

ORCHIS CRUENTA Müll. IN THE BRITISH ISLANDS

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A short note on the finding of *Orchis cruenta* O. F. Müller in the counties of Galway and Mayo has already been published (Harrison, 1949). The present paper serves to expand the description of this interesting boreal species, and provides additional distributional and cytological data.

Orchis cruenta was described by Müller in Oeder's *Flora Danica* in 1782 from Rörös in central Norway. Synonyms, icones and exsiccata are cited by Pugsley (1935) and by Vermeulen (1947). By the latter author the species is renamed *Dactylorchis cruenta* (Müll.) Vermeulen, following his elevation of Klinge's subgenus *Dactylorchis* to the rank of genus. Vermeulen states that he has been unable to locate the type-specimen of Müller, and the description given in his paper of 1947 is based upon a plant from Frösön, Jämtland, Sweden, 170 miles E.N.E. of Rörös, which he names as the lectotype, in Herb. L. M. Neuman, Lund, and is augmented from comparison with Swiss, Russian and other Scandinavian material. It is couched in general terms, and may thus be said to refer to a population rather than to an individual. Other descriptions of *O. cruenta* which may be said to define populations in that some attempt is made to indicate the ranges of variation of taxonomic characters are those of Klinge (1898), Ascherson and Graebner (1907, where the plant is named *O. incarnatus* subsp. *cruentus*) and E. and A. Camus (1928). The latter accounts seem largely to be based upon Klinge's original work.

The earlier treatment of *O. cruenta* by the two Reichenbachs (H. G. L. Reichenbach, 1832; H. G. Reichenbach, 1851) is marred by numerous inconsistencies. The "*Orchis cruenta* Roch." of the former should, according to Ascherson and Graebner (1907) and Vermeulen (1947), fall under *O. cordigera* Fries. *O. cruenta* Müll. is represented by the elder Reichenbach's "*Orchis haematodes*," although the diagnosis of this plant is by no means identical with that of the original. The younger Reichenbach provides a plate (t. 43, I) purporting to depict *O. cruenta* Müll. The species is, however, treated in the text in his complex system of subgrouping under *Orchis incarnata* as 2. *Sublatifoliae*, a. *brevicalcaratae* bb. *rhombilabia cruenta*. The "*O. haematodes*" of his father is relegated to 1. *Incarinatae verae*, where it features as a synonym of a. *lanceata*. Again the caption appended to the plate of this plant shows little agreement with the text, since the plant is there entitled "*O. matodes* Rchb." (*sic*) under the general heading "*Orchis incarnata* L." Neither the figure of *O. cruenta* Müll. (t. 43, I) nor that of *O. matodes* Rchb. (t. 46, I) shows the feature most characteristic of the species: the presence of anthocyanin pigmentation on both surfaces of the leaf. The only case in which this character

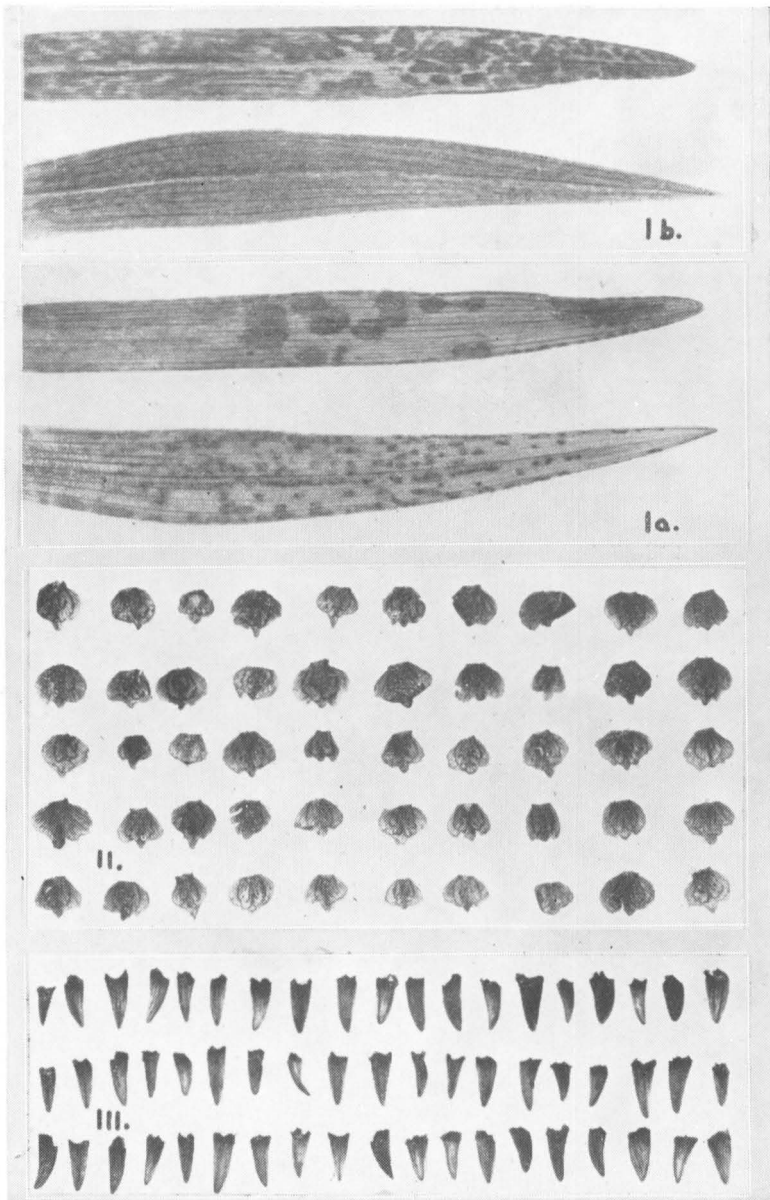


Plate I 1 (a) Upper and (b) lower surfaces of a pair of leaves from two different plants of *O. cruenta*. (Natural size).
 ii. Lips from homologous flowers from fifty different individuals (c. natural size).
 iii. Spurs from fifty-seven different individuals (c. natural size).

is illustrated is in a supplementary plate (t. 170, II) of *Orchis salina* Turcz. This figure might well represent a form of *O. cruenta* Müll., and it is significant that *O. salina* is placed in the supplementary text with *O. haematodes* Reichb. p. under 1, *Incarnatae verae*, a. *lanceata* (that is, *O. cruenta* Müll. sensu Reichb. p.).

Five varieties of *O. cruenta* Müll. are recognised by L. M. Neuman (1909) in his treatment of the Scandinavian forms of the species. These are: α *subelliptica*, β *subtriangularis*, γ *brevifolia*, δ *lanceolata* and ϵ *haematodes*. The first two are broad-leaved forms (maximum leaf width 2-2.5 cm.), differing from each other in a labellum character. Vars. *brevifolia* and *lanceolata* are narrow-leaved plants (maximum leaf width 1-1.5 cm.), the former with exceedingly short, recurved leaves. Var. *haematodes* is a resuscitation of the elder Reichenbach's "*O. haematodes*," differentiated, according to Neuman's brief diagnosis, mainly through the possession of a greater number of bract-like leaves between the upper foliage leaf and the spike.

The continental range of *O. cruenta* was greatly extended by Pugsley's discovery in 1933 of a plant undoubtedly connected with that of Müller in two regions near Zermatt in Switzerland. Two years later the plant was found in Graubünden by Gsell (1935). Pugsley's description of the Swiss plant (Pugsley, 1935) is apparently based upon selected specimens, and gives little indication of variation—certainly it is not adequate to associate the Swiss race with any particular one of Neuman's varieties. That of Gsell gives some useful biometrical data and an indication of the range of variation of certain characters. The most recent continental find has been that reported by Wilmott (1938), who identified the plant in material from the French Alps. The excellent photograph which accompanies his description portrays a plant which may have affinities with Neuman's var. *subtriangularis*. The inter-relationships of the continental forms are discussed further below.

Brief consideration must be given here to certain erroneous former records of *O. cruenta* from the British Isles. The first record of the species from a British locality occurs in a note by H. Goss (1899) in which it is stated to occur on the Cumberland fells at an altitude of 1000 ft., the identification having been made by Rolfe. Druce (1910) subsequently recorded the plant from Teesdale, Durham, again on the basis of identifications made by Rolfe. In 1916, T. A. Stephenson reported *O. cruenta* from Hawkshead, N. Lancs., and from the Isle of Arran—"corroborated at Kew," presumably also by Rolfe. Druce apparently had some suspicion of these last records, since he saw differences between the plant concerned and that illustrated in Müller's original *Flora Danica* plate. All of these records preceded the establishment by the Stephensons in 1920 of their *Orchis purpurella* as a distinct species. After that date it became clear that all the previous records of "*Orchis cruenta*" from the British Isles referred to *O. purpurella*, and moreover that it had been the practice of certain continental authorities to refer plants of *O. purpurella* to *O. cruenta*, no doubt as

Vermeulen (1947) suggests, as the result of the misleading plate published of the latter species by the younger Reichenbach. This point was demonstrated by Druce (1920), for whom plants of *O. purpurella* were named as *O. cruenta* by Lindman. In a further elucidation of the relationship of *O. purpurella* with other marsh orchids, the Stephenson (1921) pointed out the marked differences between their plant and the *O. cruenta* of Müller. From examination of Druce's herbarium material, they decided that *O. cruenta* is nearer to *O. incarnata* (*O. latifolia* L. sec. Pugsl.) than to *O. purpurella*—"as compared with the minute dots of *purpurella* it has not only more angular markings, but also bright purple blotches on both sides of the leaves." They finally concluded (1922) that "it is now certain that previous records of *cruenta* from Britain are incorrect; the plants found must be assigned to *purpurella*." Druce had already reached this conclusion (1921), and had shown that the original record of Goss was at fault as a result of Rolfe's misnaming. He withdrew his own record for *O. cruenta* in Teesdale, stating that the plants there, too, fall under *O. purpurella* Steph.

The nomenclatural confusion which surrounds *O. cruenta* arises, as in the case of so many other dactylorchids, largely from the extreme inherent variability of the species. Among the dactylorchids, the observation of Camp and Gilly, in a recent discussion on the structure and origin of species (1943), applies with particular force: "the species is not necessarily a particular kind of organism; the species is a kind of population." To be of use in comparative studies, descriptions of taxonomic units within the group must necessarily take into account the range of variation found in natural populations.

The following description is based upon two random mass collections of more than one hundred individuals each from the colonies of *O. cruenta* on the limestone shores of Lough Carra and Lough Mask. For assistance in recording biometrical data I am indebted to Prof. A. R. Clapham and to Dr Y. Massey.

DESCRIPTION

LEAF CHARACTERS.

Number. There are normally two or three membranous leaves ensheathing the stem just above the tubers. Counting the lowest green leaf as the first, and that below the first floral bract as the last, even though it may be bract-like, the distribution of the number of leaves per plant in the populations examined is as follows: 3 leaves, 1%; 4 leaves, 22%; 5 leaves, 68%; 6 leaves, 8%; 7 leaves, 1%. The modal class for leaf number among the Irish plants is thus 5, with about a third as many with 4.

Size and shape. The leaves are characteristically lanceolate or linear-lanceolate, slightly keeled and broadest about one-third of their length from the base. They are normally erect, slightly recurved, and dispersed regularly along the length of the stem. Population parameters for the dimensions of the largest leaf are as follows:

Length (from top of sheath to tip): Range, 5-15 cm.; mean, 8.42 cm.; standard deviation, 2.49 cm.

Width (at broadest point): Range, 0.9-2.1 cm.; mean, 1.25 cm.; standard deviation, 0.29 cm.

Marking. Leaf marking was absent from 35% of the plants examined. The majority of the remainder showed the extraordinary distribution of anthocyanin pigmentation exclusive to *O. cruenta* among the European orchids. The marking is of a reddish-purple or violet hue, dispersed in fine dots or larger spots and blotches, sometimes forming dark bars running parallel to the leaf venation, sometimes forming fields or zones of colour interrupted only occasionally by small rectangular greenish islands, and often covering the entire leaf surface. Except in about 2% of the individuals examined, this marking was repeated on both surfaces of the leaf. The pigment seems to be located in sub-epidermal cells on each surface, and the patterning on the two surfaces is thus not necessarily coincident. This point is illustrated in the photograph of upper and lower surfaces of a pair of leaves reproduced in Plate I, i. The intensity of pigmentation can only be assessed visually; separating the range of variation into five arbitrary classes and taking no account of variation in pattern, the distribution of the Irish plants is as follows: Nil, 35%; Light, 28%; Medium, 14%; Heavy, 12%; Very heavy, 11%.

STEM.

Measured from immediately above the tubers (the point at which the stem parts with a vertical pull at the level of the lower leaves) the stature of the plants examined varied from 19 to 46 cm. The mean of all plants was 31.42 cm., and the standard deviation, 4.80 cm. The stem is invariably hollow, the cavity usually exceeding half the total diameter. In those individuals with heavily marked leaves, the stem is generally suffused with a similar violet or purple coloration, particularly in the upper parts. In others it is striated or flecked with pigment, the markings being continuous with those of the upper leaves or floral bracts.

INFLORESCENCE AND FLOWERS.

The inflorescence of Irish plants of *O. cruenta* is somewhat less dense than in native *O. latifolia* L. sec. Pugsl., and ranges in length from 3 to 7.5 cm., with 11 to 42 flowers. The bracts, which are spotted like the upper leaves, exceed the flowers in the lower part of the inflorescence. The flowers are small and possess a range of lilac-purple colours, with no trace of the flesh or maroon tint of *O. latifolia*. The lateral sepals are erect or slightly reflexed, marked with a pattern of fine dots or short bars. The labellum is entire or obscurely tri-lobed, often reflexed laterally in the fresh state. The range of variation in shape is illustrated in Plate I, ii. The dimensions are as follows:

Width (at broadest point): Range, 4.5-9.0 mm.; mean, 6.38 mm.; standard deviation, 1.04 mm.

Length (measured from spur mouth): Range, 4.25-7.50 mm.; mean, 5.82 mm.; standard deviation, 0.74 mm.

The spur is thick, curved and bluntly conical (Plate I, iii). The dimensions are:

Length: Range, 5.5-9.25 mm.; mean, 7.65 mm.; standard deviation, 0.76 mm.

Width (flattened): Range, 2.0-4.0 mm.; mean, 2.91 mm.; standard deviation, 0.47 mm.

The ovaries are strongly ridged, and commonly flecked with reddish-purple in the manner of the floral bracts and upper part of the stem.

CYTOLOGY.

Root- and tuber-tips were fixed in the field in Lewitsky's modification of Navaschin's solution, and sections were cut at 12 μ . The chromosomes of the dactylorchids are small, and tend to lie in compact groups, or even to form chains (e.g., *O. ericetorum*; Hagerup, 1944). This makes accurate determination of their number difficult. The disadvantage may to some extent be overcome by staining with Johansen's methyl violet method, and carrying the differentiating and destaining action of the final picric-alcohol and clove oil baths to the point where only the outlines of the chromosomes remain visible. Overlapping and clumped groups may then be separated into their individual components with far greater ease than when the chromosomes are stained deeply and uniformly. Forty plates were counted in material from four plants. The chromosome number was found uniformly to be



Fig. 1. *Orchis cruenta* Müll.: metaphase plate from root tip. $\times c.$ 3000.

$2n = 40$. A well-spread metaphase plate is illustrated in fig. 1. This finding is in accordance with that of Heusser (1938) for Swiss material of *O. cruenta*, and places the plant in the diploid series to which belong the other members of Pugsley's *Latifoliae verae*.

O. CRUENTA IN RELATION TO OTHER BRITISH DACTYLORCHIDS.

With *O. latifolia* L. sec. Pugsley (*O. incarnata* auct. mult.), *O. cruenta* forms the subsection *Latifoliae verae* of the subgenus *Dactylorchis*

Klinge in Pugsley's classification (1935). *O. latifolia* L. sec. Pugsl. is represented in the British Islands by a wide range of varieties, almost all of which are clearly distinguished from *O. cruenta* by the complete absence of leaf markings. As has been seen, populations of *O. cruenta* always contain a high proportion of individuals in which the characteristic marking is present on both sides of the foliage leaves, and in which the bracts and upper parts of the stem are "cruentate"—flecked with reddish-purple pigment. Other differences which distinguish *O. cruenta* from the *O. latifolia* forms are found in flower colour and shape, and in the size, shape and distribution of the leaves. The lilac-purple flower colour is quite distinct from the straw, flesh, salmon, crimson-red series of tones found in many *O. latifolia* forms (var. *Gemmana* Pugsl.; var. *ochroleuca* (Boll) Pugsl.; var. *coccinea* Pugsl.), and in fact is almost as distinct in the fresh state from the reddish-purple colours of the other *latifolia* varieties (var. *pulchella* (Druce) Pugsl. and var. *cambrica* Pugsl.). Closest to *O. cruenta* amongst the *O. latifolia* forms is var. *pulchella*, some populations of which contain individuals with light pin-point leaf spotting reminiscent of that found in *O. purpurella* T. & T. A. Steph. But the leaf marking in *pulchella* is restricted to the upper surface of the foliage leaves, never extending to the bracts or the stem. The labellum of *pulchella* is considerably larger than in *O. cruenta* (c. 8×8 mm., in contrast with c. 6×6.5), the leaves are broader, more recurved and more numerous, and the stem less fistular. The var. *pulchella* is, moreover, an early flowering plant of mildly acid sphagnum bog (frequently with *Sphagnum squarrosum* in Ireland), while *cruenta* flowers in late June and early July, and is apparently restricted to the highly calcareous type of marsh habitat described below.

COMPARISON WITH CONTINENTAL *O. CRUENTA*.

It is clear from the continental literature that *O. cruenta* is as variable throughout its range as are *O. latifolia* L. sec. Pugsl. and *O. majalis* Reichb. Nevertheless, there is a substantial body of agreement between the various descriptions of the species, and there can be little doubt that the Irish plant here described falls within the "Rassenkreis" to which the northern forms of Müller, Klinge and Neuman, and the Alpine forms of Pugsley, Gsell and Wilmott belong. As in the *O. majalis* complex, there seems to be a wide variation in leaf size and shape. The original plate of Müller portrays a rather broad-leaved plant, close to Neuman's var. *subelliptica* (the leaf dimensions given by Neuman for this variety, which was based upon plants from Frösön, Jämtland, are 6-7 cm. × 2 cm.). I understand from Dr H. Smith of Uppsala that the broad-leaved plant is the more common in southern Sweden. Jämtland was, however, also the source of the material upon which Neuman's varieties *subtriangularis* and *lanceolata* were based, the former with a leaf size given as 5-7 cm. × 2-2.5 cm., and the latter, 6-12 cm. × 1-1.5 cm. It is difficult to tell from Neuman's account how well defined were the populations to which these dimensions refer, and it should be noted that Vermeulen (1947) states that the material he saw from this important

Swedish locality showed a very wide range of variation in leaf width*. Klinge, presumably describing Russian material, quotes the dimensions of the largest leaf as 6-8 cm. \times 1-1.5 cm.; dimensions which are accepted without modification in the accounts of Ascherson and Graebner (1907) and of Camus (1928-9). Gsell's dimensions for the Graubünden plants (5-9 cm. \times 1.5-1.8 cm.) define a broad-leaved race, no doubt similar to that represented by the broad-leaved plant illustrated by Wilmott (1938). Summarising the above:

(1) Narrow-leaved and broad-leaved races of *O. cruenta* occur in the Scandinavian region, the former tending possibly to have a more northerly and the latter a more southerly distribution;

(2) the narrow-leaved form is probably the more common in northern Russia;

(3) the Alpine form is characteristically broad-leaved.

While the Irish plants show considerable variation in leaf width (0.9-2.1 cm.), the mean width is 1.25 cm., and the race must therefore be regarded as relatively narrow-leaved. If Neuman's varieties are accepted, then the Irish race is closest to his var. *lanceolata*.

DISTRIBUTION AND ECOLOGY

In Ireland, *O. cruenta* appears to be limited to suitable habitats around the lakes of the Galway-Mayo limestone basin. Its distribution in this area has been explored in some detail by Mrs H. Gough, Mrs D. Teacher and Major R. F. Rutledge (June, 1950). The localities now known are as follows:

East Mayo (v.-c. H.26). Lough Carra: plentiful near Keel Bridge at the south end of the lake, extending up the west shore north of Partry and occurring on some of the islands; also plentiful at Cloonee and on the east shore north of Cloonee. Lough Mask: abundant at Aghinish, and occasional on the lake shore further north. Lough Corrib: occasional on the north-east shore near Castletown.

North Galway (v.-c. H.17). Occasional at Annaghdown, on the north-east shore of Lough Corrib.

The main continental range of *O. cruenta* (*sens. lat.*) lies between latitudes 55° and 65° N., although at the head of the Gulf of Bothnia and possibly in western Russia it approaches the Arctic Circle. The plant is now known from six or seven Alpine localities, following Pugsley's initial discovery of it near Zermatt in 1933. A record for a "race" of the species (*O. cruentus* B *Seemenii* Ascherson & Graebner, 1907) exists for a locality on the Isle of Borkum. Schulze (in Ascherson and Graebner, p. 721) considered this to be a form of *O. in-*

*My own measurements of leaf size made in July 1950 on 25 plants from a colony near Hammerdal in Jämtland, one of the type localities for Neuman's var. *lanceolata*, gave the following results: length 9-14 cm., mean 11.40 cm.; width 0.9-1.9 cm., mean 1.15 cm. In a collection of 100 plants from Omberg in Östergötland some 350 miles south of this locality, the dimensions of the largest leaf were as follows: length 6-14 cm., mean 9.24 cm., width 0.7-2.2 cm., mean 1.29 cm. The distinction between these two Swedish populations in this character is thus hardly significant.

carnata (*O. latifolia* L. sec. Pugsl.). This race is now extinct (*vide* Vermeulen). For reasons outlined above, the Scottish and northern English records quoted by Ascherson and Graebner, Camus, and other continental authors must now be disallowed.

The European distribution of the species, as now known, is thus as shown in the accompanying map, fig. 2. For the spot records of the



Fig. 2. *Orchis cruenta* Müll. : European distribution.

plant from the Scandinavian area I am indebted to Dr E. Hultén, who kindly supplied me with an advance map from his remarkable *Atlas* (1950).* To these I have added a record from Götland (Petterson, 1947).

**O. cruenta* is placed by Hultén in his Group 14: "North-European plants with a boreal-montane tendency", among the species *without* a central European range. Its presence in the Alps means that it should feature, rather, in the second section of this Group, in which are listed plants possessing central European (often sub-alpine) ranges in addition to their more extensive northern areas.

East of the area shown on the map, the range of the species extends through central and northern Russia, reaching, according to Nevski, east of Lake Baikal. Details of the eastern Siberian range are not available.

O. cruenta generally occurs in small colonies in calcareous marshes and fens, and occasionally in salt-marshes. In Ireland, as for example about Lough Carra, it is a member of an *open* association dominated by *Schoenus nigricans*. This occurs in a belt of varying width extending down to the water's edge, and is subject to frequent inundation. The substratum is a white, highly calcareous deposit, soapy in texture, with a pH ranging from 8.2-8.4 in the samples examined and a solubility in acid of 70-85% dry weight. Characteristic associates include *Ranunculus Flammula*, *Lythrum Salicaria*, *Cirsium dissectum*, *Anagallis tenella*, *Samolus Valerandi*, *Pinguicula vulgaris*, *Juncus acutiflorus*, *Scirpus pauciflorus*, and occasionally *Cladium Mariscus*. The plant rapidly thins out in the drier *closed* associations, at and just above the flood level, which have a richer orchidaceous flora including *Gymnadenia conopsea*, *Anacamptis pyramidalis*, *Orchis Fuchsii*, and, locally, *Epipactis palustris*.

The foregoing distributional data suggest that *O. cruenta* must be added to the problematical little group in the flora of the British Islands which Matthews (1937) has termed the Northern-Montane. This includes plants with a fairly wide lowland distribution in northern Europe which possess disjunct localities further south, mostly in sub-alpine areas. Other examples in the Irish flora with this type of distribution are *Potentilla fruticosa*, *Calamagrostis neglecta* and *Salix phylicifolia*. The comparative sparsity of *O. cruenta* in central Europe suggests that it is of northern origin, and that the Alpine and Irish colonies represent relict stations from late glacial times when the species probably occupied a more extensive region south of the glaciated zone. During the ensuing climatic amelioration the main mass of the species is likely to have migrated northwards to its present station, while the immigration of a vigorous lowland flora eliminated the species in its southern stations except for isolated areas in which it is fitted by specialised ecology to meet competition. In Switzerland, one may suppose that such conditions are found in calcareous sub-alpine marshes. Gsell emphasises the fact that the Graubünden stations are all above the 1800 m. level, that is, at a greater altitude than that at which *O. incarnata* is commonly found. In Ireland, the present distribution may be explained on the assumption that survival was possible in calcareous marsh areas due to the early check to the immigration of potential competitors caused by the opening of the English Channel and the widening of the Irish Sea.

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