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PLANT PORTRAIT

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1099. *Neottia ovata* (L.) Hartm.

Orchidaceae

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Summary

Neottia ovata (TWAYBLADE) is illustrated here (t. 1099). It is a widespread, temperate Eurasian species. A detailed description is provided, with notes on cytology and habitat. Given its wide distribution and the diverse range of habitats where it occurs, its conservation status is Least Concern in Europe. Probably as a reflection of its dependence on mycorrhizal fungi for its whole life history, it is not a plant known from cultivation; it should be enjoyed as an intriguing member of our native orchid flora.

INTRODUCTION

Linnaeus (1753) recognised relatively broadly circumscribed genera of Orchidaceae, but many of the species were soon transferred to other genera by other botanists. For example, *Ophrys* L. originally included species now treated in 11 other genera (Jarvis & Cribb, 2008). *Neottia ovata* (L.) Hartm. (TWAYBLADE or COMMON TWAYBLADE, the subject of this account) was one of the species originally included in Linnaeus' broad concept of *Ophrys* (as *O. ovata* L.), but it had been transferred to at least six other genera by the early 1820s.

Neottia Guett. is a member of tribe Neottieae (subfamily Epidendroideae), and the subtribe includes taxa with varying degrees of dependence on mycorrhizal fungi, and the loss of photosynthetic ability and the shift to total dependence on fungi have occurred several times in the subtribe. The non-green (achlorophyllous) species were often placed in separate genera than their photosynthetic relatives (e.g. Lallemand et al., 2019, and references therein); in one such example, *N. ovata* and photosynthetic relatives including *N. cordata* (L.) Rich. (LESSER TWAYBLADE) were widely treated as species of *Listera* R.Br., with *Neottia* being traditionally reserved for achlorophyllous species such as *N. nidus-avis* (L.) Rich. (BIRD'S-NEST ORCHID).

Although the lack of chlorophyll and true leaves makes *N. nidus-avis* immediately distinguishable from *N. ovata*, the flowers of these species closely resemble each other (as noted by Darwin, 1877). In addition, species of *Listera* and *Neottia sensu stricto* form a clade in phylogenetic analyses but are not reciprocally monophyletic (e.g. Lallemand et al., 2019; Peng

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et al., 2022). Due to the morphological similarities and the results of the phylogenetic analyses, most standard works therefore now treat *Listera* as a synonym of *Neottia* (e.g. Chase et al., 2003, 2015; Pridgeon et al., 2005; POWO, 2023). *Neottia sensu lato* (including *Listera*) comprises 79 species (POWO, 2023), three of which are native to Britain: *N. cordata*, *N. nidus-avis* and *N. ovata*.

TWAYBLADE (= "two leaf", from *Zweiblatt* in German: Lyte, cited by Grigson, 1955, 1974) refers to one of the more obvious characteristics of *N. ovata* and *N. cordata* (the two opposite leaves). Occasional individuals of *N. ovata* have three or four leaves; if there are three, the third is smaller and can be located above or below the main pair of leaves (e.g. Davies, Davies & Huxley, 1983.) "Sweethearts" (a local name from Somerset) also alludes to the paired leaves (Grigson, 1955). Of the other local names listed by Grigson, "adder's tongue" and "man orchis" (from Wiltshire and Somerset, respectively) refer to the shape of the labellum. Grigson (1955) also wrote that *N. ovata* was first recorded in Britain in 1548 by Turner (as "martagon") and that Gerard (in his *Herbal*) stated that the flower of 'twayblade' or 'herbe bifoile' resemble "a gnat, or a little gosling newly hatched" - many will struggle to see this latter resemblance!

With yellowish-green flowers, *N. ovata* is not one of our showiest native orchids, and Brooke (in Brooke & Bone, 1950) asked 'If the orchids represent the 'Royal Family' of flowering plants, what are we to say of the undistinguished and far-from-regal twayblade?'. Bersweden (2017) commented on its 'amazing ability to disappear into the background while in plain sight' and, while it is one of the most abundant species of orchid in Britain, he continued 'I suspect its extremely camouflaged flowers are considerably under-recorded'.

Neottia ovata produces nectar and a terpene-rich floral fragrance. As a result, it is visited by a wide range of insects, with members of Diptera being frequent visitors. The main pollinators are, however, ichneumonids and sawflies (Hymenoptera) and beetles (Coleoptera) (Nilsson, 1981). Darwin thought this species to be 'one of the most remarkable of the whole order', and he described its floral structures in detail in his book on orchid pollination (Darwin, 1877, in part based on an earlier study by Hooker, 1854). In particular, he was fascinated by the rostellum (a structure separating the stigma and stamen in the column) which expels 'viscid matter' violently when touched (Darwin, 1877, p 117), a mechanism he had only otherwise observed in *N. nidus-avis*. This sticky drop results in an efficient pollination mechanism:

> "When touched by the visiting insect – led thither by the nectar-baited pathway up the narrow lip – a small explosion occurs, a drop of the adhesive matter is expelled, and cements the pollinia to the insect's head ….. Later, the rostellum rises again, leaving the stigma clear for an insect arriving with pollinia from another flower …. so well co-ordinated is the mechanism, that the pollinia are invariably removed. … The twayblade appears to be a constant species, varying little in ordinary situations: probably because the mechanism has reached so high a degree of efficiency that further evolution is unnecessary." [Brooke in Brooke & Bone, 1950, pp. 60-61].

Mean fruit set has been recorded to be *c.* 40%, but this can vary dramatically, depending on the weather conditions. Artificial pollination has demonstrated that *N. ovata* is self-compatible, but spontaneous autogamy occurs rarely, if ever (Kotilínek, Těšitelová, & Jersáková, 2015, and references therein).

Despite the constancy referred to by Brooke (Brooke & Bone, 1950), plants with abnormal flowers (including peloric forms with petal-like lips or lip-like petals) are not uncommon (e.g. Allen & Woods, 1993). Possibly as a result of the sophisticated pollination mechanism, *N. ovata* has not been recorded to form hybrids with other species.



PLATE 1099 *Neottia ovata* REINHILD RAISTRICK

With some species that produce chlorophyll and some that do not, *Neottia* is a textbook example for studies on the loss of photosynthesis and the evolution of obligate dependence on mycorrhizal fungi. Even green (photosynthetic) orchids are dependent on mycorrhizal (normally "rhizoctonia"-type) fungi, at least for seed germination and early developmental stages, and the shift from autotrophy (in plants that produce their own food by photosynthesis) to mycoheterotrophy (in plants that rely on fungi for their nutrition) is normally associated with a shift to ectomycorrhizal fungi. Partially mycoheterotrophic species therefore present an opportunity to track this shift. Given its broad habitat range (see below), *N. ovata* was selected as a study organism by Wang et al. (2023), who hypothesized that grassland and woodland individuals of *N. ovata* were likely to associate with "rhizoctonia"-type and ectomycorrhizal fungi, respectively. Their results, however, showed that "rhizoctonia"-type fungi play the major role in nutrition of plants of *N. ovata* in both habitats.

CULTIVATION

Under natural conditions, in *N. ovata* the time interval between seed germination and its appearance above ground is generally three to four years, and seedlings are entirely dependent on mycorrhizal fungi for at least three years. Beyond this period, seedlings and adult plants both appear to obtain some nutrition from mycorrhizal fungi (Kotilínek et al., 2015, and references therein).

Seeds of *Neottia ovata* can be germinated under *in vitro* conditions, symbiotically or asymbiotically (with or without a fungus, respectively), but information on later stages of seedling development is sparse (Kotilínek et al., 2015, and references therein). Probably in part due to its dependence on a fungal associate for much (or all) of its life cycle, we are not aware of *N. ovata* being successfully grown to flowering size from seed in cultivation. With sympathetic management of grassland and other habitats, it can be enjoyed in nature as an intriguing, if rather subdued, member of our native orchid flora.

NOMENCLATURE AND DESCRIPTION

Neottia ovata (L.) Hartm., Handb. Skand. Fl.: 331 (1820).

NOTE: The combination *Neottia ovata* is often attributed to Bluff & Fingerhuth (1825), but Hartman's combination predates this.

Homotypic synonyms include:

Ophrys ovata L., Sp. Pl.: 946 (1753). "Habitat in Europae subhumidis pratis". Lectotype: Specimen 1056.10 (LINN); designated by Renz in Nasir & Ali, Fl. Pakistan 164:8, 1984.
Epipactis ovata (L.) Crantz, Stirp. Austr. Fasc., ed. 2, 2: 473 (1769).
Listera ovata (L.) R.Br. in W.T.Aiton, Hortus Kew. 5: 201 (1813).
For other homo- and heterotypic synonyms, see POWO (2023).

A long-lived perennial with a short horizontal creeping *rhizome c.* 5 mm in diameter bearing numerous *roots*, but no storage organ. *Stem* green to brownish, (10–)20–60(−75) cm high, with whitish pubescence above the leaves. *Leaves*, normally 2, opposite (rarely 3 or 4), 4–13 cm long, 3–8 cm wide, clasping, joined to the lower third of the stem, oval, mucronate, with 3–5 prominent veins. *Inflorescence* lax, 7–25 cm. *Flowers* (15)20–80(100), greenish-yellow (sepals sometimes purplish). *Petals* and *sepals*, oval, 4–5 mm long, curved inwards to form a loose hood

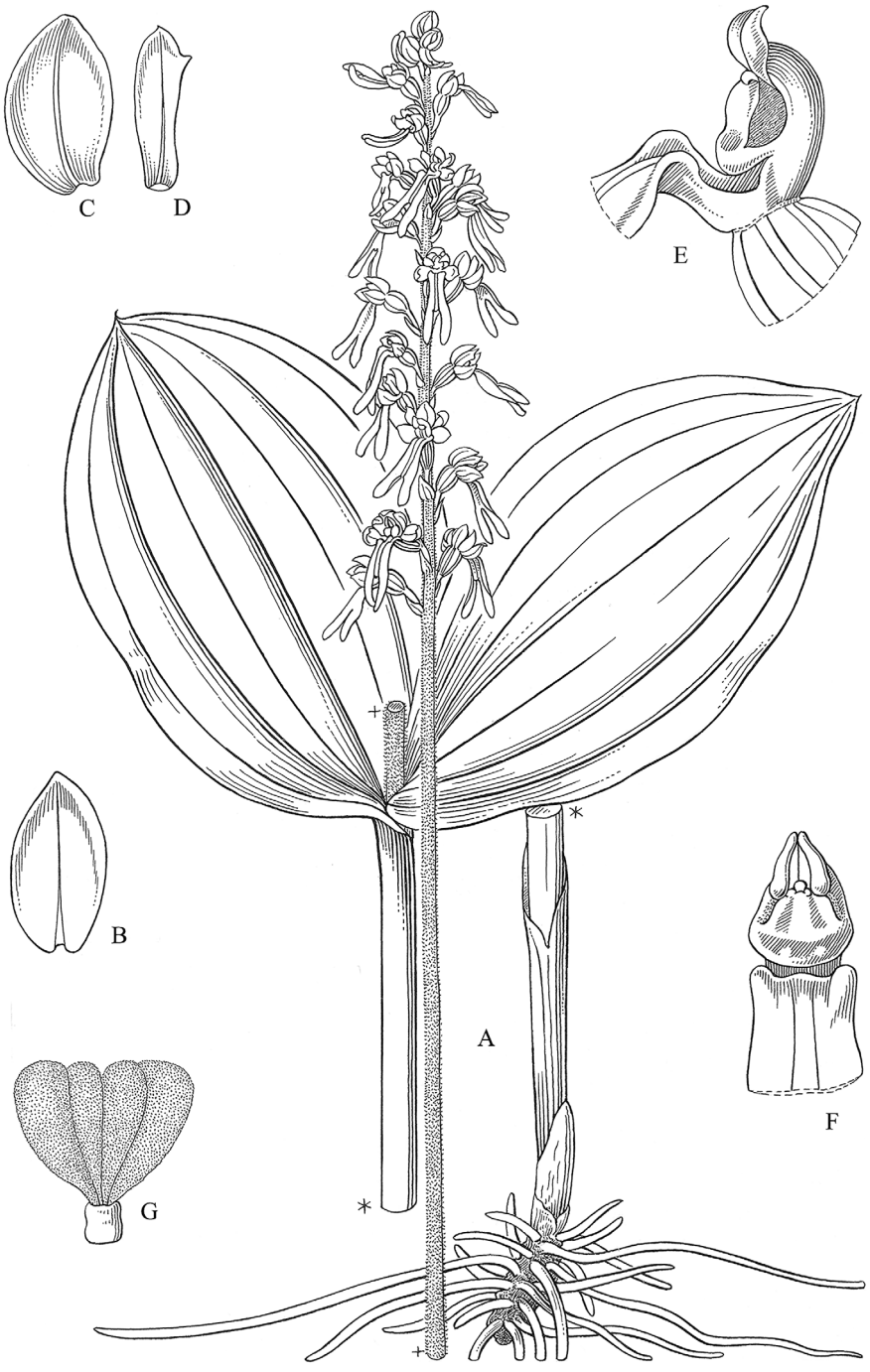


FIGURE 1 **Neottia ovata**. A, plant habit, ×1; B, dorsal sepal, ×6; C, lateral sepal, ×6; D, petal, ×6; E, base of lip and ovary, with column, side view, ×10; F, column, from below, ×10; G, pollinia, ×20. Drawn by Stella Ross-Craig for *Drawings of British Plants* part XXVIII Hydrocharitaceae, Orchidaceae (1971).

around the column. Sepals 2 mm wide, petals 1 mm wide. *Labellum* pendent, 7–15 mm long, sharply bent, with a nectar groove at the base. Labellum tip split into two elongate lobes. No spur. *Ovary* globose, ribbed. *Pedicel* twisted, 3–6 mm long.

(Based on Delforge, 1995, and Kotilínek et al., 2015). See Plate 1099 (based on material observed on Lindisfarne, off the north-east coast of England) and Figure 1.

CYTOLOGY. $2n = 32–42$; the variation has been attributed to a variable number of B (supernumary) chromosomes (Kotilínek et al., 2015, and references therein), and there is geographical variation in their occurrence (e.g. Vosa, 1983).

DISTRIBUTION. A widespread Eurasian species, occurring from Iceland and Ireland in the west to Irkutsk and Buryatia (Russia) and the eastern Himalayas (POWO, 2023). It has also been introduced in Ontario (Canada) (Elliott & Cook, 1970; Anderson & Goltz, 1982). It occurs from sea level to *c*. 2400 m.

It is one of the most widely distributed orchid species in Britain, occurring from Orkney in the north to the south coast of England. It is, however, absent from Shetland and much of the Scottish Highlands. It is widespread in Ireland, but it is absent or less common in coastal regions of southern Ireland (BSBI, 2023).

HABITAT. *Neottia ovata* occurs in a wide range of habitats and species communities. It can be found in open woodland, but it does not tolerate deep shade. It can be found on weakly acidic to weakly alkaline substrates under moderately dry to damp conditions (Kotilínek et al., 2015). Allan & Wood (1993) in their book on Scottish orchids wrote that *N. ovata* occurs in an 'extremely wide range of habitats but flourishes best in open, moist woodland on base-rich soils', while also occurring in natural habitats as diverse as machair, dune slacks and limestone pavements and, as a 'pioneering species', on 'bings' (spoil heaps from mining) and disused railway lines. The first author (MFF) remembers finding it for the first time in an abandoned quarry when walking to Hadrian's Wall from Bardon Mill (Northumberland) in the early 1970s.

FLOWERING TIME. May to July.

IUCN CATEGORY AND CONSERVATION. *Neottia ovata* has not been assessed for the Global Red List, but it has been assessed as Least Concern at the European level (Rankou, 2011). Given its wide distribution and its broad climatic and ecological range, it is probably among the least threatened species of Orchidaceae, and it is not likely to be impacted by climate change in the near future. However, a decline in the number of populations has been recorded in Britain, Ireland and elsewhere, largely attributed to changes in agricultural practice (Fay, 2015; Kotilínek et al., 2015; and references therein).

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