phytoptus eriobia* Nal. 1922 (see GBIF – this is presumably an error)
= *Eriophyes macrochelus psilomerus* var. *aceris campestris* Nal. 1922 (see Jeppson et al. 1975; this is the deutogyne of *A. macrocheluserinea*. Note that this is distinct from *E. m. psilomerus*, which is the deutogyne of *A. pseudoplatanea*)

The gall description is based on gall M 005 in Maidstone (2013, 2021), Nalepa (1922) and Redfern & Shirley (2011), the latter only for erineum position and colour, as well as other British observations. Nalepa (1922) notes that the erineum 'shows the great diversity of the same erineum on *Acer pseudoplatanus* [i.e. the erineum of *Aceria pseudoplatanea*], both in the hair form and in the shape and distribution of the erineum. The erinea … are sometimes irregularly delimited, flat, crooked in appearance, sometimes rounded, sharply delimited and cushion-like … The hairs are … short in the flat erineum and on the leaf upperside, longer-stalked in the cushion-like erineum; they are not only on the lamina, but also on the veins'. Jeppson et al. (1975) refer to the hairs as 'capitate papillae'. Roskam (2019) notes that *A. macrocheluserinea* galls can cause some bulging. Nalepa (1922) lists *Eriophyes macrochelus psilomerus* var. *aceris campestris* 'often in large numbers', *Phyllocoptes aceris* (= *Aculops aceris*) and *Oxypleurites serratus* Nal. 1892 (= *Shevtchenkella serrata*) as inquilines. However, *E. m. p.* var. *a. campestris* is actually the deutogyne of *A. macrocheluserinea* (Jeppson et al. 1975).

EAc4 cf. *Aceria lophophyes* (Nal. 1922)
≡ *Eriophyes macrochelus lophophyes* Nal. 1922
= *Aceria macrochela lophophyes* (Nal. 1922)

The gall description is based on gall M 008 in Maidstone (2013, 2021), who suggests that the causer is either *Aculops acericola* or *A. lophophyes*, and personal observations from St Nicholas Fields in York. Pflanzengallen has images of *A. lophophyes* galls on Field Maple from Thüringen (under the name '*Aceria macrochela lophophyes* Nal.') that appear similar to the corresponding British galls, although the hair morphology is not visible.

Judging by Nalepa (1922), *A. lophophyes* would seem the most appropriate name to give the causer of M 008. Nalepa describes the erinea as 'small, rounded accumulations of flat, broadened hair formations in the vein angles, but also scattered on the underside of the leaf. In severe infections these crests of hair are not confined to the vein angles, but are also found scattered as small crumbs of various sizes on the lamina, especially on the leaf indentations, near the leaf edge, which is then slightly bent down; even the petioles then have loose hairs. The tufts are initially whitish, hyaline, and take on a splendid crimson colour in sunny areas; later they turn brown. The hairs do not grow on the veins like those of [*Cecidophyes gymnaspis*], but on the leaf surface, which shows small, flat, sometimes yellowish-coloured elevations at these points on the upperside. [The hairs] are

multicellular, flat, spread-out, mostly branched trichome formations'. He lists *Oxypleurites serratus* (= *Shevtchenkella serrata*) and a *Tegonotus* sp. as inquilines.

Aculops acericola, meanwhile, appears to be an inquiline rather than a gall-causer; moreover, following the interpretation of Jeppson et al. (1975) – which I align to here – it is not found on Field Maple, but on Sycamore. Nalepa (1922) certainly knew it only as an inquiline. Nalepa actually described two related inquiline species, *Phyllocoptes aceris* on Field Maple and *P. acericola* on Sycamore, but later synonymised them under *P. aceris* (Nalepa 1922). However, Jeppson et al. (1975) consider them distinct species, noting that females of *A. acericola* are smaller than those of *A. aceris*. Jeppson et al. (1975) and Alford (2018) state that *A. acericola* is an inquiline in erinea of *Eriophyes psilomerus* (= *A. pseudoplatanea*) on Sycamore, Alford emphasising that it is not a gall-causer. Jeppson et al. (1975) state that *A. aceris* is an inquiline in erinea of *E. eriobius* (= *A. macrocheluserinea*) on Field Maple. Nalepa also listed *P. aceris* as an inquiline in erinea of *A. pseudoplatani*: assuming that host tree is the main delimiter of *P. aceris* from *P. acericola*, this inquiline would actually be *P. acericola*. Bagnall & Harrison (1928) noted *P. aceris* on Field Maple in galls of *Eriophyes macrochelus* (it is unclear what precise species is being referred to here – it might be *Aceria macrochela*, but equally it could possibly be *A. macrocheluserinea*, alluding to its old name *E. m. eriobius*) and *E. macrorrhynchus* [sic] (= presumably *Aceria macrorhyncha* (Nal. 1889), although Bladmineerders states that this is found only rarely on Field Maple). Arthur Morel Massee (1899-1967), in a work described by DBIF simply as 'Acarina: Eriophyidae' from 1965 (I have been unable to obtain a copy of this work), notes *A. acericola* on Sycamore from 'Thames' and 'Humber'. Massee did publish 'The Gall Mites (Arachnida: Acarina: Eriophyidae) of Kent' (Massee 1961) and also a checklist of British eriophyids held at the Department of Zoology in the British Museum (Massee 1964); perhaps these have some relation to the 1965 work, which might also be a mis-citation. Connold (1901) named mites found in 'pustulate galls on leaves of sycamore' (Roper 2011) prior to 1902 in Hastings as *Phyllocoptes acericola*. Based on the description, the galls are likely to be caused by *Aceria cephalonea* (Nal. 1922) or *A. macrorhyncha*. Presumably, *A. acericola* is an inquiline in these galls. There appears to be a similar, although more confused, situation in Bernini et al. (2002), who use the name '*Aculus acericola*' to describe 'red pimple galls' on Sycamore that look from the photo provided like galls of *A. cephalonea*. The NHMW list includes *Aculus acericola* (Nal. 1894) on Sycamore. I suspect that *Aculus acericola* is synonymous with *Aculops acericola*, with *Aculus* possibly being a typo.

However, most British authors appear to consider *A. acericola* a gall-causer, perhaps erroneously, including Stubbs (1986), Swanton (1912) and Biggs (2007), 'typically in vein axils of *A. pseudoplatanus*' (Spooner 2019). Seminal European works also consider *A. acericola* a gall-causer, including on Field Maple (when the mite concerned may actually be *A. aceris*). Bladmineerders (and Roskam 2019) include Field Maple as a host of *A. acericola*, Bladmineerders describing the hairs of *A. acericola* erinea as 'spiralled and lengthened', although Roskam, following gall 68 in Buhr (1964), is tentative: 'With reservation, also the malformation reported as "yellow tufts" consisting of longer, widened, densely felt-like hairs, reported as "Erineum abnorme" is caused by *Aculops acericola*'. However, Nalepa (1922) determined the causer of the 'Erineum abnorme' as *A. lophophyes*, not *A. acericola* or *A. aceris*, which he did not find in these galls (although *A. aceris* could plausibly be found here). Davis et al. (1982) describe *A. aceris* as an erineum-causer on Field Maple and Sycamore (as well as Sugar Maple *Acer saccharum* Marshall), although the latter presumably refers to *A. acericola*.

It is not clear what evidence is being drawn on by any of these authors to claim that *A. aceris*/*acericola* is a gall-causer rather than the inquiline that Nalepa knew based on his meticulous observations. I am sceptical of *A. aceris*/*acericola* being anything other than an inquiline; claims to the contrary have probably been biased by associations of mite names with galls without examining the mites.

Robbins (1994) includes a 'l/s [lower surface] filz-gall, chiefly in the vein angles' on Field Maple that he equates to 'Buhr 68-70'. It is unclear whether Robbins means that he has found all three gall types, or whether the gall is from within this range. Buhr's 68-70 are all associated with vein angles and veins, varying in the hair morphology and degree of leaf bulging (Buhr 1964). At least one of these galls (e.g. 68 or 69) may be the same as EAc4, whilst the others could possibly represent variation in this gall. Buhr describes 70 as 'krümelige' (crumbly), which I have also noticed in old galls of EAc4 at St Nicholas Fields, although in other respects (e.g. the noted lack of leaf bulging), Buhr's 70 sounds rather like EAc2 (see below).

Robbins (1994) also describes a gall 'in 1993 on a spray of *Acer campestre*' with an unknown causer: 'On the larger leaves there were patches of dense erinea adjacent to the petioles and small patches also in several of the vein-angles: the hairs were quite different from those of *Aceria eriobia* [= *A. macrocheluserinea*] which occurred on one of the leaves, nor do they correspond to any of the descriptions given by Buhr (B.67-70). Additionally, on the two smallest leaves the hairs were scattered somewhat loosely over the l/s, they occurred around the margin, which was incurled, and also extended to the petiole: on the leaf-margins and the petioles of these two leaves the hairs were red, but were yellowish on the others.' I am reluctant to include this as a separate entry in the key for several reasons. Firstly, Robbins does not describe the hair morphology. Secondly, it is not clear if the hairs of the erinea on the smaller leaves are different from EAc3 (the former gall sounds rather like EAc4). Thirdly, the galls appear to be based on a single spray of Field Maple. Cecidologists should nonetheless keep an eye out for any erinea on Field Maple that do not conform to EAc1, 2, 3 or 4.

Although *A. aceris* should be expected as an inquiline on Field Maple and *A. acericola* on Sycamore, we should be open to the possibility that *A. acericola* could be vagrant on Field Maple, and *A. aceris* a vagrant on Sycamore.

EApl1 cf. *Aceria platanoidea* (Nal. 1922)
≡ *Eriophyes macrochelus eriobius* var. *platanoidea* Nal. 1922
≡ *Eriophyes macrochelus eriobius* var. *platanoideus* Nal. 1922
= *Eriophyes platanoidea* (Nal. 1922)
= *Eriophyes platanoideus* Nal. 1927 (there may be several errors with this name given by GBIF, which erroneously calls it the basionym of *A. platanoidea*. The year is possibly incorrect, and the name should probably be a *combinatio nova*)

The gall description is based on Spooner (2019), who found and identified the gall in 2019 in Surrey, as well as a draft of Redfern & Shirley (2022 in press) and Nalepa (1922). It may be the same as the gall recorded by Burkill (1934) in 1933 in Surrey (Spooner 2019). Nalepa (1922) described the erineum thus: 'The hairs have very short stalks, mostly in the shape of buttons or tops, later in the shape of a goblet or cup. The turfs are widely spread, usually not sunken into the leaf surface, but

hairy turfs are also found which are deeply sunken into the leaf blades, similar to [the erinea of *A. pseudoplatani*]'. He listed *Oxypleurites serratus* (= *Shevtchenkella serrata*) and an unknown variety of *Phyllocoptes gymnaspis* as inquilines.

Roskam (2019) notes *A. macrocheluserinea* and *A. pseudoplatani* (see below) on Norway Maple; perhaps they can be found on this host as vagrants. Although Pflanzengallen (https://www.pflanzengallen.de/pflanzenverzeichnis.php?letter=A) shows a picture of '*Aceria pseudoplatani*' erinea on Norway Maple, without checking the hairs, these look identical to EApl1, so I suspect that the identification is erroneous.

EApl2 cf. *Rhynchaphytoptus magnificus* (Hodgkiss 1913)

The gall description is based mainly on gall M 010 in Maidstone (2013, 2021), who suggests *A. acericola* as a possible causer (*A. lophophyes* appears to be known only from Field Maple). Again, I am sceptical of any treatment of *A. acericola* or *A. aceris* as a gall-causer. Spooner (2019) suggests that such galls may correspond to an unnamed mite gall (no. 65) on this host in Buhr (1964), and notes that they match galls of the North American species *R. magnificus*, which seems to be the most appropriate placeholder causer name. It is interesting that even the sharp-eyed Nalepa failed to spot this vein angle erineum in his studies.

Bladmineerders and Davis et al. (1982) note *C. gymnaspis* (see above) from Norway Maple, so recorders should perhaps keep an eye out for EAc2-type galls on this host, or perhaps *C. gymnaspis* would appear as a vagrant/inquiline; Davis et al. (1982) note that *C. gymnaspis* is both an erineum-causer and vagrant, but do not clarify on which hosts the mite uses which strategy.

EAps1 *Aceria pseudoplatani* (Corti 1905)
≡ *Eriophyes pseudoplatani* Corti 1905
= *Eriophyes macrochelus pseudoplatani* (Corti 1905)
= *Eriophyes macrochelus* var. *pseudoplatani* (Corti 1905)
= *Eriophyes eriobius pseudoplatani* Nal. year unknown sensu Alford (2018)
= *Aceria macrochela pseudoplatani* (Corti 1905) (see Bladmineerders)
= *Eriophyes phyllerites* Nal. 1922 (see Jeppson et al. 1975; this name refers to the protogyne of *A. pseudoplatani*)
= *Aceria phyllerites* (Nal. 1922)

The gall description is based on British observations, including gall M 013 in Maidstone (2013, 2021) and 'Type B' in Leach (2005), which are likely to be referring to the same gall/causer. Leach (2005) describes the hair morphology as 'slimmer, tubular and twisted, and much less swollen than Type A' (Type A corresponds to EAps2 below). Maidstone (2021) describes the hairs as 'sausage-shaped'. These descriptions match the equivalent galls found at St Nicholas Fields in York on Sycamore (pers. obs.), and are consistent with Corti's (1905) original description of *A. pseudoplatani* galls: 'Large patches of cylindrical hairs on the underside, sometimes even slightly swollen at the apex, dense; alteration and hypertrophy of mesophyll tissues and discoloured yellowish bulges on the upper side' (translated from the original Italian). Leach (2005) also notes a distinct yellow discoloration on the upper leaf surface above and surrounding the erinea. Roskam (2019) notes that the hairs of *A.*

pseudoplatani erinea may be 'weakly club-shaped, the apical part sometimes curved or also crooked'. Overall, the most important hair features appear to be that they are relatively long and unswollen compared to the hairs of *A. pseudoplatanea* galls, although the degree of swelling might be variable. Indeed, John Robbins knew *A. pseudoplatani* erinea as being 'variedly broadened at or towards the tips' (Leach, 2005). Leach (2005) notes of the erineum colour: 'turning from whitish-cream to a much paler (tan) brown than Type A'. Intriguingly, Corti (1905) noted of the colour: 'The hairs had, at the time I collected them, assumed a ruby colour; but they are whitish when they are younger' (translated from the original Italian). 'Ruby' is an unusual colour for *A. pseudoplatani* galls, being more associated with galls of *A. pseudoplatanea* (see below), although based on British observations, this colour is not unheard of in *A. pseudoplatani* galls, especially on purple-leaved Sycamore varieties (e.g. Maidstone 2013, 2021). Leach (2005) apparently equated his Type A galls most closely to Robbins' *A. pseudoplatani* galls, lamenting the confusing fact that Robbins' galls caused bulging; however, the Type A galls probably correspond to another of Robbins' galls, which do not contradict Leach's observations (see footnote to EAps2 below).

Nalepa (1922) described the erinea as follows: 'roundish, initially yellowish, later browning hairy lawns on the underside of the leaf in bumpy upward swellings of the leaf blade. Hairs cylindrical-cube-shaped, strongly curved and matted, rarely hooked'. He listed *Eriophyes macrochelus eriobius* var. *pseudoplataneus* (i.e. protogynes of *A. pseudoplatanea*), *E. m. psilomerus* (i.e. deutogynes of *A. pseudoplatanea*), *E. phyllerites* (i.e. deutogynes of *A. pseudoplatani*), *Phyllocoptes aceris* (i.e. presumably *Aculops acericola*) and *P. gymnaspis* var. *pseudoplatani* (= *Cecidophyes pseudoplatani*) as inquilines.

I am led to believe that Jeppson et al. (1975) are erroneous in their description of *A. pseudoplatani* (in their case, *Eriophyes pseudoplatani*) erinea. The authors describe *E. pseudoplatani* as 'from rather small yellowish undersurface erineum patches near leaf veins, usually located basally, on European Sycamore maple'. This is not the case based on Nalepa (1922); Jeppson et al.'s description sounds more like the second variety of Nalepa's *A. pseudoplatanea* erineum. Indeed, Jeppson et al. note that 'Nalepa always expressed doubt as to the precise maker of this erineum', which is not the case for Nalepa's *A. pseudoplatani* erinea but *is* the case for the second variety of the *A. pseudoplatanea* erineum (see below). The erineum that Jeppson et al. describe is probably caused by *A. pseudoplatanea* (i.e. *Eriophyes psilomerus*, to use the Jeppson et al. name – see below). The same error seems to be made by Alford (2018) (see below).

Bizarrely, Winter (1983) lists *A. pseudoplatani* as occurring on Field Maple, not Sycamore. This must surely be an error, unless Winter examined the mites and found *A. pseudoplatani* as a vagrant (Winter did not examine mites, as far as I am aware). Furthermore, Darlington (1968) calls the causer of EAps1 '*Eriophyes megalonyx*', which is an unusual name to choose. It appears to be a synonym of *Aceria macrochela* (see GBIF) – perhaps Darlington was alluding in a confusing way to the old name *A. macrochela pseudoplatani*, but it may equally simply be an error.

Nalepa (1922) also described a 'double-sided' erineum on Sycamore with an unknown causer: 'Flat tufts of hair of irregular shape, scattered on the leaf underside but also on the upperside near the leaf margin, often fringing the indentations and denticles. The hairy turf on the underside corresponds to yellow spots on the upperside, but occasionally loose hairy turfs [on the upperside]

are apparently not formations of their own, but are probably caused by the stimulus that emanated from the mites that produce the … turf on the leaf underside and [travelled] through the thickness of the leaf blade [to] the cells of the upper epidermis, [which] are responsible for hair formation … The patches of hair are irregularly delimited, of small size and mealy or downy appearance and yellowish-white, later brown in colour; the hairs are similar to those of [the erineum caused by *A. pseudoplatani*]; in some lawns there are large numbers of hooked hairs. At present, no specific judgment can be made about the producer of this erineum: *E. macrochelus pseudoplatani* [i.e. *A. pseudoplatani*] is generally assumed to be present in large numbers alongside *E. phyllerites* [i.e. the deutogyne of *A. pseudoplatani*] in the hairy lawn; it is not probable that a species so remote from *E. m. pseudoplatani* should produce the same or at least very similar hair formations'. It is unclear whether Nalepa actually found *A. pseudoplatani* in the erinea or whether he is just assuming they are present; nonetheless, it does seem likely that this is a form of the *A. pseudoplatani* erineum. I am unaware of any British records of this erineum type. Nalepa (1922) listed *E. m. eriobius* var. *pseudoplataneus* (i.e. *A. pseudoplatanea*), *E. m. psilomerus* (i.e. *A. pseudoplatanea* deutogynes) and *P. aceris* (i.e. presumably *A. acericola*) as inquilines in this erineum.

EAps2 cf. *Aceria pseudoplatanea* (Nal. 1922)
≡ *Eriophyes macrochelus eriobius* var. *pseudoplataneus* Nal. 1922
= *Eriophyes pseudoplataneus* Nal. 1922 sensu GBIF (this is erroneously given as the basionym)
= *Aceria pseudoplataneus* (Nal. 1922)
= *Eriophyes psilomerus* Nal. 1922 sensu Jeppson et al. (1975)
= *Eriophyes psilomera* Nal. 1922
= *Aceria psilomera* (Nal. 1922)
= *Aceria macrochela psilomera* (Nal. 1922) (see Bladmineerders)
= *Eriophyes macrochelus psilomerus* Nal. 1922 (see Jeppson et al. 1975; this is the deutogyne of *A. pseudoplatanea*. Note that this is distinct from *E. m. p.* var. *aceris campestris*, which is the deutogyne of *A. macrocheluserinea*)

The gall description is based on British observations, including gall M 015 in Maidstone (2013, 2021), 'Type A' in Leach (2005), Robbins (2000) and Robbins' descriptions in Leach (2005), with observations on changes over time taken from Nalepa (1922). It is presumably the same as Buhr's (1964) gall no. 56, matches the description of *A. pseudoplatanea* galls by Roskam (2019), and is consistent with Nalepa's erinea of *Eriophyes macrochelus eriobius* (Nalepa 1922). Leach (2005) found 85% of the Type A erinea to be adjacent to, and restricted by, major leaf veins. Leach (2005) describes the hairs as 'rather squat', with 'swollen almost globular apices'. Maidstone (2021) describes the hairs as 'bead-headed'. These descriptions fit well with the equivalent gall found at St Nicholas Fields on Sycamore (pers. obs.), which has even been found on the same leaf as the erineum of *A. pseudoplatani* (see photos in key). I have seen some images of EAps2-type galls with yellowing above, so lack of yellowing may not be a consistent character. I have opted for the Bladmineerders name *Aceria pseudoplatanea* as the placeholder simply because it seems to agree better with the feminine-sounding Latin gender of *Aceria*, although GBIF states that the accepted name is *A. pseudoplataneus*. I see no reason why the species could not equally be called *Aceria psilomera*, since both protogyne and deutogyne names were coined at the same time (Nalepa 1922), so my choice is fairly arbitrary from this perspective too, although there is something to be said in aligning with

Bladmineerders (which opts for the protogyne-derived name *pseudoplatanea* rather than the deutogyne-derived *psilomera*).

Nalepa's use of the name *eriobius* on Sycamore is synonymous with *psilomerus*, whose type host is Sycamore (Jeppson et al. 1975). There are distinct morphological differences between the mites causing the 'purple erineum' on Sycamore (i.e. *A. pseudoplatanea*) and the mites causing the 'purple erineum' on Field Maple (i.e. *A. macrocheluserinea*), although the two species cause similar galls (Jeppson et al. 1975). 'Since there are these distinctions, and since there is lack of data on experimental transfers, the conclusion here is that these purple erineum mites on the two different hosts are closely related but specifically distinct' (Jeppson et al. 1975). Although Maidstone (2021) suggests *A. macrocheluserinea* as a causer of the swollen-haired Sycamore erineum (based on Roskam (2019)), it is more likely to be a vagrant if present at all on this host. An observation that could support the *pseudoplatanea*/*macrocheluserinea* distinction is that where Field Maple and Sycamore are in close proximity, they do not always share the swollen-haired erineum (Robert Maidstone pers. comm.). Jeppson et al. (1975) state that Nalepa referred to the causer of the purple Sycamore erineum as '*Eriophyes macrochelus eriobius* var. *pseudoplatani* (Corti)': this is actually not the case in Nalepa (1922), and indeed would seem to be erroneous on two counts: Nalepa gives the variety as *pseudoplatanea*, not *pseudoplatani*, and Nalepa is the coiner of this name, not Corti. I worry that this discrepancy in Jeppson et al. (1975) has confused other authors, such as Alford (2018), given the similarity of *E. m. e.* var. *pseudoplatani* to *E. m. pseudoplatani*, which is a synonym of *A. pseudoplatani*.

Nalepa (1922) described the swollen-haired erineum on Sycamore as occurring 'in two forms, which often appear side by side on the same leaf'. The first form is 'on the leaf underside, rarely also on the upperside … scattered randomly over the leaf surface, irregular, not always sharply defined, thin, flat, sometimes slightly sunken, initially whitish, later sometimes reddening, finally brown hairy lawns, corresponding to yellow spots on the upperside of the leaves. Hairs short, thin, with protuberances from the head or mushroom-shaped extensions'. He listed *Eriophyes macrochelus psilomerus*, *Phyllocoptes aceris*, *P. stylotrichus* Nal. 1920 (presumably = *Rhinophytoptus stylotrichus* (Nal. 1920)) and *Tegonotus fastigatus* Nal. 1892 (= *Neotegonotus fastigatus* (Nal. 1892)) as inquilines, although *E. m. psilomerus* is actually the erineum-causer; presumably, Nalepa listed it separately because, as in the case of *A. macrocheluserinea* (see above), he mistook it to be a distinct species even though it was the deutogyne of the causer.

The second form of this erineum that Nalepa (1922) described is 'On the leaf underside in the vein angles at the leaf base, sharply defined, cushion-like, thickened, initially greenish-yellow hairy lawns, spreading from the vein angles along the main underside veins, in severe infections also scattered over the leaf surface. The attack of the parasites is not usually confined to the lower leaf surface; narrow, stripe-like tufts of hair form along the veins on the upper leaf surface … or numerous, roundish spots scattered over the leaf surface. Hairs thick, long, gradually widening from the base and not sharply separated from the head or hat-like flared end, later funnel- or goblet-shaped. The hairs stretch out from the leaf surface, but also from the sides of the main veins at the leaf base. The producer of this erineum form could not be determined with certainty: *Eriophyes macrochelus eriobius* Nal. was found before long, then *E. m. psilomerus* Nal. outnumbered it'. Despite Nalepa's uncertainty, there is a strong suggestion that *A. pseudoplatanea* (*E. m. eriobius*) is again the causer

of this erineum, becoming dominated by its deutogyne (*E. m. psilomerus*) as the season progresses. Nalepa (1922) listed *E. phyllerites* (i.e. the protogyne of *A. pseudoplatani*), *P. aceris* (i.e. presumably *Aculops acericola*), *P. dorsalis* and *P. gymnaspis* var. *pseudoplatani* (= *Cecidophyes pseudoplatani*) as inquilines.

Nalepa's first erineum type seems the closest to what we know in Britain, although Nalepa's description of yellow spots on the leaf upperside seems to be rare if present at all here. Similarly, Alford (2018) provides a photo of the gall caused by '*Eriophyes psilomerus*' that, without seeing the hair morphology, matches EAps2 well, but a description that is a little confusing. Alford states: 'The leaves of sycamore … are often disfigured by large, irregular erinea induced by this generally common gall mite. Each gall appears as a pale green to brownish blister on the upper surface of the leaf, with the underside densely clothed in whitish to purplish hairs. Such galls occur from May onwards, and gradually darken as they mature. Although infested foliage looks unsightly, tree growth is not affected'. The description of a 'blister' over each erineum does not really seem to be an EAps2 character – although some bulging may occur, it seems to be minimal, at least based on British observations. Otherwise the description is largely consistent with EAps2 (although leaf discolouration is noted, again highlighting the possible unreliability of this character for British specimens, assuming they are caused by the same species).

I am unaware of any definitive British record of the second erineum type, although intriguingly, Robbins knew a similar-sounding erineum on Sycamore 'on underside of leaves form[ing] a narrow band alongside the mid-rib and veins. Hairs … are shortish and lie thickly', caused by an unknown mite (Leach 2005). Perhaps this is the second *A. pseudoplatanea* erineum; we should certainly keep an eye out for it in Britain. Alford (2018) also seems to describe this erineum, and indeed provides a photo of it, albeit under the apparently erroneous causer name *Eriophyes eriobius pseudoplatani* (= *A. pseudoplatani*), describing the erinea as 'yellowish to brownish … on the underside of the leaves. The galls occur from May onwards, and tend to be concentrated alongside and at the junctions of the major veins … Although infested leaves are often extensively galled, the foliage is not distorted'. Alford omits the erineum type caused by *A. pseudoplatani*, suggesting that he has conflated *A. pseudoplatani* and *A. pseudoplatanea* as Jeppson et al. (1975) appear to have done (the latter authors call the causer of what appears to be Nalepa's second *A. pseudoplatanea* erineum type, '*Eriophyes pseudoplatani*' – see footnote to EAps1 above). A possibly related error is that the NHMW list calls both *A. pseudoplatanea* and *A. psilomera* junior synonyms of *A. pseudoplatani*.

Robbins (2000) noted an erineum in vein angles on Sycamore 'not accompanied by any bulging or yellowing'; he suggested that this was possibly caused by *Phyllocoptes acericola* (= *Aculops acericola*), ruling out *Coptophylla gymnaspis* (= *Cecidophyes gymnaspis*) because it is, 'I am informed, restricted to Field Maple' and because its erineum hairs 'are different, being close to normal hairs in appearance'. Unfortunately, Robbins did not describe the hair morphology of his galls in this paper, but the implication is that they are more modified than those of *C. gymnaspis*. However, Robbins did know erinea on Sycamore that 'lie on underside of leaves in the vein angles and alongside the midrib. Hairs … are much broadened apically', caused by an unknown mite (Leach, 2005). I suggest that this is the same gall as noted in Robbins (2000). Although the possibility was not considered by Robbins, it seems plausible that these galls are the same as EAps2. This would resolve the discrepancy with previous literature noted by Robbins, that his galls did not cause leaf bulging

despite this apparently being a feature of *A. acericola* galls; a lack of bulging does, however, seem to be a feature of EAps2 (note that *A. acericola* is unlikely to be a gall-causer in reality). Swanton's (1912) *P. acericola* gall may be the same as Robbins', i.e. EAps2. In the words of Swanton (1912), 'The characteristic gall of *P. acericola* … is a very slight swelling on the upper surface of the leaf, with the corresponding depression on the lower one filled with a mass of swollen hairs. It is situated between the larger veins'. The observation of 'very slight swelling' is not what one would immediately associate with EAps2, although could potentially be consistent; 'swollen hairs' is certainly consistent, however.

Bladmineerders includes an entry for *Aceria pseudoplatanea* as causing an erineum on Field Maple, Norway Maple and Sycamore as well as Greek Maple *Acer heldreichii* Orph. ex Boiss., but notes that it is known only from the Balkans and perhaps Austria, with records of *A. pseudoplatani* on Sycamore in north-west Europe unlikely to be confused with *A. pseudoplatanea*. I find this description rather mystifying; it would presumably read differently if sources such as Nalepa (1922) and Jeppson et al. (1975) had been consulted.

Nalepa (1922) found erinea on Sycamore, accompanying *A. pseudoplatanea* erinea, similar to those caused by *C. gymnaspis* on Field Maple, i.e. abnormal hairiness of the veins. However, despite investigating 'more than 40 specimens', he failed to find any *C. gymnaspis* in these erinea. His conclusion was that *A. pseudoplatanea* may cause erinea like this on the veins. He also described a complexity of other variations in the forms of the Sycamore erinea (especially those caused by *A. pseudoplatanea*), including in their shape, distribution on the leaf surface, and hair morphology. He suggested that these were due to the overlapping gall induction of different species, e.g. *A. pseudoplatani* and *A. pseudoplatanea*, contrasting these with the relatively uniform erineum forms on other hosts, such as Beech *Fagus sylvatica* L. or indeed Norway Maple. For instance, he noted unusual *A. pseudoplatanea* erineum hairs 'whose ends, which are more or less disc-like, protrude into lateral blind sac-like protuberances, which intervene between the same protuberances of the neighbouring hairs. Intermediate forms of the hair formations mentioned are not infrequently observed'. He also described distinct erinea side-by-side without a clear border between them. The fact that so many different eriophyoid species could be found on Sycamore (or Field Maple) leaves was felt by Nalepa to have important implications for the prevalence of such chimeric galls.

EAps3 cf. *Cecidophyes pseudoplatani* (Nal. 1922)
≡ *Phyllocoptes gymnaspis* var. *pseudoplatani* Nal. 1922
= *Phyllocoptes pseudoplatani* (Nal. 1922) Liro 1947 (GBIF erroneously gives '*Phyllocoptes pseudoplatani* Nalepa, 1922' as the basionym)
= *Coptophylla pseudoplatani* (Nal.) Roivainen 1950
?= *Cecidophyopsis pseudoplatani* (Nal. 1891) (see Bladmineerders)

This erineum and its causer are mysterious entities both in Britain and elsewhere. Whether this erineum or its causer can truly be found in Britain is somewhat unclear; I include it in the key out of caution, and we should in any case look out for such galls in Britain. The erineum description is based on Nalepa (1922), who described 'Abnormal whitish hairs on the veins and hair tufts in the vein angles on the leaf underside [… occurring] more rarely alone, but more frequently together with [erinea of *A. pseudoplatanea* and *A. pseudoplatani*]', whose causer he called *Phyllocoptes gymnaspis*

var. *pseudoplatani*. This is one of the few cases where Nalepa gives insufficient information in the erineum description (e.g. the shape of the hairs); how are we to distinguish this erineum from the abnormally hairy veins apparently caused by *A. pseudoplatanea*? The only way seems to be if hair tufts in the vein angles are found, as Nalepa (1922) stated that the latter erineum does not grow on the leaf surface in vein angles. Hopefully, distinguishing a 'tuft' of hairs from the normal *A. pseudoplatanea* erinea patches is possible, although I know of no illustrations of the former erineum.

Given the difficulty in distinguishing *A. pseudoplatanea* and *C. pseudoplatani* erinea, it is hard to make sense of Robbins' erineum on Sycamore with 'hairs not markedly broadened apically', whose causer he called *Coptophylla gymnaspis*, although he did not comment on the position of the erineum (Leach 2005). This might be the erineum of either *A. pseudoplatanea* or *C. pseudoplatani*, but is unlikely to reveal the presence of *C. gymnaspis*, which is restricted to Field Maple if Nalepa (1922) is to be believed. Indeed, Robbins (2000) admitted that *C. gymnaspis* was restricted to Field Maple! Jeppson et al. (1975) consider *Coptophylla gymnaspis* only from Sycamore, noting that it causes extra hair growth on the leaf underside. This is confusing, because it is ambiguous as to whether the authors are referring to *P. gymnaspis* var. *pseudoplatani* (this would be most likely given the host), or the *Cecidophyes gymnaspis* that is better known on Field Maple. See also the footnote to EAc2 above.

Oddly, the only references to *C. pseudoplatani* from Britain that I have come across are from hosts other than Sycamore. Massee (1965) found *Coptophylla pseudoplatani* at 'Channel, Thames' on Field Maple, and DBIF also lists Norway Maple as a host of *Coptophylla pseudoplatani*. Davis et al. (1982) describe *Coptophylla pseudoplatani* as both an erineum-causer and vagrant on Norway Maple, whilst Bladmineerders uses the mystifying name of *Cecidophyopsis pseudoplatani* (Nal. 1891), drawing on Scandinavian works by Rovainen, even though this name is absent from the NHMW list – a name that may be synonymous with *Cecidophyes pseudoplatani* since Bladmineerders gives *Coptophylla pseudoplatani* and *Phyllocoptes pseudoplatani* as synonyms – to describe a vagrant mite on Norway Maple. If these records from non-Sycamore hosts are correct, we should expect *Cecidophyes pseudoplatani* as (presumably) a vagrant on them. However, I do wonder whether there has been some confusion with mite names. Perhaps Massee confused *C. pseudoplatani* with *C. gymnaspis*, for instance. There is surely much to resolve in this taxonomic corner.

Implications for record verification

What implications does the key have for verifying records, particularly on iRecord (https://irecord.org.uk/home) (see Buckton 2022)? Table 2 provides suggestions on how verifiers should deal with records of each of the galls presented in the key above. I have virtually tested the key and Table 2 on British photos of *A. macrocheluserinea* and *A. pseudoplatani* galls on iRecord, iNaturalist (https://www.inaturalist.org/home), iSpot (https://www.ispotnature.org/), GBIF (https://www.gbif.org/) and NBN Atlas (https://nbnatlas.org/), finding only EAc3, EAc4 (my own photos), EAps1 and EAps2, which has helped to refine the descriptions of these galls. In particular, I was interested to see an EAps2 on Sycamore on iRecord (record ID 3275300) that showed a small patch of erineum on the leaf upperside (in addition, the erineum colour is an amazing garish pink!). There are photos of EApl1 on the British Plant Galls Facebook group (https://www.facebook.com/groups/1649308048444607). There are several British records of *A.*

acericola on GBIF and NBN Atlas but without photos, which makes them difficult to verify. EAc1 is apparently absent altogether from the modern British consciousness.

To accept records as correct, high-magnification images of the erineum hairs are often necessary, although none of the galls is above Recording Grade 3 (see Buckton 2022). I see no good reason why records of all the erinea types apart from EAps3 cannot be accepted if sufficient evidence is provided (although the relevant names would need to be added to the UKSI and filter through to iRecord before they can be verified on this platform with their corresponding mite names). I would feel more cautious about accepting records of EAps3 until it becomes clear how distinct hair 'tufts' on Sycamore are from other erineum patches.

For doubtful records, new aggregate names are possible. Any undetermined erineum on Field Maple can be named *Aceria macrocheluserinea* agg.; on Sycamore, *Aceria pseudoplatani* agg.; and on Norway Maple, *Aceria platanoidea* agg. Chris Raper has added these aggregate names to the UKSI, which will eventually filter through to iRecord as available names for recorders and verifiers to use.

Table 2. Suggestions for how records of British *Acer* erinea should be dealt with by verifiers (e.g. on iRecord) in light of the new key. Note that a specimen sent to the verifier may replace the need for photos. Careful judgement will be needed regarding the decision to 'accept as considered correct' (see Buckton 2022). Recording Grades are based on Buckton (2022). UKSI = UK Species Inventory.

Gall and causer	**Host**	**Criteria for accepting species-level record as correct**	**Decision if species-level record not acceptable**	**Recording Grade and other notes**
EAc1 *Aceria carinifex*	*Acer campestre*	Clear photos of erineum on upperside over vein and bulge or keel below.	Accept as *Aceria macrocheluserinea* agg.	Grade 2. If this gall does indeed occur in Britain, it must surely be rare.
EAc2 cf. *Cecidophyes gymnaspis*		Clear photos of erineum restricted to veins.		Grade 3. If the erineum extends onto the leaf blade, it may be caused by e.g. *A. lophophyes*.
EAc3 *Aceria macrocheluserinea*		Clear photo of erineum on leaf blade away from leaf base; ideally, high-magnification photo showing bead-headed hairs.		Grade 2. No other erinea occurring across the main leaf blade are currently known on Field Maple in Britain.
EAc4 cf. *Aceria lophophyes*		Clear photos of erineum in vein angles, especially near petiole, with corresponding leaf bulge, and high-magnification photo showing curled hairs.		Grade 3. Care is needed to separate from the other erinea on Field Maple.
EApl1 cf. *Aceria platanoidea*	*Acer platanoides*	Clear photo of erineum mainly on lamella away from veins; ideally, high-magnification	Accept as *Aceria platanoidea* agg.	Grade 2.

		photo showing squat, apically swollen hairs.		
EApl2 cf. *Rhynchaphytoptus magnificus*		Clear photos of erineum in vein angles near petiole with corresponding leaf bulge, and high-magnification photo showing straight hairs.		Grade 3. I suggest that photos showing erinea restricted to the vein angles near the petiole with bulging, but without photos of the hairs, could be accepted as considered correct.
EAps1 *Aceria pseudoplatani*	*Acer pseudoplatanus*	Clear photo of erineum mostly on lamella away from major veins and high-magnification photo showing long tubular hairs; ideally a photo showing the degree of leaf bulging and yellowing.	Accept as *Aceria pseudoplatani* agg.	Grade 3. The degree of leaf bulging and yellowing may not be such a reliable character to distinguish EAps1, but it could be a useful pointer for distinguishing from EAps2. I suggest that photos showing erinea mostly away from major veins (especially if there is clear leaf bulging), but without detail of the hair shape, could be accepted as considered correct.
EAps2 cf. *Aceria pseudoplatanea*		Clear photo of erineum mostly adjacent to and delimited by major leaf veins and high-magnification photo showing short bead-headed hairs; ideally a photo showing the degree of leaf bulging and yellowing.		Grade 3. The degree of leaf bulging and yellowing may not be such a reliable character to distinguish EAps2, but it could be a useful pointer for distinguishing from EAps1. Care may be needed to separate EAps2 from EAps3; presumably, the swollen hairs are a unique EAps2 feature.
EAps3 cf. *Cecidophyes pseudoplatani*		Clear photo of abnormal hair tufts in the vein angles.		Probably Grade 3. Erinea on the veins could be confused with those apparently caused by *A. pseudoplatanea*.

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