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Ophrys apifera Huds. × *O. insectifera* L., a natural hybrid in Britain

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ABSTRACT

The well-established population of *Ophrys* × *pietzschii* Kümpel (*O. apifera* Huds. × *O. insectifera* L.), known since 1968 in Leigh Woods, Bristol, N. Somerset, v.c. 6, has been found to agree closely in floral characters with the artificial hybrid created in Germany. The distinctive characteristics of the hybrid are described, the most important being features of the labellum, especially its lobing and coloration. The performance of the hybrid is discussed in the context of the habitat, ecological conditions and vegetation of Leigh Woods. Reference is also made to the existence of the hybrid on the Continent, including a possible natural hybrid in the French Jura. The Leigh Woods plants represent the first recorded natural population of the hybrid, and the only population now extant in Europe. It appears that the binomial *O.* × *pietzschii* was in fact not validly published, as no preserved specimen was indicated as holotype.

INTRODUCTION

In early summer 1968 four orchids of unusual flower structure, suspected as being hybrids between *Ophrys insectifera* L. (*O. muscifera* Huds.) and *O. apifera* Huds., but regarded at the time as falling within the range of variation of *O. insectifera*, were found in an old quarry in Leigh Woods, Bristol (Willis 1969). The hybrid was then unknown, but three years later it was described and illustrated in colour (Kümpel 1971), it having originated as the result of artificial cross-pollination in the wild in East Germany. Subsequently the Leigh Woods plants were recognized as *O.* × *pietzschii* (Pankhurst 1977, Willis 1978).

The performance of the British plant has been monitored over the years and is described in relation to the environmental conditions and associated vegetation in Leigh Woods. This paper also describes the diagnostic characteristics of the hybrid, and gives details of the artificial hybrid in Germany and also of a putative natural hybrid in France.

PRODUCTION OF THE ARTIFICIAL HYBRID

Details of the origin of the artificial hybrid in East Germany are given by Kümpel (1970, 1971, 1977). In 1962, the late Karl Pietzsch transferred the pollinia of *O. insectifera* to *O. apifera* in their natural habitat in the Halle district, Lower Unstrut, East Germany (*O. insectifera* had almost finished flowering when the first flowers of *O. apifera* were opening). In 1967, the first flowering hybrid plants (three in all) were seen. Flowering, which was in the first half of June, continued well in following years, a fourth plant appearing in 1970. However, this small population subsequently disappeared, the last flowering specimen being seen in 1975 (H. Kümpel pers. comm. 1978).

DESCRIPTION OF THE HYBRID

All four of the plants arising from the artificial cross-pollination agreed closely in floral characteristics. A Latin diagnosis of the hybrid has been given by Kümpel (1971, 1977), who listed other *Ophrys* hybrids (Kümpel 1977; see also Danesch & Danesch 1972). For convenience, a translation of the Latin diagnosis is given here: Plant height 14–23 cm. Inflorescence with 3–6 large flowers. Flower 23 mm from the tip of the unpaired sepal (outer perianth segment) to the tip of the appendage. Sepals first dull

TABLE 1. COMPARISON OF THE MAJOR DIAGNOSTIC FEATURES OF *O.* × *PIETZSCHII* WITH THOSE OF THE PARENTAL SPECIES

	O. insectifera	*O.* × *pietzschii*	*O. apifera*
Outer perianth segments	Pale green	Dull green-pink	Pink-white to strongly pink or rose-red
Labellum	± flat	Convex	Strongly convex
Lower lateral lobes	± in one plane	Bent back	Rolled back
Protuberance of upper lateral lobes	Absent	Very small	Small to large
Appendage	Absent	Short, pointing downwards	Long, pointing backwards
Blotch	± square, without central spot	Arching transverse band, or ± square with indistinct central spot	A surrounding basal field with dark-brown centre
Connective appendage	Rudimentary, blunt	Short, pointed	Long, S-shaped, tortuous

yellow-green, later, especially at the margins, rose-pink but always dullish. Paired sepals at first more strongly bent back than those of *O. insectifera*, but much less than those of *O. apifera*. Median sepal strongly erect, later slightly turned forward, and the paired sepals then in line. Petals (inner perianth segments) dark brown, oblong-lanceolate, broader at the base, slightly hairy on the upper surface and about one-third as long as the sepals. Labellum dark-brown also, convex, 5-lobed. Upper lateral lobes densely covered with dark hairs on the outer parts, hemispherically curved, each lobe terminating in a triangular reflexed point, and with a small glabrous forward-tilted protuberance. Lower lateral lobes paler at the margin, almost ochre-coloured, glabrous and reflexed so strongly that they almost touch one another at the back, the labellum appearing very narrow from the front. The appendage appears like a fifth lobe, much smaller than in *O. apifera*, reddish, rounded 3-cornered, turned downwards, and exceeding the lower lateral lobes. The lead-grey blotch does not reach the base of the lip, originating in the region of the lateral lobes and occupying the middle of the labellum as a transverse arc, drawn out in two blunt corners. The marking varies. Sometimes a dark violet central spot can just be recognized, sometimes lateral spots and a girdle-like connection to them are faintly visible. Between the blotch and the base of the labellum is a dark forwardly-arched basal region, as in *O. insectifera*. The column resembles that of *O. apifera* more in form and colour; connective appendage short and acuminate. Staminode spots are present. Self-fertilization, normal in *O. apifera*, has not, as yet, been observed.

The structure of the flower of *O.* × *pietzschii* is intermediate between that of the parents in nearly every feature. The most important distinctive characteristics of the hybrid are the structure and marking of the labellum and the nature of its lobes and terminal appendage, the appearance of the connective appendage (anther point) and, to a lesser extent, the colour and disposition of the outer perianth segments. The chief differences between the hybrid and the parents are given in Table 1, which is based on the distinctions recognized by Kümpel (1977).

The holotype of *O.* × *pietzschii* was said to be in the Nature Reserve 'Tote Täler' near Freyburgh, Unstrut (Kümpel 1977). Since no herbarium specimen was designated, strictly the name *O.* × *pietzschii* was not validly published.

THE OCCURRENCE OF *O.* × *PIETZSCHII* IN LEIGH WOODS

FEATURES OF THE HABITAT AND ASSOCIATED VEGETATION

The hybrid occurs on the fairly flat low floor (*c.* 35–40 ft O.D.) of an old, long since re-vegetated, quarry of Leigh Woods, N. Somerset, v.c. 6. The woods flank the western bank of the river in the Avon Gorge and are known to be of considerable antiquity and have a rich flora (Hope-Simpson & Willis 1955). Until about 1928, stone was mined in six quarries, close to the towpath at the foot of the woods. Details of the geology of the area and of the quarries are given by Vaughan & Reynolds (1936). The northern

section of the wood is on Old Red Sandstone, but the hybrid occurs in the more southerly part on Carboniferous Limestone. Here exposures are predominantly north- and east-facing, and consist for the greater part of Black Rock Limestone and Gully Oolite. Rainfall is in excess of 800 mm per year (at Long Ashton, about 4 km away, the average annual rainfall is 922 mm). The site is moderately well drained, and the soil, although deeper than on the more precipitous Bristol side of the Gorge, is fairly shallow.

The vegetation of the southern part of Leigh Woods provides a rich example of that developed on Carboniferous Limestone in the Bristol region. The major tree species are *Quercus petraea*, *Fraxinus excelsior*, *Ulmus glabra* and *Tilia cordata*, the last being characteristic of the area. The genus *Sorbus* is well represented; *Sorbus aria*, *S. aucuparia* and *S. torminalis* are present, and, mostly in the more open areas, *S. anglica*, *S. bristoliensis*, *S. eminens*, *S. porrigentiformis* and *S. wilmottiana*. The ground flora is diverse, and includes *Aquilegia vulgaris*, *Cardamine impatiens*, *Carex digitata*, *Convallaria majalis*, *Hypericum androsaemum*, *Polygonatum odoratum* and *Potentilla tabernaemontani*. Certain of the St Vincent's Rocks rarities are also present, e.g. *Arabis scabra*. Bryophytes are numerous (Willis 1964), the quarries containing a substantial number of less common species. *Ophrys insectifera* occurs sparingly under light shade in a number of places, and is associated with *O. apifera*, which is infrequent, at several sites. *O. apifera* var. *trollii* is also known in small quantity from Leigh Woods (see White 1912 for early records), as well as a virescent form of *O. insectifera*, approaching the 'peloric condition' (Sandwith 1963). Other orchids include *Anacamptis pyramidalis*, *Dactylorhiza fuchsii* (common especially in the quarries), *Epipactis helleborine* (scattered), *Listera ovata* and *Spiranthes spiralis* (regularly flowering along the towpath and in grassy areas); *Neottia nidus-avis* has also been recorded.

In the long-disused, wooded quarry where *O.* × *pietzschii* is found, there are rather few plants of *O. insectifera*, and only the occasional specimen of *O. apifera*. However, both species occur in somewhat larger numbers not far away. In the particular quarry, where conditions are somewhat open, with scrub and small tree cover, rather light shade is cast by *Betula pendula*, *Cornus sanguinea*, *Corylus avellana*, *Fraxinus excelsior*, *Sorbus aria* (*s.s.*) and *Tilia cordata*. Other woody plants include *Acer campestre*, *Betula pubescens*, *Clematis vitalba*, *Crataegus monogyna*, *Ligustrum vulgare*, *Salix caprea*, *Taxus baccata*, *Viburnum lantana* and *V. opulus*. Among the herbaceous plants of the quarry are *Eupatorium cannabinum*, *Euphorbia amygdaloides*, *Hieracium pilosella*, *Inula conyza*, *Orobanche hederae*, *Pimpinella saxifraga*, *Prunella vulgaris*, *Succisa pratensis* and *Teucrium scorodonia*. In two quadrats (of 1m side), each including one hybrid orchid, recorded in 1978 (C. M. Lovatt pers. comm. 1978) herbaceous plants included *Bellis perennis*, *Brachypodium sylvaticum*, *Carex flacca*, *Centranthus ruber*, *Fragaria vesca*, *Hypochoeris radicata*, *Linum catharticum*, *Listera ovata*, *Lotus corniculatus*, *Origanum vulgare*, *Plantago lanceolata*, *Poa nemoralis*, *Senecio jacobaea*, *Solidago virgaurea* and *Sonchus oleraceus*. Bryophytes in close proximity to the hybrid orchids included *Lophocolea bidentata*, *Bryum pseudotriquetrum*, *Eurhynchium praelongum*, *E. striatum* and *Brachythecium rutabulum*.

The hybrid orchids occur in rather open parts of the quarry, some being scarcely shaded, although several specimens are under bushes. One plant is associated with scree fragments, and there is moderate litter cover elsewhere.

THE PERFORMANCE OF THE HYBRID

When the hybrid was first seen in Leigh Woods by Dr M. Flower, Dr I. D. R. Stevens and Professor M. C. Whiting in 1968, four specimens were noticed. These plants bore up to seven flowers per inflorescence and were up to about 40 cm tall. The flowers were approximately 20 mm from the tip of the outer perianth segment to the appendage of the labellum. Photographs show details of these plants (Willis 1969). Although the possible hybrid origin of the plant was considered in 1968, the opinion of J. P. M. Brenan and P. F. Hunt then was that these specimens could be included within the considerable variation of flower structure found in *O. insectifera*.

In 1971, six plants, of similar 'aberrant' flower structure, found by S. Harris were reported from the same Leigh Woods quarry (Willis 1972). In 1973, eight specimens were found in the same locality in a survey of the less common plants of the Avon Gorge (Hendry & Pearson 1973). In mid June 1974, Mrs O. M. Stewart did a painting of the plant, again from the same quarry (O. M. Stewart pers. comm. 1976). The drawing shows five flowers in an inflorescence; Mrs Stewart also noted that one plant bore two spikes, which were at least 38 cm tall. Subsequently the painting was sent to the Royal Botanic Gardens, Kew, and the identity of the plant as the hybrid was strongly suspected (P. Taylor pers. comm. February 1976). In June 1976 the plant was examined and photographed in the quarry by

R. J. Pankhurst in the company of J. M. Mullin. Confirmation of the determination of the hybrid was subsequently given by P. F. Hunt and also by P. Taylor, P. Cribb and J. J. Wood at Kew. An exhibit of the plant was set up by R. J. Pankhurst at the B.S.B.I. Exhibition Meeting in November 1976 (Pankhurst 1977). More recently, H. Kümpel (pers. comm. 1978) has confirmed the plant as concurring with the artificial hybrid in all of the major characteristics of the flower.

Observations made in the quarry in 1978 by C. M. Lovatt (pers. comm. 1978) showed a flowering period from 8th June (early flowers) to 30th June (flowers over). On 5th June *O. insectifera* was in full flower, but *O. apifera* was only just coming into flower. Five specimens of the hybrid were noted, ranging in height from 17 to 31 cm (average 26 cm), with 2–5 flowers (average 4) per inflorescence and 2–4 leaves per plant. These plants were somewhat smaller than those of previous years. Two of the specimens each produced one capsule (1·5 cm long), but it is not known whether these resulted from selfing, crossing with other plants of the population or back-crossing with adjoining *O. insectifera*. An insect was seen by C. M. Lovatt on one flower of the latter species, and it flew off with one of the pollinia stuck to it. Only two species of insects are known to be regular visitors to *O. insectifera* (Proctor & Yeo 1973), males of the solitary wasps *Argogorytes mystaceus* (L.) (*Gorytes mystaceus*) and *Argogorytes fargeii* (Shuckard) (*Gorytes campestris*). *Argogorytes mystaceus* is known to be locally common and widespread in England and Wales, and *A. fargeii* is a rare or very rare species in the southern counties of England and Wales (M.E. Archer pers. comm. 1979). The flight period of the former is from May to July, and of the latter in June and July.

Although *A. mystaceus* is known to visit *O. insectifera* in southern France (Godfery 1929) and in Scandinavia (Wolff 1950; Kullenberg 1950, 1961), and to be very specific, it has not been observed to effect pollination in Britain. Casual visitors to *O. insectifera* appear to be rare (Godfrey 1929), and only very rarely does *A. mystaceus* visit any orchid other than *O. insectifera*. Because of this specificity, hybridization in *Ophrys* is not likely to be more than a rare event (Proctor & Yeo 1973). Nevertheless, a large number of hybrids within the genus are known in Europe (Danesch & Danesch 1972), although only four in addition to the present one have been recorded for Britain (Hunt 1975). In Britain self-pollination of *O. apifera* appears to be the rule and seed-set substantial, but many flowers of *O. insectifera* fail to set seed (Summerhayes 1951; Kullenberg 1950).

In 1979, flowering was poor, as only two flowering spikes were seen in late June; these persisted well into July. One of the spikes bore six flowers and was 41.5 cm tall, but the other was shorter (26.5 cm), with only two flowers.

Overall, from the period 1968 to 1979, there seems to have been a fairly steady flowering performance of the hybrid in Leigh Woods, averaging 5 or 6 specimens per year, of average height 30–35 cm. Its flowering period, while later than that of *O. insectifera*, is fairly similar to that of *O. apifera*.

It is hoped to study capsule production further. In the interests of conservation, no plants have been examined with respect to underground parts.

THE EUROPEAN DISTRIBUTION OF THE HYBRID

THE ARTIFICIAL HYBRID

The vegetation of the nature reserve near Freyburgh, East Germany, where the artificial hybrid was produced is developed under favourable climatic and environmental conditions, and is Xerobrometum with scattered bushes (H. Kümpel pers. comm. 1978). Growing together with the parental *O. apifera* and *O. insectifera* are *O. sphegodes* (frequent), *O. insectifera* × *O. sphegodes*, *Epipactis atrorubens*, *Listera ovata*, *Orchis militaris*, *O. purpurea*, *O. militaris* × *O. purpurea*, *O. tridentata* and *Platanthera bifolia*. No artificial hybrids were seen after 1975; these specimens were shorter than those of the more persistent Leigh Woods population of natural hybrids.

THE NATURAL HYBRID

The first recorded natural hybrids are from Leigh Woods, and this is the only population known to have continued to flower over a ten-year period. Conditions for the production and survival of the hybrid in Leigh Woods may perhaps be more favourable than elsewhere, although flowering times of the parents appear to be fairly similar in southern England and on the Continent. Danesch & Danesch (1975) give the flowering period of *O. insectifera* for the Continent from early May to mid June, and of

O. apifera from the beginning of June to early July. On the Continent there may be an overlap in the flowering of the parents of some two weeks, but in Britain the overlap period may be somewhat longer.

A single record of a possible natural hybrid has been made in the French Jura. On an excursion on 28th May, 1969, led by H. Sundermann (1970, 1975, and pers. comm. 1979; see also Danesch & Danesch 1972), he found and reported a plant (two specimens were seen) from near Ceyzériat (46°10′N, 5°20′E) which had a number of similarities to the hybrid (H. Sundermann pers. comm. 1979). The plant was in a dry grassy place on limestone, where the shrubs included *Buxus sempervirens*, *Cornus sanguinea*, *Juniperus communis* and *Prunus spinosa*. Orchids were well represented, as, besides *O. apifera* and *O. insectifera*, *O. fuciflora* and *O. sphegodes*, *Aceras anthopophorum*, *Anacamptis pyramidalis*, *Gymnadenia conopsea*, *Himantoglossum hircinum*, *Listera ovata*, *Orchis mascula*, *O. militaris* and *Platanthera bifolia* were present. The hybrid could not, however, be found in June 1976 (H. Sundermann pers. comm. 1979).

The plant from the French Jura was fairly tall (30-35 cm), with about eight flowers in the spike. The labellum bore a quite large lead-grey blotch. However, the lateral lobes of the labellum, although present, were little developed and the large middle lobe was strongly turned in, giving a bluntly rounded appearance (the terminal appendage was not visible from the front). This plant differs from the artificial hybrid and the Leigh Woods plants in several other features (such as size and orientation of perianth segments, the blotch spreading to the lower lip zone), and in the opinion of H. Kümpel (pers. comm. 1979), the Jura specimens are better considered as abnormal forms of *O. insectifera*. The view that a mutation is involved is not ruled out by H. Sundermann (pers. comm. 1979). Further light could be shed on the situation if hybrids are found elsewhere, or if the results of the reciprocal cross (with *O. insectifera* as female) are investigated.

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