

The species of *Oenothera* L. in Britain

K. ROSTAŃSKI

Institute of Botany, Silesian University, Katowice, Poland

ABSTRACT

An account is given of the 15 species of *Oenothera* which have been recorded from the wild in Great Britain; of these, ten belong to subgenus *Oenothera*, two to subgenus *Hartmannia*, and three to subgenus *Raimannia*. Only four species, given here in descending order of frequency, are common: *O. erythrosepala* Borbás, *O. biennis* L., *O. cambrica* Rostański, and *O. stricta* Ledeb. There are no post-1960 records for five of the other eleven species.

O. biennis and *O. rubricaulis* Klebahn seem to be native European species, and *O. fallax* Renner arose in Europe as the hybrid *O. erythrosepala* (female) × *O. biennis* (male). *O. erythrosepala* was introduced from N. America in the middle of the 19th century, and *O. cambrica* perhaps in the 18th century, although its area of distribution in N. America is unknown at present. *O. stricta* originated from Chile in the 19th century. The other species came from N. and S. America in the 19th and 20th centuries as repeated, non-persistent introductions.

The relatively small number of specimens of *O. biennis* seen compared with the large number of literature records is explained by misidentifications as this species of other species, e.g. *O. cambrica*, *O. fallax*, *O. erythrosepala* and even *O. stricta*. Similarly *O. parviflora* has been greatly over-recorded (most records refer to *O. cambrica*), and all records of *O. ammophila* Focke, *O. suaveolens* Desf. ex Pers., *O. grandiflora* Aiton and *O. odorata* Jacq. are erroneous.

A key to the species is provided, as are notes on the history and origin of *Oenothera* in Europe and the value and variability of certain taxonomic characters in the genus.

INTRODUCTION

Munz (1965) divided the genus *Oenothera* into 15 subgenera; most of the species commonly occurring in Europe belong to subg. *Oenothera* (type species: *O. biennis* L.). Although the representatives of the other subgenera (*Hartmannia* and *Raimannia*) are easily distinguished (with the exception of *O. stricta* Ledeb. ex Link and allies), specimens belonging to the typical subgenus are often wrongly identified, and there is a great deal of confusion in the literature. The two main reasons for these problems are the differing concepts of the species which are held by various workers, and the variability of certain characters.

This paper discusses these two problems, outlines the history and origin of *Oenothera* in Europe, and provides a key to and descriptions of the 15 species and various hybrids of the genus which have been found in the wild in Britain.

THE CONCEPT OF SPECIES IN *OENOTHERA* SUBGENUS *OENOTHERA*

There are two concepts of the species in *Oenothera*: the American and the European. The American concept, as represented by P. A. Munz (Munz 1965), is based on the cytogenetical researches of Cleland (1954, 1958, 1972). The history of this view is connected with the application to American biennial *Oenotheras* of the names used by Linnaeus: *O. biennis* L. and *O. muricata* L. But the type specimens preserved in LINN show that neither of these species, which were collected in Europe, corresponds to any North American taxon. As I have elsewhere stated, the first is *O. biennis sensu stricto*, and the second corresponds to the European *O. rubricaulis* Klebahn. Following Cleland's view, Munz (1965) divided American *O. biennis sensu lato* into three subspecies (*caeciarum* Munz, *centralis* Munz and *austromontana* Munz) omitting subsp. *biennis* as not growing in North America. All these subspecies included long lists of synonyms, which represent various taxa described by

Gates (1936), Gates & Catcheside (in Gates 1933), Sturtevant (1931), Bartlett (1914), Atkinson & Bartlett (in Bartlett 1913), and Hornemann (1813) as species or varieties. *O. muricata* was included in *O. biennis* subsp. *caeciarum*. *O. erythrosepala* Borbás was regarded as a true species "apparently as an escape on both the Atlantic and Pacific seaboards . . . and also in the interior as in Michigan" (Munz 1965). *O. parviflora* L. was divided into two subspecies: *parviflora* and *angustissima* (Gates) Munz, each with long lists of synonyms which again represent taxa described by the above-mentioned and other authors. Likewise, *O. strigosa* (Rydb.) Mack. & Bush was divided into three subspecies: *strigosa*, *canovirens* (Steele) Munz and *cheradophila* (Bartlett) Munz; *O. depressa* Greene (*O. salicifolia* Desf. ex G. Don in the present paper) was included in subsp. *canovirens*. *O. strigosa* was later treated as the synonym of *O. villosa* Thunb. by Dietrich & Raven (1976) who, basing the latter upon Thunberg's African type specimen of 1792, proposed a subdivision of this species into the following subspecies: *villosa* (including as synonyms *O. depressa* and *O. hungarica* Borbás), *strigosa* (Rydb.) Dietrich & Raven and *cheradophila* (Bartlett) Dietrich & Raven.

According to the above American point of view, only the following species should be distinguished in Europe: *O. biennis*, *O. erythrosepala*, *O. parviflora* and *O. villosa*, with further subdivisions into taxa of lower ranks.

The European concept of species is represented by the views of O. Renner. The cytogenetical studies of this famous geneticist and taxonomist led him to distinguish in Europe several taxa at the rank of species (Renner 1942, 1950, 1956). According to Renner, these taxa represent populations which are characterized by a particular chromosome complement (Renner Complex) and a constant phenotype, and which should be placed in distinct species. These phenotypes may be defined easily by the sizes of flowers and the proportions of their elements, by the colour of both midribs and sepals, and by the presence or absence of red colour on the stem, axis of the inflorescence and tubercles (papillae) of the stem and ovaries, etc. Following this concept some European authors recognized as good species taxa described earlier by Desfontaines (1815), Borbás (1902, 1903),

TABLE 1. VARIATION IN SIZE OF FLORAL PARTS OF FOUR SPECIES OF *OENOTHERA* ACCORDING TO TIME OF YEAR

Date	Hypanthium (mm)	Sepal-tips (mm)	Anthers (mm)	Stigma-lobes (mm)	Petals (mm)
<i>Oenothera erythrosepala</i> (1979)					
20.VI	46	8	14	9	53×65
16.VII	42	6	13	7	42×48
12.IX	35	2	8	7	37×41
25.IX	30	2	6	6	30×33
24.X	25	1	5	7	27×31
<i>Oenothera fallax</i> (1961)					
7.VII	38	2	7	10	22×27
19.VII	35	2	7	8	20×24
9.VIII	33	2	7	9	24×28
6.IX	30	2	5	7	21×24
2.X	27	2	4	5	15×18
<i>Oenothera biennis</i> (1961)					
7.VII	32	4	7	8	23×29
17.VII	30	3	7	8	21×26
25.VIII	28	3	5	6	19×22
6.IX	28	3	5	6	18×21
<i>Oenothera parviflora</i> (1961)					
13.VII	40	3	4	5	10×10
17.VII	40	3	5	5	10×10
3.VIII	38	3	5	5	8×8
25.VIII	38	3	4	5	9×9
30.IX	40	3	3	5	10×10

Focke (1904), Klebahn (1914) and by Renner himself, and they began to describe new strains as new taxa. Such authors are Scholz (1956), Rostański (1965, 1968a, 1977), Kappus (1966), Hudziok (1968), Linder & Jean (1969), Gutte & Rostański (1971), Sodano (1978–9) and Jehlík & Rostański (1979). Keys to the identification of these species have been published in some European Floras or other works by Flössner *et al.* in Wünsche-Schorler (1956), Linder (1957, 1965), Tacik (1959), Kloss (1963), Rostański (1965, 1966, 1975, 1976), Raven (1968), Soó (1966), Damboldt (1975) and Oberdorfer (1970).

However, some European authors accepted the American concept and endeavoured to recognize collective species, distinguishing within them some subspecies or varieties, e.g. Tischler (1950), Janchen (1951) and Garcke (1972). Renner (1956, p. 247) criticized these authors, writing as follows: "wenn Tischler (1950 s. 57 f.) unter Berufung auf Cleland das primitive der Floren aufgreift, als Arten nur *O. biennis* und *O. muricata* gelten lässt und die von mir unterschiedenen Arten wie *rubricaulis*, *suaveolens* auf der einen, *ammophila*, *parviflora* usw. auf der anderen Seite nur als Subspezies der beiden Hauptarten bestehen lässt, so kann ich dem nicht zustimmen. Diese Arten sind klar geschiedene Biotypen, stärker voneinander verschieden . . . als manche anerkannte Arten von *Epilobium*."

Nevertheless, in this paper, as in all my earlier ones, I accept Renner's concept of species in *Oenothera*. This was also the concept of Linnaeus, as shown by the type specimens of *Oenothera*

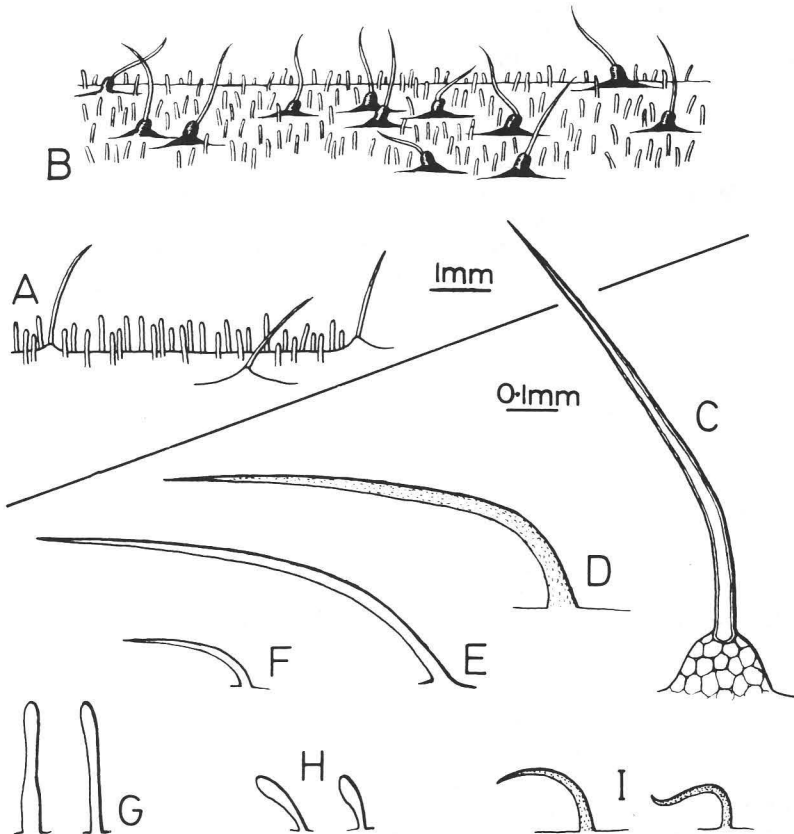


FIGURE 1. Indumentum in *Oenothera* subgenus *Oenothera*. A, part of surface of hypanthium of *O. rubricaulis* with glandular and stiff eglandular hairs; B, part of surface of ovary of *O. fallax* with glandular hairs and eglandular hairs with red bulbous bases; C, detail of last hair-type; D, arcuate stiff hair with verrucose surface; E & F, arcuate stiff hairs with smooth surface; G, glandular hairs; H, clavate hairs; I, crispate hairs with verrucose surface.

preserved in LINN. These species each have their own individual history, which determines their present-day pattern of distribution. They can hybridize in mixed populations to produce hybrids which often may be described as new taxa.

THE IMPORTANCE AND VARIABILITY OF CERTAIN CHARACTERS

Although the species of *Oenothera* subgenus *Oenothera* defined according to the European concept generally possess more or less constant characters, they have some peculiarities which must be taken into consideration during determination.

a. Shape of leaves. The narrow-leaved species are not variable, but the broad-leaved ones, e.g. *O. biennis*, *O. rubricaulis* and *O. suaveolens* Desf. ex Pers., may sometimes also possess narrow, lanceolate leaves, which can lead to wrong identification.

b. Size of flowers. Small-flowered species are always small flowered, but large-flowered ones may bear flowers as little as half their normal size—especially after their main flowering season. Both the sepal-tips and the petals may show this phenomenon. Table 1 gives measurements of various floral parts of four species grown in my garden in Poland in 1961 and 1979. Therefore, the main (earliest) phase of blooming is the best time for the identification of *Oenothera*.

c. Changes in fruit pubescence during development of the inflorescence. There are important specific characters in fruit pubescence, but these vary in different parts of the fruiting spike. On the inflorescence generally there are both stiff eglandular hairs and glandular hairs (Fig. 1). Some species possess both these types along the whole length of the inflorescence, but, in those species which do not develop glandular hairs in the older (lower) half, they can appear in the upper, youngest part of the spike, e.g. in section *Strigosae*. But the sequence of development of the various kinds of hairs is a major specific character.

d. Variation in development of some colour characters. There are some species which always have green sepals, but in the case of species with red sepals the development of anthocyanin may be prevented by low light intensity. This applies also to the midribs. White midribs are always white, but normally red ones may be white, especially in shade.

e. Variation in inflorescence erectness. There are some species in which the inflorescence tip is bent over, e.g. section *Parviflorae*. But this character may be easily overlooked, because often it can be seen only at the beginning of the flowering period, after which the axes of the inflorescence may be erect. On the other hand, accidental curving of the inflorescence tip may sometimes occur among the straight-growing species, where it is of no taxonomic importance.

Herbarium specimens are naturally collected in different phases of development, so that their proper identification is often difficult and misinterpretations of some characters may take place. Hence taxonomists studying *Oenothera* put the main stress on the investigation of living plants.

The appearance of the flowers in bud is an important character which should be carefully noted, particularly in relation to the size and form of the sepal-tips (Fig. 2A, B). Similarly the shape of the apex of the capsule teeth is valuable (Fig. 2C, D).

While collecting, some colour and size characters should be noted: colour of midribs of lower and upper stem leaves; presence or absence of red punctulation on green parts of stem, rhachis and fruits; extent of red striping, tingeing or dotting on buds; and colour of young rhachis at tip. The length/width ratio of petals should also be measured on fresh flowers.

Before pressing for the herbarium the whole plant should be cut in pieces to obtain several parts of stem with lower, middle and upper leaves and with inflorescence.

The pubescence may be best observed using the stereo-microscope.

In mixed populations consisting of two or more species, new taxa resulting from crossing can appear. These hybrids need to be analysed in detail, in respect to both their taxonomic characters and their genetical peculiarities. Sometimes such new taxa are constant in appearance and form extensive populations. In such cases they can be regarded as new species, e.g. *O. fallax* Renner.

Here and there may also occur unknown new aliens from other countries. In these cases the development of their populations and their homogeneity must be observed. The characters of these newcomers should be compared to the corresponding ones of the well-known species, leading to the

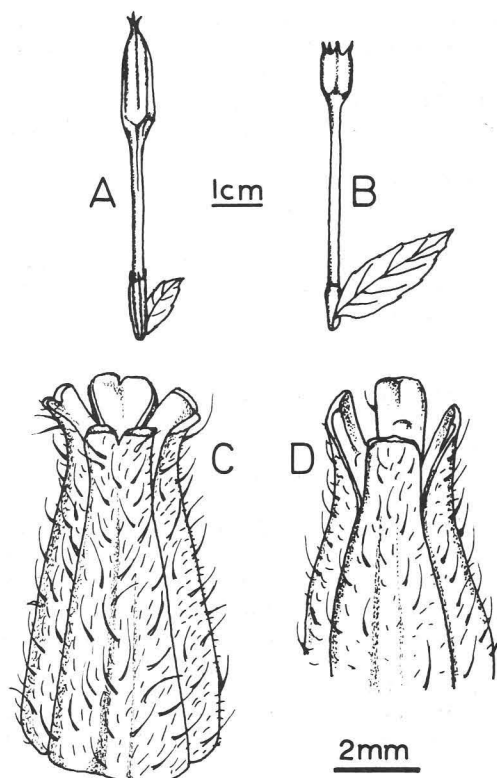


FIGURE 2. Characteristics of buds and capsules. A, bud of *O. fallax* with sepal-tips appressed below; B, bud of *O. parviflora* with sepal-tips separated; C, apex of capsule of *O. salicifolia* with emarginate teeth; D, apex of capsule of *O. cambrica* with truncate teeth.

establishment of the differences between them. The correctness of any new determinations should be verified by a specialist.

ORIGIN OF OENOTHERA SUBGENUS OENOTHERA IN EUROPE

In the European flora there have been recognized and described a total of 59 species and hybrids, a greater part of which (44) was described as new taxa during the last 25 years (Renner 12 taxa, Hudziok 16, Rostański 9, Rostański & Gutte 2, Linder & Jean 1, Kappus 1, Jehlík and Rostański 1, Soldano 2).

According to their origin the following groups can be distinguished:

1. European species which do not occur in North America: *O. biennis* sensu stricto, *O. rubricaulis* and *O. suaveolens*.
2. North American arrivals in Europe from the 17th to 20th centuries: *O. syrticola* Bartl., *O. salicifolia*, *O. erythrosepala*, *O. parviflora*, *O. silesiaca* Renner, *O. cruciata* Nutt. ex G. Don, *O. chicaginensis* De Vries ex Renner, *O. perangusta* Gates, *O. turoviensis* Rostański and perhaps *O. cambrica* Rostański.
3. Hybrids which originated in Europe from the crossing of either: (a) European and American species: *O. × braunii* Doell (= *biennis* × *parviflora*), *O. × fallax* Renner em. Rostański (= *erythrosepala* × *biennis*, treated as a species in this paper), *O. × issleri* Renner ex Rostański (= *biennis* × *syrticola*), *O. × heiniana* Teyber (= *syrticola* × *suaveolens*), *O. × oehlkersi* Kappus (=

- erythrosepala* × *suaveolens*), *O.* × *drawerti* Renner ex Rostański (= *salicifolia* × *suaveolens*), *O.* × *punctulata* Rostański & Gutte (= *biennis* × *chicaginesis*), *O.* × *polgari* Rostański (= *suaveolens* × *salicifolia*), *O.* × *hoelscheri* Renner ex Rostański (= *salicifolia* × *rubricaulis*), *O.* × *wienii* Renner ex Rostański (= *rubricaulis* × *salicifolia*); or (b) two American species: *O.* × *purpurans* Borbás (= *salicifolia* × *erythrosepala*) and *O.* × *slovaca* Jehlík & Rostański (= *salicifolia* × *turoviensis*).
4. Species of unknown origin: e.g. *O. ammophila* Focke, *O. ersteinensis* Linder & Jean, and various species or hybrids described by Hudziok, Rostański and Soldano.

Oenotheras occurring in Great Britain came here variously from the Continent or direct from America; probably none is native except for recent hybrids which originated here, e.g. *O.* × *britannica* (= *erythrosepala* × *cambrica*).

HISTORY OF *OENOTHERA* IN GREAT BRITAIN

Oenothera has been a subject of interest for British botanists from the beginning of the 17th century. The seeds of the first *Oenothera* to have appeared in the botanical literature were collected in Virginia by John Morus (or Morris?), the physician and philosopher, and were then sent from England to Prosper Alpinus in Italy, who called it *Hyosciamus virginianus* and made a drawing (Wein 1931, Rostański 1968b). This species belongs to section *Parviflorae* and seems to me to be near to or identical with *O. syrticola* (apart from its 5 petals!). It is certainly not *O. biennis*, as was thought by Linnaeus and most later authors. A primitive figure of *Oenothera* (named as *Lysimachia siliquosa virginiana*) was given by Parkinson (1640), but now it is impossible to state which species it represents.

The oldest British herbaria from the 17th and 18th centuries contain some *Oenotheras*, which were either collected in the field or cultivated in gardens. The following species, named with pre-Linnaean nomenclature, are represented in various Horti Sicci in **BM**:

O. biennis sensu stricto:

Lysimachia siliquosa virginiana major—HS 168: 215 (Bannister Herbarium)

Lysimachia lutea corniculata virginiana—HS 57: 8, no. 175

Lysimachia virginiana flore luteo—HS 45: 23 (Sloane Herbarium)

Lysimachia lutea corniculata—HS 321: 39 (Herbarium Boerhavianum)

Onagra latifolia flore sulphureo—Hortus Cliffortianus

Lysimachia lutea corniculata—HS 333: 15 (Dr Uvedale, c. 1650)

O. cambrica (probably):

Lysimachia siliquosa virginiana—HS 139: 11 (near Oxford, Duchess of Beaufort)

O. parviflora sensu stricto:

Lysimachia lutea virginiana pannonica quibusdam—HS 9 (H. Sloane, 1682)

Lysimachia virginiana—HS 13: 57, no. 2

Onagra angustifolia caule rubro flore minori (Inst. R.H. 302) (= *Oenothera angustifolia* Miller, 1768, nom. illeg.)—HS 295: 69 (Chelsea Physick Garden, 1768)

In the first half of the 19th century Forbes Young cultivated interesting *Oenotheras*, perhaps in his own garden in Cotham Lodge: *O. muricata* (*O. rubricuspis* Renner ex Rostański) in 1826, *O. parviflora* in 1829, *O. cruciata* in 1831, and *O. spectabilis* Hornem. in 1832. He collected also some specimens in the wild: *O. cambrica* (named *O. biennis*) in 1840 from Peckham fields; and *O. stricta* in 1837 from Wandsworth (specimens in **BM** and **K**).

Among the botanists who paid particular attention to *Oenothera* in the current century and often collected very interesting specimens should be mentioned the following:

C. Bailey, who discovered great populations of *O. erythrosepala* (named *O. lamarckiana* De Vries) at St Anne's-on-Sea in 1904 (Bailey 1907, 1915);

E. S. Marshall, who discovered *O. cambrica* at Berrow in 1906 and sent it to W. O. Focke, the discoverer of *O. ammophila* in the Friesian Islands. This specimen was by mistake determined by

Focke as *O. ammophila* and that is why this name began to be used in British literature, later to be replaced by the name *O. parviflora* (Perring & Walters 1962, p. 148);

R. R. Gates, who at the beginning of his famous *Oenothera* investigations researched *Oenothera* in Cheshire and Lancashire (Gates 1914) and then worked out Canadian *Oenotheras* in cultivation in Regent's Park, London (Gates 1936);

J. E. Lousley, an eminent investigator of alien plants in England, who collected many different specimens of *Oenothera* in various regions of Great Britain. These specimens are often very difficult to name, because many of them represent individuals varying from the typical in some way, or quite unknown adventive taxa;

B. M. Davis, who attempted (Davis 1926) to elucidate the history of *Oenothera* in England in the light of knowledge at that time and described a new species, *O. cantabrigiana* Davis (Davis 1940);

D. McClintock, who investigated *Oenothera* in Guernsey (McClintock 1975), collected *O. renneri* H. Scholz from Scotland in 1962 and grew it in his garden, and similarly *O. cambrica* from South Wales in 1969. His specimens and seeds sent to me were grown in my experimental field and enabled me to describe the last mentioned species as new;

C. A. Stace, who analysed the problem of hybridization of *Oenothera* in Britain (Stace 1975);

J. C. Bowra, who made observations on *Oenothera* populations near Warwick (Bowra 1980);

M. McC. Webster, who collected interesting specimens of *Oenothera* in Scotland, e.g. *O. renneri* in 1966, *O. longiflora* L. in 1964 and *O. fallax* in 1978.

Fairly numerous localities of various species of *Oenothera* have been published in local Floras from near the end of the 19th century onwards. Mostly these were under the names of *O. biennis*, *O. erythrosepala* (or *O. lamarckiana*), *O. ammophila* and *O. stricta* (or *O. odorata* Jacq.), since these are the taxa most frequently covered in the British Floras. Clapham (1952) dealt with five species in full: *O. biennis*, *O. erythrosepala*, *O. grandiflora* Ait. (*O. suaveolens*), *O. stricta* and *O. ammophila*. The descriptions of the first two of these, which are widespread in Britain, are good. The description of *O. ammophila* is correct with regard to the "infl. drooping for a considerable distance behind the tip. Sepals tinged and spotted with red. Petals 11–16 mm", but this species has not occurred in Britain. Small-flowered plants of *O. cambrica* will key out as *O. ammophila* in Clapham's account. *O. grandiflora* is native to southern U.S.A. (Munz 1965) and has not occurred in Europe, being a short-day plant which does not reach flowering in European conditions (fide W. Stubbe of Düsseldorf). *O. suaveolens* is a distinct species of southern Europe which has not occurred in Britain. Clapham (1962) added *O. parviflora* to the above five species, saying that it is closely related to *O. ammophila*.

Perring & Walters (1962) mapped the distribution of *O. biennis*, *O. erythrosepala*, *O. parviflora* and *O. stricta*, but stated in relation to the first two species: "There is acknowledged taxonomic confusion here and the records should be treated with caution". My examination of herbarium specimens of these two species confirms this statement. The distribution they give of *O. stricta* is representative but that of *O. parviflora* corresponds in the greater part to that of the then undescribed *O. cambrica*, especially in Wales and southern England.

Twenty years ago I started to study *Oenothera* in Europe. From 1965 to 1970 I determined British specimens from CGE, E and K. Of course, I had some problems with naming certain specimens and I made some errors. For instance I identified *O. coronifera* Renner (it was a form of *O. erythrosepala*), *O. nuda* Renner ex Rostański (which may be a Canadian newcomer near *O. victorini* Gates), and *O. chicaginensis*. The last mentioned, previously named in Britain as *O. parviflora* or *O. ammophila*, was *O. cambrica*, which I later (Rostański 1977) described as a new species. *O. renneri*, collected in Scotland by D. McClintock in 1960, was recorded by me for the first time.

In September 1977 I visited Britain and examined the specimens of *Oenothera* in the British herbaria mentioned by McClintock (1978). Thanks to the help of S. G. Harrison and G. Ellis in Cardiff I made an interesting field trip in S. Wales to see the *locus classicus* of *O. cambrica* in Pembrey and other localities of this species and *O. erythrosepala* (Rostański & Ellis 1979).

From 1977 to 1981 I revised specimens from some other British herbaria (ABS, GL, LTR, MANCH and UCNW) and also from Lady Anne Brewis (Blackmoor), Mrs M. Briggs (Horsham), Q. C. B. Cronk (Cambridge), T. Edmondson (Chester), J. C. Bowra (Warwick), M. A. Hyde (Woolverstone), Dr C. A. Stace (Leicester), Mrs F. le Sueur (Jersey) and R. C. Palmer (Oxford).

On the basis of these records I worked out the distribution of the British species as indicated

below. Bowra (1980) has already reported on my determinations of his specimens from Warwick. The distributions on the Continent are based on my own examination of *Oenothera* specimens received from various European herbaria in the years 1960–1980.

SPECIES OF *OENOTHERA* OCCURRING IN GREAT BRITAIN

The 15 species treated in the following account are classified into the following subgenera and sections. The sections of subgenus *Oenothera* follow those of Rostański (1965), although they are considered series or subseries by Dietrich (1978).

Subgenus *Oenothera*

Section *Oenothera*: 1. *O. biennis* L.; 2. *O. cambrica* Rostański; 3. *O. erythrosepala* Borbás; 4. *O. fallax* Renner; 5. *O. rubricaulis* Klebahn; 6. *O. perangusta* Gates

Section *Strigosae* Rostański: 7. *O. salicifolia* Desf. ex G. Don; 8. *O. renneri* H. Scholz

Section *Parviflorae* Rostański: 9. *O. parviflora* L.; 10. *O. rubricuspis* Renner ex. Rostański

Subgenus *Hartmannia* (Spach) Munz: 11. *O. rosea* L'Hérit. ex Aiton; 12. *O. tetraptera* Cav.

Subgenus *Raimannia* (Rose) Munz: 13. *O. laciniata* Hill; 14. *O. longiflora* L.; 15. *O. stricta* Ledeb. ex Link

In Britain the four most frequent species, in descending order of abundance, are *O. erythrosepala*, *O. biennis*, *O. cambrica* and *O. stricta*. In central Europe, on the other hand, the sequence is *O. biennis*, *O. rubricaulis*, *O. salicifolia*, *O. erythrosepala*, *O. parviflora* and *O. renneri*.

Besides these species, and various hybrids involving the first three of them, I have seen a number of herbarium specimens which I cannot identify with certainty. Most are similar to one or other of the 15 species, and probably would be identified as such if complete specimens were available, but others most closely resemble different species not certainly recorded from Britain. For example, a specimen collected on Walton Common, Surrey, v.c. 17, in 1961 by D. Philcox (K) appears close to *O. lipsiensis* Rostański & Gutte, and a specimen collected from Cofton, S. Devon, v.c. 3, in 1915 by E. S. Marshall (BM) appears close to *O. victorini*. *O. argentinæ* Léveillé & Thell. was recorded by Riddelsdell *et al.* (1948) from Avonmouth Docks, W. Gloucs., v.c. 34, in 1932, but I have not seen the specimen and various varieties of this species are placed under different species by Dietrich (1978). A few other species have been grown in England, e.g. *O. cruciata* by Forbes Young at Cotham Lodge in 1831 (K), but have not been recorded in the wild.

In the following account I have only cited herbarium material seen by me. Obviously this represents but a fraction of the total in existence, and a particularly small fraction of the modern collections, but I hope that the records quoted will form a sound basis for future studies.

Since I am not an expert on *Oenothera* outside subgenus *Oenothera*, I have provided only brief diagnoses of species from subgenera *Hartmannia* and *Raimannia*, but have also given a reference to a fuller, authentic description by Munz (1965) or Dietrich (1978).

KEY TO SPECIES

Two distinct hybrids and two distinct varieties are also included

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|----|--|----|
| 1. | Capsule oblong, fusiform or cylindrical, without wings; petals yellow | 2 |
| 1. | Capsule clavate, the basal part sterile and narrowed, the distal part thicker, fertile and ribbed or winged (subgenus <i>Hartmannia</i>) | 18 |
| 2. | Capsule cylindrical, usually somewhat tapering upwards, c. 6–8 mm wide at base; seeds prismatic, sharply angled (subgenus <i>Oenothera</i>) | 3 |
| 2. | Capsule oblong-fusiform, usually enlarged towards apex, about 2–4 mm wide at base; seeds not angled (subgenus <i>Raimannia</i>) | 16 |
| 3. | Capsule-teeth obtuse or truncate (rarely somewhat emarginate); ovary with stiff hairs and glandular hairs | 4 |
| 3. | Capsule-teeth distinctly emarginate; ovary and young capsule whitish appressed | |

	strigose, without glandular hairs at least in lower part of inflorescence; petals 7–25 mm (section <i>Strigosae</i>)	15
4.	Sepal-tips appressed at least below, their apices usually arcuate-divergent; tip of stem erect; cauline leaves various; petals 10–50 mm (section <i>Oenothera</i>)	5
4.	Sepal-tips erect, separated from their bases in bud; cauline leaves lanceolate; tip of stem ± nodding before anthesis then usually erect; petals less than 20 mm (section <i>Parviflorae</i>)	14
5.	Stem without red bulbous-based hairs on green parts; sepals always green; petals 15–30 mm	6
5.	Red bulbous-based hairs on stem, rhachis and ovaries	7
6.	Cauline leaves elliptic or elliptic-lanceolate; petals broader than long; rhachis and capsules with numerous glandular hairs	1. <i>O. biennis</i>
6.	Cauline leaves lanceolate; petals ± as broad as long; lower capsules without glandular hairs	2. <i>O. cambrica</i> var. <i>impunctata</i>
7.	Petals 30–50 mm; style long with stigma-lobes spreading above the anthers; sepals red-striped; capsules red-punctulated, with numerous eglandular and glandular hairs	3. <i>O. erythrosepala</i>
7.	Petals 10–35 mm; style with stigma-lobes spreading between anthers or at their apices	8
8.	Sepals red-striped	9
8.	Sepals green; leaf midribs red	12
9.	Rhachis reddened at tip; all capsules glandular with some red bulbous based hairs	10
9.	Rhachis green; lower capsules with only eglandular hairs; upper ones with eglandular and glandular ones	11
10.	Leaves elliptic or elliptic-lanceolate, often crinkled, with red or white midribs; petals 20–30 mm, broader than long; capsules densely pubescent	4. <i>O. fallax</i>
10.	Leaves lanceolate or narrowly lanceolate, flat, with red midribs; petals 10–20 mm, as broad as long; capsules with glabrous spaces along the valvae	6. <i>O. perangusta</i> var. <i>rubricalyx</i>
11.	Petals 15–20 mm, slightly pubescent outside at base or glabrous	4 × 2. <i>O. fallax</i> × <i>O. cambrica</i>
11.	Petals 25–35 mm, distinctly pubescent outside at base	3 × 2. <i>O. erythrosepala</i> × <i>O. cambrica</i>
12.	Rhachis always green at tip; petals 20–30 mm; lower capsules with eglandular hairs only; capsule-teeth up to 2 mm, obtuse; leaves lanceolate, flat	2. <i>O. cambrica</i> var. <i>cambrica</i>
12.	Rhachis red or reddened at tip; petals 10–20 mm; all capsules with numerous glandular and eglandular hairs; capsule-teeth shorter	13
13.	Hypanthium 15–25 mm; leaves elliptic or elliptic-lanceolate, wavy; papillae funnel-shaped; capsule pilose	5. <i>O. rubricaulis</i>
13.	Hypanthium 30–32 mm; leaves lanceolate, flat; papillae cylindrical; capsules with glabrous spaces along the valvae	6. <i>O. perangusta</i> var. <i>perangusta</i>
14.	Sepal-tips 2–3 mm, distinctly separated in bud; buds green, sometimes turning red in late flowering phase; petals 6–12 mm; capsule with glandular and eglandular hairs	9. <i>O. parviflora</i>
14.	Sepal-tips 2–4 mm, less separated in bud; buds reddened between sepal-tips from start of flowering; petals 12–18 mm; capsule with mostly glandular hairs	10. <i>O. rubricuspis</i>
15.	Cauline leaves oblong-lanceolate with wavy margins and curved tips, with reddish midribs; young rhachis red; inflorescence loose; flowers often cleistogamous; papillae on stem and rhachis very low, red	7. <i>O. salicifolia</i>
15.	Cauline leaves lanceolate, flat or channelled, with white midribs; tip of rhachis green, rarely slightly reddened; inflorescence compact; flowers open; papillae usually green	8. <i>O. renneri</i>
16.	Stems usually branched, decumbent; leaves sinuate-pinnatifid; mature buds nodding, the younger ones erect; petals 5–18 mm	13. <i>O. laciniata</i>

16. Stem erect; leaves serrate; buds erect; petals 15–40 mm 17
 17. Cauline leaves 15–60 × 10–30 mm; hypanthium 60–100 mm; petals 20–40 mm ..
 14. *O. longiflora*
 17. Cauline leaves 60–180 × 6–25 mm; hypanthium 20–45 mm; petals 15–35 mm 15. *O. stricta*
 18. Petals rose to red-violet, 5–10 mm; hypanthium 4–8 mm; capsule 3–4 mm wide with
 ± 1 mm wide wings 11. *O. rosea*
 18. Petals whitish or pink, 20–35 mm; hypanthium c. 10 mm; capsule 6–8 mm wide with
 2–3 mm wide wings 12. *O. tetraptera*

DESCRIPTION AND DISTRIBUTION OF TAXA

Subgenus *Oenothera*

Oenothera subgenus *Euoenothera* Munz, Revista Universitaria Univ. Catol. Chile, **22**: 262 (1937).

Biennial herbs making rosette of leaves in first year and erect flowering shoots in the second. Leaves toothed. Flowers yellow, vespertine; hypanthium long-cylindrical. Capsule sessile, ± tapering upwards; seeds prismatic, angled.

Section *Oenothera*

Axis of inflorescence erect, with glandular and stiff hairs. Cauline leaves elliptic or elliptic-lanceolate or rarely lanceolate, flat or wavy. Petals 10–50 mm. Sepal-tips connected at least at their bases in bud. Capsule-teeth obtuse, rarely emarginate.

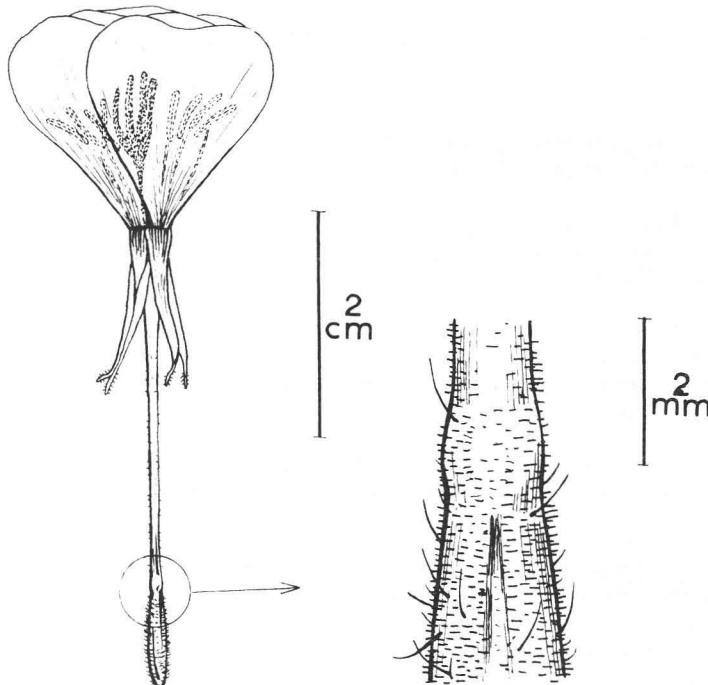


FIGURE 3. Flower of *O. biennis* with enlarged transitional part between ovary and base of hypanthium.

1. *Oenothera biennis* L., Sp.Pl. 346 (1753).

Synonyms: *Onagra biennis* (L.) Scop., Fl.Carn., ed. 2, 1: 628 (1772); *Onagra europaea* Spach, Hist. Veg. (Phan.), 4: 359. (1835); *Oenothera biennis* subsp. *biennis* sensu Munz, N. Amer.Fl., II (5): 132 (1965).

Figure 3.

Stem 100–150 cm, simple or branched, with appressed arcuate hairs and longer stiff hairs on bulbous coniform green papillae (papillae red on red splotches on stem). Leaves elliptic to elliptic-lanceolate or oblanceolate, slightly denticulate, flat, somewhat pubescent, with red midrib (except in shade). Rhachis green at tip, strongly glandular-pubescent. Buds green; sepal-tips 2–3 mm, appressed below, somewhat divergent above. Hypanthium 28–35 mm. Petals obcordate, distinctly broader than long, 15–30 × 18–35 mm (linear in var. *leptomeres* Bartlett), yellow (pale yellow in f. *sulphurea* De Vries). Anthers 5–10 mm. Stigma-lobes spreading between anthers, 5–15 mm. Capsule 20–35 mm, green, glandular-pubescent with arcuate simple or bulbous-based stiff hairs; teeth obtuse.

Sand-dunes, sandy river shores, waste places, railway banks and sidings, etc. Temperate Europe, E. Asia (Primorskij Kraj in eastern U.S.S.R., southern Sachalin, northern Japan). Unknown in U.S.A.

In Britain *O. biennis* is the second most common species of *Oenothera*, occurring northwards to Invergowrie (56°29'N). The earliest British record dates from c. 1650 (Hortus Siccus Vol. 333, **BM**); there are many fairly early records from Lancashire, to which it was perhaps introduced from the Continent.

- W. Cornwall, v.c. 1: Between Brea and Cassock Hills, 1953, R. H. Good (**LTR**); Padstow, 1957, R. W. David (**LTR**).
- S. Devon, v.c. 3: Plymouth, 1846, S. Goulding (**MANCH**).
- Somerset, v.c. 5 or 6: Woolchester (?), 1857, H.P.R. (**BRIST**).
- Wight, v.c. 10: St Helen's Spit, 1899, A. Loydell (**OXF**).
- N. Hants., v.c. 12: Hogmoor Enclosure, Longmoor, 1978, A. Brewis (**herb. A.B.**); The Slab, Bordon, 1979, A. Brewis (**herb. A.B.**); Aldershot, 1980, A. Mundell (**KTU**).
- E. Sussex, v.c. 14: Isfield, 1884, T. Hilton (**BM**); Nr Crawley, 1906, H. S. Thompson (**CGE**); Camber Sands, 1952, R. C. Palmer (**OXF**).
- E. Kent, v.c. 15: Sandling, 1883, H. Lamb (**MNE**).
- W. Kent, v.c. 16: Bexley, 1843, E. Edwards (**MANCH**); North Cray Woods, 1845, J. W. Rimmington (**MANCH**); Woolwich Arsenal, 1954, J. F. Hall (**MNE**).
- Surrey, v.c. 17: Battersea Fields, 1847, H. Taylor (**OXF**); Thames Ditton, 1864, H. C. Watson (**BM**); Witley, near the station, 1880 & 1888, E. S. Marshall (**CGE, BRISTM**); Weybridge Heath, 1900, J. Fraser (**K**); Crooksbury, 1922, H. W. Monckton (**RNG**); Godalming, 1933, T. J. Foggitt (**BM**); Dulwich Woods, Camberwell, 1958, J. E. Lousley (**RNG**); Walton Common, 1979, R. M. Burton (**herb. R.M.B.**).
- Middlesex, v.c. 21: Cottage Garden, 1780, Smithian Herb. No. 655.2 (**LINN**); S. Kensington, 1907, G. A. Boulanger (**BM**); Hanwell, Rubbish Hill, 1947, A. H. G. Alston (**BM**); Rubbish tip, Hounslow Heath, 1961, D. Philcox & C. C. Townsend (**K**); Sunbury-on-Thames, 1930, J. E. Lousley (**RNG**); Same place, 1972, B. M. Gerrans (**BM**).
- Berks., v.c. 22: Enborne, 1895, A. B. Jackson (**BM**); Rubbish heap near Wellington College, 1916, H. W. Monckton (**RNG**); Tubney Wood, 1965, R. C. Palmer (**OXF**); Wokingham, 1965, H. J. M. Bowen (**OXF**).
- Oxon, v.c. 23: Banbury, 1872, A. French (**BM**); Headington, 1896, G. C. Druce (**OXF**); Oxford, 1909, G. C. Druce (**OXF**).
- E. Suffolk, v.c. 25: Woodbridge, 1810, D. Turner (Herb. Smith, **LINN**); Same place, 1829, C. Stewart (**CGE**); Suffolk coast, 1811, G. R. Lather (**K**); Kessingland, 1935, J. B. Evans (**BM**).
- W. Suffolk, v.c. 26: Mildenhall, 1953, M. Southwell (**CGE**).
- E. Norfolk, v.c. 27: Thorpe Plantation, 1834, R. J. Mann (**K**); Holt, 1896, A. Wallis (**CGE**).
- Camb., v.c. 29: Kennet, 1950, M. Southwell (**CGE**).
- Beds., v.c. 30: Luton, 1901, D. M. Higgins (**BM, RNG**); Maulden, 1931, M. Brown & J. E. Little (**CGE**).
- E. Gloucs., v.c. 33: Cheltenham, 1948 & 1950, C. C. Townsend (**K**).
- Warks., v.c. 38: Warwick, 1977 & 1979, J. C. Bowra (**herb. J.C.B.**).
- Salop, v.c. 40: Shifnal & Ruckley, 1890, Bullock (**OXF**).
- Merioneth, v.c. 48: Aberdovey, 1850, V. H. Painter (**ABS**); Same place, 1875, H. E. Fox (**OXF**); Same place, 1980, C. J. Vaughan (**OXF**); Barmouth, 1867, M. A. Lawson (**BM, OXF**); Same place, 1871, W. E. Backhouse (**E**); Same place, 1884, W. Pamplin (**OXF**); Same place, 1905, E. M. Walker (**CGE**); Same place, 1960, P. Benoit (**K**).

- Caerns., v.c. 49: Castle Bank, Bangor, 1876, J. T. C. Williams (NMW); Morfa Bychan, nr Portmadoc, 1890, J. E. Griffith (NMW).
- N. Lincs., v.c. 54: Lace, Sea Hull (?), 1862, R. T. Lowe (BM).
- Leics., v.c. 55: Knighton Clay Pit, Leicester, 1950, E. K. Horwood (LTR).
- Notts., v.c. 56: Boughton Brake, nr Ollerton, 1963, L. F. Bowden & G. C. Hillman (BM); Newark, 1891, H. Fisher (TUR).
- Cheshire, v.c. 58: Caldý, W. Kirby, 1893, G. V. C. Last (K); Winnington, 1915, W. Horton-Smith (MANCH); Birkenhead, Bidston Moors, 1934, T. Green (LIV).
- S. Lancs., v.c. 59: Many records, including: Sandhills N. of Liverpool, 1805, J. Shepherd (LINN); Same place, 1821, W. Gardiner jun. (LTR); Same place, 1825, W. Wilson (CGE); Nr Liverpool, no date but c. 1830, ex herb. Conway (NMW); Sandy coast, 1832, N. Tyacke (OXF); Birkdale dunes, 1899, J. A. Wheldon (NMW); Same place, 1929, F. W. Holder (LIV); Same place, 1974, C. A. Stace (LTR); Ainsdale dunes, 1928 & 1947, F. W. Holder (LIV); Hightown, 1904 to 1913, J. A. Wheldon (BRIST, CGE, K, MANCH, NMW, OXF); Southport, 1835, B. H. Allen (CGE); Same place, 1851, J. Dugdale (BM); Same place, 1883 to 1891, C. Bailey (MANCH); Same place, 1915, J. D. Firth & E. C. Howell (OXF); Freshfield, 1869, G. E. Hunt (K); Same place, 1880, A. French (BM); Same place, 1913, R. H. Compton (CGE); Formby, 1878, J. A. Wheldon (GL); Same place, 1882, R. Brown (LIV); Crosby, 1825, W. Borrer (K); Same place, 1862, V. W. Benn (LIV); Same place, 1871 to 1879, J. H. Lewis (BM, LTR, MANCH, OXF); Same place, 1891, E. Gibson (LIV); Same place, 1916, W. G. Travis (LIV); Same place, 1930, C. T. Green (LIV); Hillside, 1931, J. W. Holder (LIV); Altcar, 1912, R. H. Compton (CGE); Same place, 1932, E. Vachell (NMW); Mersey View, Waterloo, 1872, D. H. L. (MANCH).
- W. Lancs., v.c. 60: Ansdell, 1904, J. A. Wheldon (NMW); St Anne's-on-Sea, 1898, J. A. Wheldon (NMW); Lytham, 1963, A. E. Ratcliffe (LIV).
- S.W. Yorks., v.c. 63: Linthwaite, 1959, R. Lancaster & C. E. Shaw (RNG).
- Ayrs., v.c. 75: Doonfoot, 1854, no collector (GL).
- Angus, v.c. 90: Invergowrie, 1926, R. H. Corstorphine (BM).

I have seen only one specimen of *O. biennis* var. *leptomeres*:

Middlesex, v.c. 21: Acton, 1907, A. Leydal (BM).

Forma *sulfurea* probably occurs in Britain, but is impossible distinguish other than in the fresh state.

Hybrids of *O. biennis* as female parent.

O. biennis × *O. cambrica*

Stem and rhachis green, but red-punctulated on green parts; leaves lanceolate or elliptic-lanceolate, with white or pink midrib; sepal-tips 1–2(4) mm; hypanthium 25–33 mm; petals glabrous, 13–20 mm; anthers and stigma-lobes 4–6 (9) mm; stigma-lobes spreading between anthers; capsule green, slightly pubescent with stiff and glandular hairs and with glabrous spaces along the valves; the number of glandular hairs in fruiting spike increasing upwards.

N. Hants., v.c. 12: Woolmer Pond, 1979, A. Brewis (herb. A.B.); The Slab, Hogmoor Lane, 1978, 1980, A. Brewis (KTU).

Warks., v.c. 38: Emscote, nr Warwick, 1977, 1979, 1980, J. C. Bowra (herb. J.C.B.).

O. biennis × *O. erythrosepala*

O. × *albivelutina* Renner, Ber. dt. bot. Ges., 60: 460 (1942), nomen nudum.

Stem and rhachis red-punctulated (rarely not); leaves elliptic to elliptic-lanceolate, with white or pink midrib; buds green or striped brownish-red; sepal-tips 3–4(6) mm; hypanthium (25)30–35(40) mm; petals c. 35 mm, glabrous or slightly pilose at base without; anthers 6–10(13) mm; stigma-lobes 4–8(10) mm, exceeding anthers or spreading between them.

N. Hants., v.c. 12: Longmoor, by disused railway, 1980, A. Brewis (herb. A.B.).

W. Sussex, v.c. 13: West Worthing, 1928, A. J. Crosfield (K).

N. Essex, v.c. 19: Colchester, 1881, J. D. Gray (BM).

- Herts., v.c. 20: Rickmansworth, J. M. Bryan (CGE).
 W. Suffolk, v.c. 26: Mayday Farm, Elveden-Brandon, 1961, P. D. Sell (CGE); Same place, 1961, J. E. Lousley (RNG); Same place, 1970, D. McClintock (herb. D.McC.).
 Beds., v.c. 30: Luton, 1901, D. M. Higgins (CGE).
 Warks., v.c. 38: Emscote, nr Warwick, 1977, 1978, 1980, J. C. Bowra (herb. J.C.B.).
 Cheshire, v.c. 58: Muldsworth, 1968, J. Edmondson (K).
 S. Lancs., v.c. 59: Norkton (?), Midland Station, 1875, G. C. Druce (OXF); Southport, Birkdale, 1933, T. J. Foggitt (BM); Same place, 1974, C. A. Stace (LTR); Freshfield, 1905, C. T. Green (BM); Same place 1950, T. R. Leycock (MANCH); Ainsdale, 1971, C. A. Stace (LTR).
 W. Lancs., v.c. 60: St Anne's-on-Sea, 1907, C. Bailey (OXF, MANCH); Same place, 1912, R. H. Compton (CGE); Ansdell, 1912, R. H. Compton (CGE).

The record for Guernsey (McClintock 1978) comes from Renner (1942, pp. 460–461): “Aus den Samen der *O. biennis* von der Insel Guernesey (leg. Ewald) gingen mehrere Individuen des Bastardes *O. (biennis × Lamarckiana) albivelutina* hervor, mit getupften Stengel, ziemlich schmalblättrig, in der Mehrzahl weissnervig, eine davon rotnervig”.

O. biennis × *O. fallax* (effectively a backcross)

This differs from *O. biennis* only in its red-punctulated stem and rhachis.

- S. Lancs., v.c. 59: Birkdale, nr Southport, 1974, C. A. Stace (LTR).

O. biennis × *O. cambrica* × *O. erythrosepala*

Stem green, not red-punctulated; leaves elliptic-lanceolate, with white midrib; glandular hairs only in upper part of the inflorescence; hypanthium c. 30 mm; buds green; sepal-tips 5–6 mm; petals glabrous, 25–35 mm; anthers 8–11 mm; stigma-lobes 6–10 mm, exceeding anthers.

- Warks., v.c. 38: Emscote, nr Warwick, 1979, 1980, J. C. Bowra. (herb. J.C.B.).

2. *Oenothera cambrica* Rostański, Fragm.Fl.Geobot., 23: 285 (1977).

Synonyms: *O. parviflora* auct.brit., non L.; *O. foliis lanceolatis dentatis caule hispido* Miller, Gard. Dict., 2: 126 (1771).

Figures 4, 2D.

Stem 60–100 cm (in cultivation up to 150 cm), often branched in lower half (in dunes sometimes with lowest branches lying on sand with ascending tips), green or reddish, strongly punctulated with red splotches, with numerous stiff hairs on red bulbous bases and shorter arcuate hairs (red splotches and redness of bulbous-based hairs absent in var. *impunctata* Rostański). Leaves elliptic-lanceolate or lanceolate, with reddened midrib, slightly denticulate to ± entire, flat, ± pubescent. Rhachis green but red-punctulated (not in var. *impunctata*), with glandular hairs only in upper part. Buds green; sepal-tips 3–5 mm, appressed below, somewhat divergent above. Hypanthium 25–35 mm. Petals yellow, glabrous, obcordate, as broad as long or somewhat narrower, 20–30 × 21–28 mm. Anthers 6–12(14) mm. Stigma-lobes spreading between anthers, 6–16 mm. Capsule 30–40(45) mm, green, with hairs with red bulbous bases (green in var. *impunctata*); upper ones with glandular hairs as well; teeth up to 2 mm, obtuse.

Sand-dunes, sandy sea-shores, railway banks, waste places.

This species is confined to Wales, Jersey and southern England northwards to Llangollen (52°58'N), but its origin is uncertain. The oldest specimen definitely attributable to *O. cambrica* was collected in Cardiff in 1833, but an 18th century specimen in Hortus Siccus Vol. 139 (BM) might also belong here. It is now the third most frequent species in Britain. Its distribution in Wales was mapped by Rostański & Ellis (1979).

It seems probable that this species was introduced from Canada in the 18th century. The specimen portrayed in Miller (1771, pl. 189, fig. 1) seems to correspond to *O. cambrica*, as does the description

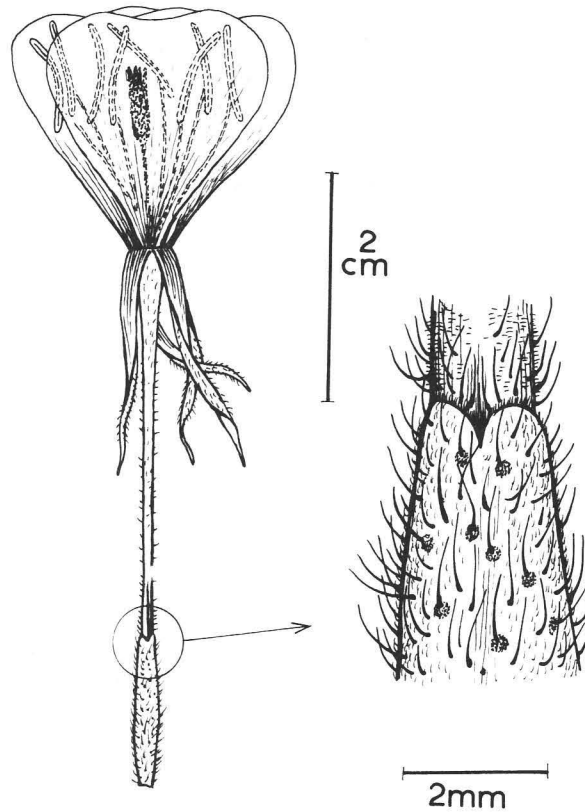


FIGURE 4. Flower of *O. cambrica* with enlarged transitional part between ovary and base of hypanthium.

on p. 126. The author writes that this species “grows naturally in Canada” and supposes that “having been long cultivated in gardens the seeds were scattered and thereby propagated the plants in so great plenty, as to appear as it was native of England”. In addition, a specimen from one strain of *O. novae-scotiae* Gates “with large flowers” cultivated in Regent’s Park, London, by Gates from seed coming from Middleton, Nova Scotia, Canada (**BM**) seems to be near to *O. cambrica*.

Guernsey: Port Soif, 1967, D. McClintock (**herb. D.McC.**).

Jersey: St Brelade’s Bay, 1867, H. E. Fox (**OXF**); Same place, 1871, C. Bailey (**MANCH**); St Aubin’s Bay, 1884, F. J. Hanbury (**BM**); Same place, 1898, L. V. Lester-Garland (**K**); Same place, 1900, J. Piquet (**OXF**); Same place, 1906, G. C. Druce (**OXF**); Same place, 1924, F. le Sueur (**JSY**); Route de Trinité, 1925, F. le Sueur (**JSY**); Mt Maco Quarry, 1962, J. Fluck (**JSY**); St Ouens, 1969, J. E. Lousley (**RNG**); Val de la Mare, 1973, F. le Sueur (**JSY**).

W. Cornwall, v.c. 1: Penzance, 1854, I. M. Roper (**BRISTM**); St Just, 1934, J. L. Dawson (**E**).

E. Cornwall, v.c. 2: Rock, 1930, H. E. Fox (**OXF**).

S. Devon, v.c. 3: Exmouth, no date, W. K. Crotch (**CGE**).

N. Devon, v.c. 4: Braunton Burrows, 1915, E. S. Marshall (**BM, E**); Same place, 1915, W. A. Shoolbred (**NMW**); Same place, 1917, A. B. Colte (**OXF**); Same place, 1958, J. Evans (**BRISTM**); Same place, 1958, E. F. Warburg (**OXF**); Same place, 1968, G. Paxman (**LANC**); Same place, 1980, J. G. Keylock (**LANC**).

N. Somerset, v.c. 6: Burnham, 1861, J. Sadler-Gale (**OXF**); Same place, 1880 to 1906, J. W. White (**BRIST**); Same place, 1883, W. B. Waterfall (**MANCH**); Same place, 1912 & 1919, R. H. Compton (**CGE**); Same place, 1927, V. S. Summerhayes (**K**); Berrow, 1906, E. S. Marshall (**BM, BREM, E**); Same place, 1910, A. Ley (**LTR**); Same place, 1916, C. Bucknall (**BRIST**); Same place, 1938, J. E. Woodhead (**LANC**); Same place, 1951, C.I. & N.Y. Sandwith (**K**); Same place, 1955, A. H. G. Alston (**BM**); Same place, 1955, J. W. Evans (**BRISTM**); Portishead railway sidings, 1939, J. E. Woodhead (**LANC**).

- Wight, v.c. 10: unlocalized, 1973, A. Brewis (**herb. A.B.**).
- S. Hants., v.c. 11: Hayling Island, 1960, S. Warren (**CGE**); Same place, 1980, A. Brewis (**herb. A.B.**); Southampton Docks, 1958, J. E. Lousley (**RNG**).
- N. Hants, v.c. 12: Woolmer Forest, 1978, A. Brewis (**herb. A.B.**); Slab, Bordon, 1979, A. Brewis (**herb. A.B.**).
- W. Sussex, v.c. 13: West Wittering, 1930, Miss Hotham (**CGE**); Same place, 1953, M. B. Mallinson (**LTR**); Same place, 1978, M. Briggs (**herb. M.B.**); Pilsley Island, 1978, M. Briggs (**herb. M.B.**).
- W. Kent, v.c. 16: Shorne, Arles Pit, 1974, J. E. Lousley (**RNG**); Stone, Horns Cross Pit, 1974, E. G. Philp (**MNE**).
- Surrey, v.c. 17: Peckham Fields, 1840, J. Forbes Young (**BM**).
- Berks., v.c. 22: Didcot, 1977, R. C. Palmer (**herb. R.C.P.**).
- Oxon, v.c. 23: Roman Way, Oxford, 1972, R. C. Palmer (**OXF**); Same place, 1977, K. Rostański (**KTU**).
- E. Suffolk, v.c. 27: Sizewell, 1834, C. M. Lemann (**CGE**).
- W. Gloucs., v.c. 34: Bristol, 1867, S. Brody (**RISTM**); Same place, 1869, H. Trimen (**BM**); Same place, 1937, C. I. Sandwith (**BRIST**); Sharpness Docks, 1952, C. C. Townsend (**K**); Same place, 1956 & 1962, J. E. Lousley (**BM, RNG**).
- Mons., v.c. 35: Abercarn, 1924, A. E. Wade (**NMW**); Monmouth, 1928 & 1930, C. I. Sandwith (**BRIST**); Newport Docks, 1935, C. I. Sandwith (**BRIST**); Newport, 1954, J. S. L. Gilmour (**CGE**); Redbrook, 1936, S. G. Charles (**NMW**); Whitebrook, 1948, S. G. Charles (**NMW**); Rogerstone, 1963, A. P. Conolly & H. Reeve (**LTR**).
- Warks., v.c. 38: Emscote, nr Warwick, 1977, 1979, 1980, J. C. Bowra (**herb. J.C.B.**).
- Glam., v.c. 41: Many records, including: Cardiff, banks of Taff, 1833, Mr Daw (**GL**); Cardiff, 1921 to 1954, A. E. Wade (**NMW**); Same place, 1977, K. Rostański (**KTU**); Gwaelod-y-gardh, 1970, D. McClintock (**herb. D.McC.**); Briton Ferry, 1858, H. Boswell (**OXF**); Pentyrch, 1879 & 1892, C. T. & E. Vachell (**NMW**); Crymlyn Burrows, 1892, E. F. Linton (**BM**); Same place, 1933, H. A. Hyde (**NMW**); Same place, 1961, A. John (**ABS**); Gower, 1890, A. B. Sampson (**K**); Oxwich, 1908, A. H. Trow (**UCSW**); Same place, 1977, K. Rostański (**KTU**); Whitmore Bay, Barry Island, 1902, R. Williams (**ABS**); Barry Docks, 1969, D. McClintock (**herb. D.McC.**); Jersey Marine, Swansea, 1948, J. E. Lousley (**RNG**); Same place, 1977, K. Rostański (**KTU**); Radyr, 1920, R. L. Smith (**NMW**); Kenfig Burrows, 1951, C. W. Bannister (**BM**); Same place, 1977, K. Rostański (**KTU**); Whitford Burrows, 1956, A. E. Wade (**NMW**); Same place, 1977, K. Rostański (**KTU**); Merthyr Mawr, 1966, V. Lavelly (**RNG**); Dyffryn Woods, 1971, A. M. Pell (**NMW**); Danygraig, 1939, J. A. Webb (**NMW**); Nantgarv, 1934, E. M. MacAllister (**E**).
- Brecks., v.c. 42: Glanrhyd to Ystradgynlais, 1941, J. A. Webb (**NMW**).
- Carms., v.c. 44: Pembrey Burrows, 1899, E. S. Marshall (**BM, CGE**), Same place, 1970, D. McClintock (**Holotypus, KTU**); Same place, 1977, G. Ellis (**NMW**); Same place, 1977, K. Rostański (**KTU**); Bynea (?), 1939, J. A. Webb (**NMW**); Kidwelly, 1930, A. E. Wade (**NMW**); Same place, 1943, J. A. Webb (**NMW**); Ferryside, 1960 to 1966, R. F. May (**NMW**); Same place, 1977, K. Rostański (**KTU**); Laugharne Burrows, no date, G. I. Thomas (**NMW**).
- Pembs., v.c. 45: Tenby Burrows, 1867, no collector (**BM**); Saundersfoot, 1925, H. A. Hyde (**NMW**); Same place, 1930, A. E. Ellis (**LANC**); St Dogmaels, 1975, G. Ellis (**NMW**).
- Cards., v.c. 46: Glandyfi to Ynyslas, 1955, T. A. Wilkins (**NMW**); Aberystwyth, 1975, A.D.Q. Agnew (**ABS**).
- Monts., v.c. 47: Dovey Junction Station, 1953, P. M. Benoit (**NMW**).
- Merioneth, v.c. 48: Aberdovey, 1875, H. E. Fox (**MANCH**); Barmouth Station, 1906, R. H. Goode (**BM**); Harlech Point, 1956, Woodhead (**NMW**); Same place, 1980, J. C. Bowra (**herb. J.C.B.**).
- Caerns., v.c. 49: Morfa Bychan, 1955, E. K. Horwood (**LTR**); Portmadoc, no date, J. E. Lousley (**RNG**).
- Denbs., v.c. 50: Trevor to Llangollen, 1954, A. E. Wade (**NMW**).
- N.E. Yorks., v.c. 62: Carthan Dunes, Redcar, 1958, J. E. Lousley (**RNG**).

Var. impunctata:

- Oxon, v.c. 23: Oxford, Roman Way, 1977, K. Rostański (**KTU**).
- Glam., v.c. 41: Jersey Marine, Swansea, seed collected 1973 by D. McClintock, grown 1975 in Katowice by K. Rostański (**Holotypus, KTU**; **paratypes, K, KTU, NMW**); Cardiff Castle grounds, 1954, J. W. Davies (**NMW**); Dunes at Oxwich, nr Swansea, 1977, G. Ellis (**NMW**); Pembrey, 1971, D. McClintock (**herb. D.McC.**).

Hybrids of *O. cambrica* as female parent.

O. cambrica × *O. biennis*

Stem and rachis red-punctulated; leaves lanceolate, with pink midrib; glandular hairs present along

whole length of rhachis; hypanthium 23–30 mm; buds yellow-green; sepal-tips 1–4 mm; petals glabrous, 15–30 mm; anthers 5–10 mm; stigma-lobes spreading between anthers, 5–12 mm.

W. Cornwall, v.c. 1: The Towans, Phillack, Hayle, 1937, J. E. Lousley (RNG).
Warks., v.c. 38: Emscote, nr Warwick, 1979, J. C. Bowra (herb. J.C.B.).

O. cambrica × *O. fallax* (effectively a triple-hybrid)

Stem and rhachis red-punctulated; leaves lanceolate or oblanceolate, with white or pink midrib; glandular hairs more frequent towards apex of rhachis; hypanthium 25–30 mm; buds green; sepal-tips 1–2 mm; petals glabrous or slightly pilose at base without, 20–25 mm; anthers 4–5 mm; stigma-lobes spreading between anthers, 7 mm.

Warks., v.c. 38: Emscote, nr Warwick, 1979, J. C. Bowra (herb. J.C.B.).

O. cambrica × *O. erythrosepala*

Stem and rhachis red-punctulated or not; leaves lanceolate or elliptic-lanceolate, with pink or white midrib; glandular hairs more frequent towards apex of rhachis; hypanthium 25–35 mm; buds green; sepal-tips 2–6 mm; petals glabrous or very slightly pilose at base without, 25–35 mm; anthers 5–11 mm; stigma-lobes 6–13 mm, almost exceeding anthers.

N. Hants., v.c. 12: By tank establishment, Hogmoor, 1978, 1979, 1980, A. Brewis (herb. A.B.).
Warks., v.c. 38: Emscote, nr Warwick, 1977, 1979, 1980, J. C. Bowra (herb. J.C.B.).
Glam., v.c. 41: Oxwich dunes, 1977, K. Rostański & G. Ellis (KTU).

3. *Oenothera erythrosepala* Borbás, Magyar Bot. Lapok, 2: 245 (1903).

Synonyms: *O. lamarckiana* auct., non Séringe in DC., Prodr., 3: 46 (1828); *O. lamarckiana* De Vries, Mutationstheorie, 1: 151–378 (1901); *O. vriesseana* Léveillé, Monogr. Oenoth. 368 (1909); *O. glazoviana* Micheli in Martius, Fl. Bras., 13 (2): 178 (1882); *O. grandiflora* subsp. *erythrosepala* (Borbás) Löve & Löve, Op. bot., 5: 258 (1961).

Dietrich (1978, p. 617) wrote on the nomenclature of this species as follows: "Although the name *O. glazioviana* Micheli (1882) antedates *O. erythrosepala* Borbás (1903) and we believe that these names refer to the same entity, as indicated by the synonymy above, I am not making the substitution at the present time pending further studies . . . will clarify the taxa involved".

Figure 5.

Stem up to 180 cm, simple or branched, green or reddish, strongly punctulated with red splotches, with spreading short hairs and longer stiff hairs with red bulbous bases. Leaves elliptic to oblong-lanceolate, with white or reddish midrib, denticulate, somewhat pubescent, often strongly crinkled, rarely flat. Rhachis green but red-punctulated, reddened at apex, with numerous glandular hairs and stiff hairs with red bulbous bases. Buds red-stripped when ripe (rarely green at start of flowering phase), strongly glandular-pubescent; sepal-tips 3–8 mm (sometimes 2 mm in autumn), appressed below, somewhat divergent above. Hypanthium 30–40 mm. Petals glabrous or rarely slightly pilose without, yellow, broadly obcordate, broader than long, 30–50 × 32–58 mm (but often much smaller in autumn). Anthers 10–13 mm. Stigma-lobes considerably exceeding anthers, 6–10 mm. Capsule green or red-stripped when young, 20–35 mm, densely glandular and with long stiff hairs with red bulbous bases; teeth concave to ± obtuse.

Sand-dunes, roadsides, railway tracks, waste places, etc. Introduced into Europe from North America in the middle of the 19th century as an ornamental; suggestions that it arose in Europe as a mutation are fanciful. Bailey (1915) wrote: "In 1858 a firm of London nursery men introduced seeds into England from Texas without being aware that they were those of *lamarckiana* . . . From these seeds it may be inferred that all the modern examples of the species have been derived". Lehmann (1922) gave the following information, taken from Dombain (Floral Magazine 1862): "We

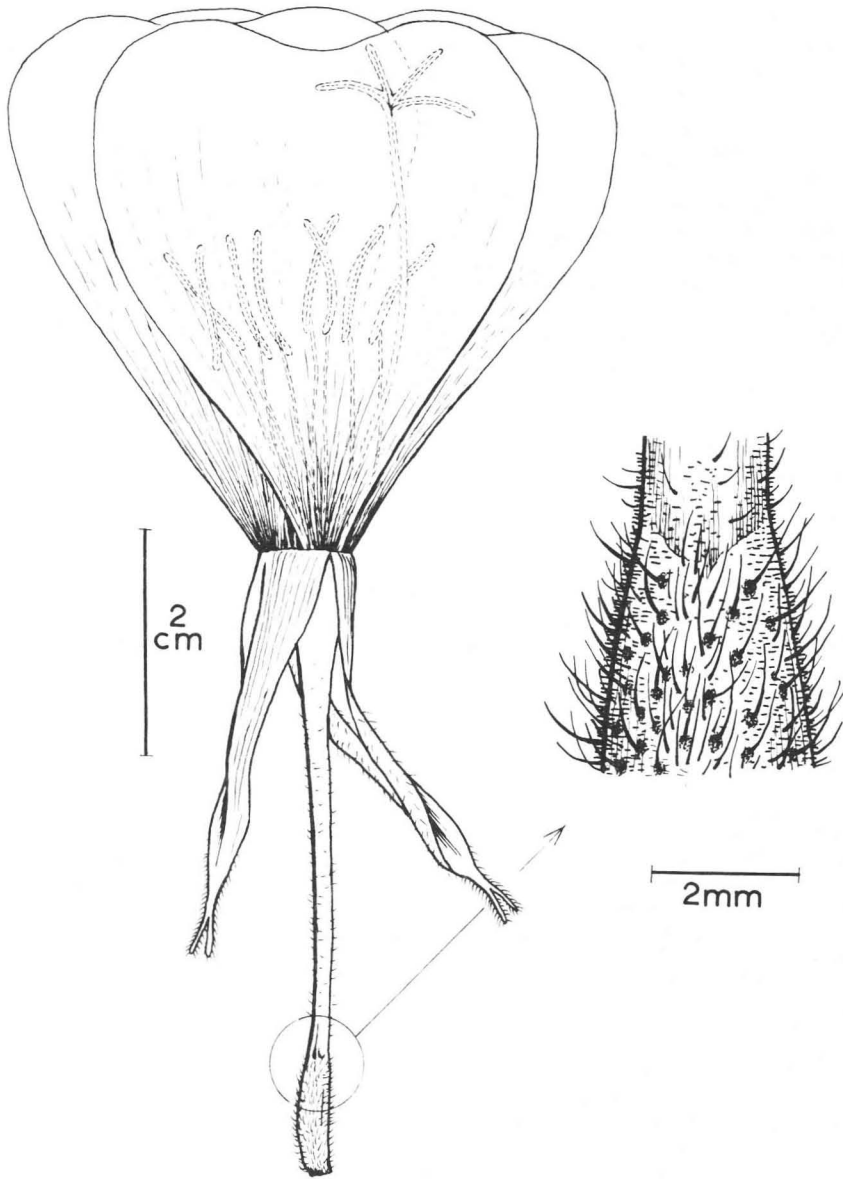


FIGURE 5. Flower of *O. erythrosepala* with enlarged transitional part between ovary and base of hypanthium.

received, about four years ago, some seed from Texas unnamed. When we flowered it, we sent some blooms to Dr. Lindley, who pronounced it to be *Oenothera Lamarckiana*, a species we believe introduced into England by Mr. Drummond". De Vries (1905, p. 384) wrote: "Die Samenhandlung von Ernst Benary zu Erfurt, aus deren Kulturen die jetzt bei Hilversum wildwachsenden Oenotheren stammen, hat die *O. lamarckiana* zum ersten Male im Jahre 1861 in ihrem Katalog eingeführt und zwar infolge einer Empfehlung der Royal Horticultural Society in London". Later, Lehmann (1922, p. 37) wrote: "Zur selben Zeit wurde die *O. lamarckiana* in den meisten europäischen Grossamenhandlungen eingeführt, zuerst wohl von Carter & Holborn, London, von wo sie auch Benary in Erfurt bezogen haben soll". Therefore the supposition by Gates (1915, p. 16)

that '*O. lamarckiana*' "established itself on the Lancashire coast between 1785 and 1796 . . . and 1805, when it was observed in Lancashire in abundance" has no supporting evidence. The *Oenothera* to which Gates referred "was gathered . . . on the coast a few miles off Liverpool where millions of the same species have been observed by Dr. Bostock and Mr. John Shepherd, perfectly wild and covering a large tract between the first and second range of sand-hills" (Sowerby 1806), and was true *O. biennis*, as shown by the specimen collected by J. Shepherd in 1805 (**K**). It is now widely naturalized in Europe, and even more widespread (east to the Caucasus) as a casual or garden escape. The oldest European specimen known to me was grown in the Leningrad Botanical Garden in 1864 (v.v. Herder e seminibus de Haag, no. 2150, **LE**). However, a specimen under the name '*Oenothera spectabilis* Hornem.' cultivated at Cotham Lodge in 1832 by Forbes Young (**K**) resembles *O. erythrosepala*, but has more hairy capsules and shorter petals (30 mm).

O. erythrosepala is the commonest species of the genus in Britain, although the earliest wild-collected specimen (from the Isle of Wight) is not much over 100 years old (1866). It occurs northwards to Barbaraville, E. Ross (57°42'N) and in Northern Ireland (Co. Down, v.c. H38). The distribution in Wales has been mapped by Rostański & Ellis (1979).

Guernsey: Le Vau de Morel, Pleinmont, 1972, R. de Sansmerez (**JSY**).

Jersey: St Aubin's and St Helier, 1906, G. C. Druce (**OXF**); Samares (?), 1924, F. le Sueur (**JSY**).

Sark: 1953, B. Sowerby (**BM**).

W. Cornwall, v.c. 1: Tresco, Scilly, 1967, F. Russel & J. E. Lousley (**RNG**); Newquay, no date, G. G. Druce (**OXF**); Padstow, 1957, R. W. David (**LTR**).

E. Cornwall, v.c. 2: Carlyon Bay, 1952, L. M. Hill & F. J. Taylor (**LTR**).

S. Devon, v.c. 3: Lyme Regis to Seaton, 1935, W. C. Worsdell (**K**); Dawlish Warren, 1959, J. E. Lousley (**RNG**).

N. Devon, v.c. 4: Braunton Burrows, 1931, R. Meinertzhagen (**BM**); Same place, 1939, J. E. Woodhead (**LANC**); Same place, 1949, E. K. Horwood (**LTR**); Same place, 1957, G. A. Matthews (**BM**).

N. Somerset, v.c. 6: Burnham sand-hills, 1944, H. Williams (**LTR**).

Dorset, v.c. 9: Poole, 1927, W. E. Grevithick (**K**); Lytchett Minster to Broadstone, 1952, R. H. Goode (**LTR**).

Wight, v.c. 10: Niton, 1866, J. R. E. (**OXF**).

Hampshire, v.c. 11/12: Sewage works, 1878, G. C. Druce (**BM**).

S. Hants., v.c. 11: Exbury, 1926, R. Jindbay (**K**); Hayling Island, 1980, A. Brewis (**KTU**).

N. Hants., v.c. 12: Liss, 1908, E. Hoult (**K**); Woodmoor Forest, 1978, A. Brewis (**herb. A.B.**); The Slab, Bordon, 1979, A. Brewis (**herb. A.B.**); Aldershot, 1980, A. Mundell (**KTU**).

E. Sussex, v.c. 14: Brockhurst, East Grinstead, 1933, F. J. Hanbury (**BM**).

E. Kent, v.c. 15: Littlestone, no date, E. C. Wallace (**RNG**); Lympne, no date, E. Birchall (**OXF**); Littlestone-on-Sea, 1915, A. J. Crosfield (**K**); Folkestone Sands, 1958, F. Rose (**MNE**); Rubbish heap nr Dungeness Station, 1913, R. H. Compton (**CGE**).

Surrey, v.c. 17: Spontaneous in Kew Gardens (cultd in 1911), 1920, W. B. Turrill (**K**); Same place, 1931, T. A. Sprague (**K**); Same place, 1948, J. Souster (**K**); Same place, 1952, W. T. Stearn (**BM**); Wisley to Pyrford, 1923, J. E. Lousley (**RNG**); Weybridge, 1924, J. Fraser (**K**); Mitcham Rubbish Tip, 1930 & 1956, J. E. Lousley (**RNG**); Ham, 1952, S.R.C. & T.R.S. (**K**); Juniper Hall, Dorking, 1960, S. Sherwood (**LIV**); Walton Common, 1961, D. Philcox (**K**); Bagshot, no date, E. V. Watson (**RNG**); Mickleham, no date, J. R. Sealey & S. Ross-Craig (**K**).

S. Essex, v.c. 18: Hawkwell, 1933, R. S. Vine (**K**).

N. Essex, v.c. 19: Colchester, 1881, J. D. Gray (**CGE**).

Herts., v.c. 20: Hitchin, 1923, J. E. Little (**BM, CGE**).

Middlesex, v.c. 21: Drayton Brooks, 1906, G. C. Druce (**OXF**); Uxbridge, 1907, U. R. Sharron (**BM**); Southgate, 1915, H. S. Redgrove (**BM**); Teddington, 1925, L. J. Foster (**RNG**); Newgate Street to St Pauls, 1959, M. E. Robson (**RNG**).

Oxon, v.c. 23: Henley, 1935, T. Chapple (**BM**); Port Meadow, 1957, R. F. Norris (**RNG**); Same place, 1965, H. J. M. Bowen (**OXF**).

Bucks., v.c. 24: Marlow, 1956, J. Wallace (**LIV**).

E. Suffolk, v.c. 25: Woodbridge, 1913, R. H. Compton (**CGE**); Beccles, 1934, J. E. Lousley (**RNG**).

W. Suffolk, v.c. 26: Cockfield, 1871, C. C. Babington (**BM**); Barton Mills, 1955, M. Southwell (**CGE**).

E. Norfolk, v.c. 27: Wymondham, no date, Miss Pomeroy (**OXF**); Yarmouth, 1910, S. H. Bickham (**CGE, LTR**).

W. Norfolk, v.c. 28: East Wretham, 1916, A. R. Horwood (**NMW**); Narborough, 1950, E. K. Horwood (**LTR**); Thetford, 1961, P. D. Sell (**CGE**).

Cambs., v.c. 29: Cambridge, 1940, H. Gilbert-Carter (**CGE**); Same place, 1970, S. M. Walters (**CGE**); Trumpington to Hauxton, 1951, P. D. Sell (**CGE**); Hauxton Mill, 1958, P. D. Sell (**CGE**); Earith, river bank, 1951, P. D. Sell (**CGE**).

Beds., v.c. 30: Flitton, 1962, P. D. Sell (**CGE**).

- Hunts., v.c. 31: Conington rubbish tip, 1948, J. G. Dony (**BM**); Same place, 1961, C.E.G. Tutin (**LTR**).
 E. Gloucs., v.c. 33: Ashton, 1888, J.W.W. (**LIV**); Staymesgarth, Cleave, 1915, C. Bailey (**MANCH**);
 Leckhampton, Cheltenham, 1951, C. C. Townsend (**K**).
 W. Gloucs., v.c. 34: Bristol, 1935, E. Y. E. Bell (**LTR**); Same place, 1938 & 1940, C. I. & N. Y. Sandwith
 (**BRISTM**).
 Mons., v.c. 35: Tintern, 1943, R. Lewis (**BM**); Abergavenny, 1959, A. E. Wade (**NMW**); Yvns-ddu, 1968, A. E.
 Wade (**NMW**).
 Worcs., v.c. 37: Charlton, 1958, J. E. Lousley (**RNG**).
 Warks., v.c. 38: Emscote, nr Warwick, 1977 & 1979, J. C. Bowra (**herb. J.C.B.**); Nr Southam, 1978, J. Ford
 (**herb. J.C.B.**).
 Glam., v.c. 41: Canton, Cardiff, no date, J. W. Davies (**NMW**); Blackpill, 1941, J. A. Webb (**NMW**); Horton
 Burrows, 1945, E. Vachell & J. A. Webb (**NMW**); Port Eynon, 1948, J. E. Lousley (**NMW, RNG**); Kenfig,
 1951, C. W. Bannister (**BM**); Black Cork Inn, 1954, V. Edwards (**NMW**); Swanbridge, 1954, A. E. Wade
 (**NMW**); Swansea, Black Pill, 1977, K. Rostański (**KTU**) Oxwich, 1977, K. Rostański (**KTU**).
 Carms., v.c. 44: Burry Port, 1916, G. C. Druce (**OXF**); Same place, 1965, R. F. May (**NMW**).
 Pems., v.c. 45: Goodwick, 1950, L. M. Hill & F. J. Taylor (**LTR**); Lydstep Haven dunes, 1957, E. K. Horwood
 (**LTR**); Haverfordwest, 1963, T. A. W. Davis (**NMW**).
 Cards., v.c. 46: Llanbadarn, 1970 & 1975, R. G. Ellis (**NMW**).
 Merioneth, v.c. 48: Barmouth, Llanhedo, 1928, no collector (**LIV**); Mochras, nr Harlech, 1954, B. W. Ribbons
 (**GL**); Harlech, 1965, E. V. Watson (**RNG**).
 Caerns., v.c. 49: Llandudno, 1960, L. J. Larsen (**NMW**); Abersoch, 1958, A. P. Conolly (**LTR**).
 Flints., v.c. 51: Rhuddlan, 1971, G.W. (**BM**).
 N. Lincs., v.c. 54: Grimsby, 1913, G. Walworth (**NMW**).
 Leics., v.c. 55: Wanlip, 1957, J. M. Hartshorn (**LTR**).
 Derbys., v.c. 57: Repton, 1882, E. D. Bostock (**LTR**); Bakewell, Haddon Closes, 1960, P. W. Ball (**LIV**).
 Cheshire, v.c. 58: Caldly, W. Kirby, 1893, G. V. C. Last (**K**); Bidston Junction, Birkenhead, 1905, C. T. Green
 (**BM**); Bidston, 1912, Harrison (**LIV**); Boughton Hall, Chester, 1925, C. Waterfall (**OXF**); Hoole Village, nr
 Chester, 1968, J. Edmondson (**K**).
 S. Lancs., v.c. 59: Southport, 1891 to 1907, C. Bailey (**MANCH**); Same place, 1913, G. Walworth (**NMW**);
 Walton Gaol, 1912, J. A. Wheldon (**NMW**); Birkdale, 1913, R. H. Compton (**CGE**); Same place, 1928, T. J.
 Foggitt (**BM**); Same place, 1974, C. A. Stace (**LTR**); West Kirkby, 1914, Ellis (**LIV**); Crosby, 1939, J. W.
 Holder & T. N. Frankland (**LIV**); Ainsdale, 1946, J. W. Holder (**LIV**); Same place, 1952, E. M. Rosser & B.
 Benick (**MANCH**); Same place, 1971, C. A. Stace (**LTR**); Formby, 1957, E. F. Greenwood (**LIV**); Seaforth,
 1960, R. K. Brummitt (**LIV**); St Helens, 1976, Liverpool Bot. Soc. (**LIV**).
 W. Lancs., v.c. 60: St Anne's-on-Sea, 1904–1908, C. Bailey (**BRIST, CGE, E, K, LTR, MANCH**); Same place,
 1912, Miss Lee (**LIV**); Same place, 1912, J. Evans (**BRISTM**); Same place, 1913, R. H. Compton (**CGE**); Same
 place, 1932, E. Vachell (**NMW**); Lytham, 1909, no collector (**BRIST**); Bryning Warton, 1971, E. F.
 Greenwood (**LIV**).
 S.E./Mid W. Yorks, v.c. 61/64: Selby, Olimpia Mills, C. I. Sandwith (**BRIST**).
 W. Lothian, v.c. 84: Linlithgow, 1871, B. Balfour (**OXF**).
 E. Ross, v.c. 106: Barbaraville, 1978, M. McC. Webster (**BM**).

Hybrids of *O. erythrosepala* as female parent.

O. erythrosepala × *O. biennis* = *O.* × *fallax*, treated as a separate species in this account.

O. erythrosepala × *O. cambrica* = *O.* × *britannica* Rostański, **hybr.nov.** (Fig. 6)

Ab *O. erythrosepala* Borbás, cui similis, differt petalis minoribus, 25–35 mm longis, ad basim in externa parte pilosis, stylo brevioribus infra antheras vel supra apicibus eius positus, apicibus sepalorum brevioribus, 1–3(5) mm longis. Provenit in Britannia intra populationes specierum parentalium.

HOLOTYPE: Sandy ground near sea, Oxwich dunes, Glam., v.c. 41, 14/9/1977, K. Rostański & G. Ellis (**KTU**).

Stem, rhachis and ovaries with red bulbous-based hairs; leaves lanceolate, with white or pink midrib; hypanthium 30–40 mm; buds red-striped; sepal-tips 1–3(5) mm; petals 25–35 mm, distinctly

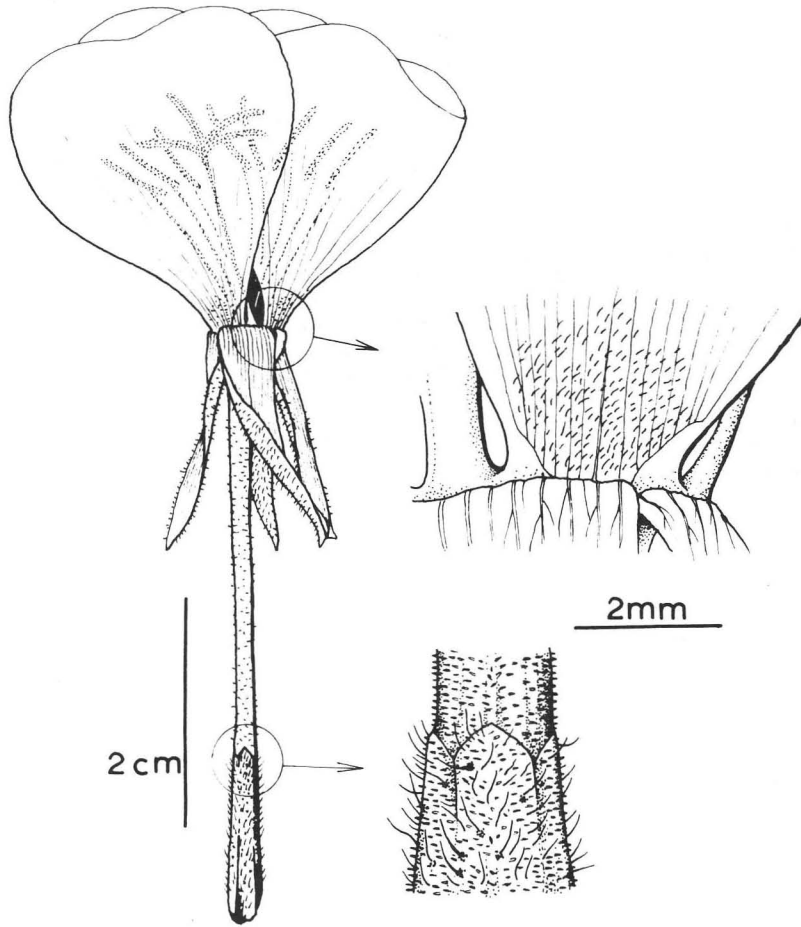


FIGURE 6. Flower of *O. × britannica* with enlarged transitional part between ovary and base of hypanthium, and enlarged part of petal base from outside.

pilose at the base without; anthers 6–10 mm; stigma-lobes spreading between anthers or somewhat longer, 5–8 mm; lower capsules hirsute, upper ones with increasing number of glandular hairs, sometimes with glabrous spaces along the valves.

N. Hants., v.c. 12: The Slab, Bordon, 1979, A. Brewis (**herb. A.B.**).

Oxon, v.c. 23: Oxford, Blackfriars Road, 1977, K. Rostański (**KTU**).

Warks., v.c. 38: Emscote, nr Warwick, 1979, 1980, J. C. Bowra (**herb. J.C.B.**).

Glam., v.c. 41: Holotype above; Canton, Cardiff, 1956, J. W. Davies (**NMW**); Kenfig dunes, 1963, R. M. Speed (**ABS**).

The backcross to *O. cambrica* has flowers like those of *O. × britannica* but with green buds and shorter hypanthia (c. 25 mm).

Warks., v.c. 38: Emscote, nr Warwick, 1980, J. C. Bowra (**herb. J.C.B.**).

The backcross to *O. erythrosepala* has flowers like those of *O. erythrosepala* (with a long style and petals) but the bases of the petals are distinctly pilose without.

N. Hants., v.c. 12: Hogmoor Lane, 1980, A. Brewis (KTU).

Glam., v.c. 41: Black Pill, Swansea, 1977, K. Rostański & G. Ellis (KTU); Oxwich dunes, 1977, K. Rostański & G. Ellis (KTU).

Plants which appear to be crosses between *O.* × *britannica* and *O. fallax* (effectively *O. biennis* × *O. cambrica* × *O. erythrosepala* but differing from that, see under *O. biennis*) have flowers like those of *O. fallax* (with a short style) but the bases of the petals are distinctly pilose without.

Warks., v.c. 48: Emscote, nr Warwick, 1980, J. C. Bowra (herb. J.C.B.).

O. erythrosepala × *O. fallax* (effectively a backcross)

Stem, rhachis and capsules red-punctulated, with glandular and eglandular hairs; leaves elliptic-lanceolate, crinkled, with red midrib; buds red-striped; sepal-tips 2–3 mm; hypanthium 30–34 mm; petals 30–37 mm, glabrous; anthers 7–9 mm; stigma-lobes slightly exceeding anthers, 3–6 mm.

S. Lancs., v.c. 59: Birkdale dunes, 1974, C. A. Stace (LTR).

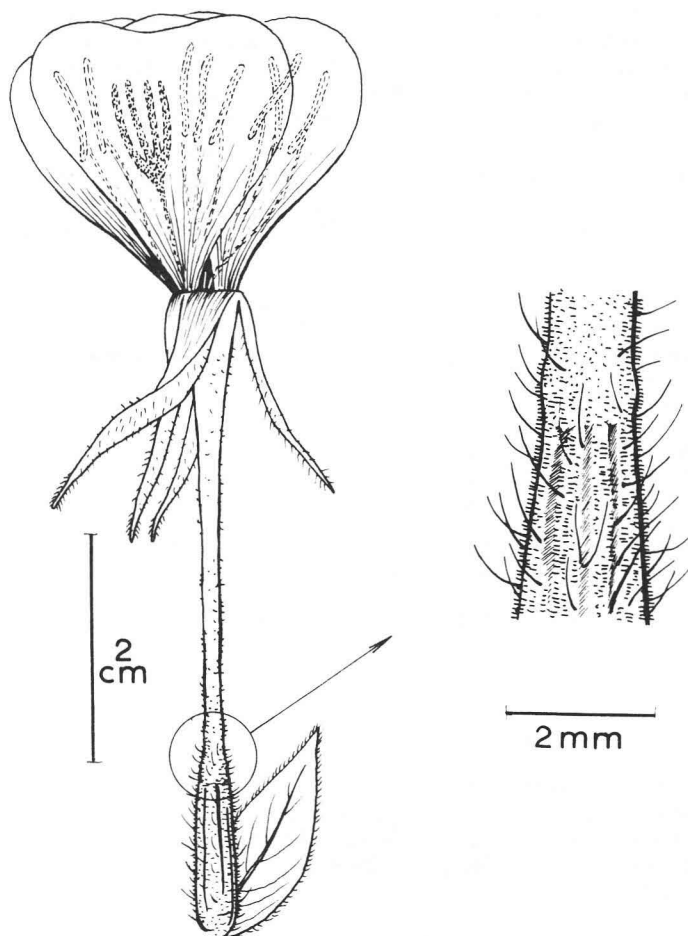


FIGURE 7. Flower of *O. fallax* with enlarged transitional part between ovary and base of hypanthium.

4. *Oenothera fallax* Renner, Zeitschr. Abst. Vererb., **18**: 176 (1917), emend. Rostański, Fragm. Flor. Geobot., **11**: 507 (1965).
 Synonyms: *O. cantabrigiana* B. M. Davis, Genetics, **25**: 435 (1940); *O. velutirubata* Renner, Ber. dt. bot. Ges., **60**: 461 (1942).
 Figures 7, 1B, 2A.

Stem often over 100 cm, often with branches from low down, green or somewhat reddened, distinctly red-punctulated, with numerous long stiff hairs with bulbous red bases and shorter arcuate hairs. Leaves elliptic to ovate-lanceolate, with white or reddish midrib, denticulate, pubescent, the lower ones crinkled. Rhachis green, red-punctulated, reddened at apex, with numerous glandular hairs and stiff hairs with red bulbous bases. Buds red-striped, with stiff and glandular hairs; sepal-tips 2–4 mm, appressed below, divergent to appressed above. Hypanthium 30–40 mm. Petals yellow, obcordate, broader than long, 20–30 × 22–34 mm. Anthers 3–10 mm. Stigma-lobes spreading between anthers, 5–10 mm. Capsule green, red-striped when young, 20–30 mm, red-punctulated, with numerous glandular hairs; teeth obtuse to emarginate.

This taxon arose as a hybrid between *O. erythrosepala* (female) and *O. biennis* (male). It is constant in its characters (unlike the reciprocal hybrid) and is often grown in botanic gardens under the name *O. lamarckiana*.

It is found in the wild as a spontaneous hybrid and it also escaped independently from cultivation; this, added to its constancy, suggests it is best treated as a separate species.

Sand-dunes, waste places, etc. Outside Britain it has been found wild in Poland (Rostański 1965), West Germany (seen by me in 1980 along the Rhine from Düsseldorf to Kehl), East Germany (Gutte & Rostański 1971), and Czechoslovakia (Roubal 1971, Jehlík & Rostański 1979).

In Britain it was cultivated in Cambridge in 1928 (Davis 1940) and Oxford in 1977 (seen by me). The oldest British record is from Aintree, S. Lancs., in 1892 (see below). It was also collected by Bailey from St Anne's-on-Sea, W. Lancs., in 1907 (see below), and named as a "short-styled form" of *O. lamarckiana*. McClintock (1975) recorded it from Guernsey and Jersey, but I have not seen specimens.

N. Hants., v.c. 12: The Slab, Bordon, 1980, A. Brewis (**herb. A.B.**); Longmoor, 1980, A. Brewis (**herb. A.B.**).
 Surrey, v.c. 17: Mitcham, 1979, R. M. Burton (**herb. R.M.B.**).

S. Essex, v.c. 18: Grange, Loughton, seed from Tewkesbury, 1913, R. H. Compton (**CGE**).

Warks., v.c. 38: Emscote, nr Warwick, 1979, J. C. Bowra (**herb. J.C.B.**).

Glam., v.c. 41: Waste ground, Swansea, 1977, K. Rostański (**KTU**); Sand-dunes, Whitford Burrows, 1977, G. Ellis (**NMW**).

S. Lancs., v.c. 59: Aintree, 1892, G. V. C. Last (**K**); Ainsdale, 1942, no collector (**LIV**); Same place, 1971, C. A. Stace (**LTR**); Freshfield dunes, 1956, R. K. Brummitt (**LIV**); Same place, 1965, E. V. Watson (**RNG**); Birkdale, 1974, C. A. Stace (**LTR**); Ince Moors, 1969, T. Edmondson (**LIV**); Guce Moss, Wigan, 1969, T. Edmondson (**LIV**).

W. Lancs., v.c. 60: St Anne's-on-Sea, 1907, C. Bailey (**K, LTR, MANCH**).

Westmorland, v.c. 69: Between Sizerburgh and Heaves, 1975, G. Halliday (**LANC**); Near Grayrigg Tarn, Kendal, 1980, J. Thompson (**LANC**).

E. Ross, v.c. 106: Fortrose, 1978, M. McC. Webster (**BM**).

Hybrids of *O. fallax* as female parent.

O. fallax × *O. biennis* (effectively a backcross)

Stem slightly red-punctulated; rhachis green, glandular-pubescent; leaves elliptic, crinkled, with red midrib; buds at start of flowering phase slightly red-striped, then green; sepal-tips 1–3 mm; hypanthium 28–35 mm; petals glabrous, 22–28 mm; anthers 5–7 mm; stigma-lobes spreading between anthers, 7–8 mm.

Warks., v.c. 38: Emscote, nr Warwick, 1979, 1980, J. C. Bowra (**herb. J.C.B.**).

S. Lancs., v.c. 59: Ainsdale, 1971, C. A. Stace (**LTR**); Birkdale, 1974, C. A. Stace (**LTR**).

O. fallax × *O. cambrica* (effectively a triple hybrid)

Stem red below, green and red-punctulated above, rhachis glandular-pubescent, with red bulbous-based hairs; leaves lanceolate, with white or pink midrib; buds red-striped; hypanthium 35–40 mm; sepal-tips 1 mm; petals glabrous, 15–20 × 15–20 mm; anthers 3–4 mm; stigma-lobes 5 mm, spreading between anthers or slightly shorter; capsules 20–30 mm, with glandular and eglandular hairs.

N. Hants., v.c. 12: Hogmoor, 1979, A. Brewis (herb. A.B., KTU).

O. fallax × *O. erythrosepala* (effectively a backcross)

Stem, rhachis and capsules red-punctulated, with glandular and eglandular hairs; leaves lanceolate, ± flat, with white midrib; buds slightly red-striped; sepal-tips c. 3 mm; hypanthium 24–32 mm; petals 30–37 mm, sparsely pubescent at base without; anthers 9–11 mm; stigma-lobes exceeding anthers, 4–6 mm.

S. Lancs., v.c. 59: Birkdale dunes, 1974, C. A. Stace (LTR).

5. *Oenothera rubricaulis* Klebahn, Jahrb.Hamb.Anst., 31: 12 (1914).

Synonyms: *O. muricata* L., Syst.Nat., ed. 12, 263 (1767), nomen confusum; *O. biennis* var. *parviflora* Abromeit, Fl.Ost-Westpreussen, 1: 276 (1898); *O. muricata* var. *latifolia* Ascherson, Fl.Brandenb., 1: 213 (1864); *O. biennis* subsp. *rubricaulis* (Klebahn) Stomps, Rec. Trav. bot. neerl., 41: 131 (1948).

Although Linnaeus' *O. muricata* (type in LINN) is clearly the same as *O. rubricaulis*, it has most often been misapplied to species of section *Parviflorae* (e.g. *O. ammophila* Focke and *O. syrticola* Bartl.) and for this reason must be treated as a *nomen confusum* and rejected.

Figures 8, 1A.

Stem 100–150 cm, often branched in lower half, green or reddish, strongly red-punctulated, with

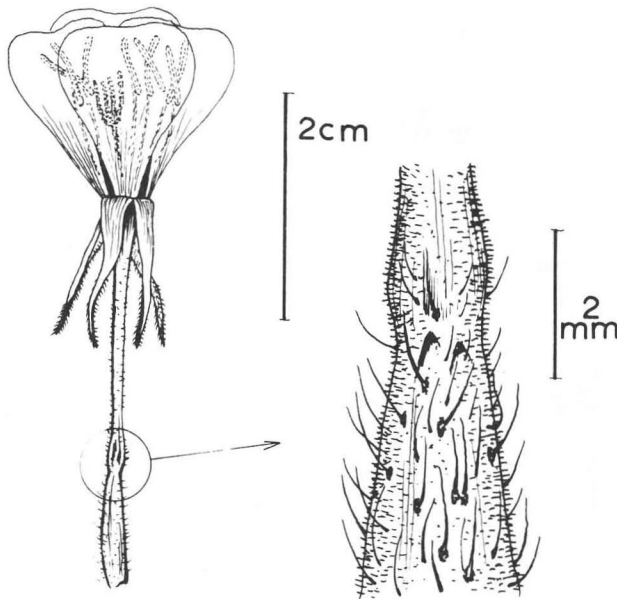


FIGURE 8. Flower of *O. rubricaulis* with enlarged transitional part between ovary and base of hypanthium.

numerous long stiff hairs with red bulbous bases and shorter appressed hairs. Leaves elliptic-lanceolate or lanceolate, with red midrib, flat or crinkled, pubescent, denticulate. Rhachis green below, reddish at tip, red-punctulated, with numerous glandular hairs and stiff hairs with red bulbous bases. Buds green, glandular-pubescent; sepal-tips *c.* 3 mm, appressed below, divergent above. Hypanthium 15-25 mm. Petals yellow, obcordate, mostly narrower than long, 10-20 × 9-18 mm. Anthers 5-8 mm. Stigma-lobes spreading between anthers, 5-8 mm. Capsule green with red stripes when young, 20-30 mm, strongly glandular and with stiff hairs; teeth obtuse.

Sandy shores of rivers and lakes in eastern Europe where it is native, but as an alien in sandy fields, railway embankments and waste places, etc. Central and eastern Europe from eastern France and southern Sweden to northern and central Russia; eastern Asia (Primorskij Kraj, U.S.S.R.).

In Britain only as a casual, and with very few recent records.

N. Somerset, v.c. 6: Berrow Church, 1951, C. I. & N. Y. Sandwith (**K**).

S. Hants., v.c. 11: Southampton Docks, 1958, J. E. Lousley (**RNG**).

Surrey, v.c. 17: Rotherhithe Commercial Docks, 1972, J. E. Lousley (**RNG**).

W. Lancs., v.c. 60: Lytham, 1965, A. E. Ratcliffe (**LIV**).

I have also seen specimens near *O. rubricaulis*, and perhaps this species, from Middlesex, v.c. 21(**OXF**); Warks., v.c. 38 (**CGE**); and Glam., v.c. 41(**RNG**).

6. *Oenothera perangusta* Gates, *Canad. Field Nat.*, **64**: 142 (1950).

Figure 9.

Stem 50-100 cm, mostly simple, green with red diffusion, red-punctulated, with scattered appressed

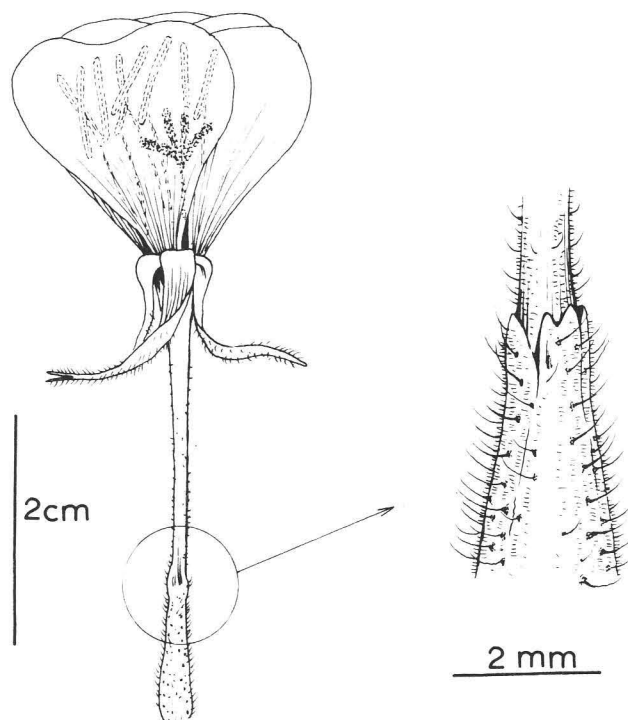


FIGURE 9. Flower of *O. perangusta* with enlarged transitional part between ovary and base of hypanthium.

hairs and long stiff hairs with red bulbous bases. Leaves narrowly lanceolate, with red midrib, flat, pubescent, slightly denticulate. Rhachis green or somewhat reddened at tip, red-punctulated, with numerous glandular hairs and stiff sometimes recurved hairs with red bulbous bases. Buds green (red-stripped in var. *rubricalyx* Gates), with glandular and stiff hairs; sepal-tips *c.* 2 mm, appressed. Hypanthium 30–32 mm. Petals yellow, obcordate, about as long as broad, 10–20 × 10–20 mm. Anthers *c.* 6 mm. Stigma-lobes spreading between anthers, *c.* 6 mm. Capsule green, red-punctulated, 25–35 mm, with stiff hairs with red bulbous bases and glandular hairs, but glabrous on midribs of capsule valves; teeth short, somewhat emarginate.

This species was described from Canada in 1950, but I have seen earlier collections from Britain, Sweden, Finland and U.S.S.R. Among European species it appears closest to *O. rubricaulis*.

In Britain found only as a rare casual in waste places, etc.

N. Devon, v.c. 4: Saunton Burrows, 1972, J. E. Lousley (RNG).

W. Kent, v.c. 16: Stone, 1974, J. E. Lousley (BM).

Surrey, v.c. 17: Hurst Park Race-course, 1963, J. E. Lousley (BM, RNG).

E. Suffolk, v.c. 25: Ipswich, 1975, M. A. Hyde (herb. M.A.H.).

Glam., v.c. 41: Nantgarw, 1935, E. Vachell (NMW); Abercynon, 1961, K. Chamberlain (UCSW).

Cheshire, v.c. 58: Hoole Village, nr Chester, 1968, J. Edmondson (K).

I have also seen a specimen close to *O. perangusta*, and perhaps that species, from Northants., v.c. 32 (K).

Section *Strigosae* Rostański, Fragm. Flor. et Geobot., **11**: 509 (1965).

Axis of inflorescence straight, with long arcuate stiff hairs and shorter closely appressed ones adhering to stem; glandular hairs sometimes appearing in later phase of development. Cauline leaves lanceolate, flat or wavy. Petals 7–25 mm. Sepal-tips appressed in bud. Capsule-teeth distinctly emarginate.

7. *Oenothera salicifolia* [Desf., Tabl. École Bot., ed. 2, 271 (1815), nomen nudum] Desf. ex G. Don, Gen. Syst., **2**: 685 (1832).

Synonyms: *Onagra salicifolia* (Desf. ex G. Don) Spach, Hist. Vég. (Phan.), **4**: 361 (1835); *Oenothera depressa* Greene, Pittonia, **2**: 216 (1891); *Onagra depressa* (Greene) Small, Bull. Torr. Bot. Club, **23**: 170 (1896); *Oenothera hungarica* Borbás, Magyar Bot. Lapok, **2**: 243 (1903); *Oenothera bauri* Boedijn, Zeitschr. Abst. Vererb., **32**: 360 (1924); *Oenothera strigosa* (Rydb.) Mack. & Bush var. *depressa* (Greene) Gates, Tax. Genet. *Oenothera* 34 (1958); *Oenothera biennis* subsp. *bauri* (Boedijn) Tischler, Chromos. Gefässpfl. Mitteleur. **57** (1950); *Oenothera strigosa* subsp. *hungarica* (Borbás) Löve & Löve, Op. bot., **5**: 257 (1961); *Oenothera villosa* Thunb. subsp. *villosa* sensu Raven & Dietrich, Ann. Mo. bot. Gard., **63**: 382 (1976).

Figures 10, 2C.

Stem 100–200 cm, mostly unbranched, green, usually tinged red below, red-punctulated, with soft crispate short hairs and long stiff hairs with small red coniform bases. Leaves lanceolate, with midrib white at first but turning red at base later, crinkled and with twisted apex, appressed-pubescent. Rhachis green or reddish below, with reddened tip, slightly red-punctulated, with arcuate spreading hairs and shorter appressed hairs, with glandular hairs developing later. Flowers cleistogamous or chasmogamous. Buds red-stripped, whitish-pubescent; sepal-tips *c.* 3 mm, appressed. Hypanthium 28–35 mm. Petals yellow, glabrous, obcordate, about as long as broad, 15–20 × 15–20 mm. Anthers 5–8 mm. Stigma-lobes spreading between anthers, 6–11 mm. Capsule grey-green, red-punctulated when young, 30–45 mm, with whitish appressed hairs and the upper ones also with glandular hairs; teeth emarginate.

The inflorescence of this species is distinctly 'loose', with a mean of 0.51 capsules cm⁻¹ of rhachis;

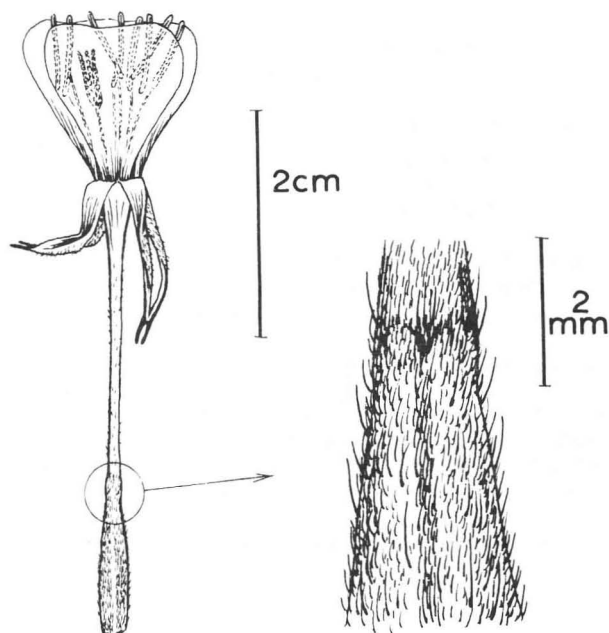


FIGURE 10. Flower of *O. salicifolia* with enlarged transitional part between ovary and base of hypanthium.

comparable figures are 1.11 in *O. biennis*, 1.18 in *O. erythrosepala*, 1.49 in *O. fallax* and 2.04 in *O. parviflora*.

Sandy river shores, railway banks, waysides and fallow ground on the Continent, to which it was introduced from N. America in the first half of the 19th century (Rostański 1966). Now distributed from France to U.S.S.R.

A very rare casual in Britain, with no very recent records.

W. Gloucs., v.c. 34: Bristol, no collector or date but before 1918 (OXF).

Glam., v.c. 41: Splott, Cardiff, 1927, R. L. Smith (NMW); Same place, 1926, R. Melville (K).

Mid-W. Yorks., v.c. 64: Baildon, 1962, J. E. Lousley (RNG).

I identified as this species the specimen illustrated in the paper of Gates (1910, pl. 29) named by the author as *O. multiflora* Gates nom. provis.: "Plant belonging to a race known as *O. multiflora*, originally derived from the English coast near Liverpool" (Gates 1910, p. 184). "This race was descended from a single individual grown at Woods Hole in 1908" (Gates 1910, p. 176). I have omitted the name *O. multiflora* in the above list of synonyms of *O. salicifolia* because Gates (1910, p. 193) wrote as follows: "the forms described under the names *multiflora*, *multiflora elliptica* . . . are not pure species or even true breeding races".

8. *Oenothera renneri* H. Scholz, Wiss. Zeitschr. Pädag. Hochsch. Potsdam, 2: 206 (1953).

Synonyms: *O. strigosa* (Rydb.) Mack. & Bush subsp. *canovirens* (Steele) Munz, N. Amer. Fl., II(5): 132 (1965), pro parte; *O. mollis* Renner, Planta, 47: 238 (1956), nom. illegit.; *O. strigosa* subsp. *mollis* (Renner) Weihe in Garcke, Ill. Fl. Deutschl., 23rd ed., 982 (1972).

Figure 11.

Stem 60–100 cm, mostly simple, green or slightly reddened, commonly not punctulated, with soft crispate spreading short hairs and long stiff hairs with small green or rarely red coniform bases. Leaves lanceolate, with midrib white or rarely somewhat pink at base, flat, usually softly hairy,

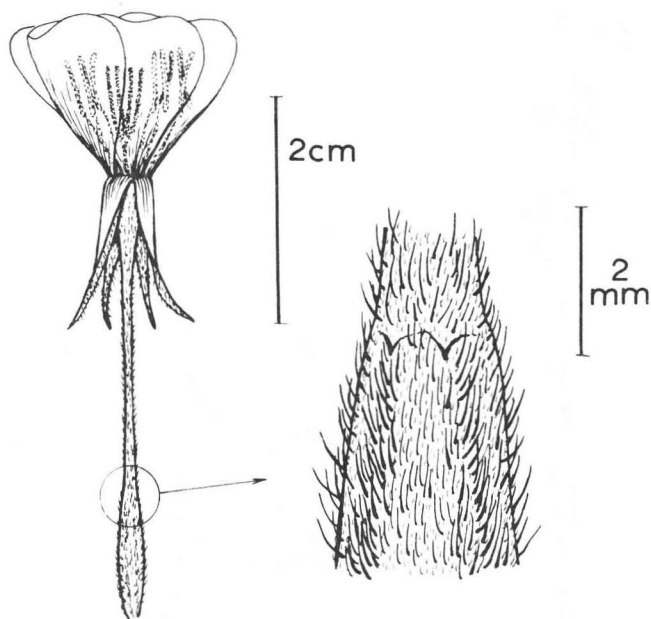


FIGURE 11. Flower of *O. renneri* with enlarged transitional part between ovary and base of hypanthium.

slightly denticulate. Rhachis green or somewhat reddened at tip, not or slightly red-punctulated, with soft arcuate spreading hairs. Buds green or red-striped, whitish-pubescent; sepal-tips 1–3 mm, appressed. Hypanthium 20–35 mm. Petal yellow, obovate, about as broad as long but variable in size, 7–25 × 7–25 mm. Anthers 4–9 mm. Stigma-lobes spreading between anthers, 4–9 mm. Capsule grey-green, 25–40 mm, with whitish appressed hairs; teeth emarginate.

A N. American species rarely found in central and northern Europe and the Far East.
A very rare casual in Britain.

S. Lancs., v.c. 59: Birkdale, nr Southport, 1907, C. Bailey (**MANCH**).

Midlothian, v.c. 83: Borthwick railway tip, nr Fushiebridge, 1964, J. E. Lousley (**CGE, RNG**) (wrongly attributed to *O. cambrica* by McClintock (1978)); Same place, 1966, M. McC. Webster (**BM, RNG**). A similar plant, perhaps the same species, was collected from the same place in 1962 by M. McC. Webster (**K**); Cultivated from seed from same place, 1969, D. McClintock (**herb. D.McC.**).

Section *Parviflorae* Rostański, Fragm. Flor. Geobot., **11**: 512 (1965).

Axis of inflorescence bent at tip before flowering, then remaining bent or becoming straight, with stiff and glandular hairs. Cauline leaves lanceolate, flat. Petals 6–18 mm. Sepal tips ± separated in bud, straight or arcuate. Capsule-teeth obtuse or slightly emarginate.

9. *Oenothera parviflora* L., Syst.Nat., ed. 10, 998 (1759).

Synonyms: *O. pachycarpa* Renner ex Rudloff, Gartenbauwiss., **3**: 499 (1930); *O. muricata* subsp. *parviflora* (L.) Tischler, Chromos. Gefässpfl. Mitteleur. **57** (1950).

Figures 12, 2B.

Stem 100–150 cm, simple or branched, green to dark red, slightly red-punctulated or not, with short arcuate hairs and long stiff hairs with green or pinkish bulbous bases. Leaves lanceolate, with red

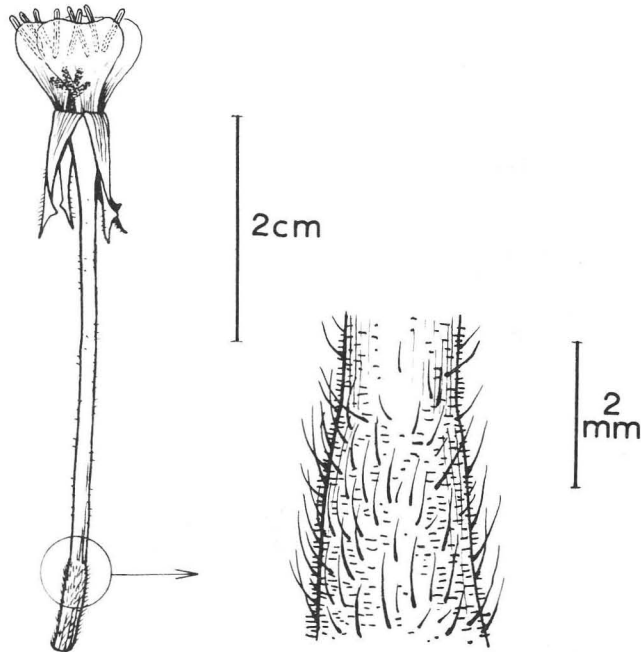


FIGURE 12. Flower of *O. parviflora* with enlarged transitional part between ovary and base of hypanthium.

midrib, slightly pubescent, denticulate. Lower bracts longer than flowers, Rhachis green, slightly red-punctulated, with glandular hairs and long stiff hairs with green or pink bulbous bases. Buds green but those developing late in season brown-red, with glandular hairs and stiff hairs; sepal-tips 2–3 mm, thick, erect and separated. Hypanthium 30–40 mm. Petals yellow, glabrous, obovate, about as broad as long, 6–12 × 6–12 mm. Anthers 4–6 mm. Stigma-lobes spreading but often falling short of anthers, 4–6 mm. Capsule green, with thick wall, 20–30 mm, with glandular hairs and stiff hairs; teeth somewhat emarginate.

A N. American species found only as a very rare casual in Europe (Britain, France, E. and W. Germany, Poland, U.S.S.R. and Czechoslovakia).

In Britain it was cultivated in the Chelsea Physick Garden in 1768 (specimen in Hortus Siccus Vol. 295, **BM**), but it did not establish itself in the wild.

Almost all the plants in Britain recorded as *O. parviflora* are in fact *O. cambrica*, as explained above (see also Rostański & Ellis 1979). There are only two genuine records, both Welsh and neither recent.

Glam., v.c. 41: Aberdare, no date but c. 1905, H. J. Riddelsdell (**OXF**); Port Talbot Docks, 1905, H. J. Riddelsdell (**BM**).

10. *Oenothera rubricuspis* [Renner, Ber. dt. bot. Ges., **63**: 131 (1951), nomen nudum] Renner ex Rostański, Fragm.Fl.Geobot., **11**: 512 (1965).

Synonyms: *O. muricata* auct. subsp. *rubricuspis* (Renner ex Rostański) Weihe in Garcke, Ill.Fl.Deutschl. 982 (1972); *O. parviflora* L. subsp. *angustissima* (Gates) Munz, N.Am.Flora **2**(5): 123 pro parte (1965).

Figure 13.

Stem turning red, red-punctulated, with short arcuate hairs and long stiff ones with red bulbous

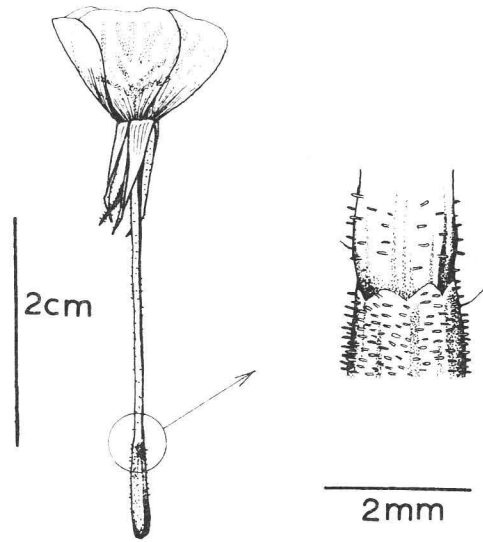


FIGURE 13. Flower of *O. rubricuspis* with enlarged transitional part between ovary and base of hypanthium.

bases. Leaves lanceolate, denticulate or nearly entire, slightly pubescent to subglabrous, dark green with red midrib. Lower bracts shorter than flowers or nearly so. Rhachis green, red-punctulated, with many glandular hairs and scattered stiff hairs with red bulbous bases. Fruiting spike less dense than in previous species. Buds turning red in upper part; sepal-tips red, 2–4 mm, erect, thin and separated. Hypanthium 25–35 mm. Petals yellow, glabrous, obovate, as broad as long, 12–18 × 12–18 mm. Anthers 3–6 mm. Stigma-lobes spreading between anthers or below them, 5–8 mm. Capsule green, with thin wall, with hairs almost all glandular, 18–25(30) mm; teeth obtuse or truncate.

This is a N. American species, the origin of which is unknown, but it seems to me to be near *O. angustissima* Gates. Gates' specimen of *O. angustissima* from Ithaca, New York (**BM**), differs from *O. rubricuspis* in its shorter hypanthia (25 mm) and longer capsules (c. 35 mm).

O. rubricuspis is a very rare casual in Europe, recorded only from Wales, Belgium and W. Germany. It was cultivated in 1782 in Göttingen under the name *O. muricata* (**BM**), and in 1826 in Britain (Cotham Lodge) by Forbes Young (**K**).

There is only one British record in the wild.

Glam., v.c. 41: Grangetown, Cardiff, 1922 & 1923. R. L. Smith (**NMW**).

Subgenus *Hartmannia* (Spach) Munz, Amer.Jour.Bot., **19**: 755 (1932).

Perennial herbs. Leaves subentire to pinnatifid. Flowers yellow, or white to rose or purplish, vespertine or diurnal; hypanthium funnellform. Capsule club-shaped, ribbed or winged, attenuate at base into a sterile pedicel-like portion or truly pedicellate; seeds obovoid, not angled.

11. *Oenothera rosea* L'Herit. ex Aiton, Hort.Kew., **2**: 3 (1789). In Smithian Herbarium (**LINN**) sub nom. *O. lyrata* L. fil. no. 655.20-21.

Stems erect, ascending or decumbent, 10–50 cm, more or less strigulose throughout. Leaves oblanceolate to oblong-ovate, subentire to sinuate-denticulate and even pinnatifid at base of blade,

obtuse to acute, 15–30 mm. Bracts linear-lanceolate. Flowers diurnal; hypanthium 4–8 mm, strigulose-canescens; sepal-tips 1 mm; petals rose to red-violet, broadly obovate, 5–10 mm; anthers 2.5–4 mm. Style equalling stamens; stigma-lobes *c.* 2 mm. Capsule obovoid, 8–10 × 3–4 mm, somewhat winged, passing at base into hollow ribbed pedicel 5–20 mm; seeds oblong-obovoid, *c.* 0.6 mm (Munz 1965, pp. 83–84).

A Central American species with only two British records.

N. Somerset, v.c. 6: Tailand House, garden weed, 1928, J. W. White (CGE).
Glam., v.c. 41: Maindy Pool, Cardiff, 1938, R. L. Smith (NMW).

12. *Oenothera tetraptera* Cav., Icon. Desc., 3: 40 (1796).

Stem decumbent or ascending, branched, 15–50 cm, strigulose with spreading hairs. Leaves oblanceolate to lanceolate, irregularly sinuate-pinnatifid with large terminal lobe to even subentire. Bracts lanceolate, acuminate. Flowers vespertine; hypanthium hirsute, about 10 mm; buds reddish; sepal-tips minute, free in bud; petals pink or whitish, 20–35 mm, broadly obovate. Capsule obovoid, 10–15 × 6–8 mm, hirsute, winged, narrowed into ribbed pedicel 5–25 mm; seeds obovoid, *c.* 1.3 mm (Munz 1965, p. 83).

A central American species with a single British record.

Surrey, v.c. 17: Menton, John Dunes, 1932, D.G.C. (CGE).

Subgenus *Raimannia* (Rose) Munz, Amer.Jour.Bot., 22: 645 (1935).

Annual or perennial herbs. Leaves entire to pinnatifid. Flowers yellow or white, usually vespertine; hypanthium cylindrical. Capsule linear to oblong-fusiform, usually enlarged upwards, sessile; seeds subcylindric or narrowly obovoid, not sharply angled.

13. *Oenothera laciniata* Hill, Hort.Kew 172 (1768).
Synonym: *O. sinuata* L., Mant. Alt. 228 (1771).

Annual or perennial. Stem usually branched, decumbent, 20–30(50) cm, usually finely strigose with or without spreading stiff hairs. Leaves oblanceolate to oblong lanceolate, sinuate-pinnatifid or -dentate, sometimes quite entire, 20–60 × 5–15 mm, the lower petiolate, the upper sessile. Flowers solitary in upper axis; hypanthium 15–35 mm; buds erect or nodding, sepal-tips free, up to 2 mm; petals yellow, drying red, 5–18 mm, broadly obovate to obovate; style equalling or exceeding stamens; stigma-lobes 2–4 mm. Capsule cylindrical, usually somewhat arcuate and divaricate, 10–35 × 2–3 mm, sessile or short-pedicelled; seeds 1 mm, pitted (Munz 1965, p. 109).

A North American species not recorded in Britain since 1928.

W. Gloucs., v.c. 34: Bristol, 1927, C. I. Sandwith (K); Tewksbury, 1912, R. H. Compton (CGE).
Glam., v.c. 41: Cardiff Docks, 1925, R. L. Smith & C. I. Sandwith (NMW).
Flints., v.c. 51: Prestatyn, 1928, J. D. Massey (NMW).
Leics., v.c. 55: Kirby Muxloe, no date, F. A. Sowter (BR).
S. Lancs., v.c. 59: Canalside, Ford, 1903, J. A. Wheldon (NMW); Liverpool, 1928, G. V. C. Last (K).
W. Lancs., v.c. 60: St Anne's-on-Sea, 1906, C. Bailey (MANCH).

14. *Oenothera longiflora* L., Mantissa Alt. 227 (1771).

Annual or biennial. Stem unbranched or with arcuately ascending side branches arising from near

rosette, 40–80 cm, long-villous and sparsely glandular-pubescent. Cauline leaves oblong to elliptic or narrowly ovate to ovate, short-acute, truncate to subcordate at base, sessile, 15–60 × 10–30 mm, mostly irregularly serrate, with flat or undulate margins; bracts oblong to ovate, short-acute to subobtusate, sessile, shorter than capsules, 10–30 × 10–30 mm. Hypanthium 60–100 mm, often streaked with red; buds red in lower part; sepal-tips 1–3 mm, erect or divergent; petals broadly obovate, yellow with red spot at base, 20–40 mm; anthers 7–13 mm; stigma-lobes 6–12 mm, spreading between anthers or above. Capsule curved, 30–45 × 3–4 mm; seeds elliptic, 1.5–2 mm (Dietrich 1978, p. 509).

A native of S. America (Brasil, Uruguay, Argentina) with one British record.

Selkirk., v.c. 79: Galashiels, introduced with wool, 1964, M. McC. Webster (CGE).

15. *Oenothera stricta* Ledeb., Mem.Acad.St. Petersb., **8**: 315 (1822).

Synonyms: *O. striata* Ledeb. ex Link, Enum.Hort.Berol.Alt., **1**: 377 (1821). (H. F. Link misspelled Ledebour's epithet as "*striata*" in publishing the species (Dietrich 1978, p. 536)); *O. agari* Gates, Canad.Field Natur., **41**: 24 (1927). Type specimen of Ledebour preserved in LE (seen by me).

Annual or biennial. Stem erect or decumbent, unbranched or with side branches arching upward, 35–150 cm, pubescent below, villous and glandular-pubescent above. Cauline leaves lanceolate, acute, sessile, flat or slightly undulate at margins, remotely serrate, 6–18 × 0.6–2.5 cm. Bracts lanceolate to ovate, acute, sessile, truncate to subcordate at base, 20–35 × 7–15 mm, shorter than capsules, with reddish margins. Hypanthium 20–45 mm; buds green or reddened; sepal-tips erect or divergent, 1–3 mm; petals broadly obovate, yellow with red spot at base, 15–35 mm; anthers 5–11 mm; style short; stigma-lobes 3–6 mm. Capsule shortly villous, 30–50 × 3–4 mm, enlarged in upper half; seeds elliptic, smooth, brown, 1.3–1.8 mm (Munz 1965, p. 110; Dietrich 1978, p. 536).

A native of Chile.

This is the only species of *Oenothera* outside subgenus *Oenothera* which is naturalized in Britain, and it is now the fourth most common species (after *O. erythrosepala*, *O. biennis* and *O. cambrica*). It occurs mainly on maritime sands, but also in waste places, in Jersey, Guernsey, England, Wales and Scotland as far north as Selkirk (55°33'N), according to Dietrich (1978). Its distribution in Wales was mapped by Rostański & Ellis (1979).

Jersey: Many records, including: St Clements, no date, Dr Graham (GL); Grève d'Azette, 1849, Casborne (CGE); Le Dick, 1860, no collector (JSY); Trinité, 1862, no collector (JSY); St Brelade's Bay, 1865, C. Bailey (CGE); Same place, 1870 & 1900, F. Piquet (JSY); Same place, 1879, W. Hillhouse (CGE); Millbrook, 1877, O. F. Cooper (LTR); St Aubin's Bay, 1859, A. M. Norman (BR); Same place, 1879, J. Comber & J. C. Melville (BM, MANCH); Same place, 1892, F. R. Tennant (CGE); Road to Gorey Station, 1883, F. B. Webb (LTR).

Guernsey: Vale, 1847, C. C. Babington (CGE), first record in British Isles; L'Ancrese, 1886, M. Dawber (MANCH).

W. Cornwall, v.c. 1: Penzance, 1854, J. M. Roper (BRISTM); Gwennap, 1903, F. H. Davey (E); Coverach, 1926, G. C. Druce (BAS, fide Dietrich 1978); Cadywith, 1873, W. M. Rogers (LANC).

E. Cornwall, v.c. 2: Par, 1920, L. T. Medlin (K).

S. Devon, v.c. 3: Laira, nr Plymouth, 1852, Blitt (BM); Dawlish Warren, 1924, S. G. Carter (CGE); Same place, 1929, F. A. Sawter (BR); Same place, 1951, Trew (CGE).

N. Devon, v.c. 4: Braunton Burrows, 1977, M. Tulloh (herb. M.T.).

N. Somerset, v.c. 6: Brean, 1882, J. W. White (MANCH); Brean Down, 1883, J. W. White (GL); Brean sandhills, 1926, J. W. White (BRIST); Burnham, 1873, Melville (E); Same place, 1900 & 1906, J. W. White (BRIST, MANCH); Same place, 1906, E. S. Marshall (CGE); Same place, 1906 & 1917, H. Thompson (CGE); Same place, 1927, E. Vachell (NMW); Same place, 1931, T. Frankland (LIV); Same place, 1939, A. E. Wade (CGE); Same place, 1910, E. S. Gregory (CGE); Same place, 1912, R. H. Compton (CGE); Berrow, 1879, Davis (K); Same place, 1915, H. S. Thompson (CGE); Same place, 1956, E. Hodgson (LANC).

Dorset, v.c. 9: Wareham, 1884, Fawett (BM).

Wight, v.c. 10: St Helens, 1874, no collector (GL); Same place, 1881, C. Bailey (MANCH); Same place, 1933, H. Foster (BR); Bembridge, 1894, J. A. Preston (MANCH).

- S. Hants., v.c. 11: Bournemouth, 1944, Alston (**BM**).
 N. Hants., v.c. 12: Blackmoor, 1968, J. E. Lousley (**BM**); Farnborough Airfield, 1980, A. Mundell (**herb. A. Brewis**).
 W. Sussex, v.c. 13: Littlehampton, 1892, E. S. Marshall (**CGE**).
 E. Kent, v.c. 15: Nr Sandwich, 1860, A. Irvine (**MANCH**); Sandwich Bay, 1946, F. Rose (**MNE**); Same place, 1948, J. E. Lousley (**CGE**).
 W. Kent, v.c. 16: Catford, 1910, Lowne (**K**).
 Surrey, v.c. 17: Esher Station, 1873, H. C. Watson (**CGE**); Croydon, 1873, Bennett (**E**); Bisley, 1958, Burkill (**E**); Wandsworth, 1837, Forbes Young (**BM**); cultivated in Regent's Park as *O. agari* Gates, 1928, R. R. Gates (**CGE**).
 Middlesex, v.c. 21: Twickenham, 1867, no collector (**BM**).
 E. Suffolk, v.c. 25: Chelmondiston, 1975, M. A. Hyde (**herb. M.A.H.**).
 E. Norfolk, v.c. 27: Yarmouth Cemetery, 1901, S. H. Bickham (**CGE**).
 Beds., v.c. 30: Potton, 1950, J. G. Dony (**CGE**).
 Mons., v.c. 35: Stonehouse near Newport, 1972, S. Irvine (**NMW**).
 Herefs., v.c. 36: Ross-on-Wye, 1837, A. Knight (**CGE**).
 Warks., v.c. 38: Warwick, 1870, Bromwick (**BM**).
 Glam., v.c. 41: Cardiff, East Moors, 1876, J. Storrie (**NMW**); Porthcawl, 1916, P. W. Richards (**NMW**); Between Newton and Porthcawl, 1941, E. M. Thomas (**NMW**).
 Carms., v.c. 44: Pembrey, 1964, R. F. May (**NMW**).
 Merioneth, v.c. 48: Aberdovey, 1875, H. E. Fox (**MANCH**); Between Aberdovey and Towyn, 1919, J. C. Melville (**BM, NMW**).
 Cheshire, v.c. 58: Bickley, 1902, Beer (**BM**).
 S. Lancs., v.c. 59: Southport, 1853, H. Graham (**LIV**); Same place, 1865, J. Coward (**CGE**); Burnham, near Liverpool, 1852, E. Simony (**BP**); Same place, no date, J. Stephenson (**MANCH**).
 N.E. Yorks., v.c. 62: Scarborough, 1873, T. W. Nettleship (**CGE**).
 Selkirks., v.c. 79: Selkirk, 1911, I. M. Hayward (**E**); Same place, 1966, M. McC. Webster (**E**, fide Dietrich 1978).

ACKNOWLEDGMENTS

The gathering of the data for this paper was made possible by the help of many persons and Institutions. I am most grateful to the authorities of the Silesian University in Katowice for the support of my voyage to England and Wales in 1977, and to Mr D. McClintock, who initiated my interest in British evening-primroses, provided me with specimens and seeds, and helped me during my stay in Britain. Mr S. G. Harrison and Mr G. Ellis similarly helped me in Wales.

Among the other persons to whom I am specially indebted for their assistance I wish to mention: Dr S. M. Walters and Dr D. Briggs (**CGE**), Mr J. F. M. Cannon, Mr J. Lewis and Mr A. O. Chater (**BM**), Mr P. S. Green (**K**), Mr F. White and Mr R. C. Palmer (**OXF**), Dr S. L. Jury (**RNG**), Dr J. Challice (Long Ashton) and Mrs St Schramm (London).

I am also very grateful to Mr Jerzy Zygmunt of Czestochowa, for the preparation of the Figures; to Mr J. Bevan and Mr G. Ellis, for checking and correcting the English and Welsh localities respectively; to Dr C. A. Stace, for improvements to the English of this paper; and to the B.S.B.I., for the provision of funds for retyping.

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(Accepted January 1981)