BROOMRAPES OF BRITAIN AND IRELAND

A field guide to the holoparasitic Orobanchaceae

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INTRODUCTION

Broomrapes (*Orobanche* L. family Orobanchaceae) are among Britain's most curiously beautiful and least understood plants. In recent years, these unusual parasitic plants have sparked interest among plant enthusiasts, in a similar way to orchids. Broomrapes are renowned for being taxonomically challenging. Plants which are distinct in the field can become brown and featureless when pressed

which has led to the incorrect determination of herbarium specimens. Confusion has been compounded by intra-specific variation in some species, confusing synonymies, names cited incorrectly and species with poor type specimens and descriptions. Nevertheless, identification of British broomrapes in the field should normally be straightforward with careful examination. This book seeks to give clear and detailed accounts of each species so that they may be identified reliably. All species known to occur in the British Isles are covered, including one or two casual species that may be extinct, or at least seen very infrequently here. Photographs have been selected to capture as much of the intraspecific variation within a species as possible – distinct colour forms, for example. Many of the photographs were kindly provided by other botanists and enthusiasts from up and down the country, so that populations could be well represented geographically. The maps included are courtesy of the Botanical Society of the British Isles (BSBI) and give an indication of past and current distributions. As can be seen from these maps, most species of broomrape in Britain are rare and many are erratic in their appearance; in fact the remaining populations of a handful of species exist literally on a cliff edge! Generally such populations require some level of intervention, such as clearance of encroaching scrub; the outlook for some is precarious indeed. It is hoped that this book will stimulate interest in broomrapes broadly, and promote their much-needed conservation focus in the British Isles. For each species we give the conservation status listed currently, as provided for GB by Cheffings and Farrell, 2005; for England by Stroh et al., 2014; Wales by Dines, 2008 and Ireland by Wyse-Jackson et al., 2016. Where we feel that the statuses may be in need of review we provide revised assessments and the rationale behind these. Several of our species are protected legally from collection or damage within at least part of their British or Irish ranges. In Britain this protection is accorded under Schedule 8 of the Wildlife and Countryside Act, 1981 as amended. No species are protected in Eire under the comparable legislation, the Flora (Protection) Order, 2015 although *O. hederae* Duby is accorded protection in Northern Ireland under Schedule 8 of the Wildlife (N. Ireland) Order, 1985 as amended by the Wildlife and Natural Environment Act (N. Ireland), 2011.

THE BROOMRAPE FAMILY

The broomrape family (Orobanchaceae) comprises about 90 genera and 1600 species of annual and perennial herbs and shrubs (Schneeweiss, 2013). With the exception of three genera (*Lindenbergia, Rehmannia* and *Triaenophora*) now included in the family (see below), all are parasitic, therefore reliant to a varying degree on other plants – their so-called hosts, for nutrition. The current circumscription of the Orobanchaceae follows the disintegration and reassessment of the Scrophulariaceae at the end of the last century (Olmstead et al., 2001) as a consequence of molecular data. This means that modern guides contradict earlier traditional floras in places, for example, the past assignment of toothworts (*Lathraea*) to the Scrophulariaceae rather than to the Orobanchaceae. However, even a century ago Boeshore (1920) had made a very compelling case on morphological grounds for the unification of the parasitic taxa into one family.

Molecular phylogenetic analyses have transformed our understanding of relationships in the Orobanchaceae (Schneeweiss et al., 2004a; Li et al., 2019). As stated above these have led to a re-circumscription of the family that formerly comprised exclusively holoparasitic *Orobanche* and a few related genera (Beck-Mannagetta, 1930). Based on DNA evidence, the Orobanchaceae was expanded to include all hemiparasites and the few remaining holoparasites (such as *Lathraea* L.) that were placed formerly in the Scrophulariaceae (Young et al., 1999; Wolfe et al., 2005; Bennett and Mathews, 2006; McNeal et al., 2013). The sister group to the parasitic Orobanchaceae has been shown by various studies to be the Asian non-parasitic genus *Lindenbergia*, now also included frequently in the broadened Orobanchaceae (Young et al., 1999; Wolfe et al., 2005; Bennett and Mathews, 2006; Park et al., 2008; McNeal et al., 2013; but see Fischer, 2004). More recently the

Rehmanniaceae (including the two non-parasitic genera, *Rehmannia* and *Triaenophora*), also shown as sister (Albach et al., 2009; Xia et al., 2009), has been merged within the Orobanchaceae as well (Angiosperm Phylogeny Group, 2016). Holoparasitism has therefore evolved independently from hemiparasitic ancestors on multiple occasions in the family (McNeal et al., 2013).

The largest of all parasitic plant families (Schneeweiss, 2013), the Orobanchaceae, is represented on every continent except for Antarctica. Some species in the family have a profound effect on both natural and agricultural systems. For example Yellow Rattle (*Rhinanthus minor* L.) parasitises grasses, supressing their dominance, so enabling a diversity of other flora to prosper. Meanwhile striga (*Striga* spp.) destroys billions of dollars' worth of cereals and legumes in Africa and Asia every year. Some species of broomrape (*Orobanche* and *Phelipanche* Pomel) are also pernicious weeds of various crop species around the Mediterranean Basin and the Middle East.

Broomrapes belong to the genera *Orobanche* and *Phelipanche.* Although still grouped as one genus, *Orobanche,* by many authors*,* DNA sequence analysis and cytological differences have demonstrated that *Phelipanche* forms an independent lineage, and so it is treated as distinct in this guide and not as a sub-genus, or section (Trionychon) of *Orobanche*. The two other past sub-genera (*Myzorrhiza* and *Gymnocaulis*) are exclusively American in distribution. They share morphological and cytological features and some host preferences with the genus *Phelipanche,* to which molecular data (see for example McNeal et al., 2013) also link them. On karyological and phylogenetic grounds the small Asian genus *Phelypaea,* striking plants with single large scarlet flowers, shows greater affinities to *Orobanche s.str.* than that does to *Phelipanche* (Schneeweiss et al., 2004b). Further divisions within *Orobanche* have also been proposed, eg. Carlón et al., 2008 have suggested that on morphological and phylogenetic grounds that the rather distinctive polyploid Mediterranean parasite of *Rosmarinus*, *Orobanche latisquama* should be treated in its own genus *Boulardia* F.W. Schultz. Other closely related genera include *Cistanche,* a diverse genus of robust parasites (sometimes called 'desert broomrapes' or 'desert hyacinths') – typically on the roots of shrubs, and widespread across dunes, deserts and semi-arid regions of the Old World. Our understanding of species diversity in the genus *Cistanche* is still rudimentary. *Lathraea* is a further genus of holoparasites, distantly related to *Orobanche,* and resolved within a lineage shared with *Euphrasia*, *Parentucellia*, *Odontites* and *Rhinanthus* (Li et al., 2019). This small genus of plants, known as toothworts, are typically parasitic on the roots of trees in wooded habitats across temperate Europe and Asia. The two species of toothwort that grow in Britain (one of which, *L. clandestina,* is not native) are also included in this guide, even though technically speaking they are not broomrapes, because of their similar appearance and life history.

LIFE CYCLE AND BIOLOGY

Parasitic plants attach to, and feed from, the roots and stems of other plants. Over 1% of all flowering plants are parasitic to a degree and this strategy has evolved at least 12 times independently. Parasitic plants are very diverse and range from herbaceous plants to trees, and a handful of highly reduced parasites that grow embedded in their host and lack all trace of leaves and roots (endoparasites) – for example Southeast Asian *Rafflesia,* the largest flower in the world. All parasitic plants can be classified broadly into two major groups: the **hemiparasites**, which are photosynthetic, and the **holoparasites,** which lack chlorophyll and rely entirely on a host plant for carbon. They can also be divided into those that are **facultative**, meaning that they can live without a host, or **obligate** meaning that they require a host to complete their life cycle. Finally, they can be divided into those that attach to their host plants' roots and those that attach to the host plants' stems. Broomrapes (and toothworts that are included here also) are all obligate root holoparasites.

Broomrapes emerge above ground in the form of a flowering spike that is devoid of functional leaves (these are reduced to bracts at the base of the stem). The life history of most species is rather poorly known, particularly with respect to their longevity. Many species are demonstrably annuals, and are able to germinate and set seed in the same year, for example *O. minor* Sm. and *O. crenata* Forssk.; unsurprisingly such species have a tendency to occur as weeds in fields and gardens. Some species are perennial – often weakly so; indeed fresh flowering spikes can be seen occasionally growing alongside withered spikes from the previous year, for example *O. rapum-genistae* Thuill.. Rather more commonly broomrapes are monocarpic, dying after flowering. For example *O. hederae* flowers two years after germinating, but seldom shows unequivocal evidence of perennation. The life history and longevity of broomrapes is also influenced by, or coordinated with, their host plants' physiologies. For example ivy broomrape sown on *Tetrapanax* (Araliaceae) – an alien host – can flower and set seed within a single year, rather than the two years it takes on ivy, its typical host.

The fruiting spikes of broomrapes produce many thousands of minute seeds (of similar size to those of orchids), that are wind-dispersed following release from their capsules. The large quantity of seeds, their wind dispersal, and their ability to be washed into crevices, together maximises opportunities for the parasites to encounter the roots of a suitable host plant. Mainly self-pollinating species such as *O. minor* will always set seed. Others, particularly those with larger, fragrant flowers, are predominantly outcrossing and appear to set rather smaller quantities of seed (or in some specimens, no seed at all), such as *O. caryophyllacea* Sm.

Broomrape seeds show considerable abilities to remain viable but dormant, in some instances for 20+ years. They germinate only following a conditioning period of suitable temperature, and in response to chemical signals produced by host plants' roots. These signals include strigalactones, which are exuded by the roots to signal to symbiotic arbuscular mycorrhizas in the soil. Differences in signal responsiveness and perception by the parasite, as well as differences in signal production by the host, influence the level of parasite germination and establishment. Host signals also govern later stages of the host-parasite interaction; in a successful interaction, the radicle of the broomrape seedling attaches to the host root via a **haustorium** – the physiological bridge via which the parasite intercepts its nutrition. On a compatible host, the parasite develops a small yellowish tubercle. In some species this is accompanied by a profusion of fleshy root-like starch-storage structures. Eventually, an inflorescence is produced – typically in early summer (most British species flower from late May to early July, but there are several exceptions). The flowering period is often short-lived, in small specimens of *P. ramosa* (L.) Pomel even just a matter of days. The dried fruiting spikes are woody and often remain long after the plant has died.

Each species of broomrape has a preferred host, for which the underlying determinants are complex and multifaceted. The success or failure of the various developmental stages outlined above, influence the host specificity of the parasite. The development of the parasite is also determined by other host attributes, such as root architecture and spread, and growth rate. If we consider two subspecies of *O. minor*, the seed of subsp. *maritima* (Pugsley) Rumsey (adapted to sea carrot) is able to germinate on red clover (a typical host of subsp. *minor*) however seedlings cannot attach and develop on this host; meanwhile subsp. *minor* is able to develop on both hosts, but performs much better on red clover (Thorogood et al., 2009a). The latter has a very broad host range and can parasitise numerous hosts from 16 orders (Thorogood et al., 2009b). That said, it does show a preference for particular families, such as Fabaceae, Asteraceae and Apiaceae (Sánchez-Pedrada et al., 2020). Moreover, races can shift to new hosts. For example var. *heliophila* is associated with *Brachyglottis* (native to New Zealand) and cannot establish on clovers, based on the authors' growth trial experiments. Presumably a race adapted to native Asteraceae (such as var. *compositarum*) shifted onto this novel host, in a similar way to species that have shifted from their natural hosts to cultivated crops elsewhere in the world (*O. crenata,* for example). Closely related broomrapes can

often infect one another's hosts in some cases. For example *O. hederae* grows happily on sea holly (*Eryngium* spp.) which is the host of its sister species *O. amethystea* Thuill. Host identify can be useful for broomrape identification, but clearly for some species, this is problematic (*see Identification*).

NON-PHOTOSYNTHETIC PLANTS IN THE BRITISH ISLES

Broomrapes are the most numerous and diverse group of British flowering plants lacking in chlorophyll. The inability to photosynthesise means that non-green plants must have some alternative mechanism by which they obtain their nutrition. In practice this means reliance on other organisms, whether through fungi associated with other, usually, woody plants (**myco-heterotrophs**), or directly through parasitism. In both cases the typical morphological reductions, such as the loss of leaves and an emphasis on the reproductive structures results in many parallels and similarities. The myco-heterotrophs in the British Isles are found in two families: the Ericaceae and the Orchidaceae. In both cases there is evidence of increasing reliance on fungal partners in certain lineages and apparent transitional examples that retain some photosynthetic activity.

Hypopitys monotropa Crantz (syn. *Monotropa hypopitys* L.) – the Yellow Bird's-nest was previously assigned its own family, the Monotropaceae, distinguished by its myco-heterotroph nature, but is now considered to belong to the Ericaceae, along with the wintergreens. There are two British taxa, treated currently as subspecies, distinguished by their hairiness and chromosome number, with many intermediates that may represent hybrids. Typically, they are plants of deep shade and leaf litter under beech or conifers, or more rarely amongst willows in dune-slacks, and always associated with fungi of the genus *Tricholoma*.

In the Orchidaceae some normally photosynthetic but markedly mycorrhizal orchids may produce chlorophyll-less mutants, such as *Epipactis purpurata* Sm. (as f. *rosea* (Erdner) P. Delforge), which does produce leaves, but the whole plant has a purplish-pink colouration. The 'committed' myco-heterotrophs have dispensed with leaves, although some, such as the Coral-root orchid (*Corallorhiza trifida* Châtel.), do still retain some chlorophyll activity in parts of the floral structures. The most frequently encountered is the Bird's-nest Orchid (*Neottia nidus-avis* (L.) Rich.) a species of shady deciduous woodlands, generally on calcareous soils. The only other example in the British flora is the most elusive of our flowering plants, the Ghost Orchid (*Epipogium aphyllum* Sw.). All can be distinguished readily from the broomrapes and toothworts by their floral structures: *Hypopitys* has radially symmetric flowers, 10 stamens and globose capsules; the orchids have inferior ovaries, pollen dispensed in bundles (pollinia) from a single anther, borne with the stigma on a specialised structure, the column.

Aside from the broomrapes and toothworts the only other British holoparasites are the dodders (*Cuscuta* spp.). Like *Hypopitys* these were once accorded their own family status on account of their parasitic life-style; the dodders are now regarded as a sub-family of the Convolvulaceae. Like the bindweeds they are twining, scrambling plants, but unusually they have no root system and extract nutrients through their specialised haustoria which penetrate the stems of their hosts. The whole plant consists of a tangle of fine, highly coloured filaments, the small flowers in globose sessile heads at intervals. There are two native British species: *Cuscuta epithymum* (L.) L., typically parasitic on *Calluna* and *Ulex* on heathlands but also found on chalk grasslands, and *C. europaea* L., a parasite of *Urtica dioica* L. by riversides. The bright orangey-yellow alien *C. campestris* Yunck. is a parasite of Carrots (*Daucus carota* L.) but is perhaps most often found on Niger (*Guizotia abyssinica* (L. *f.*) Cass. from contaminated garden bird food. All are uncommon and the natives are declining.

HABITATS AND ECOLOGY

Each species of broomrape has its own distinct host range, habitat and ecology, however as a rule of thumb, broomrapes tend to occur in open, dry sunny habitats where their host plants are plentiful. Such habitats include chalk grassland, scree, cliff tops, rocky ledges, and sandy dunes. There are exceptions of course. *Orobanche rapum-genistae* tends to grow in relatively undisturbed nutrient-poor pastures and thickets (as well as in coastal habitats); meanwhile *O. hederae* frequents moist and shady, rocky places such as coastal forests on limestone cliffs. Furthermore, some species have expanded beyond the habitats of their natural range. *Orobanche hederae* which, as a native, is most frequent on the coasts of the southwest, is now widespread across southern Britain in urban environments where it has spread from windswept seed or from deliberate introductions. Forms of *O. minor* are also now frequent in disturbed environments, where at least one form has shifted to a cultivated host (var. *heliophila* Thorogood & Rumsey on *Brachyglottis*) and can appear in large numbers in car parks, amenity plantings and gardens. Native forms of this species, including subsp. *maritima* and var. *pseudoamethystea* Thorogood & Rumsey are most probably restricted to coastal stations but the species has probably been introduced regularly in sown clover leys. Other species primarily occurring in agricultural situations and thus not considered native include the now extinct *Phelipanche ramosa* and *Orobanche crenata.* The latter infests pea and bean crops in its native Mediterranean, and occurs in arable fields, as well as in the adjacent field margins, where it has been introduced accidentally in southeast Britain.
Globally the majority of Broomrape species have narrow host ranges and grow exclusively on perennial host plants, thus being at least potentially perennial themselves. This trait combination has been proposed as the ancestral one in *Orobanche* and *Phelipanche* (Manen et al., 2004) and agrees with the hypothesis that parasite specialization tends to be associated with predictable resources (Ward, 1992), i.e. long-lived hosts, as shown in animal parasites (Sorci et al., 1997; Sasal et al., 1999). These species are usually found in natural ecosystems, where they are often uncommon compared with their potential hosts, and they do not harm their hosts in an obvious way (Teryokhin, 1997). In contrast, a few *Orobanche* and *Phelipanche* species have wide host ranges and grow on annual hosts and are thus (at least facultatively) annuals themselves. These species are usually found in anthropogenically disturbed ecosystems, where they are often frequent and can cause severe to lethal damage to their host plants, thus showing a weedy behaviour (Parker & Riches, 1993; Teryokhin, 1997). This is particularly pronounced in economically important pest species such as *Orobanche crenata* and *Phelipanche aegyptiaca*, which can cause major yield losses (Riches & Parker, 1995; Musselman et al., 2001). It is therefore hypothesized that shifts in host range and life history play an important role in the evolution of weediness in *Orobanche* and *Phelipanche* (Schneeweiss, 2006), as well as their speciation (Thorogood et al., 2009b).

Many species are unpredictable in their appearance and abundance and vary greatly in number (sometimes by several orders of magnitude) at a given site from year to year. Their considerable seed bank may lie dormant in the soil for many years in the absence of a suitable host plant, therefore broomrapes often respond to disturbance events, which facilitates contact between parasite seeds and host roots. Hence, unstable environments such as cliffs and dunes are a stronghold for natural populations of annual species such as *O. minor, O. minor* subsp. *maritima* and *O. picridis* F.W. Schultz). Whilst such habitats are inaccessible and must afford the plants some protection, they are particularly vulnerable to encroachment by secondary vegetation and scrub that outcompetes their host plants, stabilises substrates, and reduces opportunities for parasite seed-host root contact. Disturbance of grassland habitats can lead to the emergence of large stands of *O. minor*, for example on road cuttings; such a proliferation occurred in the 1990s around Stansted Airport, following its expansion. Similarly the re-routing and upgrading of the A1M in Yorkshire provided new habitat for *O. reticulata* Wallr. which had long been known from the banks of the old road, probably a vestige of

a larger grassland population now lost to agriculture. At sites where populations have declined or disappeared, disturbance may well catalyse their re-establishment.

The rather exacting requirements for a particular habitat and host plant, and the requirement for at least some soil disturbance, probably explains why nearly all British broomrapes are rare and local. Some have retracted markedly within their former range, for example *O. rapum-genistae*, whilst others have always been very local, *O. caryophyllacea* for example. This species grows only on downs and dunes in east Kent, not far from the populations of *O. picridis* on the White Cliffs of Dover. Both species have a predominantly southerly distribution, extending to Asia Minor and North Africa, and their restriction to the very far southeast of Britain indicates a mere foothold into the northernmost extreme of their range. Populations of these species, though long-established, may have originated from wind-swept seed from Continental Europe, since both are common in northern Holland; there *O. picridis* is not restricted to chalky sea cliffs as it is in Britain, and grows in dunes and even on ruderal sites where it is often an altogether more robust plant.

TAXONOMIC HISTORY

Such unusual and striking plants unsurprisingly have long attracted attention and aroused interest. Early herbalists rarely differentiated species and the woodcut illustrations they provide often lack features critical for identification. It is clear though that *Orobanche rapum-genistae*, the species responsible for the genus' common name, was a familiar plant and much more frequent than today. As early as 1548 William Turner recorded it in Northumberland as "newe chappel floure" (Britten, 1881) and it was well known to Gerarde (1597) who lists it in his famous herbal with its host, as though a strange manifestation of that plant. While it is possible to deduce the presence in the British Isles of other species such as *O. elatior* through the publications of Ray, the first explicit mention was not made until the third edition of his *Synopsis Methodica* in 1724 when we have ' *Orobanche flore minore J.B*. [=*O. minor*] ..found by Mr. Rand in a field of Oats two miles beyond Rochester'. The late discovery of this species does give credence to the view that it is primarily an introduction here. Other locally frequent species such as *O. hederae* were, however, also unknown, or at least were overlooked. Its first date of publication was as late as 1841 (see Pearman, 2017) although we can be certain that it was the plant seen "upon roots of Ive at Chateau des Marais, Guernsey" in 1726 by Thos. Knowlton (McClintock, 1975). Our other species being so rare or highly localised it is perhaps not so surprising that they evaded description until the late 18th century, or even later, for example, *O. reticulata* was first reported in 1909 (Rumsey & Jury, 1991); although paradoxically early British botanists were familiar with *Phelipanche ramosa,* a species now effectively extinct in this country. This had been a frequent crop weed of Hemp in the East Anglian region where many of our most notable botanists lived and worked. Within the British Isles a strong interest in the genus was shown by such worthies as Sir James Smith and Charles Sutton. They would almost simultaneously describe *O. minor* as a new species, the latter also formally recognised *O. elatior* (Sutton, 1797), the former describing *O. caryophyllacea* but from foreign material, long before it was first recorded in the British Isles by his namesake, but not relative, G.E Smith (Smith, 1829). Much later the genus would occupy the attention of Arthur Bennett and subsequently H.W. Pugsley, who would go on to describe several new taxa at specific and infraspecific level (Pugsley, 1940).

Problems have been posed for taxonomists by these highly reduced plants from the dawn of the discipline. Linnaeus the father of the modern binomial taxonomic system working in the mid-18th century only recognised five species in Species Plantarum (Linnaeus, 1753). Based in the Scandes he can be excused as being unfamiliar with the living plants, but his names such as "*O. major*" have long been the source of confusion and dispute and he clearly did not understand the plants, or their

points of distinction (Turland & Rumsey, 1997). In fact none of his names are currently accepted within *Orobanche* sensu stricto! The first attempt at a global monograph of both the genus *Orobanche* sensu lato (and the family as then circumscribed) was made by the Austrian botanist Gunther Beck von Mannagetta (Beck-Mannagetta, 1890). His final account in Die Pflanzenreich (Beck-Mannagetta,1930) is still required reading for anyone with an interest in these plants. His protégé in Vienna, Alexander von Gilli continued to work on the genus in Europe (Gilli, 1965), Turkey and Asia into the 1970s (Gilli,1982) , but was not in the end responsible for the influential account in Flora Europea, where a very conservative broader specific concept was ultimately adopted by David Webb and Arthur Chater (Chater & Webb,1972).

The traditional intrasectional structures proposed by the various authors for *Orobanche* s.str.were not all confirmed by internal transcribed spacer molecular data (ITS) in the first major phylogeny produced for the genus (Schneeweiss et al., 2004a). For example the grex *Speciosae* put forward by Beck-Mannagetta (1930) that included *O. crenata*, was found to nest within the *O. minor* group. The DNA data also revealed negligible intraspecific sequence divergence between accessions; however given that *O. crenata* showed no sequence divergence from *O. minor* or related species (which are very distinct from the former), it appears that ITS sequence data are unable to resolve all taxa adequately. Other sequence data, such as sequence characterised amplified regions (SCARs) have revealed genetic divergence among closely related taxa in the complex *minores* group (Thorogood et al., 2008; 2009b). Here, the significance of co-evolution and host-mediated speciation, corroborated by detailed molecular studies alongside cultivation experiments, has revealed considerable cryptic diversity that traditional field-based taxonomic methods struggle to accommodate (Thorogood et al., 2008). How such cryptic races in the British Isles correspond with those further afield remain to be determined. Certainly British *O. minor* subsp. *maritima* is closely related to the Mediterranean coastal species *O. litorea* Guss*,* but in the absence of a broadly-sampled, well resolved phylogeny, such relationships remain undetermined. Advanced technologies such as a hyb-seq NGS-based approach may resolve such challenges as those described above.

In the Mediterranean, Asia Minor and the Middle East – the centre of diversity for the genus, authors have tended to treat newly identified host specific races with restricted geographic ranges as distinct species (see Cárlon et al., 2001, 2003, 2005, 2008; Pujadas-Salva &Crespo, 2004; Pujadas-Salva et al., 2005, Pujadas-Salva et al., 2008; Domina & Danin, 2014; Zare & Dönmez, 2014; Piwowarczyk, 2015). Few have been included in phylogenetic analyses, and their genetic relatedness remains unexamined. Taken together, the data available suggest that a combined approach encompassing broad-scale sampling, careful examination of micro-morphological features, ecological (host) data, as well as advanced DNA sequencing technologies will be required to tease apart relatedness in the most challenging taxa. Until we reach such a stage, taxonomy in the genus is likely to remain in a state of some flux.

IDENTIFICATION

Whilst it is not always possible to identify closely related species in herbaria, or from photographs, with careful observation identification in the field is usually straightforward in British species. Populations are often variable in robustness, colouration (such as the stigma lobes) and hairiness, therefore care should be taken not to rely on a single character in isolation. Characters that are especially important to observe include the shape of the corolla, the presence or absence of dark glands on the corolla, the colour and degree of fusion of the stigma lobes, the position, shape and size of the lobes of the upper and lower corolla lips and the presence or absence of glands on their margins, the length, shape and venation of the calyx (though this may vary even on a single plant) and the extent to which the segments are fused together (connate) under the flower, the height of insertion of the stamens (i.e. the distance from the base of the corolla tube that the filament

becomes free), the position and degree of the stamen hairiness and glandulosity (above and below. The nature and extent of hairiness and the extent and nature of the swelling to the shoot base are also useful characters. The presence of bracteoles is an easy way to distinguish *Phelipanche* from *Orobanche* (the former are also typically bluish or purplish-mauve in colour). In fruit the two genera can easily be distinguished as the capsules of *Phelipanche* do not remain fused at the apex as they do in *Orobanche*.

Most of the British species have a restricted host range and it is therefore important to identify the host where possible. For some species this is straightforward: *O. rapum-genistae* will always be found within a stone's throw from its typical host – a broom or gorse bush. For species with a broad host range, such as *O. minor*, in mixed vegetation reliable identification of the host can be all but impossible. Indeed the authors have excavated host-parasite connections of related species in the Mediterranean and established the emergent parasite to be several metres away from the host, with several seemingly possible host plants growing much closer by. An overlap in the host range of different species can also present difficulties. *Orobanche minor* can grow on ivy (though rarely), which is of course the predominant host of the similar species *O. hederae*. It may also grow (and luxuriantly) on thistles (*Carduus* spp. and *Cirsium* spp.) the hosts of *O. reticulata*. For these reasons, host plant identification alone is never a reliable diagnostic.

The most taxonomically challenging group in the British broomrapes is the subsection *minores* (Beck-Mannagetta) Teryokhin (Teryokhin, 1997) - a group of similar, small-flowered species (with corollas typically <20 mm) that are notoriously challenging to identify in the field, and that preserve poorly in herbaria. Three species belonging to this group occur in the British Isles: the widespread *O. minor* and the rare *O. picridis*, which co-occur in Kent, and *O. hederae*, which is most frequent in the southwest but increasingly common in urban areas. Furthermore, in its broadest circumscription, *O. minor* s.l. comprises multiple taxa some of which may be morphologically indistinct, but which have distinct host ranges, ecologies, evolutionary histories and distributions. For example subsp. *maritima* is established to be genetically distinct from subsp. *minor*, and is physiologically adapted to its local host – the sea carrot (*Daucus carota* L. subsp. *gummifer* (Syme) Hook. *f.*). Meanwhile forms of subsp. *minor,* though morphologically cryptic, are also host specific and ecologically distinct. For example var. *heliophila* grows almost exclusively on *Brachyglottis* in planted areas, whereas var. *pseudoamethystea* grows on sea holly and other maritime hosts in coastal habitats. These host-defined forms of broomrape seem to be in the process of incipient speciation – that is to say, they are on an evolutionary path to forming new species. Confusion among these taxa has been propagated by misidentification in popular photographic field guides to the British flora – for example *O. hederae* depicted as *O. minor, O. minor* subsp. *maritima* depicted as *O. picridis* and *O. minor* var. *pseudoamethystea* depicted as *O. minor* subsp. *maritima* (e.g. Gibbons & Brough, 2007; Sterry & Cleave, 2012.)

Orobanche minor aside, the species limits in the British species are relatively well understood. Not so in the Mediterranean which is the centre of diversity for the genus, where a spate of new species have been described in recent years (e.g. Carlón et al., 2001,2003,2005,2008; Pujadas-Salva & Crespo, 2004; Pujadas-Salva et al., 2005, Pujadas-Salva et al., 2008; Domina & Danin, 2014; Zare & Dönmez, 2014; Piwowarczyk, 2015). Genus-wide, in the absence of a well-sampled tree based on DNA sequence data from species samples across their ranges, alongside type specimens, identification of closely related taxa is likely to remain challenging.

The species described in the following pages are ordered by their genetic relatedness (Schneeweiss et al., 2004a). This is the most scientific and objective system for organising the taxa, and means that those that are most similar will appear side by side, for easy comparison.

USING AND UNDERSTANDING THE SPECIES ACCOUNTS

The species described in the following pages are ordered by their genetic relatedness (Schneeweiss et al., 2004a). This is the most scientific and objective system for organising the taxa and means that those that are most similar will appear side by side, for easy comparison.

Having arrived at a possible identification through the key one should consult the appropriate species account. Each of these begins with the taxon's name, author and its original place of publication and selected synonyms. The synonymy cited is not exhaustive but aims to capture the names likely to be encountered in more recent (i.e. post 1960) literature. This is followed by a concise tabulation of the conservation status for Great Britain, its constituent countries where assessments have been published, and Ireland. Where we believe these assessments require revision we state so and give our proposed re-assessment with reasoning.

After some initial remarks we give a detailed description before outlining the key distinguishing features. This is followed by comments on likely causes of confusion, before we outline the known host range, the habitats and ecology and present the most up to date distribution maps. In these, through the use of three defined date classes, we can see ancient historical decline (pre 1930); distribution through the major period of recording for the first two BSBI Atlas projects (1930- 1999) and what we might regard as the current distribution (post 2000). The accounts conclude with information relating to the variation each taxon demonstrate, which alongside the illustrations chosen represent the spectrum of variation expected and should help with the identification of difficult and atypical examples.

KEY TO THE BRITISH SPECIES

1. Flowers with 2 bracteoles, similar to the calyx teeth and external to them (1 bracteole + 2 calyx teeth each side of the flower); mature capsule valves free……2
1. Flowers without bracteoles; each flower with a 2-4 toothed calyx; capsule valves remaining joined distally……3

2. Stem usually simple, c.8 mm across; corolla 18-26(-30) mm; on *Achillea millefolium* ……*Phelipanche purpurea*
2. Stem often branched, slender, c. 5 mm across; corolla *small,* 10-15(-17) mm; on various cultivated hosts…… *Phelipanche ramosa*
[nb.The very rare casual *P. aegyptiaca* has larger more inflated corollas (>18mm) with hairy anthers]

3. Lower lip of corolla with minute glandular hairs at the margins……4
3. Margin of the lower lip of the corolla eglandular (glandular hairs may be frequent elsewhere on the corolla) ……7

4. Stigma lobes reddish or purplish……5
4. Stigma lobes yellow……6

5. Stigma lobes just touching; corolla suffused dark red, usually ≤20 mm long; calyx teeth entire, c. as long as the corolla tube (very local)…… *O. alba*
5. Stigma lobes widely spaced; corolla pale (not suffused dark red), usually ≥20 mm long; calyx teeth entire or bifid, shorter than the corolla tube (rare, in southeast England)…… *O. caryophyllacea*

6. Stigma lobes distant; filaments hairless at least in the basal third, inserted ≤2 mm above the base of the corolla tube (on woody legumes in natural habitats)…… *O. rapum-genistae*
6. Stigma lobes just touching; filaments hairy below, inserted 2-3 mm above the base of the corolla tube (on Berberidaceae in cultivated habitats)…… *O. lucorum*

7. Calyx with 2 lateral lips partially fused on the lower-side; filaments inserted (3)4-6 mm above the base of the corolla tube……*O. elatior*
7. Calyx with 2 lateral lips free on both the upper- and lower-side; filaments inserted 2-4(5) mm above the base of the corolla tube……8

8. Corolla with sparse dark glands (mostly distally), curved strongly along the back……*O. reticulata*
8. Corolla without dark glands (often with pale ones), curved a little, or straight along the back……9

9. Corolla large (20-30 mm) and open, campanulate, fragrant; filaments sparsely hairy along their length……*O. crenata*
9. Corolla small (10-22 mm) and ± tubular, scentless; filaments hairless or hairy mostly at the base……10

10. Corolla tube constricted just behind the mouth; corolla with acute to subacute lower lobes; stigmas yellow (rarely orange or reddish) ……*O. hederae*
10. Corolla tube not conspicuously constricted; corolla with blunt lower lobes; stigmas pink or purple (only yellow in all-yellow variants) ……11

11. Plant pale, hairy; upper lip porrect; filaments inserted ≥3 mm above the base of the corolla tube, their bases with shaggy covering of whitish hair; calyx with long filiform limbs (rare: Isle of Wight and east Kent) ……*O. picridis*
11. Plant variously suffused with purple; upper lip forwardly directed; filaments inserted ≤3 mm above the base of the corolla tube, their bases hairless to hairy; calyx teeth acute, sometimes very slender but not filiform (widespread) ……*O. minor*

1. GREATER BROOMRAPE

Orobanche rapum-genistae Thuill., Fl. Paris, 2nd ed., 317 (1800)

CONSERVATION STATUS
GB: NT; England: VU (A_{2c}); Wales: LC; Ireland: NT (A_{2c})
Nationally Scarce

REMARKS
The specific name means literally ‘turnip of broom’, a reference to the swollen stem base of the plant, attached to the roots of its host (that is typically broom). Once a common plant in the British countryside, now very much declined.

DESCRIPTION
A brownish, yellowish, or reddish perennial, often clumped. Flowering stem simple, 20-90 cm, glandular-hairy, strongly swollen at the base, usually a dull brownish colour, sometimes reddish or pinkish. Inflorescence rather compact, laxer below, extending over most of the shoot, the lowest flowers well-separated. Bracts 15-30 mm, linear-lanceolate, generally markedly exceeding the flowers. Calyx 8-15 mm, each lip usually equally bifid. Corolla 20-25 mm, pale yellow or brown to

reddish outside, more strongly red inside, sub-erect to erecto-patent, campanulate, inflated at the base in front; *upper lip rather hooded, almost entire* with spreading margins, lower lip with the middle lobe largest, all lobes ciliate, rather wavy and indistinctly toothed; back of corolla curved throughout, glandular pubescent. *Stamens inserted near the base* (not more than 2 mm above); filaments *hairless* below, glandular-pubescent above. Style glandular-pubescent; *stigma lobes yellow, markedly distant*. Flowering period early May into June (rarely to early July). Visited by bees. Native, parasitic on shrubby Fabaceae tribe Genisteae, mainly broom and gorse, very rarely Dyer's Greenweed and Petty Whin.

KEY DISTINGUISHING FEATURES:
This is one of Britain's largest species, identified easily by its stature and host (shrubby Fabaceae). Key features include the almost entire upper corolla lip, stamens with hairless filament bases, inserted virtually at the base of the corolla tube, and well-separated yellow stigma lobes.

SIMILAR SPECIES:
The only similar species is *O. elatior* which is also robust and brownish (although typically tinted orange), but that grows in chalky grassland on greater knapweed and has a finely-toothed upper corolla lip (not virtually entire), and stamens inserted well above the base of the corolla tube, with hairy filament bases. *O. caryophyllacea* has a somewhat similar corolla shape and may have a similar colour but has a distinct scent and purplish stigma lobes.

HOST, HABITAT AND DISTRIBUTION:
Greater Broomrape tends to occur in rough grassland, heaths and sandy, coastal scrub, where its host plants are abundant, although it is usually found on scattered, or isolated hosts, not in dense stands. Its preferred habitats tend to be somewhat less disturbed than those of other broomrapes (which grow on loose sands, cliffs and shallow soils). Prior to the British agricultural revolution the most common Broomrape in Britain, the species is still extant in c. 20 vice-counties, but has suffered a significant, if largely historical, decline. This decline continued through the twentieth century, although a brief resurgence was heralded by the great storms of 1987, when the windfall in coniferous forestry plantations on acid soils saw the return of hosts and parasite from the soil seedbank (Rumsey & Headley, 1998). Subsequently populations have remained almost stable, although losses are still occurring and significantly the species is not being found in new sites, just recurring sporadically in old ones. In many vice-counties it is now restricted precariously to a single location, often with just one or two clumps. Suitable habitats from which the plant remains absent are plentiful and in an increasingly favourable climate for this Mediterranean species which suggests poor seed dispersal to be a major contributory factor to its ongoing plight.

VARIATION
There exists significant variation in corolla and stem colour. Pure yellow forms lacking purplish pigmentation - f. *flavescens* Durand (syn. f. *hypoxantha* G. Beck) have been photographed in N. Hants. (VC.12) and may occur elsewhere. Chater & Webb (1972) recognised three subspecies in Europe, our plant being subsp*. rapum-genistae*. The plant is locally plentiful on the southwest sea cliffs of Jersey and Alderney. Here it parasitises prostrate broom (*Cytisus scoparius* subsp. *maritimus*) exclusively, even though 'ordinary' broom (*Cytisus scoparius* subsp. *scoparius*) does occur there. The plant is brownish with stem bases with numerous bracts and devoid of flowers. Further work may reveal this ecotype of the species to be genetically distinct and worthy of infraspecific status.

2. CLOVE-SCENTED BROOMRAPE

Orobanche caryophyllacea Sm. in Trans Linn. Soc. Lond. 4: 169 (1797).

CONSERVATION STATUS
GB: NT (D); England: NT(D)
Nationally Rare
The plant may be present annually in large numbers in Kent, at Sandwich Bay and in small quantity sporadically at various sites around Folkestone from Sugar Loaf hill, east to Samphire Hoe and inland around Church Hougham. There are no recent records from the Kearsney/ Temple Ewell area and it may be lost from its most westerly site at Sandgate, were last recorded in 1991. The contraction of range and general decline in habitat quality and extent may mean it should be revised to EN ($B_{1,2\ bi\text{-}v}$) at English and GB level, or at least VU (D_1) if detailed repeated census established the annual population was fewer than 1,000.
Protected under Schedule 8 of the Wildlife and Countryside Act, 1981

REMARKS
The plant was discovered in the Folkestone area by the Rev. Gerard Smith in May 1828 and subsequently found by him around Dover (Smith, 1829) and west to Sandgate. It was later discovered on the sandhills at Deal and Sandwich, from where it is most familiar to visiting botanists nowadays. Victorian records from Scotland, N. Wales and more recently Suffolk are all thought to be misidentifications (eg. Sandford, 1992), or the result of mixing of labels in herbaria.
It has always been rare in the British Isles. The very visible abundance in some years at Sandwich have tended to lessen concerns over this species' survival here. However even there seed-set can be very poor, the plant easily damaged by users of the beach area. Around Folkestone and at its most inland locations sites have been lost and appearances are sporadic. It is surely deserving of greater conservation attention.

DESCRIPTION
A rather short, stocky annual (rarely perennial) with simple flowering stems 15-40(-50) – occasionally clumped; stems glandular-hairy, whitish, pale yellow or pale pink in colour with rather numerous dark brown bracts at the very base. Flowers typically rather few flowers in a lax spike smelling quite strongly of cloves, especially in warm weather. Bracts ovate-lanceolate, acuminate, *shorter* than the flowers. Calyx 10-17 mm, entire to ± equally bifid. Corolla 20-32 mm, a similar colour to the stem, densely glandular-hairy, erecto-patent, *broadly campanulate*, broadest just behind mouth, ± uniformly curved, upper lip notched with the lobes erect upon opening, lower lip with subequal glandular-ciliate almost fringed lobes. Stamens inserted 1-3 mm *above the base of the corolla tube*, filaments hairy below, glandular above. Stigma *dark purple, lobes distant*. Flowering period mid-May to June (rarely into July). Visited and pollinated by bumblebees. 2n=38. Native, parasitic on Rubiaceae.

KEY DISTINGUISHING FEATURES:
A pale, fragrant, large-flowered plant with broadly campanulate corolla and dark, separated stigma lobes.

SIMILAR SPECIES:
The colour, form and ecology of this plant make it unmistakable in the British Isles. On the continent, *O. teucrii* Holandre is a similar species that grows on *Teucrium* and is widespread in Northern Europe, and *O. apuana* Domina & Soldano is a similar species that grows on *Santolina* in central Italy; *O. lutea* Baumg. is also a similar continental species that has yellow stigma lobes.

HOST, HABITAT AND DISTRIBUTION:
One of our rarest broomrapes, this species has always been very local in Britain, and is restricted to east Kent, where it is perhaps the result of wind-blown seed from the continent (populations grow in similar habitats on the adjacent mainland). The best-known site is on stabilised dunes at Sandwich in

Kent where it grows on *Galium verum,* and to a lesser extent, on *G. album.* Here the relatively stable population can produce hundreds of spikes in a year and is afforded some protection from the conservation focus on other rarities with which it co-occurs, such as the lizard orchid (*Himantoglossum hircinum*). Elsewhere it is exceptionally scarce and has suffered decline, for example on the chalk downs and undercliff above Samphire Hoe in Dover and in similar situations around Folkestone, extending westwards to Sandgate. Here the plant parasitises *G. album*, the taller, rather purplish plants occurring in very small numbers. Seed set is low (the plant is reliant on cross-pollination), so the establishment of new populations is hampered. Persistence in cultivation where deliberately introduced, as in the Natural Order beds at Kew where it persisted for over 50 years, suggests that the species distribution is not limited by climatic factors and its hosts are ubiquitous.

3. THYME BROOMRAPE

Orobanche alba Stephan ex Willd., Sp. Pl. 3: 350 (1800)
(syn. *O. rubra* Sm.)

CONSERVATION STATUS

GB: LC; England: LC; Ireland: LC
Nationally Scarce
Familiar to most British botanists from the Lizard peninsula in Cornwall where a fluctuating population may be locally abundant in some well-visited areas, but total population size is difficult to estimate. Elsewhere in England the plant has been recorded from fewer than 5 sites since 2000, with very low numbers, produced sporadically and subject to various threats. For England at least LC seems too optimistic and a category of NT(D) might be more appropriate.

REMARKS

Our plant was described from Cave Hill, Belfast by J. E. Smith in Sowerby (1805) under the name of *Orobanche rubra* Sm. The material was sent by J. E. Templeton and listed by him in his unpublished manuscript Flora Hibernica from c.1793. (Pearman, 2017). It was not until much later that the British and Irish plant was identified as being a reddish variant of the continental *Orobanche alba* Stephan ex Willd. This is an extremely variable species in the Balkans and S.W. Asia but relatively invariable in the British Isles which marks the western extremity of its distribution and where the forma *rubra* (Hook.) Beck predominates.

DESCRIPTION

A short, stocky reddish annual (or monocarpic perennial) with simple flowering stems, usually 8-25 cm; stems *dark orange-red*, short-glandular-hairy, slightly swollen with numerous reddish scales at base. Inflorescence lax, with few flowers, slightly fragrant. Bracts 12-25 mm, lanceolate, acuminate, glandular, *slightly shorter or equalling* the length of the corolla. Calyx 8-16 mm usually *entire*, occasionally bidentate, about equalling the corolla tube. Corolla 15-25 mm, rather shiny pale cream, usually *strongly suffused dull reddish-purple*, glandular-pubescent especially distally, erecto-patent, slightly curved, more strongly so at the basal and distal ends; tube *campanulate-cylindrical*; upper lip entire or 2-lobed with somewhat spreading margins; lower lip glandular-ciliate, the 3 lobes about equal, the middle just the largest. Stamens inserted 1-3 mm *above the base of the corolla tube*; filaments slightly hairy below, glandular above. Stigma lobes reddish or purplish, the lobes touching. Flowering period late May and June (rarely into early September). Flowers visited by bumblebees. 2n=38. Native, parasitic on *Thymus drucei* Ronniger in the British Isles, on a much wider range of Lamiaceae elsewhere.

KEY DISTINGUISHING FEATURES:

In Britain, this plant is almost always strongly tinted red and grows in rocky habitats. Other key features include the fragrant flowers, campanulate-cylindrical corolla with distinct dark glands and the (usually) entire calyx teeth.

SIMILAR SPECIES:
Historically this species has been confused with small specimens of *O. minor* and *O. hederae,* but its distinctive morphology and ecology make it unmistakable in Britain. On the continent the plant is much more variable (usually paler) and could be confused with *O. caryophyllacea* (which has distant, dark purple stigma lobes) and other species such as *O. gracilis* Sm. (which has yellow stigma lobes).

HOST, HABITAT AND DISTRIBUTION:
In Britain this plant grows on *Thymus* on rocky slopes, screes and sea cliffs, usually on basic or ultrabasic rock (basalt, limestone and serpentine). Though widespread, the plant is absent from much of the country, is rare, local and has declined. In Cornwall – a stronghold – it is now virtually restricted to the Lizard Peninsula where it is fairly frequent, especially around Kynance Cove but numbers fluctuate markedly from year to year. Inaccessibility probably affords the plant some protection. The plant has occurred in gardens in Somerset and Surrey, perhaps introduced with the host and has not persisted. Rather bizarrely a single individual was reported (doubtfully – the specimen had yellow stigmas) in grazed grassland in Wilts., close to the Hants. border, in 2015, but the unusual specimen has not recurred.

4. THISTLE BROOMRAPE

Orobanche reticulata Wallr., Orob. Gen. 42 (1825).

subsp. ***pallidiflora*** (Wimm. & Grab) Hayek.

(syn. *O. pallidiflora* Wimm. & Grab.; *O. reticulata* subsp. *procera* (Koch) Dostál)

CONSERVATION STATUS
GB: NT (D); England: NT(D)
Nationally Rare
The plant has been recorded in 11 sites post 2000, but was known from over 15 more, largely within the current area of occupancy, in the period 1987-1999. If this reflects genuine loss as opposed to under-recording the species may qualify as EN (A_{2a}) and is almost certainly VU ($C_{2\,ai}$). Detailed re-survey is required.

Protected under Schedule 8 of the Wildlife and Countryside Act, 1981.

REMARKS
The form in the UK is referable to subsp. *pallidiflora*, treated by some (eg. Kreutz, 1995) as a distinct species. The nominate subspecies is a shorter plant of alpine situations, with a subtly different corolla shape, the flowers more densely dark-glandular, filaments more densely glandular above, and a narrower host range but including examples of the Dipsacaceae.

Foley (2000) argued that our plant should be called subsp. *procera* (Koch) Dostál, the defining characters given for the earlier name *pallidiflora* he felt being ambiguous, pale flowered forms existing in subsp. *reticulata,* but he had been unable to see type material of the latter.

DESCRIPTION
A pinkish to purplish annual (rarely a weak perennial) with simple stems 15-70(-81) cm, glandular-hairy, typically liver-coloured (± yellowish or purplish), slightly swollen below. Inflorescence rather dense above, laxer below, often occupying c. the upper third of the stem, the lowermost flowers

often well-separated. Bracts 12-25 mm, narrowly triangular equal to, to shortly exceeding corolla, rather dark (contrasting the flowers). Calyx 7-12 mm, bifid, upper segment largest. Corolla 12-22 mm, *pale* creamy-yellowish, purple distally (especially the margins), *with sparse, dark glands* (especially distally), broadly cylindrical-campanulate; upper lip with 2 spreading lobes, the lower lip with 3 equal lobes, the middle rather square; all lobes more or less toothed. Corolla tube somewhat broadened above the insertion of the stamens, the back curved strongly above the base and behind the upper lip. Stamens inserted 2-4 mm above the base of the corolla; filaments hairless to sparsely hairy below, somewhat glandular to hairless above. *Stigma lobes dark purple*, just touching at base. Flowering period June (rarely into August). Native, parasitic on thistles, most frequently *Cirsium arvense* (L.) Scop. and *C. eriophorum* (L.) Scop.

KEY DISTINGUISHING FEATURES:
Rather robust, creamy or purple spikes with flowers with dark glands and dark purple stigma lobes, and the corolla curved strongly behind the upper lip.

SIMILAR SPECIES:
Robust specimens of *O. minor* can resemble *O. reticulata* (and also parasitise thistles), but the former have narrower, typically less arched corolla tubes which lack dark glands and the filaments are never glandular hairy above.

HOST, HABITAT AND DISTRIBUTION:
This rare species has been reported reliably from fewer than thirty localities, almost exclusively on Magnesian limestone in northwest Yorkshire, often associated with the floodplains of the major rivers but also Roman roads. The most frequent hosts are *Cirsium arvense* (L.) Scop.and *C. eriophorum* (L.) Scop. but other thistles are also parasitised. It grows in unimproved pastures, along roadsides, in waste places and grassland overlying limestone. None of the extant populations are extensive, all fluctuate markedly in number and many are endangered by changes in land use. Not described as British until 1909, having been found on Hetchell Crags by J.F. Pickard in 1907. The first known British specimen was collected in the 1830s in Notts. No subsequent finds have been made in the county but the magnesian limestone does extend into the area and its natural vegetation has been extensively destroyed. Paradoxically, due to the detailed study of this rare plant by Headley, Hughes & Jeavans (1998), more is known about its autecology than for any other British species.

5. PICRIS BROOMRAPE

Orobanche picridis F.W.Schultz, Bot. Lit.-Blatt. 5: 504 (1830).

CONSERVATION STATUS
GB: EN; England: VU($D_{1,2}$); Wales: Not Listed but RE
Nationally Rare
The losses from Wales (1860s) and Cambridgeshire (1930s) are historical and too ancient for consideration when assessing using IUCN criteria. While there has been deterioration of habitat in the St. Margaret's area and around Dover and increased rates of coastal erosion pose threats throughout the British range, healthy populations still exist on the Kent coast and the plant is increasing very locally on the Isle of Wight (mainly in one thriving cliff-top population). Numbers fluctuate markedly but recently the number of plants has exceeded the threshold for VU(D_1) in most years, the species still qualifies under VU (D_2) if the Kent populations are considered as 1-2 locations, as they are contiguous, under the same management/ownership and facing the same threats.

Protected under Schedule 8 of the Wildlife and Countryside Act, 1981

REMARKS
Britain's rarest native broomrape in terms of distribution and population size and the most misunderstood in terms of its past records. Previously known as *O. artemisiae-campestris* Vaucher ex Gaudin– now shown to be a closely related species and also *O. loricata* Rchb. a later synonym of that segregate species. The most thermophilous British native species and the last to commence flowering, in some years well into August. Rather invariable in the British Isles although plants may differ markedly in stature.

DESCRIPTION
A slender, *pale* annual with simple flowering stems, (10)20-60 cm, virtually hairless to glandular-hairy, pale yellowish, often tinged dull purple, with few brown scales below, and scarcely swollen at the base. Inflorescence rather dense apically, the flowers usually restricted to top half of the stem. Bracts 12-20 mm, *narrowly* ovate-acuminate, recurved, equalling to just exceeding the flowers, papery dark brown, contrasting the pale flowers. Calyx 10-15 mm, with segments entire or unequally bifid; the segments *slender*, acuminate, 1-veined or 3-veined, the outer veins very indistinct. Corolla 14-22 mm, *very pale, ivory* to yellowish, veined purple-lilac distally, virtually hairless to glandular-hairy, the upper lip emarginate to bifid, porrect to erect, ± forming a standard; the lobes of lower lip subequal, or the middle the largest, rather square in shape; all lobes crisped and toothed; the back of the corolla curved at base, then *virtually straight;* corolla with brown papery patches upon opening. Stamens inserted (2-) 3-5 mm above the base of corolla; filaments with *conspicuously dense white hairs below*. Stigma lobes *dark* purple (often blackish, especially in Kentish populations), contrasting the pale flowers, just touching. Rather late flowering, from May (on the Isle of Wight) into June and July (in Kent). 2n = c. 38* & 38. Native, parasitic almost exclusively on *Picris hieracioides* L.

KEY DISTINGUISHING FEATURES:
A very pale plant with contrasting bracts and stigma lobes, slender, with flowers rather large relative to the slender stems; the calyx lobes are long and slender, the upper segment with one conspicuous vein only and in most British plants the calyx lobes are +/- entire not conspicuously bifid; the bracts more or less exceed the flowers and are often conspicuous at the top of the spike. Flowering is typically almost a month later than *O. minor* with a peak in July and into August.

SIMILAR SPECIES:
This species is closely related to the widespread and co-occurring *O. minor*, which typically flowers a month earlier and all the diagnostic characters overlap with the extremes found in that species; small specimens of both species can be particularly confusing. Careful observation of all characters highlighted above is crucial, and reliable identification from photos and poor herbarium specimens can be problematic. Importantly even small specimens of *O. picridis* usually have dark purple (not pinkish) stigma lobes which contrast strongly with the pale corollas. Herbarium specimens have corollas of a distinctive orangey colour.

HOST, HABITAT AND DISTRIBUTION:
This very rare plant has a distinct ecology in Britain where surviving populations are virtually restricted to the edges and ledges of chalk sea cliffs, or rocky debris and slumped soil at their foot. It is parasitic almost exclusively on *Picris hieracioides*, but was seen once on *Pilosella officinarum* in Kent. Depauperate specimens have also been observed growing on *Inula conyza* by the authors in 2020. Though widely recorded across Southern England most records have proved erroneous. A genuine specimen exists from Giltar Head, Pembs. and the plant was known from an area around Comberton and Haslingfield in Cambridgeshire for almost a century; the few populations extant today are restricted to the Dover and Deal area of east Kent and on the west coast of the Isle of

Wight. Its penchant for steep and unstable chalky ledges affords it protection in some populations, however encroachment of scrub and shading by trees on the undercliffs seems to have caused the decline of others. The increased rate and extent of coastal erosion threatens the plant's survival in both of its British locations. Though unlikely, colonisation from wind-swept seed from the continent is not impossible; populations thrive on the dunes of north Holland nearby.

6. IVY BROOMRAPE

Orobanche hederae Duby, *Bot. Gall.* 1: 350 (1828).

CONSERVATION STATUS

GB: LC; England: LC; Wales: LC; Ireland: LC

Accorded protection in Northern Ireland under Schedule 8 of the Wildlife (N. Ireland) Order, 1985 as amended by the Wildlife and Natural Environment Act (N. Ireland), 2011.

REMARKS

First discovered in the British Isles on Guernsey in 1726 the plant was found subsequently along the southwest coast of England, Wales and in the Killarney area of Ireland. This species was at first confused with *O. minor* and was included in it by Bentham & Hooker (1930) who considered the stigma colour and 'other trifling characters' indistinct. One of the most frequently encountered species in the British Isles and the only native which is increasing through spread into urban situations. Usually to be found in considerable abundance and density where it occurs and often with the remains of past generations still apparent.

DESCRIPTION

A purplish, monocarpic biennial (rarely weakly perennial) with simple flowering stems, 10-60(-105) cm, strongly suffused purple, glandular pubescent usually markedly swollen and yellowish at the base. Spike typically rather long and lax (to dense above), often with *flowers from near ground level*, and with a conspicuous broad, pointed 'bud' of unopened flowers. Bracts 12-22 mm, equalling or exceeding the flowers, ovate-lanceolate to lanceolate, acuminate and *minutely toothed* near the tip. Calyx 10-15 mm, bifid or entire. Corolla (10-)12-20(-22) mm, dull cream tinged reddish-purple; sparsely glandular or almost hairless, erecto-patent to patent tube slightly inflated below, usually *constricted distally*; upper lip entire to emarginate, the lobes forwardly directed or spreading; lower lip with middle lobe just the largest, all sub-acute, crisped and toothed; corolla rather straight along the back, except at the base. Stamens inserted well above the corolla base (by 3-4 mm); filaments virtually hairless below, occasionally sparsely glandular above. *Stigma lobes partially united, yellow* (sometimes tinted pink or reddish-orange). Flowering period June to November + (the latest flowering species here). 2n=38*. Native, naturalised in artificial habitats east of its native range; parasitic on Araliaceae and rarely Apiaceae.

KEY DISTINGUISHING FEATURES:

Distinguished easily by its habitat (typically rather shady areas with abundant ivy), its long purple spikes with flowers almost throughout, i.e. from near ground level, and (usually) yellow stigmas. Corolla narrow and pinched towards the tip, the lobes rather acute and with somewhat lacerated edges. The species has the longest flowering period sometimes even to be found flowering at new year.

SIMILAR SPECIES:

This plant is mistaken frequently for *O. minor* (which can also grow on *Hedera,* but very seldom), from which it can be distinguished most readily by its yellow stigma lobes (that in *O. minor* are usually pinkish, and yellow only in all-yellow forms). It also has a different corolla shape (somewhat

dorso-ventrally constricted behind the mouth), flowers extending over most of the stem, and a broad, pointed top to the spike.

HOST, HABITAT AND DISTRIBUTION:
This is one of our most common broomrapes and seems to be steadily increasing. It is particularly frequent in the southwest on wooded sea cliffs and at the base of (and on) old walls, particularly in limestone areas. Native Atlantic populations are parasitic predominantly on *Hedera hibernica* (G. Kirchn.) Bean*;* those naturalised further east also grow on *Hedera helix* L.*,* and on a range of other Araliaceae in gardens, including *Tetrapanax, Fatsia,* and x *Fatshedera.* Interestingly it also appears from time to time on garden cultivars of *Eryngium* (the host of its sister species *O. amethystea,* which is absent in Britain).

VARIATION
The most significant variation occurs in plant pigmentation; pale plants are not infrequent and the striking yellow forma *monochroa* Beck (nb. not *monochroma* as is sometimes and perhaps understandably used) is increasingly being found, largely away from the species' native range suggesting some deliberate horticultural introduction. In some areas, such as in parts of Hampshire around Winchester and Alresford it is the only form present. Variation also exists in stigma colouration. Populations with a more pinkish orange cast to the stigma can be more easily mistaken for *O. minor*.

7. COMMON BROOMRAPE

Orobanche minor Sm**.**, Eng. Bot. 6: 422 (1797).
subsp*.* ***minor***
var*.* ***minor***

CONSERVATION STATUS
GB: LC; England: LC; Wales: LC; Ireland: Not Evaluated

REMARKS
Taxonomically the most complex species, in which races adapted to different hosts are known to be physiologically and genetically distinct, but are difficult to distinguish based on morphology alone. The most common species in the British Isles.

DESCRIPTION
A pinkish-purple annual with simple flowering stems (5-)10-60 cm, glandular-puberulent to hairy, yellowish or reddish-brown, tinged to a variable degree with purple, scarcely swollen below. Spike usually rather lax (to dense apically) with rather numerous flowers. Bracts 6-22 mm, ovate-lanceolate to lanceolate-subulate, acuminate, equalling to just exceeding the corolla. Calyx 6-14 mm long, equally to unequally bifid, rarely entire. Corolla 10-18(-20) mm, creamy-yellow, *curved regularly throughout* (or sharply inflected at the base then curved), purplish suffused to a variable extent, hairless to glandular-hairy, upper lip emarginate or slightly bilobed with the lobes directed forwards; lobes of lower lip sub-equal or with the central the largest, all lobes crisped and denticulate, without prominent bosses. Stamens inserted 2-3.5 mm above the corolla base; *filaments virtually hairless to sparsely hairy below*. *Stigma lobes typically pinkish-purple, to reddish-purple* (or yellow in all-yellow variants), just touching at the base to partially united. Flowering period late May to June (rarely into to mid-September). n = 19, 2n = 38. Native (in some forms) and also introduced. Parasitic on a wide range of hosts, especially Fabaceae and Asteraceae.

KEY DISTINGUISHING FEATURES:
A (typically) purplish, rather small-flowered and slender annual. Corolla tubular, not widened upwards, its back curved ± evenly throughout.

SIMILAR SPECIES:
Infraspecific taxa can be very difficult to distinguish (see next descriptions) and close attention must be paid to the characters emphasised above, and to ecology. The most similar species to *O. minor* is the very rare (but co-occurring) *O. picridis,* which is a pale plant with slender stems, darker stigmas, straighter-backed corollas and very slender bracts and calyx lobes. Pale forms of *O. minor* with rather attenuated calyx lobes and rather hairy filaments can be confusing, but never have the purple (often even blackish) stigma lobes present in British populations of *O. picridis.* It is also confused regularly with *O. hederae* that differs in its yellowish stigma, corollas with a distinct constriction behind the corolla mouth and more acute corolla lower lip lobes.

HOST, HABITAT AND DISTRIBUTION:
Our most common broomrape, this is a highly variable and widespread plant that is possibly not native to the British Isles, except persistent populations in coastal areas, on fixed dunes and shingle (see var. *pseudoamethystea*). The common form described above (subsp. *minor* var. *minor*) is often casual or sporadic and particularly common on roadsides, in disused chalk and gravel pits, and sown leys; it is widespread but most common in southern Britain. Red clover (*Trifolium pratense*) is perhaps the most frequent host, it can parasitize numerous plants, so host identity is of little diagnostic value.

Key to infraspecific taxa of *O. minor*

1. Plant purplish throughout; spikes lax to dense; hosts and habitats various……..3

1. Plant always entirely yellow……2

2. Plant short (to 25 cm), with a dense spike, often *sub-globose* apically, corollas <12mm, calyx short, usually entire. Channel Islands - growing on Asteraceae tribe Cichorieae — extinct (?)……. **subsp*. maritima* var*. hypochoeridis***

2. Plant short to tall (up to c. 60 cm), spike lax to moderately dense, corollas usually >13mm, calyx variable - usually unequally bifid. Hosts various. But for colour, indistinguishable from *O. minor* subsp. *minor*…… **subsp. *minor* f. *lutea***

3. Stem typically glandular-pubescent, short to tall (up to c. 60 cm). Bracts equalling to exceeding the corolla; calyx 7.5-16 mm, entire or bifid. Lower lip with sub-equal, broadly rounded lobes, *lacking* prominent contrasting yellow bosses. Stigma lobes just fused, becoming distant with age. Hosts various……. 4

3. Stem glandular-puberulent, short (to 35 cm). Bracts not exceeding the corolla; calyx short, 6-10 mm, often *entire*. Lower lip with middle lobe largest, reniform, with two *prominent* yellow bosses. Stigma lobes partially fused. Host *Daucus carota* subsp. *gummifer* (rarely *Plantago* or Asteraceae)……. **subsp. *maritima***

4. Flowers patent (rarely sub-erect in fruit), 5-8 mm in diameter, variably suffused purple and typically glandular-pubescent. Hosts and habitats various……. 5

4. Flowers conspicuously *sub-erect* (especially so in fruit), *slender*, 3.5-5 mm in diameter, pale and sub-glabrous. Hosts Asteraceae (especially *Crepis*), rarely other families……. **subsp. *minor* var. *compositarum***

5. Plant slender to robust but rarely clumped (i.e. without many stems arising from one tuber), monocarpic; corolla typically tinted pale purple; filaments slightly hairy at the base. Hosts and habitats various……6

5. Plant usually *clumped*, perennating; corolla basally white, *strongly flushed purple* distally; filaments *densely hairy at the base*. Host *Brachyglottis* (occasionally other shrubs), in cultivated and landscaped environments……. **subsp. *minor* var. *heliophila***

6. Stem scarcely swollen below. Spike lax to dense; corolla often purplish, with *regularly curved* dorsal line (or sharply inflected at the base); upper lip not distinctly bilobed; filaments inserted 2-3.5 mm above corolla base. Hosts numerous, often Fabaceae and Asteraceae; often in disturbed or grassy habitats, coastally and inland……. **subsp. *minor* var. *minor***

6. Stem *bulb-like at the base*. Spike often dense; corolla (>15mm) strongly tinted purple, with *flattish* dorsal line, *geniculate* at the tip, *bilobed* upper lip and a high filament insertion (≥3 mm above the base). Parasitic on *Eryngium maritimum* and other halophytes, exclusively in maritime habitats ……. **subsp. *minor* var. *pseudoamethystea***

Orobanche minor

subsp. *minor*

var. *compositarum* Pugsley in J. Bot. (Lond.)78:111 (1940).

CONSERVATION STATUS:

Not Evaluated. Poorly recorded and much misunderstood which would warrant a DD category if any decline were thought to have occurred.

REMARKS:

Described by Pugsley to take account of plants that had been confused with *O. picridis* because of their hairier filaments, pale flowers and parasitism on Asteraceae. These characters and that of the sub-erect corollas may have arisen independently in distinct lineages and the wider host range also suggests that this taxon may a bit of a dumping ground of actually disparate plants. Molecular and genetic studies to resolve this have not yet proved possible.

DESCRIPTION:

Flowering stems 10-50 cm, slender, glandular pubescent to sub-glabrous, usually pale reddish-brown. Spike usually lax throughout, rarely dense. Bracts and calyx as in var. *minor*. Corolla 10-16(-18) mm slenderer than in var. *minor* (width to c.5mm), sub-glabrous, *sub-erect* (not horizontal) at anthesis, less heavily pigmented. Filaments somewhat hairy to c.mid-point. Other characters as in var. *minor*.

KEY DISTINGUISHING FEATURES:

The combination of pale, narrowly tubular corollas that are arching to sub-erect and with conspicuously hairy filaments help distinguish this only rather subtly different variant of Common Broomrape.

SIMILAR TAXA:
Difficult to differentiate from other forms of the highly variable *O. minor*. It may resemble *O. hederae* particularly when both are past flowering.

HOST, HABITAT & DISTRIBUTION:
Host usually *Crepis* (Asteraceae). Recorded most reliably on sandy soils in Surrey and East Anglia, and in coastal areas elsewhere, especially on *C. capillaris* Wallr. and other Asteraceae. At least one example annotated by Pugsley as a Paratype at BM! is parasitic on *Trifolium pratense*. Plants answering this taxon's description have also been seen by the authors on this host and on *Smyrnium olusatrum* L. (Rumsey & Jury, 1991). Possibly closely related to var. *heliophila* (which can also produce sub-erect flowers, especially in fruit). Plants from Suffolk parasitising *Brachyglottis* were recorded as var. *compositarum* (Sanford, 1992).

BRACHYGLOTTIS BROOMRAPE
***Orobanche minor* Sm.**
subsp. *minor*
var. *heliophila* Thorogood & Rumsey in British & Irish Botany 2:230 (2020)

CONSERVATION STATUS
Recently described (Thorogood & Rumsey, 2020) and therefore Not Evaluated in the national Red-lists. If regarded as a Neophyte it would not be evaluated, although if recently evolved and largely restricted to the British Isles worthy of consideration. Increasing, widespread if sometimes ephemeral and locally abundant and therefore we regard it as LC.

REMARKS
A form of *O. minor* subsp. *minor* that is morphologically rather cryptic but clearly host-defined, growing almost exclusively on *Brachyglottis* × *jubar.*

DESCRIPTION
A more or less robust annual, or weak perennial. Flowering stems 1-5(10), typically clumped from the base, (5-)15-60(70) cm (clumps often with spikes of varying height), glandular-pubescent, yellowish below, reddish-brown to purple above. Stems scarcely swollen below. Spike often many-flowered, usually lax below and dense to crowded apically in larger specimens. Bracts 9-22 mm, ovate-lanceolate to lanceolate-subulate, acuminate, equalling to just exceeding the corolla. Calyx purple, 6-14 mm long, equally to unequally bifid. Corolla 10-18 mm, glandular-pubescent, basally white, conspicuously flushed and veined with purple towards the upper 1/3 or 1/2, curved regularly throughout or inflected at the base then curved, upper lip emarginate to bilobed with the lobes often slightly reflexed; lobes of lower lip sub-equal, all lobes strongly crisped to sub-crenate-denticulate; corolla erecto-patent to sub-erect in fruit. Stamens inserted 2-3 mm above the corolla base; *filaments typically white-hairy below*. Styles purplish, reflexed apically (especially when mature). Stigma lobes slightly exserted, pinkish-purple to purplish-orange, rather distant. Flowering period late May (rarely into mid-September). Parasitic on *Brachyglottis* × *jubar.*

KEY DISTINGUISHING FEATURES:
Distinguished most easily by its ecology (artificial habitats where its host has been planted). Typically clumped with multiple stems arising from a stock, often perennating. Spikes often many-flowered.

SIMILAR TAXA:

Morphologically very similar to *O. minor* subsp. *minor* var. *minor* but typically more robust with many spikes arising from a single specimen, corolla whitish at the base and rather strongly pigmented distally, and hairy-based filaments.

HOST, HABITAT AND DISTRIBUTION:
Parasitic on *Brachyglottis* × *jubar* and occasionally other shrubs (such as *Veronica* spp.) in cultivated and landscaped habitats. Frequent in car parks and gardens throughout the British Isles except for the far north; most common in the southeast. Cultivation trials show that the plant cannot establish on clovers (a frequent host of *O. minor* subsp. *minor* var. *minor*).

SEA HOLLY BROOMRAPE
Orobanche minor Sm.
subsp. ***minor***
var. ***pseudoamethystea*** Thorogood & Rumsey in British & Irish Botany 2:231 (2020)

CONSERVATION STATUS
Recently described (Thorogood & Rumsey, 2020) and therefore Not Evaluated by the national Red-lists. Best treated as DD pending further research.

REMARKS
Possibly the British form of *O. minor* subsp *minor* most likely to be a native, this plant has been much-confused historically with *O. minor* subsp. *maritima* and with *O. amethystea* (a species not native to Britain).

DESCRIPTION
An annual with simple flowering stems (5-)10-60 cm, glandular-pubescent, reddish-brown, tinged strongly with *purple* (especially when young). Spike often dense and many-flowered in taller specimens. Stem base *conspicuously swollen (bulb-like) below*. Plant often forming lax clumps with specimens of varying sizes. Bracts 10-22 mm, lanceolate-subulate, acuminate, equalling to just exceeding the corolla. Calyx red-brown, 10-14 mm long, unequally bifid (rarely entire). Corolla 10-18(-20) mm, whitish-cream, *rather flat dorsally, then inflected at the tip (not evenly curved)*, veined and tinted purple, weakly glandular-pubescent, upper lip *bilobed* with the lobes directed forwards; lobes of lower lip sub-equal, all lobes crisped and denticulate, without prominent bosses. Stamens inserted 3-3.5 mm above the corolla base; filaments sparsely hairy below. Stigma lobes pinkish-purple, partially united. Flowering period late May and June (into early July). n = 19, 2n = 38. Parasitic on sea holly (*Eryngium maritimum*) and other herbs of sandy and shingly shores, particularly Apiaceae and Asteraceae, e.g. *Crithmum maritimum*.

KEY DISTINGUISHING FEATURES:
A plant defined as much by its ecology as its morphology, and perhaps variable depending on host identity. Key features include the robust purplish stems, often devoid of flowers in the lower half, rather flat-backed corolla, geniculate towards the tip, and bilobed upper lip.

SIMILAR SPECIES:
Frequently misidentified as *O. minor* subsp. *maritima* and depicted as such in some popular field guides. Whilst var. *pseudoamethystea* does share some characteristics with subsp. *maritima* (coastal ecology, parasites of Apiaceae, purple stems with swollen bases) the latter is very distinct, for example in its unequally 3-lobed lower corolla lip with conspicuous yellow bosses. Also (historically) confused with *O. amethystea,* a continental species that is absent from the British Isles and also parasitic on *Eryngium* spp. but with a larger corolla (to 23 mm) and longer, more acuminate calyx segments and typically a more reddish-brown colouration.

HOST, HABITAT AND DISTRIBUTION:
Parasitic on *Eryngium maritimum* and other halophytes on coastal dunes and shingle in east Kent (Sandwich Bay and Deal), and locally along the coasts of southern Britain and South Wales: Isle of Wight (formerly), Devon, Cornwall, Scillies, Channel Islands (and also the north coast of France, Belgium and the Netherlands).

CARROT BROOMRAPE
Orobanche minor Sm.
subsp. ***maritima*** (Pugsley) Rumsey, Watsonia 26(4): 474 (2007).
(syn. *O. maritima* Pugsley)

CONSERVATION STATUS
GB: LC; England: LC; Wales: Not Evaluated
Nationally Scarce
Recorded from VC.44-46 in Wales but perhaps requiring review. The host *Daucus carota* subsp. *gummifer* is however known from all around the coast, north to Anglesey and so the parasite is to be expected.

REMARKS
A British native first reported in Britain in 1845 by Rev. W. S. Hore from on the cliffs at Whitsand Bay, Cornwall identified wrongly as the continental *O. amethystea*. Later described at the species level by Pugsley (1940).

DESCRIPTION
Flowering stem 10-30(-40) cm, *strongly pigmented with purple*, glandular-puberulent, usually with a pronounced *bulbous base* from which several stems may arise. Flowers few to many in a dense spike. Bracts 8-16 mm, lanceolate from a broad base, usually not exceeding the corollas. Calyx 6-10 mm, entire or unequally bifid, *shorter* than the corolla tube. Corolla 10-17 mm, sparsely glandular, sharply inflected at base; upper lip entire to emarginate; lower lip with *middle lobe the largest, reniform*, with *pronounced yellowish bosses*; all lobes crisped and denticulate; tube pale dull yellow, veined purple, strongly curved at the base then ± straight. Filaments hairless to sparsely hairy below, inserted 2-3 mm above the corolla base. Stigma lobes partially united, purple. Flowering period late May to June (rarely into early August). Parasitic on *Daucus carota* subsp. *gummifer.*

KEY DISTINGUISHING FEATURES:
A strictly maritime plant with purple stems with minute hairs (puberulent), rather straight-backed corolla, the lower lip with middle lobe the largest, reniform, with conspicuous yellowish bosses. Almost always on sea carrot (*Daucus carota* subsp. *gummifer*) on sea cliffs and dunes.

SIMILAR SPECIES:
Distinguished from the widespread subsp. *minor* by the characters stressed above. Although superficially similar, this is a distinctive maritime taxon with squatter corollas compacted in the top third of the spike. Superficially similar to *O. picridis* (with which it co-occurs in east Kent) but with more purple stems and shorter bracts and calyx lobes, the corolla mouth with distinctive bosses.

HOST, HABITAT AND DISTRIBUTION:
A rare plant, the distribution pattern of which matches that of its main host, sea carrot, *Daucus carota* subsp. *gummifer.* Exclusively coastal, it occurs on southern sea cliffs and dunes, particularly loose sands and shallow turf on the rocky shelves of cliffs –similar habitats to those of *O. picridis* (the

two species grow together in Kent). The plant exhibits a broader than normal host and habitat range in Cornwall, the Scillies and Channel Islands, and at the disjunct eastern end of its range on the chalk cliffs and dunes of Kent; here populations co-occur with subsp. *minor* and gene flow may occur between them. This rare plant is afforded some protection by the inaccessibility of its habitat. It also occurs on the north Atlantic coast of France and has been shown to be closely related to the southern European *O. litorea,* indicating divergence from a widespread continental maritime lineage.

Orobanche minor Sm.

var. ***hypochoeridis*** (Beck) Rumsey in Watsonia 26(4):476 (2007).

CONSERVATION STATUS:
Not Evaluated. Believed to be EX.

REMARKS:
An intriguing local variant, the source of much confusion and whose relationships are still uncertain. Referred to (incorrectly) as var. *flava* E. Regel in earlier British floras (Regel's plant is just a yellow subsp. *minor*) but originally was likened not to *O. minor* but to *O. ritro* (=*O. elatior*). Known only with certainty from fixed dunes in the Channel Islands. Not recorded recently, and possibly extinct.

DESCRIPTION:
Flowering stem 8-18(-25) cm, glandular-pubescent, yellow, *with numerous long bracts at the base*. Spike *dense to sub-globose*. Bracts 6-14 mm, ovate lanceolate, equalling corollas. Calyx 6-10 mm, entire almost filiform. Corolla 10-14 mm, sparsely glandular, curved throughout but most sharply inflected at the base. Upper lip emarginate, lobes forwardly directed; lower lip with +/-subequal lobes, all crisped and denticulate. Filaments sub-glabrous, inserted 3-3.5 mm above corolla base. Stigma lobes yellow, touching at base.

KEY DISTINGUISHING FEATURES:
The dense globular inflorescence of squat corollas, with high filament insertion on a short plant often with very foliose stems is characteristic.

SIMILAR TAXA:
Only likely to be confused with other pigment-less yellow forms of *O. minor,* or of *O. hederae* and *O. elatior*. The last having equally dense inflorescences. The defining features mentioned above help to differentiate this.

HOST, HABITAT & DISTRIBUTION:
Only recorded from dune systems in the Channel Islands, its past presence in Guernsey requires confirmation. Last recorded at its locus classicus, in St. Ouen's Bay, Jersey in 1951. Somewhat similar plants recorded repeatedly from Newport Docks, Glamorgan also produce yellow, dense to sub-globose spikes but lack features of the holotype (such as the stem bracts, high filament insertion) and have a different host range (mainly legumes). The plant has been cultivated at Bristol Botanic Garden where it may persist as a casual. On reconsideration, the population from Newport is unlikely to be conspecific with var. *hypochoeridis;* further work should consider DNA of the type specimen, and surveys at the locus classicus in Jersey.

VARIATION

Common Broomrape is a highly variable species that has been the subject of much taxonomic confusion. Research shows that races adapted to local hosts with distinct ecologies are divergent

and potentially in the process of forming new species. All infraspecific taxa are poorly understood and require further examination. The most obvious variation is in colouration, with anthocyanin-deficient (yellow) forms the most striking.

Orobanche minor Sm.

forma ***lutea*** (Tourlet) Thorogood & Rumsey in British & Irish Botany 2:228 (2020).

(syn. *O. minor* var*. flava* E. Regel)

CONSERVATION STATUS:

Not evaluated. Under-recorded, likely to be LC throughout as showing no evidence of decline.

REMARKS:

The original gatherings of the species in Norfolk made in the 1790s contain yellow, pigment-less plants and this colour variant occurs at low frequencies throughout the distribution of the species.

DESCRIPTION:

This is the common yellow form, identical to var. *minor,* other than in colour. Often referred to historically as var. *flava* (see above), it is a mere yellow form of the species, so we believe should be treated at the rank of 'forma'. Forma *lutea* is widespread throughout the range of the species, and shows no distinct ecology, or host specificity. An unusual population with particularly dense, sub-globose spikes that grows on sand banks and railway sidings around Newport Docks may be referred here although it has also been considered to be a yellow form of subsp. *maritima* (see var. *hypochoeridis* above).

KEY DISTINGUISHING FEATURES:

A clear yellow plant usually growing intermixed with typical examples of the species.

SIMILAR TAXA:

Only now likely to be confused with pigment-less yellow forms of *O. hederae*, *O. elatior* or the rare introduction *O. lucorum*. Corolla shape and the other defining features of these species help to differentiate this.

HOST, HABITAT & DISTRIBUTION:

Scattered throughout the British distribution of *O. minor* and appearing in the same habitats and on the same hosts, most frequently *Trifolium pratense* L. Its local persistence in parts of Suffolk is documented by Sanford (1992)

8. BEAN BROOMRAPE

Orobanche crenata Forskal, Fl. Aegypt. Arab. 113 (1775).

CONSERVATION STATUS

Not Evaluated. Alien with the potential to create severe economic damage and surely a candidate for listing on Schedule 9 of the Wildlife & Countryside Act, 1981 when reviewed.

REMARKS

A Mediterranean species that is a pernicious weed in its native region, and though rare in Britain, appears to be increasing.

DESCRIPTION
A robust annual with *dark purple,* simple flowering stems, 15-80(-120) cm, densely glandular-pubescent, somewhat bulbous at base. Inflorescence usually rather lax, with many flowers, and *strongly carnation-scented*. Bracts 15-25 mm, rather woolly, ovate-lanceolate to linear-lanceolate, acuminate. Calyx 10-20 mm, unequally bifid. Corolla (12-)20-30 mm, *white* with purplish veins especially on the lips, yellow at the base, *campanulate*, erecto-patent to horizontal; lips divergent, upper strongly bilobed forming a ± erect standard, the lower lip with large sub-orbicular lobes. Stamens inserted 2-4 mm above corolla base, with filaments hairy at least below. Stigma lobes pale - either whitish, yellow-orange or pink (rarely purple). Flowering period May to August. n=19. Introduced, rarely persistent. Usually parasitic on legume crops but with a very broad host range.

KEY DISTINGUISHING FEATURES:
The large, white, strongly scented flowers on the contrasting purple stems make this species easily recognisable.

SIMILAR SPECIES:
Identification is usually straightforward (see characters stressed above). Smaller wild specimens in its native range can be superficially similar to *O. minor* and *O. picridis*; confusion with these species in Britain is unlikely, notwithstanding the fact that plants here are less robust than those found on crops in the Mediterranean. When fresh the strong scent immediately differentiates this species, as does the pale stigma. When dead or preserved the divergent corolla lobes and hairy (villous) stems are clear diagnostics.

HOST, HABITAT AND DISTRIBUTION:
Once a very rare casual, this weedy Mediterranean species is now becoming established in South-eastern England. It was first found in South Essex in 1950 in a garden flowerbed in the Upminster/Cranham area and in the 1970s in large numbers in a nearby crop field (Adams, 2003). It has persisted sporadically on *Vicia tetrasperma* in field margins, with occasional outbreaks on legume crops in the wider area, the last record was in 2013. The same year the plant appeared in Suffolk, Kent and in the following year in Herts. In all cases it occurred in large numbers infesting cultivated field bean and pea crops, presumably having arrived as a contaminant of the crop seed. The outbreaks in the first and last were quickly dealt with by ploughing in of the parasite and crop before seed set. In the Snodland/Harvel/Meopham area in Kent the plant appears to have been present for some time before being noticed; management was prompted by a major outbreak which devastated a crop in 2013 (Rumsey, 2014). As previously in Essex, plants are still occurring sporadically on field margins in the wider area. With climate change, the plant has the potential to expand its range and possibly to become a threat to crops in the future.

9.KNAPWEED or TALL BROOMRAPE
Orobanche elatior Sutton in Trans. Linn. Soc. Lond. 4: 178 (1797).

CONSERVATION STATUS
GB: LC; England: LC; Wales: RE*

*Reported from the Cardiff area (ST27) in 2013 having previously been considered Regionally Extinct, the last record made in 1961 in ST06. Provisionally we list it as CR (D) for Wales.

REMARKS

Described by Sutton (1797), and the subject of much taxonomic confusion arising from inadequate descriptions and a confusing array of synonyms. Arguably the most robust and impressive British species.

DESCRIPTION
A *tall, stout, orange-brownish* weak perennial with simple flowering stems, (15-)25-70 cm; stems yellowish to orange, often with a rather bulbous base, usually glandular-pubescent; stems devoid of flowers and with *numerous long, brown bracts below*. Flow*ers usually numerous and densely packed, often confined to the top third of the stem*. Bracts 15-25 mm, ± equalling the flowers, lanceolate, acuminate. Calyx (6-)9-11 mm, segments united at base, usually unequally bidentate. Corolla 18-25 mm, yellow or orange with reddish-brown veins (sometimes pinkish); uniformly curved throughout, widely tubular, glandular-hairy, sub-erect to erecto-patent, sometimes patent; upper lip usually w-lobed (to virtually entire), usually spreading; lower lip three-lobed, the lobes nearly equal, crisped, denticulate. Stamens inserted 3-6 mm above the base of the corolla tube; filaments hairy below, glandular throughout. Stigma lobes yellow. Flowers attractive to bees but scentless. Flowering period rather late (except for in coastal districts), typically mid-June to July (sometimes into August). 2n=38. Native, almost exclusively parasitic on *Centaurea scabiosa*.

KEY DISTINGUISHING FEATURES:
A very distinctive plant of chalk grassland, with tall, orange-brown spikes with long bracts at the base of the stem, and numerous flowers closely packed in the upper half to third of the stem. Small, slender specimens might be confused with the alien *O. lucorum* which is similarly coloured.

SIMILAR SPECIES:
A robust plant, rivalled in stature only by *O. rapum-genistae.* Some forms of *O. elatior* have yellow stems and reddish flowers and do approach the former species; the habitat and later flowering time usually make identification in the field straightforward, furthermore *O. elatior* has a finely toothed upper corolla lip (not virtually entire), stamens inserted well above the base of the corolla tube, and less divergent stigma lobes. In the somewhat fused (connate)calyx segments joined below the flower *O. elatior* is unique amongst British broomrapes.

HOST, HABITAT AND DISTRIBUTION:
In Britain, this species grows almost exclusively on *Centaurea scabiosa* L. It has very rarely been reported on *Centaurea nigra* L. at the northern extremes of the parasite's British range. It is almost entirely restricted to chalk and Jurassic limestone unlike its predominant host which is much more widely distributed. The reasons for the limits to the distribution of the parasite are unclear but are presumed to be climatic and possibly edaphic. It is usually found on shallow soils on chalk downs, in disused chalk pits, and along roadsides. Fairly frequent in suitable habitats in Wiltshire and Cambridgeshire; rare and local elsewhere and curiously rare in Kent.

VARIATION:
A striking yellow variant which lacks the red-brown pigmentation typical of the species is infrequent but scattered throughout the British range. It has been named f. *citrina*.

10. BARBERRY BROOMRAPE

Orobanche lucorum A. Braun in Rohling, Deutschl. Fl., 3rd ed., 4: 456 (1833).

CONSERVATION STATUS
Not Evaluated. Neophyte

REMARKS
A rare introduction from Central Europe. Extensive potential habitat exists in garden and amenity plantings and it is perhaps surprising this species has not become established more widely.

DESCRIPTION

A dark *yellowish to reddish-orange,* weak perennial with simple stems, 15-50 cm, glandular-pubescent, scarcely swollen at the base; often clumped (sometimes with numerous stems). Inflorescence rather dense. Bracts 13-25 mm, oblong to lanceolate, acute to acuminate. Calyx 8-15 mm, unequally bidentate or entire. Corolla 15-22 mm, yellow tinged with red, erecto-patent to patent; upper lip ± emarginate, porrect; lower lip with conspicuously ciliate sub equal lobes. *Stamens inserted 2-3 mm above the corolla base*; filaments hairy. Stigma lobes just touching, *yellow, becoming reddish or brownish with age*. Style scarcely exserted, slightly convolute. Flowering period June to August. Introduced deliberately as a curiosity (and possibly accidentally), parasitic on *Berberis* and other species in the Berberidaceae.

KEY DISTINGUISHING FEATURES:
A yellow to reddish-orange plant, sometimes producing many spikes beneath its shrubby hosts, among ornamental plantings.

SIMILAR SPECIES:
In corolla shape *O. lucorum* is closest to *O. caryophyllacea* and *O. rapum-genistae* and somewhat intermediate in stature to these species. However, the flowers are unscented and have yellow stigmas unlike the former, and have stamens inserted higher than the latter. In general appearance it is closest to *O. elatior* although that tends to have stouter stems with more and densely packed flowers, the calyx segments connate below. Common yellow forms of *O. minor* and *O. hederae* have smaller, narrower flowers.

HOST, HABITAT AND DISTRIBUTION:

Native to Central Europe, this plant was introduced to the Botanic Gardens of the University of Oxford and St Andrews (but disappeared from the former) where it grew on *Berberis* species, its natural hosts. More recently the plant was found naturalised in an ornamental border at Brooksby Agricultural College, Leicestershire where it was parasitising a *Mahonia* sp. The plant could have been overlooked or misidentified in other locations. It was recorded erroneously from Surrey in the 19th century due to confusion with *O. elatior* (Rumsey & Jury, 1991).

11. YARROW BROOMRAPE

***Phelipanche purpurea* (Jacq.) Soják,** Čas. Nár. Mus., Odd. Přír. 140(3-4): 130 (1972).
(syn. *Orobanche purpurea* Jacq.)

CONSERVATION STATUS
GB: VU; England: VU (D_1); Wales: CR ($B_{1,2ab(v),c(iv),}C_{2a(i),}D$)
Nationally Scarce

REMARKS
Britain's only native broomrape in the genus *Phelipanche* (previously subgenus Trionychon of *Orobanche*). Most variable in terms of stem and flower colour; some plants from the Channel Islands have been erroneously ascribed to *Phelipanche arenaria*, which differs in its densely hairy anthers, larger corollas (to 35mm) and *Artemisia* host. Carlón et al., 2008 recognise four subspecies of *P.*

purpurea (Jacq.) Soják, two of which occur in Central and Western Europe. Our plants are subsp. *purpurea.* The other, subsp. *millefolii* (Rchb.) Carlón, G. Gómez, M. Laínz, Moreno Mor., Ó. Sánchez & Schneew., is also a parasite of *Achillea millefolium* but differs in being a shorter plant, with a denser inflorescence of shorter (<24mm), more conspicuously waisted, concolorous corollas, i.e. lacking whitish bosses, more intensely pigmented within and having more orbicular, overlapping lower lip lobes.

DESCRIPTION
An annual with rather stout, bluish-grey stems, 15-45 cm, simple, occasionally branched from the base (especially when damaged), glandular-puberulent, mealy, especially above; dark bluish-grey (rarely yellowish). Inflorescence dense, usually restricted to the top third of the shoot. Bracts 8-15 mm, lanceolate; bracteoles linear, shorter than calyx. Calyx 8-16 mm, mealy-hairy with lanceolate-acute teeth, equalling tube. Corolla about twice as long as the calyx, 18-26(-30) mm, dull *bluish-purple suffused with yellow at the base* (rarely pale lilac), erecto-patent or inflected, patent distally, about twice as long as calyx; tube constricted just below middle; upper lip of two sub-acute lobes recurved; lower lip of three sub-equal lobes ovate-elliptical, rounded to apiculate. Stamens inserted 5-8 mm above base of corolla, just below constriction; filaments hairless or virtually so; anthers also hairless (rarely sparsely hairy at base and along the sutures). Stigma white or pale blue. Flowering from the end of May to June (rarely into August). 2n=24. Native, parasitic on *Achillea millefolium* in Britain but on a wider range of Asteraceae tribe Anthemideae elsewhere.

KEY DISTINGUISHING FEATURES:
The presence of 2 bracteoles and blue-grey colouring are unmistakable. Dead plants are distinctive with a somewhat spreading calyx and the mature capsules free at the apex.

SIMILAR SPECIES:
This is the only native species that is bluish in colour and with flowers each with 2 bracteoles (in addition to the calyx lobes) – features characteristic of the *Phelipanche* group. The only species that could be confused with it would be *P. ramosa.* That is typically a shorter and paler branching plant, with much smaller flowers, and does not grow on *Achillea.*

HOST, HABITAT AND DISTRIBUTION:
This plant grows only on *Achillea millefolium* in Britain, usually on cliff-tops, or near the sea, although inland sites in old quarries, churchyards, pastures and on roadsides have been recorded in Leicestershire, Monmouthshire, Suffolk, Hertfordshire, Kent and, most recently, in Hampshire. Much declined and now extinct in many sites; despite this, populations are still being lost to habitat destruction, mismanagement and increased coastal erosion.

Plants on Guernsey have rather yellowish stems and paler flowers, and those on Alderney have sparsely hairy anthers which has led to confusion with the continental *P. arenaria*.

12. BRANCHED BROOMRAPE

***Phelipanche ramosa* (L.) Pomel**, Nouv. Mat. Fl. Atl. 1: 103 (1874).
(syn. *Orobanche ramosa* L.)

CONSERVATION STATUS
Regarded as a Neophyte and not evaluated. Extinct as an established crop weed for nearly 200 years.

REMARKS
The plant was the subject of much former taxonomic confusion and to this day is one of a group of closely related species that are difficult to distinguish in their native Mediterranean region. A frequent former weed of *Cannabis*, grown for fibres to provide rigging for naval vessels, in East Anglia (see Sanford, 1992). With the decline in demand and loss of its host as a crop this species became little more than a rare casual by the early 19th century.

DESCRIPTION

A *small, often branched,* rather pale annual with flowering stems 5-30 cm, slender, glandular, with a small bulbous base; yellowish suffused purple. Inflorescence rather lax, with few flowers. Bracts ovate-lanceolate, shorter than calyx; bracteoles equalling calyx, lanceolate. Calyx teeth c. 8 mm, lanceolate-acuminate, shorter than tube. Corolla 10-15(-17) mm, cream, blue or violet distally, whitish at the base, glandular-hairy, sub-erect at the base, erecto-patent distally, constricted in the middle; base inflated, *upper lip with two rounded lobes*, recurved, lobes of lower lip deflexed, obtuse, entire or denticulate. Stamens inserted 3-6 mm above corolla base, just below constriction; filaments virtually hairless at the base; anthers hairless or sparsely hairy at the base. *Stigma lobes white or bluish*. Flowering July to late September. 2n=24. Introduced but now extinct in the British Isles outside of botanic gardens or as a casual. Formerly parasitic on *Cannabis sativa,* when this was grown commercially in East Anglia, but with a very wide host range.

KEY DISTINGUISHING FEATURES:
A small branched annual, with pale lilac or mauve narrow-waisted flowers with white stigmas, parasitic on cultivated crops, or in gardens.

SIMILAR SPECIES:
The closest native species is *P. purpurea,* that usually has simple stems, much larger more intensely coloured flowers, and is largely restricted to sea cliffs and maritime habitats. The most likely source of confusion would be the appearance of other, closely related species from the Mediterranean, as casuals. *Phelipanche aegyptiaca,* for example, is similar but with larger (20-35mm), more expanded corollas, and hairy anthers.

HOST, HABITAT AND DISTRIBUTION:

A persistent casual with a lengthy history. Given the recent increase of the Mediterranean *O. crenata* in Kent, perhaps partially in response to climate change, there is potential for the plant to re-establish although its likely hosts tend to be grown under glass rather than in open-field situations. It appears erratically on Solanaceae in the taxonomic beds of Kew Gardens and at the Botanic Gardens such as those of the Universities of Oxford and Cambridge. Usually late-flowering in the British Isles (August and September).

13. EGYPTIAN BROOMRAPE

***Phelipanche aegyptiaca* (Pers.) Pomel**
[syn. *Orobanche aegyptiaca* Pers.]

CONSERVATION STATUS:
Regarded as a Neophyte and not evaluated. A potentially invasive crop weed of economic importance.

REMARKS:
Reported only once in the British Isles as a weed of tomatoes under glass in a Sussex nursery in 1952. The supporting specimen is at K! with photographs preserved in Herb. Lousley at RNG!

DESCRIPTION:
A *small, usually branched annual* with flowering stems 15-50cm, slender (to 6mm diameter), glandular-pubescent. Inflorescence rather lax. Lower flowers usually conspicuously pedicellate. Bracts (3-)6-8(-10)mm, ovate-lanceolate, shorter than the calyx: bracteoles filiform to lanceolate, shorter than calyx. Calyx teeth to 9mm, lanceolate-subulate, equalling to exceeding calyx tube. Corolla 20-35mm, lilac distally, with darker veins, cream proximally, straight or slightly curved, conspicuously waisted and infundibuliform distally. Stamens inserted 3-6mm above corolla base; filaments +/- hairy below, sometimes sparsely so above; anthers villous. Stigma lobes white or bluish. Flowering period July-Sept.

KEY DISTINGUISHING FEATURES:
The slender, usually, branched stems with very large, bracteolate, infundibuliform flowers and hairy anthers are diagnostic.

SIMILAR TAXA:
Easily confused with *P. ramosa* which is less robust and has much smaller and less expanded corollas and (usually) glabrous or sub-glabrous anthers.

HOST, HABITAT & DISTRIBUTION:
An economically important parasite of a wide range of crop species in the Middle East, North Africa and the southern Mediterranean. Parasitic mainly on Solanaceae (tomatoes, aubergines, peppers, potatoes, tobacco, etc.) it also attacks Apiaceae (carrots, fennel, celery), the Cucurbitaceae and over 70 other species, many of economic importance (Morrice & Newton, 2018). A thermophilous species more likely to affect crops grown under glass, or in gardens in the British Isles, and likely to be late-flowering (August and September). The sole reported British occurrence was from a nursery near Hastings, W. Sussex where the plant was found flowering in late Sept. 1952.

HYBRIDS
There is little documented evidence of hybridisation in the genus *Orobanche* in the British Isles, or indeed anywhere else in the world. None are recorded in Stace, Preston & Pearman's(2015) account of hybridisation and the British flora. Most species are monocarpic annuals or short-lived perennials and have no means of vegetative propagation. Any hybrids that might arise would therefore have limited opportunity for dispersal were they to be fertile, and as and when they did arise, they would be ephemeral only. Nevertheless, hybrids could have been under-recorded because they are likely to be overlooked given the taxonomic complexity of, and cryptic speciation within, the genus. Species in the *Minores* group (*O. minor* and its various infraspecific taxa, *O. picridis* and *O. hederae*) are so similar that any hybrids would probably go unnoticed (Thorogood & Rumsey, 2020). Morphological intermediates between subsp. *maritima* and subsp. *minor* do occur in Cornwall, the Scillies and Channel Islands, where the former shows a broader than normal host and habitat range, as well as at the eastern end of its range on the chalk cliffs and dunes of Kent (Thorogood et al., 2009b). Here, intermediates between *O. minor* and *O. picridis* have also been observed, and hybridisation long-suspected. Certainly hybridisation between these species is possible, and crosses have been raised

by the authors artificially (Thorogood & Rumsey, 2020), however there is no conclusive evidence of gene flow in natural populations based on DNA analysis.

Artificial hybrids have also been raised between *O. minor* and *O. hederae* (Jones, 1989; Thorogood, & Rumsey, 2020), and these species also co-occur occasionally where their habitats merge, so the possibility of natural hybridisation in these species is not out of the question either. Jones (1989) raised reciprocal crosses between these species on *Eryngium maritimum*, although only those with *O. minor* (var. *pseudoamethystea*) as the maternal parent survived to flowering. Seed produced by these hybrids contained a higher percentage of unfertilised ovules and immature seeds (c. 20%) than either parent, suggesting some incompatibility between the two species.

Finally, intermediates between *O. minor* and *O. reticulata* have also been observed in in Yorkshire, and hybrids between these species were raised in cultivation by Michael Jones (Jones, 1989). He crossed *O. minor* (female) with *O. reticulata* (male), finding no barrier to cross pollination and a mean of 592 seeds per capsule were produced. Two F_1 plants were raised to flowering on *Brachyglottis* cv 'Sunshine'; in stature, inflorescence to stem length ratio, flower density, absence of dark glands and stigma lobe morphology, the hybrids more closely approached the maternal parent. Jones also attempted hybridisation between *O. minor* and *O. rapum-genistae* and between *O. minor* and *O. gracilis*, but, given the limited number of attempts made, their failure is not conclusive evidence of definite barriers to hybridisation. Hybridisation among any of the other taxa in Britain is considered unlikely as they are rarely sympatric and synchronous in their flowering period, and because (like elsewhere), they are host-specific; hybrids may be less well-adapted to a given host plant than their parent species, and outcompeted by them.

14. TOOTHWORT

***Lathraea squamaria* L.** Sp. Pl. 2: 606 (1753)

CONSERVATION STATUS

GB: LC; England: LC; Wales: LC; Ireland: LC

REMARKS

The earliest flowering species described here, first appearing in March.

DESCRIPTION

A perennial herb with a *stout, simple, erect flowering shoot* 8-30 cm, dirty white or pale pink, slightly hairy above and with a few whitish, ovate scales below. Flowers borne in *one-sided racemes,* at first drooping, later straightening. Flowers short-stalked, each borne in the axil of a broadly ovate bract. Calyx *glandular-hairy,* tubular below, with 4 broadly triangular teeth above. Corolla *white,* tinged variably with dull pinkish-purple, slightly longer than the calyx. Capsule ovoid, with numerous seeds. Flowering from March into early May. Visited by bumble bees. 2n = 42. Parasitic on various woody plants, especially *Corylus* and *Ulmus.*

KEY DISTINGUISHING FEATURES:

The early-flowering, whitish-pink spikes are unmistakable.

SIMILAR SPECIES:
Purple toothwort (*L. clandestina*) is patch-forming, without aerial shoots, and typically has much larger, long-stalked, bright purple flowers. Yellow Bird's Nest (*Hypopitys monotropa*) has radially symmetrical creamy yellow flowers on an initially nodding flower spike, it flowers in Summer as does the brownish cream Bird's Nest Orchid (*Neottia nidus-avis*), which has inferior ovaries.

HOST, HABITAT AND DISTRIBUTION:

Parasitic on mainly on woody plants in damp woods and hedgerows, especially in chalky and limestone areas. Observed most commonly on *Corylus* and *Ulmus* but also recorded frequently on *Taxus*, *Fraxinus*, *Alnus*, *Juglans* and *Fagus*. Widespread but rarely common.

15. PURPLE TOOTHWORT

***Lathraea clandestina* L.** Sp. Pl. 2: 605 (1753)

CONSERVATION STATUS
Neophyte, deliberately introduced as an attractive horticultural novelty and therefore not evaluated. Spreading slowly from cultivated sources and showing little sign of becoming either invasive or deleterious.

REMARKS
An introduced species, grown for ornament and not infrequently seen in botanic gardens; where naturalised often downstream of garden sites. Native to Western Europe, from Belgium south to N. Spain and eastwards to C & S. Italy.

DESCRIPTION

A patch-forming *purple* perennial herb with scaly rhizomes, *lacking aerial shoots*; flowers borne in corymbose clusters, long-stalked, arising singly in the axils of fleshy rhizome-scales at, or just below the soil surface. Calyx hairless, campanulate, with 4 short triangular lobes above. Corolla *bright purple, more rarely pinkish-purple, or white, equalling to twice as long as the calyx.* Capsule globes with 4-5 seeds. Flowering from March into early May. Visited by bumble bees. 2n = 42. Parasitic on various trees, especially *Salix* and *Populus* in damp places.

KEY DISTINGUISHING FEATURES:
The patch-forming habit beneath trees, and the large claw-like purple flowers are unmistakable.

SIMILAR SPECIES:
Toothwort (*L. squamaria*) produces aerial shoots of white to dull pinkish-purple, short-stalked flowers.

HOST, HABITAT AND DISTRIBUTION:

Native to Spain, Italy, west and central France, and Belgium. Introduced to gardens across Britain and now naturalised widely, but rarely far from where it has been planted. Parasitic mainly on *Salix* and *Populus* but recorded to grow on a wide variety of other plants, including perennials, for example *Acer, Alnus, Buxus, Carpinus, Corylus, Juglans, Metasequoia, Rhododendron, Taxus* and even *Gunnera*. The colour forms are uncommon, particularly the whitish *f. albiflora* – not a true albino as the calyx retains some purplish colouration.

VARIATION:

Smaller cleistogamous flowers may form underground. The most apparent variability is in corolla colour (Armitage, 2014) with a pinkish-purple forma *rosea* J.D. Arm. and the white forma *albiflora* (Rouy) J.D. Arm.

OTHER CULTIVATED SPECIES

Broomrapes have a long history of being introduced in Britain, either by accident, as 'curiosities' in botanic gardens, or more recently, for conservation purposes. There are some species whose host plants are widespread natives, eg. *Orobanche flava* on *Petasites* spp. and *O. lutea* and *O. gracilis* which are even more generalist and will attack various legumes; their absence as natives to the British flora is perhaps surprising. The absence of others such as *O. artemisiae-campestris* and *O. coerulescens* both parasites on *Artemisia campestris*, or *O. bartlingii* on *Seseli libanotis*, is much more easily explicable because of the very scarcity of their hosts. Some species are parasites of commonly grown garden plants: *O. lucorum* on *Berberis* & *Mahonia* (which has now arrived in a British horticultural setting - see species account above), others such as *O. haenseleri*, a parasite of *Helleborus foetidus* , or *Boulardia latisquama* and *Phelipanche rosmarina*, parasites of *Rosmarinus officinalis* L., could also become established if introduced. Considering the former establishment of *Phelipanche ramosa* in Britain in the 1700s, and more recent and persistent outbreaks of *O. crenata,* there is certainly the possibility that other weedy, Mediterranean species, may establish in the future. Climatically many more species might now be expected to survive had they the means of dispersal to this country. Amongst the most likely to arrive naturally is *O. gracilis.* This is an attractive ornamental species that grows on woody Fabaceae and *Cistus.* This species was introduced by the authors to the University of Bristol Botanic Garden in 2009, where it was planted on a *Coronilla* bush, and has flowered more or less every year since, with a little re-sowing. Here other species have also been planted, including *O. picridis* that flowered in 2009 and 2010, but has not been seen since; it set seed, and may well reappear with soil disturbance (its host persists there). Similarly, *O. caryophyllacea* (and some other species including *O. crenata*) grew formerly in the order beds at Kew but disappeared as the beds were reconfigured over the years. Likewise, at the University of Oxford Botanic Garden *Orobanche flava* was established on *Petasites* species in the early 1980s (Rumsey & Jury, 1991) along with *O. lucorum* on *Berberis;* both persisted well into the 1990s. At Cambridge Botanic Gardens *Phelipanche ramosa* and *O. crenata* have both been recorded in the past and a diverse range of hosts are still parasitised by plants of *O. hederae* and other examples of the *O. minor* group (Leslie, 2019). Some of these were identified by the late Peter Sell as *O. amethystea* (specimens in CGE and see Sell & Murrell, 2009). Their identity requires further investigation but we are doubtful that they are this species.

Often neglected by botanic gardens because of perceptions of intractability in cultivation and with seed unavailable commercially, these examples demonstrate the potential for representation of broomrapes in collections and private gardens, but also the need for ongoing intervention (such as soil disturbance and re-sowing of parasite seed) to maintain populations. The University of Oxford Botanic Garden is currently re-developing the collection of *Orobanche,* both to conserve and promote awareness of these fascinating plants.

GLOSSARY OF TERMS

Acuminate, tapering to a long point.
Angiosperm, flowering plant.
Annual, completing the life cycle in one year.
Anther, fertile, pollen-producing part of the stamen, typically on a terminal stalk (**filament**).
Apex, uppermost part of a structure.
Bidentate, divided into two teeth.
Biennial, completing its life cycle in 2 years.
Bifid, divided into 2 parts, typically deeply at the apex.
Bilobed, divided into two lobes
Bract, small, leaf-like structure, often subtending (beneath) the flower.
Bracteole, small secondary bract.
Calyx, all the sepals of the flower.
Campanulate, bell-shaped.
Cleistogamous, self-fertilised within a permanently closed flower
Connate, partially joined together
Corolla, all the petals of a flower (which may form a tube).
Crenate, with round-toothed or scalloped edges.
Denticulate, toothed.
Divided, not entire; divided into teeth, lobes or leaflets.
Emarginate, notched at the apex.
Entire, whole; without distinct lobes, teeth or divisions.
Erecto-patent, between erect and spreading.
Exserted, protruding (not included, such as anthers from a corolla tube).
Filaments, the stalk of the stamen.
Genus (pl. **genera**)**,** monophyletic group of related species, the taxonomic group between the lower rank of species and the higher rank of family; the generic name is the first part of the scientific binomial.
Glabrous, not hairy.
Gland, organ of secretion, often in sticky plants; adj. **glandular** (often referring to hairs).
Globose, spherical.
Head, group of flowers crowded together at the end of a stalk.
Hemiparasite, parasitic plant that extracts some of its nutrition from another plant (the host) but which produces chlorophyll.
Herb, plant without woody parts; a soft and leafy annual, biennial or perennial in which aerial parts naturally die to ground level at the end of the growing season; adj. **herbaceous**.
Holoparasite, parasitic plant that extracts all of its nutrition from another plant (the host) and which lacks chlorophyll and a true root system.
Host specificity, the diversity of host species that can be infected by a parasite. Highly **host-specific** occur one a single host species; **generalist** parasites infect a range of species.
Host, the plant infected by the parasite.
Hybrid, offspring of a cross between two different species, races, or varieties.
Hybridisation, the formation of hybrid offspring.
Inflected, bent or folded downward.
Infundibuliform, funnel shaped
Lanceolate, lance-shaped; tapering to a point at the apex and base.
Life history, the lifespan and various phases from germination to maturity.
Lip, region of the corolla sharply differentiated from the rest (upper and lower).
Lobe, substantial division of the calyx or corolla.
Monocarpic, dying after setting seed.
Morphology, the appearance, form or structure.

Mycoheterotrophy, life history by which a non-photosynthetic plant obtains nutrition from a fungal symbiont (or sometimes from another plant via a shared fungal symbiont) living in its root system.
Native, naturally occurring in the area (not **introduced** or **naturalised**).
Ovate, oval/egg-shaped, with a tapering point and the widest near the point of attachment.
Parasite, an organism that derives nutrition from another organism (its **host**).
Patent, spreading.
Perennial, living for more than two years, generally flowering every year. Often woody at the base.
Reniform, kidney-shaped.
Sessile, not stalked.
Stamen, male reproductive organ of the flower consisting of a filament and anther (microsporangium).
Stigma, the part of the carpel or pistil that receives pollen and upon which the pollen germinates.
Subulate, narrow, broadest at their base, and tapered to an elongated tip.
Taxon (pl. **taxa**)**,** taxonomic unit of any rank, for example species, genus, subspecies or variety.
Teeth, divisions of a leaf, calyx or corolla; adj. **toothed**.
Variety, form of a species that is geographically, morphologically and or genetically distinct (but not distinct enough to warrant subspecies status).
Woolly, clothed with soft, shaggy hairs.

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Orobanche minor var. *hypochoeridis*
Orobanche minor forma *lutea*
Orobanche minor subsp. *maritima*
Orobanche minor var. *pseudoamethystea*
Orobanche picridis
Orobanche rapum-genistae
Orobanche rapum-genistae f. *flavescens* Durand
Orobanche rapum-genistae f. *hypoxantha* G. Beck
Orobanche reticulata
Orobanche reticulata subsp. *pallidiflora*
Orobanche reticulata subsp. *procera*
Orobanche rubra
Orobanche teucrii
Petasites
Phelipanche aegyptiaca
Phelipanche arenaria
Phelipanche purpurea
Phelipanche ramosa
PICRIS BROOMRAPE
Picris hieracioides
Pilosella officinarum
Populus
Rafflesia
Red clover
Rehmannia
Rhinanthus minor
Rhododendron
Rosmarinus
Rubiaceae
Salix
Santolina
Scrophulariaceae
SEA HOLLY BROOMRAPE

Striga
TALL BROOMRAPE
Taxus
Tetrapanax
Teucrium
THISTLE BROOMRAPE
THYME BROOMRAPE
Thymus
Thymus drucei
Toothwort
Triaenophora
Tricholoma
Trifolium pratense
Trifolium pratense
Ulmus
Urtica dioica
Vicia tetrasperma
YARROW BROOMRAPE
Yellow bird's nest

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