The genus *Oenothera* (Onagraceae) in Belgium

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Illustrations by S. Bellanger (fig. 2-5), W. Vercruysse (7-8), R. Barendse (10: flowers and stem; 11; 17), J. Pottier (10: hairs), R. Jean (21), P. Kalinowski (22) and F. Verloove (the others).

Abstract. – The genus *Oenothera* (Onagraceae) was thoroughly and critically revised in Belgium. This revision is based on the study of several hundreds of older and more recent herbarium specimens from all major public and some private herbaria as well as on additional fieldwork carried out since 2000. A brief history of the genus *Oenothera* in Belgium is provided. Difficulties with regard to taxonomy and nomenclature are discussed. The present treatment of *Oenothera* follows the 'European school' and is thus based on a narrow species concept for subsection *Oenothera*. In the present paper only species that have been recorded since 1950 are dealt with. As such 27 species (including stabilized hybrids) have been upheld: *Oenothera biennis*, *O. cambrica* (with two varieties), *O. canovirens*, *O. deflexa*, *O. depressa*, *O. ersteinensis*, *O. fallax*, *O. fruticosa* subsp. *glauca*, *O. glazioviana*, *O. hirsutissima*, *O. issleri*, *O. lindheimeri*, *O. nuda*, *O. oehlkersii*, *O. paradoxa*, *O. parviflora*, *O. pycnocarpa*, *O. rosea*, *O. royfraseri*, *O. rubricalyx*, *O. rubricaulis*, *O. rubricauloides*, *O. stricta*, *O. subterminalis*, *O. victorinii*, *O. villosa* and *O. wratislaviensis*. Nine additional species were only recorded before 1950. *Oenothera* is represented in Belgium by the following sections, subsections and series: sections *Gaura*, *Hartmannia*, *Kneiffia* and *Oenothera*, the latter furthermore represented by subsections *Munzia*, *Oenothera* (with the series *Devriesia*, *Linderia*, *Oenothera* and *Rugglesia*) and *Raimannia*. An identification key and photographs (mostly of typical and/or widespread species) are presented. Each species is concisely compared with related or similar species and its current distribution and naturalization status in Belgium are assessed.

Résumé. – Le genre *Oenothera* (Onagraceae) en Belgique. Le genre *Oenothera* (Onagraceae) fut inventorié en Belgique. Cette révision taxonomique est basée sur l'étude de plusieurs centaines d'échantillons d'herbier (anciens ainsi que plus récents) et des prospections de terrain à partir de 2000. L'histoire du genre *Oenothera* en Belgique est brièvement présentée et des difficultés concernant la taxonomie et nomenclature commentées. La présente révision du genre *Oenothera* suit la dite 'école européenne' pour la sous-section *Oenothera*. Dans cet article seulement les 27 taxons (y inclus quelques espèces hybridogènes) récoltés après 1950 sont retenus : *Oenothera biennis*, *O. cambrica* (avec deux variétés), *O. canovirens*, *O. deflexa*, *O. depressa*, *O. ersteinensis*, *O. fallax*, *O. fruticosa* subsp. *glauca*, *O. glazioviana*, *O. hirsutissima*, *O. issleri*, *O. lindheimeri*, *O. nuda*, *O. oehlkersii*, *O. paradoxa*, *O. parviflora*, *O. pycnocarpa*, *O. rosea*, *O. royfraseri*, *O. rubricalyx*, *O. rubricaulis*, *O. rubricauloides*, *O. stricta*, *O. subterminalis*, *O. victorinii*, *O. villosa* et *O. wratislaviensis*. Neuf taxons supplémentaires ont été récoltés uniquement avant 1950. Les taxons précités appartiennent aux sections, sous-sections et séries suivants : les sections *Gaura*, *Hartmannia*, *Kneiffia* et *Oenothera*, ce dernier en plus avec les sous-sections *Munzia*, *Oenothera* (avec les séries *Devriesia*, *Linderia*, *Oenothera* et *Rugglesia*) et *Raimannia*. Une clé pour l'identification des espèces est présentée ainsi que des photos des espèces les plus caractéristiques et/ou les plus répandues. Chaque espèce est comparée avec des espèces proches ou similaires et sa distribution et son statut (fugace/naturalisé) sont fournis.

Samenvatting. – Het genus *Oenothera* (Onagraceae) in België. Het geslacht *Oenothera* (Onagraceae) werd kritisch gereviseerd in België. Deze revisie is gebaseerd op de studie van enkele honderden herbariumspecimens (uit de belangrijkste publieke herbaria van België en uit enkele kleinere private herbaria), alsook op veldwerk, uitgevoerd sinds 2000. De his-

toriek van het geslacht *Oenothera* in België wordt geschetst en problemen met betrekking tot de nomenclatuur en taxonomie worden aangekaart. De huidige revisie volgt de zogenaamde 'Europese school' en hanteert dus een eng soortsbegrip voor de subsectie *Oenothera*. Alleen de 27 taxa (inclusief enkele gestabiliseerde hybriden) die na 1950 in België zijn waargenomen, worden uitgesleuteld en besproken: *Oenothera biennis*, *O. cambrica* (met twee variëteiten), *O. canovirens*, *O. deflexa*, *O. depressa*, *O. ersteinensis*, *O. fallax*, *O. fruticosa* subsp. *glauca*, *O. glazioviana*, *O. hirsutissima*, *O. issleri*, *O. lindheimeri*, *O. nuda*, *O. oehlkersii*, *O. paradoxa*, *O. parviflora*, *O. pycnocarpa*, *O. rosea*, *O. royfraseri*, *O. rubricalyx*, *O. rubricaulis*, *O. rubricauloides*, *O. stricta*, *O. subterminalis*, *O. victorinii*, *O. villosa* en *O. wratislaviensis*. Negen soorten werden uitsluitend voor 1950 in België aangetroffen. Het geslacht *Oenothera* wordt in België vertegenwoordigd door de volgende secties, subsecties en series: de secties *Gaura*, *Hartmannia*, *Kneiffia* en *Oenothera*, deze laatste bovendien door de subsecties *Munzia*, *Oenothera* (met de series *Devriesia*, *Linderia*, *Oenothera* en *Rugglesia*) en *Raimannia*. Een determinatiesleutel en foto's (meestal van typische en/of wijd verspreide soorten) worden eveneens gepresenteerd. Elke soort wordt vergeleken met gelijkaardige of verwante soorten en de huidige verspreiding en inburgeringsgraad in België worden kort besproken.

Introduction[1]

The genus *Oenothera* L. is not native to Belgium. Although *O. biennis* is naturalized in this country since at least the 18th century (Roucel 1792), the exact number and the true identity of the other Belgian taxa always remained unclear. This is primarily because of the very complex taxonomy of the genus, especially with regard to section *Oenothera* subsection *Oenothera*. For this group, there are two very divergent taxonomical views. According to Dietrich *et al.* (1997) the group is made up of only 13 species. This concept is usually referred to as the 'American school' but this is misleading. As early as 1958, the American botanist and geneticist Ruggles Gates already presented a taxonomic concept for *Oenothera* that for the greater part confers with the current 'European' species concept. Moreover, Dietrich is German. Rostański (1985), who represents the so-called 'European school', claimed there were 85 species and 23 hybrids. Moreover, in the past decades several additional new taxa have been described (e.g. Jehlík & Rostański 1995, Delipavlov 1998, Rostański & Ramst 2001, Rostański *et al.* 2004, Rostański 2007, Deschâtres *et al.* 2013).

As a result of a peculiar breeding mechanism (permanent translocation heterozygosity[2]) species from subsection *Oenothera* cross freely, producing off-spring that differs from either parent and developing populations that consist of many different but in fact continuous genotypes. As such, numerous, closely similar but morphologically well-delimited entities are formed. These newly arisen plants breed more or less completely true. They may be intermediate but are usually nearer one parent than the other and the degree of resemblance may vary from character to character. Some hybrids even resemble one parent species more strongly in one stage of development and the other parent at a later stage (Gates 1933). Also, when *Oenothera* species spread to new habitats, new 'species' (or mere morphotypes?) adapted to new conditions, may arise (Tokhtar & Wittig 2003). These 'microspecies' were included in one of the 13 recognized species (or hybrids of these) by Dietrich *et al.* (1997). As such, for example for *O. biennis*, there are no less than 68 'synonyms'. According to Rostański, whose work was for the greater part based on the earlier publications of Renner (1942, 1950, 1956) these mutants and hybrids are, once more or less established, preferably considered as independent species.

The choice between both concepts is not straightforward and merely a matter of opinion and there is no consensus whatsoever. However, this species concept is perhaps not applicable in North America, where the genetic variation is greater than in Europe. Wisskirchen & Haeupler (1998) presented, without judgement of their respective merits, both concepts next to one another. In our view, we consider that Dietrich *et al.* (1997) presented a too broad species concept. Under *O. biennis*, for example, numerous, easily differentiated species, are grouped together (e.g. *O. rubricaulis*) that altogether often hardly resemble *O. biennis* s.str. Other examples: *O. perangusta* is included with *O. oakesiana*, whilst the (possibly) conspecific *O. ersteinensis* is included under *O. biennis*. Also, *O. deflexa* is included in *O. parviflora* whilst both are not in the least related and actually belong to different, relatively distinct series. See also a more lengthy discussion in Rostański *et al.* (2010). In Europe, since Renner (1917), who was the founding father of the European school, a narrow species concept has been applied most of

[1] The results presented in this paper are almost exclusively based on the determinations by the first author. The text, however, was written by the second author and approved by Dr. Adam Rostański, son of the first author.

[2] Permanent translocation heterozygosity is a cytological phenomenon in which an organism is true breeding for a set of translocations involving all or part of the chromosomes.

the time although recently, in *Flora Iberica*, an exception was made (not surprisingly, the genus *Oenothera* being prepared by Dietrich; see Dietrich 2000). Van der Meijden (2005a) originally also opted for this broad species concept for the 23rd edition of *Heukels' Flora* (van der Meijden 2005b), yet eventually he accepted *O. deflexa* and *O. fallax* as two taxa, which were not recognized by Dietrich *et al.* (1997). In the most recent edition of the Belgian flora (Lambinon & Verloove 2012) numerous microspecies are accepted in taxonomically similar, complex genera (e.g. the apomictic genera *Rubus* and *Taraxacum*). For these reasons, it would be at least useful and perhaps even advisable to follow the European school, applying a narrow species concept for *Oenothera* in Belgium and neighbouring territories. This will allow tracking of changes in range and frequency and to distinguish patterns and mechanisms of distribution; application of a wide species concept would lead to considerable loss of information (Rostański & Karlsson 2010). Worthwhile mentioning is that molecular phylogenetic studies have been performed in the genus *Oenothera* (e.g. Krakos *et al.* 2014) but not yet in subsection *Oenothera*.

In 2000 the first author began a systematic revision of the Belgian *Oenothera* collections, stored in the main public herbaria (the herbarium of the Botanic Garden Meise, BR; the herbarium of the University of Liège, LG; and the herbarium of the University of Ghent, GENT) and some smaller private herbaria. Since then the second author attempted to document, as much as possible, the variation of *Oenothera* currently encountered in favourable habitats in Belgium (e.g. in seaports, coal mining spoil heaps, sand pits, landfills, railway infrastructure, sand depots, etc.).

In this paper, all species reliably recorded since 1950 are keyed out and briefly discussed. Those species that exclusively occurred as wool aliens in the Vesdre valley and species that were last collected before 1950 are excluded because they are, for the present day field botanist, of lesser interest. These species are merely cited in the classification scheme (preceded by an asterisk) and their respective records are included in the appendix of this paper.

An overview of the studies concerning *Oenothera* in Belgium and Europe

As previously mentioned the genus *Oenothera* was not well documented in Belgium. The majority of floras of the 19th and the first half of the 20th century mentioned only *O. biennis* and *O. muricata* (auct. belg. non L.) (e.g. Durand 1899), occasionally along with a few ephemeral aliens such as *O. laciniata* or *O. rosea*. Goffart (1945) added *O. glazioviana*; later, it turned out that this species was already found in Belgium since at least 1868 (Verloove 2006a). De Langhe *et al.* (1967) listed the following species: *O. biennis*, *O. erythrosepala* (syn.: *O. glazioviana*), *O. parviflora* and the ephemeral aliens *O. laciniata* and *O. stricta*. Around the mid-seventies of the 20th century the Belgian *Oenothera* collections of the herbarium of the Botanic Garden Meise (BR) were revised for the first time by an expert (Jean 1975). He confirmed the reported species of De Langhe *et al.* (1967) and added the following: *O. ammophila*, *O. atrovirens* (syn.: *O. cruciata*), *O. fallax* (as *O. biennis* × *O. lamarckiana*), *O. hungarica* (syn.: *O. depressa*) and *O. longiflora*. Recently, it became clear that *O. ammophila* as well as *O. longiflora* were misidentifications, the corresponding collections belonging respectively to *O. parviflora* and *O. affinis* (Verloove 2006a). In the subsequent editions of the Flora of Belgium the results of Jean's revision were maintained. Moreover, in Lambinon *et al.* (1998) *O. nuda* was added, a species observed in northern France (Jean 1990). In Lambinon *et al.* (2004) some provisional results from the current study were already included (mostly based on Verloove 2002). Most notable was that the Belgian populations of the 'small flowered evening primrose' were attributed to *O. deflexa* and no longer to *O. parviflora* (see further). Verloove (2006a) presented an overview of all observed species in Belgium prior to 2005 and finally, in the most recent edition of the Belgian flora (Lambinon & Verloove 2012), an extra species was keyed-out (the relatively widespread and well defined *O. fallax*). The list of ephemeral adventives was also updated.

Elsewhere in Europe, in the last decades, a reasonably good picture has been formed of the diversity and spread of the genus (mostly as a result of the continuous revisions by the first author). For many European regions there are overviews available by now. The most important (with identification keys and/or good illustrations) are presented in table 1, chronologically listed per country or region. These publications are often relevant for the *Oenothera* flora in Belgium as well. Especially north, central and east European revisions usually include species that are also found in Belgium. In contrast, for southern Europe (e.g. Italy, Portugal and Spain) there are proportionally more taxa that are not found in Belgium (and vice versa).

Finally, Dietrich (1999) offers an interesting and up-to-date overview of the genus *Oenothera* in cultivation.

Problems concerning the identification of *Oenothera*

Unfortunately, the complex taxonomy is not the only problem in the identification of *Oenothera* species. Some important diagnostic characteristics disappear on drying or become less visible: the presence or not of hairs with a red bulbous base, the colour and the size of the petals and their length and width, the red pigmentation of (parts of) the stem, the colour of the sepals, the colour of the midrib of the leaves, etc. For these reasons, it is of the utmost importance that specimens are either identified from fresh material, or with the help of field notes (especially dimensions and colour of the different plant parts). Moreover, the identification of many species needs to be carried out on flowering and fruit bearing plants.

It also is important to know that the identification of *Oenothera* species only makes sense during the first flow-

Table 1. An overview of revisions of *Oenothera* from Europe.

Countries or regions	Publications
Europe	Rostański *et al.* (2010)
Germany	Hudziok (1968), Otto (1970), Gutte & Rostański (1971), Rostański & Schnedler (1991), Gutte (1998), Haeupler & Mür (2000), Lang (2001), Jäger & Werner (2005), Rostański & Meierott (2006)
France	Rostański *et al.* (1994), Tison & de Foucault (2014)
Great Britain	Rostański (1982), Sell & Murrell (2009)
Austria	Rostański & Forstner (1982)
Eastern Europa (Baltic States, Russia, Belarus, Ukraine and Moldova)	Rostański *et al.* (2004)
Scandinavia (Denmark, Finland, Iceland, Norway and Sweden)	Rostański (2006), Rostański (2007), Rostański & Karlsson (2010)
Czech and Slovak Republic	Jehlík & Rostański (1979), Jehlík & Rostański (1995), Jehlík (1997)
Serbia and Montenegro	Zlatković *et al.* (1998); Rakaj & Rostański (2009)
Spain	Dietrich (2000)
Portugal	Rostański (1991)
Italy	Soldano (1980), Soldano (1983a, b), Soldano (1993)

ering period (for most species this is from mid-June to the end of July). During the second flowering period, the petals are almost always (much) smaller (especially in large-flowered species), the number of glandular hairs tend to increase while the number of stiff, eglandular hairs diminishes, the branching pattern changes (i.e. development of side branches below the main inflorescence or of oblique stems arising from the leaf rosette) and other characters also are often less obvious.

It is finally recommended to collect only 'typical' examples of a population. In many *Oenothera* populations – certainly those where two or more species grow in close proximity – plants with intermediate characteristics are not uncommon. These locally arisen, not-fixed hybrids will, without doubt, fail to key out properly. In this perspective, it is an illusion to think that it is possible to assign a name to each individual *Oenothera* plant. However, the identification of more or less homogeneous populations is generally feasible provided one has some field experience. In fact, in a mixed population of *Oenothera* species the difficulty mostly is to assess which plants species are the 'pure' ones and which are the hybrids.

Even if the above is taken into consideration, the identification of *Oenothera* species often remains a difficult task. The correct identification of herbarium material without accompanying field notes is, even for experts, not easy. The Belgian *Oenothera* collections of the herbarium of the Botanic Garden Meise have been reviewed by Raymond Jean (see Jean 1975), Werner Dietrich and the first author of this paper. That the conclusions of Dietrich and Rostański differ stems (mostly) from differences in taxonomical concepts. Jean, however, followed the narrow 'European' species concept and yet sometimes came to conclusions which were divergent to those of Rostański. For instance, plants which were named by Jean as "close to *O. ersteinensis*" were finally attributed to *O. deflexa* and *O. parviflora*. A collection named as "*O. hungarica*" (= *O. depressa*) is here ascribed to *O. oakesiana* although both belong to different series. Without doubt, the most striking was that nearly all *O. parviflora* collections – one of the few more or less widely spread and fully established species in Belgium – turned out to be ascribable to (the not even remotely related) *O. deflexa*. This important correction was already picked up by Lambinon *et al.* (2004).

The repeated confusion, even amongst experts, was clearly illustrated with respect to a collection of *Oenothera oakesiana* from BR (Fig. 1); this collection was

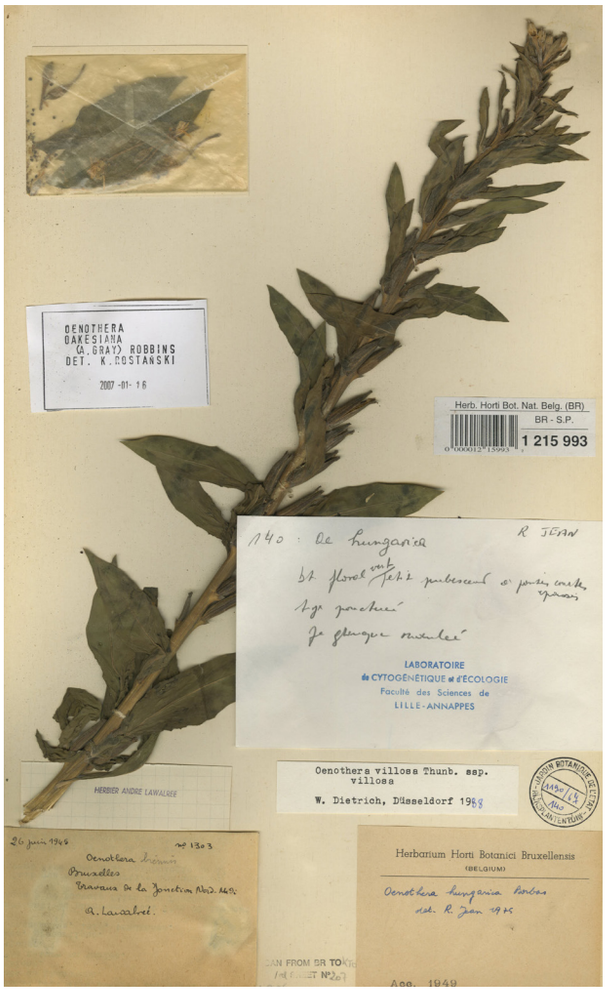


Figure 1. *Identification of species in genus* Oenothera *has often been difficult, even among experts. This collection of* Oenothera oakesiana *from BR was originally identified by A. Lawalrée as* O. biennis *and later annotated by Dietrich, Jean and the first author. It finally bears four names of species that belong to three different series.*

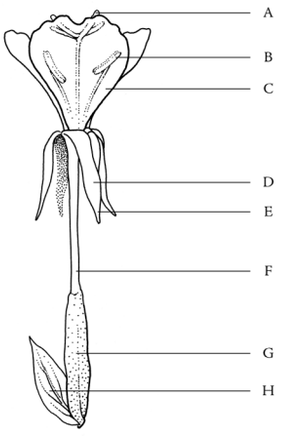


Figure 2. *Flower morphology:*
A, stigma lobes;
B, anthers;
C, petal;
D, sepal;
E, sepal tip;
F, hypanthium;
G, ovary;
H, bract.

originally identified by A. Lawalrée as *O. biennis* and later annotated by Dietrich, Jean and the first author. It finally bears four names of species that belong to three different series!

Diagnostic characters

Although similar, the species in subsection *Oenothera* are (with some experience) easily recognized in the field. The diagnostic characters, such as hairiness, colour of vegetative parts and size of floral parts (Fig. 2), are strikingly constant. However, herbarium material is frequently more difficult to identify because some characters are lost, especially in poorly prepared material (see before; also Jean 1975).

The following characters are particularly useful for an accurate identification (mostly based on Rostański & Karlsson 2010):

Mode of growth. The stem is erect in most species but ascending in a few. The tip of the growing inflorescence is erect in most species but in some, e.g. *Oenothera parviflora* and related species from series *Rugglesia*, it is drooping (as beautifully illustrated in Renner 1956). This is an important character that can easily be overlooked, e.g. in late specimens where the axis has straightened. Also, in some species of series *Rugglesia*, this character is less obvious, for instance in *O. parviflora* (Linder 1958).

Hair types (Fig. 3). There are trichomes of three main types: 1) short, soft, crispate hairs on the vegetative part of the stem and, in some species, on the ovary and fruit; 2) glandular hairs, i.e. patent, glistening, short and thick (sometimes slightly clavate) trichomes, on rachis, hypanthium, sepals, ovary and fruit in many species; and 3) long, stiff, more or less patent, straight or slightly bent hairs on most parts of the plant. In some species the hairs rise from a well-delimited, multicellular base which is often an intense red (presence of anthocyanin pigment). The shape of the thickened hair base varies. In most cases it is conical and about as high as wide; more rarely it is wide and low, as in *O. depressa*, or distinctly elongated, cylindrical and ± bent, as in *O. ersteinensis*.

Leaf shape. The relative leaf width varies between the species and, to some extent, within the species. Some are always narrow-leaved; others, like *O. biennis* and *O. cambrica* are always broad-leaved. The leaves are usually flat, but in some species they are crinkled and sometimes have a slightly twisted apex (e.g. in *O. depressa*).

Leaf hairiness. The leaves are usually sparsely hairy, but in some species, e.g. *O. hirsutissima* and in series *Devriesia* (e.g. *O. canovirens* and *O. depressa*), they appear grey-green and velvety to the touch, due to a fairly dense indumentum.

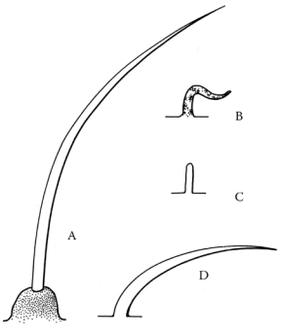
Leaf colour. The midrib of the leaves is whitish in some species, ± red in others. However, the red colour is sometimes not developed in species normally having red midribs, e.g. in specimens growing in shade.

Rachis colour. The main axis (rachis) of the inflorescence can be either green throughout as in *O. biennis* or an intense red towards the apex as in *O. ersteinensis* and *O. rubricaulis*. This character is more stable within species than the colour of leaves and sepals.

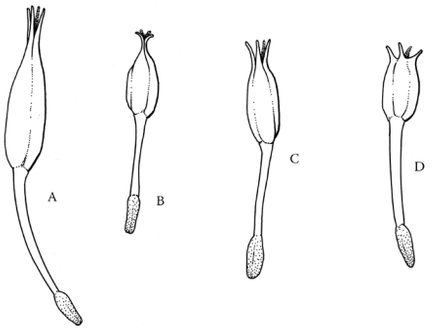
Sepal colour. The sepals are green in some species, whereas in others, e.g. *O. glazioviana*, they have red streaks or a red tinge or they may be entirely deep red (e.g. *O. rubricalyx*). The red colour is, however, not always developed. There are also species with a genetically conditioned variation in this character (e.g. *O. oehlkersii*).

Buds (Fig. 4). The sepal-tips can be entirely separated or pressed to each other in their full length, or together in their proximal part but diverging distally. The length of the sepal tips and the length of the sepals (including the tip, and measured in fully mature buds) differ between some species.

Flower size. The length and width of the petals, as well as the length/width ratio, are diagnostic. The length of the hypanthium also differs much between species; it is not correlated with petal size. Care should be taken to study



(left) ***Figure 3.*** *Hair types: A, hair with bulbous base; B, crispate hair; C, glandular hair; D, bristle hair.*



(right) ***Figure 4.*** *Flower buds and sepal tips: A, sepal tips appressed throughout; B, sepal tips appressed at base, separated at apex; C, sepal tips separated (V-shaped); D, sepal tips separated (U-shaped).*

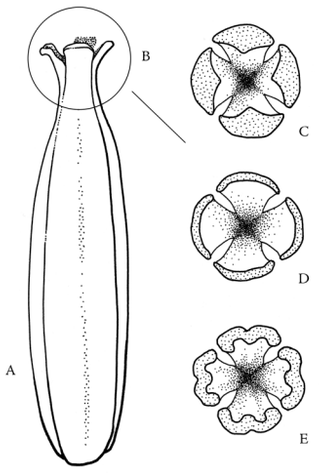


Figure 5. *Capsule and morphological variation of capsule apex:*
A, capsule;
B, capsule valve;
C, teeth acute;
D, teeth truncate;
E, teeth emarginate.

the plant at its peak of flowering. Later in season the flowers become notably smaller, especially in the large-flowered taxa. In some species the flowers are sometimes or even usually cleistogamous (e.g. *O. depressa*).

Position of stigma. The stigma is surrounded by the anthers at anthesis in most species, but distinctly raised above them in e.g. *O. glazioviana* and *O. oehlkersii*.

Hairiness of capsules. The density of trichomes of different kinds on the capsules is of major diagnostic value, but care must be taken to compare capsules at the same height, because the hairiness varies with position (i.e., between lower, older capsules and upper, younger ones). Generally, glandular hairs are more numerous on the upper, younger capsules. There are species where glandular hairs are absent on the lower (older) capsules, but present on the upper (younger) ones.

Capsule valves (Fig 5). The tips of the capsule valves are rounded, truncate or more or less emarginate. Their outline is best seen in capsules that are about to open.

Degree of naturalization of *Oenothera* in Belgium

In Belgium *Oenothera* species are mostly found in environments which have been heavily disturbed by human activity: ports and railway grounds, sand and gravel pits, dredge dumping areas, sand and mineral depots, coal mining spoil heaps, ruderalized sand dunes, etc. The flora of such environments is often rather ephemeral. Although *Oenothera* often occurs in great numbers, this is, in the most of its habitats, a temporary phenomenon. Moreover, the knowledge of the genus in Belgium is virtually non-existent and as such only the experience of the second author can serve as a basis. Because of this, the correct estimation of the extent of naturalization for many species is very difficult. Perhaps only a few species are more or less widespread and relatively common. This corresponds with previous findings: Mihulka & Pyšek (2001) indicated that only few species are successful in terms of increasing abundance while the majority of the species remain rare and local.

Probably the most widespread species for the moment is *O. deflexa*. It also appears to be the most expansive of all species. Locally, for example in the coastal sand dunes, *O. glazioviana* is also well established as is *O. fallax*. The latter is spreading vigorously, for example, in the ports of Ghent and Antwerp. This species has also become one of the most frequently found species in the west of Germany (e.g. Wittig and Tokhtar 2003). At least in the area around Ghent, *O. rubricaulis* is well established and in expansion. This species was already found in great numbers in 1985 (e.g. E. Robbrecht 2929 in BR) and it is now one of the typical species for this area. The same holds true for *O. ersteinensis* around Antwerp and in the Kempen. *O. biennis* is a perplexing case: it is, without doubt, the species with the longest history in Belgium but currently appears to be, to the greater extent, replaced by related species. Although, this species is still regularly collected, this is much less so in comparison with the other species cited before. Locally, in the second half of the 19th century, *O. angustissima* (syn.: *O. muricata* auct. belg. non L.) was more or less established, for example, along a railway track in the vicinity of Sint-Truiden (at least between 1860 and 1884). All the remaining *Oenothera* taxa are either not well known enough, or are only very locally more or less established, or (without doubt in the most cases) strictly ephemeral.

Some of the aforementioned species (e.g. *O. glazioviana*) are naturalized in great number in natural habitats, for instance in coastal dunes. In the sense of Richardson *et al.* (2000) they can probably be considered as invasive species. However, there are no indications that they replace indigenous vegetation ('transformers'). As shown elsewhere, species from other (sub-) sections that were introduced relatively recently proved to exhibit a much stronger invasive behaviour (e.g. Frean *et al.* 1997). However, Tokhtar *et al.* (2011) demonstrated that (notho-) species from subsection *Oenothera* can also act as invasive species, especially if one putative parent is of North American and the other of European origin.

Finally, an additional difficulty in assessing the degree of naturalization of *Oenothera* is the morphological plasticity of many populations. It often happens that *Oenothera* populations change strongly during the course of years: small but apparently more or less stabilized populations of rare species often disappear in a hybridization swarm of commoner species. For example, a nice population of *O. victorinii* very gradually disappeared from rough ground in the vicinity of Roeselare. The few remaining plants became less and less typical, doubtlessly as a result of introgression with the co-existing populations of *O. glazioviana* and/or *O. deflexa*, eventually disappearing altogether. The same holds true for a population of *O. hirsutissima* found on a sand storage area in the canal zone of Bruges: between 2004 and 2007 a few typical plants were collected whilst from 2008 onwards only non-defined hybrids appeared to be present. Analogously, a population of *O. wratislaviensis* in the Antwerp port area, discovered in 2007, is replaced now by plants that exhibit characters of this species, as well as of the widely

spread *O. ersteinensis*. This is a well-known phenomenon in *Oenothera*: Renner (1950) referred to it as "Der Kampf zwischen der Arten".

Geographical origin of the genus *Oenothera*

The origin of the genus *Oenothera* is quite uncertain. According to Wagner *et al.* (2007) its centre of diversity is in southwestern North America and it is now widely distributed in temperate to subtropical areas in North and South America with a few species in Central America as well. A number of species have become naturalized nearly worldwide (Frean *et al.* 1997), most likely in post-Columbian times. According to the European school, on the contrary, several species are endemic to and arose in Europe. This applies not only for the European mutants and hybrids (that are unknown in America) but probably also for some 'pure' species such as *O. biennis*. Most likely, *Oenothera* subsection *Oenothera* underwent its primary differentiation in North America but has a secondary centre of evolution in Europe (Rostański & Karlsson 2010). Quite a few originated by hybridization in Europe and became stabilized due to the extraordinary genetic mechanism mentioned above, and have subsequently become widespread. Species like *O. biennis* and *O. rubricaulis* have been present for a long time in Europe. Since exactly matching biotypes are not known in the wild in North America, early immigration and speciation has been proposed (Rostański 1968, 2004), while Dietrich *et al.* (1997) suggest a hybridogenous origin in Europe from North American taxa introduced in historic time.

Yet another possibility (comm. R. Jean, August 2014) is that *Oenothera* is, indeed, of North American origin but that species of subsection *Oenothera* already entered the Eurasian Continent, via the Bering land bridge, at the end of the last glacial period. This could explain why, genetically, 'European' species of *Oenothera* differ to such an extent from 'American' congeners. Species from subsections *Raimannia* (originating in North America) and *Munzia* (originating in South America), on the contrary, were doubtlessly introduced in post-Columbian times in Europe, have a much more limited distribution (mostly in coastal areas, without having penetrated deeper in the Continent) and are identical to plants found in their respective areas of origin.

Classification of *Oenothera* in Belgium

The overview of all the taxa collected in Belgium is divided over the different sections, subsections and series (Table 2). Taxa collected exclusively before 1950 are preceded by an asterisk (*). In the rest of this paper (except in the appendix), no further reference is made to these taxa (see earlier; also: Verloove *et al.* 2014).

This classification is in accordance with the recent revision by Wagner *et al.* (2007) with the exception of *Oenothera* subsection *Oenothera*. This implies that the genus *Gaura* L. is included in *Oenothera*.

Identification key

Despite being stable, and as such occurring in the absence of their putative parental species, *Oenothera paradoxa* and *O. wratislaviensis* have not been included in the identification key. Both are rare and relatively atypical taxa that are difficult to incorporate into the key. They are briefly described with their assumed parental species (*O. canovirens*, *O. depressa* and *O. subterminalis*). Both are hybrids between species of the series *Devriesia* and *Rugglesia*. Their capsules display an indumentum that is more or less intermediate, with an indefinite mixture of short glandular and stiff, long and eglandular hairs. From the series *Devriesia* and *Oenothera*, the unfixed hybrid *O. deflexa* × *O. depressa* has also been recorded on several occasions. As previously mentioned, it is virtually impossible to identify sporadically occurring hybrids. Plants which either cannot or only with difficulty be keyed-out belong in all probability to hybrid swarms.

The current study follows the so-called European school and thus accepts a narrow species concept. Nevertheless, it seemed also useful to always refer to the corresponding name in the taxonomic concept as defined by the so-called American school. For this reason, for every taxon of the section *Oenothera* subsection *Oenothera* the alternative name under the latter is indicated between square brackets.

1 Petals white or pink when fresh. Capsule clavate, abruptly constricted or cuneate to the base (apparently pedicellate) 2

Petals yellow when fresh (rarely pale yellow) (but in some species drying pinkish, orangish or reddish!). Capsule cylindrical or fusiform, very rarely clavate and abruptly constricted to base (only in *O. fruticosa*) 3

2 Capsule indehiscent. Seeds usually 3-4. Flowers strongly zygomorphic ..... ***Oenothera lindheimeri***

Capsule dehiscent. Seeds usually numerous. Flowers actinomorphic ..... ***O. rosea***

3 Flowers opening at sunrise. Capsule clavate, abruptly constricted or cuneate to the base (apparently pedicellate), narrowly winged .... ***O. fruticosa*** subsp. ***glauca***

Flowers opening near sunset. Capsule cylindrical or fusiform, without wings, not constricted to base 4

4 Seeds ellipsoid to globose, not prismatic and angled. Capsule fusiform, enlarged towards apex (2-4 mm wide at base). Petals yellow, often with a red spot at base (turning pinkish on drying) ..... ***O. stricta***

Seeds prismatic, distinctly angled. Capsule cylindrical, narrowed towards apex (6-8 mm wide at base). Petals yellow, unspotted (exceptionally fading whitish or pinkish on drying) 5

5 Stigma distinctly elevated above anthers at anthesis. Petals always large, 30-55 mm long 6

Stigma surrounded by anthers at anthesis or only slightly exceeding anthers. Petals small or large 9

6 Sepals entirely green or greenish yellow. Stem without hairs with red bulbous base [*O. biennis* × *glazioviana*?] ..... ***O. oehlkersii***

Sepals red-striped, suffused red or uniformly deep red. Stem with hairs with distinct red bulbous base 7

7 Leaf blade nearly plane, subentire at margin, up to 25 mm wide, the upper surface grayish green (indumentum of dense, short hairs). Hypanthium (floral tube) without or with scattered glandular hairs. Ovary and young capsule densely white hairy, without or with few glandular hairs [*O. elata*] ..... ***O. hirsutissima***

Leaf blade distinctly wavy, irregularly dentate at margin, up to 40 mm wide, the upper surface green and nearly glabrous. Hypanthium densely glandular hairy. Ovary and young capsule predominantly glandular hairy, without or with few long, white and eglandular hairs [*O. glazioviana*] 8

8 Sepals uniformly deep red ..... ***O. rubricalyx***

Sepals red-striped or suffused red ..... ***O. glazioviana***

9 Ovary and young capsules densely covered with long white hairs, without or with few glandular hairs. Cauline leaves usually lanceolate, upper surface (at least when young) grayish green with indumentum of dense, short hairs, velvety to the touch. Capsule teeth emarginate or truncate at apex [*O. villosa*] 10

Ovary and young capsules not densely white hairy, with a mixture of (predominantly) glandular and (scattered) patent eglandular hairs. Cauline leaves elliptic to lanceolate, glabrous to slightly hairy. Capsule teeth rounded or cuneate at apex, rarely slightly emarginate 12

10 Stem with numerous hairs with red bulbous base. Bracts and upper cauline leaves with distinctly wavy margins and twisted at apex. Flowers often cleistogamous ..... ***O. depressa***

Stem usually without or (rarely) with sparse hairs with red bulbous base. Bracts and upper cauline leaves with flat margins. Flowers chasmogamous, fully opening 11

11 Capsule teeth truncate at apex ..... ***O. villosa***

Capsule teeth emarginate at apex ..... ***O. canovirens***

12 Inflorescence axis slightly curved before flowering (straightening with time). Cauline leaves narrowly lanceolate, always with red midrib. Sepal tips not adhering at base, with U or V shaped sinus[1]. Petals small, at most 20 mm long (series *Rugglesia*) 13

Inflorescence axis straight from the beginning. Cauline leaves elliptic to lanceolate, with white or red midrib. Sepal tips in bud adherent at base (series *Oenothera*) 15

13 Sepal tips in bud 2-3 mm long, with U shaped sinus. Petals 6-12 mm long [*O. parviflora*] ..... ***O. parviflora***

Sepal tips in bud 2-9 mm long, with V shaped sinus. Petals 10-20 mm long 14

14 Stem dark red, at least in lower half. Sepal tips in bud 4-9 mm long [*O. parviflora*] ..... ***O. subterminalis***

Stem green or slightly suffused red in lower half. Sepal tips in bud at most 3 mm long [*O. biennis* × *oakesiana*] ..... ***O. issleri***

15 Inflorescence axis and upper half of stem without hairs with red bulbous base. Buds, sepals and inflorescence axis uniformly green 16

Inflorescence axis and upper half of stem with numerous hairs with red bulbous base. Buds, sepals and inflorescence axis either green, red, or green suffused with red 20

16 Inflorescence axis nearly glabrous (at most with very scattered, long eglandular hairs) [*O. biennis*] ..... ***O. nuda***

Inflorescence axis densely hairy, in part with short, glandular hairs 17

17 Petals 20-30 mm long [*O. biennis*] 18

Petals 10-20 mm long 19

18 Cauline leaves lanceolate. Petals about as long as wide. Lowermost (oldest) capsules without glandular hairs ..... ***O. cambrica*** var. ***impunctata***

Cauline leaves wider, elliptic to elliptic-lanceolate. Petals obviously wider than long. All capsules glandular hairy ..... ***O. biennis***

19 Petals 9-12 mm long. Hypanthium up to 30 mm long. Capsule up to 40 mm long. Sepal tips 3-4 mm long [*O. parviflora*] ..... ***O. deflexa***

Petals 10-20 mm long. Hypanthium up to 40 mm long. Capsule 30-50 mm long. Sepal tips 5-7 mm long [*O. biennis*] ..... ***O. victorinii***

20 Cauline leaves with wavy margins. Sepals always red-striped. Petals 25-30 mm long and slightly wider [*O. biennis* × *glazioviana*] ..... ***O. fallax***

Cauline leaves plane. Sepals green or suffused with red (red-striped in *O. ersteinensis* only). Petals often smaller, 10-28 mm long 21

21 Inflorescence axis at the beginning of flowering red (stem red or green) 22

Inflorescence axis at the beginning of flowering green (stem red or green) [*O. biennis*] 24

22 Pustulate hair base cylindrical, much longer than wide and often slightly curved downwards. Sepals mostly red-striped (rarely green). Stem usually entirely red [*O. biennis*] ..... ***O. ersteinensis***

Pustulate hair base conical, ca. as long as wide. Sepals green. Stem green, at least in lower half 23

23 Hypanthium 15-25 mm long. Petals 10-20 mm long and 9-18 mm wide [*O. biennis*] ..... ***O. rubricaulis***

Hypanthium 25-35 mm long. Petals 20-28 mm long and about as wide [*O. biennis*?] ... ***O. rubricauloides***

24 Petals 6-12 mm long ..... ***O. royfraseri***

Petals 15-30 mm long 25

25 Cauline leaves lanceolate, with red midrib. Petals 15-25 mm long. Hypanthium 30-40 mm long. Inflorescence lax, more or less pyramidal. Stem nearly always red, at least in lower half ..... ***O. pycnocarpa***

Cauline leaves wider, elliptic-lanceolate, with white or red midrib. Petals 20-30 mm long. Hypanthium 25-35 mm long. Inflorescence dense, oblong. Stem usually green throughout ..... ***O. cambrica*** var. ***cambrica***

[1] The shape of the sepal tips in bud is a useful diagnostic feature, especially to distinguish between series *Oenothera* and *Rugglesia*. However, this character should preferably be assessed on fresh material. See fig. 4.

Table 2. Classification of the *Oenothera* taxa collected in Belgium. Taxa collected exclusively before 1950 are preceded by an asterisk. Based on Wagner *et al.* (2007). For subsection *Oenothera* the names in the second column are those of the so-called American school.

Section *Gaura* (L.) W.L. Wagner & Hoch	
* *Oenothera curtiflora* W.L. Wagner & Hoch (syn.: *Gaura parviflora* Douglas ex Lehm.)	
Oenothera lindheimeri (Engelmann & A. Gray) W.L. Wagner & Hoch (syn.: *Gaura lindheimeri* Engelmann & A. Gray)	
Section *Hartmannia* (Spach) W.L. Wagner & Hoch	
Oenothera rosea L'Hérit. ex Ait.	
* *Oenothera speciosa* Nuttall	
Section *Kneiffia* (Spach) Straley	
Oenothera fruticosa L. subsp. *glauca* (Michaux) Straley	
* *Oenothera perennis* L.	
Section *Oenothera*	
Subsection *Munzia* Dietrich	
Series *Allochroa* (Fischer & Meyer) Dietrich	
* *Oenothera affinis* Cambess. in St.-Hilaire	
* *Oenothera indecora* Cambess. in St.-Hilaire	
Oenothera stricta Ledeb. ex Link	
Subsection *Oenothera*	
Series *Devriesia* Rostański	
Oenothera canovirens Steele	*O. villosa*
Oenothera depressa E. Greene	*O. villosa*
Oenothera paradoxa Hudziok	*O. biennis*
Oenothera villosa Thunb.	*O. villosa*
Oenothera wratislaviensis Rostański ex Rostański	?
Series *Linderia* Rostański	
Oenothera hirsutissima (A. Gray ex S. Watson) de Vries	*O. elata*
Series *Oenothera*	
Oenothera biennis L.	*O. biennis*
Oenothera cambrica Rostański	*O. biennis*
Oenothera deflexa Gates	*O. parviflora*
Oenothera ersteinensis Linder & Jean	*O. biennis*
Oenothera fallax Renner emend. Rostański	*O. biennis* × *O. glazioviana*
Oenothera glazioviana Micheli	*O. glazioviana*
Oenothera nuda Renner ex Rostański	*O. biennis*
Oenothera oehlkersii Kappus ex Rostański	*O. biennis* × *O. glazioviana?*
Oenothera pycnocarpa Atkinson & Bartlett in Bartlett	*O. biennis*
Oenothera royfraseri Gates	*O. biennis*
Oenothera rubricalyx Gates	*O. glazioviana*
Oenothera rubricaulis Klebahn	*O. biennis*
Oenothera rubricauloides Rostański	*O. biennis?*
Oenothera victorinii Gates & Catches.	*O. biennis*
Series *Rugglesia* Rostański	
* *Oenothera angustissima* Gates	*O. parviflora*
* *Oenothera cruciata* Nuttall ex G. Don	*O. parviflora*
Oenothera issleri Renner ex Rostański	*O. biennis* × *O. oakesiana*
* *Oenothera oakesiana* (A. Gray) J.W. Robbins ex S. Watson & Coulter	*O. oakesiana*
Oenothera parviflora L.	*O. parviflora*
Oenothera subterminalis Gates	*O. parviflora*
Subsection *Raimannia* (Rose) Dietrich	
* *Oenothera laciniata* Hill	

Notes on the species recorded in Belgium after 1950

For each of the species included in the key, additional information is provided with respect to its identification and differentiation from related or similar species, current and/or historical distribution in Belgium, degree of naturalization, etc. The most important synonyms have also been added. This is useful since several species were initially recognized under other names in Europe. And, finally, the probable area of origin of each species is also provided (see before).





Figure 6. Oenothera biennis. *Brugge, E-side of Boudewijnkanaal, sand storage area, August 2007. Characteristic features are the entirely green stem and sepals and the medium-sized petals.*

After having compared specimens from America and Europe, Rostański (1985) came to the conclusion that ten *Oenothera* species described from Europe were in fact already previously described from North America. However, part of this synonymy was rejected subsequently (see for instance under *O. cambrica* and *O. ersteinensis*). It may well be that none of the species described from Europe exactly match and that they are best referred to using their 'European' names (comm. R. Jean, August 2014).

• *Oenothera biennis* L., Sp. Pl. 1: 346. 1753.

Figure 6.
Probable area of origin: Eurasia?

Oenothera biennis doubtlessly was the first introduced species of the genus in Belgium. Several sources confirm its presence at the end of the 18th century when the species was already locally abundant according to Crépin (1860): "(…) dès 1792, Roucel la signalait déjà comme abondante aux environs de Bruxelles, Gand et Termonde." Yet, in the last few decades, it has been less often observed and it is even uncertain if it can really be considered as naturalized at present. From the recent distribution map of Flanders (Verloove 2006b) it does appear to be slightly expanding but it is doubtful if this reflects reality.

Oenothera biennis is easily recognizable by the medium sized petals that are wider than long, the total absence of hairs with red bulbous base, the uniformly green-colored sepals and flower buds, etc. *Oenothera deflexa* and *O. victorinii* are more or less similar but have clearly smaller petals. Most similar probably is *O. cambrica* (especially var. *impunctata*). The latter has slightly narrower leaves, petals that are as long as wide and at least the lower capsules are eglandular.

At the coal mining spoil heap of Grande Machine à Feu near Dour existed, for years, a population with pale yellow petals (last confirmed in 2007). Such plants belong to f. *sulphurea* de Vries. At the same site, it was also observed that this taxon formed hybrids with the coexisting population of *Oenothera fallax*. At various locations where *O. biennis* and *O. deflexa* occur sympatrically occasional hybrids between these species have also been observed.

• *Oenothera cambrica* Rostański, Fragm. Florist. Geobot. 23(3-4): 285. 1977.

Figure 7.
Probable area of origin: Europe?

Oenothera cambrica is a rare but possibly overlooked species (see before for the differentiation with the related *O. biennis*). For a long time it was known only from the British Isles (from where it was initially described; Rostański 1977) but more recently it has also been observed in the northwest of France (comm. D. Mercier). The typical variety (var. *cambrica*) has a red punctuate stem whilst var. *impunctata* Rostański has a uniformly green stem. In the last few years both varieties have been collected, in Roeselare (2001) and in Zwijnaarde (2007, 2014).

For some taxa which were described in Europe, it finally turned out that these were documented before in America. Rostański (1985) cited ten such cases, including



Figure 7. Oenothera cambrica *(var.* cambrica*). Zwijnaarde (Gent), roadside, August 2014. This taxon resembles* O. biennis *but the stem is clearly red-punctate.*

Oenothera cambrica. From this, the correct name for *O. cambrica* appeared to be *O. novae-scotiae* Gates. However, according to Dietrich (1991) the type of this species is certainly not identical with *O. cambrica*, nor with *O. biennis* and probably more closely related to *O. parviflora*. Whichever taxonomical concept is used, the name *O. novae-scotiae* cannot be used for *O. cambrica*.

• *Oenothera canovirens* Steele, Contr. U.S. Natl. Herb. 13(10): 365-366. 1911.

= *O. renneri* H. Scholz, Wiss. Z. Pädagog. Hochschule Potsdam, Math.-Naturwiss. Reihe 2: 206. 1956.

= *O. velutinifolia* Hudziok, Verh. Bot. Vereins Prov. Brandenburg 105: 103. 1968.
Probable area of origin: North America.

Oenothera canovirens is a very rare species in Belgium. It was last collected in 1959 from a sand raised site in Antwerpen-Linkeroever. Along with *O. depressa*, it belongs to the series *Devriesia*. Typically, these species have dense, stiff white hairs (with or without a few, barely visible glandular hairs) on the young fruits and leaves are densely hairy and velvety to the touch. Moreover, the upper leaves are often conspicuously falcate. Confusingly, they easily form hybrids with species of the series *Oenothera*; these hybrids display a much less typical assemblage of characters. The putative hybrid of *O. canovirens* and *O. subterminalis* (= *O. wratislaviensis*), a taxon that is also found in areas where one or both parental species are absent, has recently been collected on several occasions, including, for example, the port of Antwerp, in the Baai van Heist and at an abandoned coal mining site in Hensies. This hybridogenous species differs from *O. canovirens* by the clearly red striped flower buds, the red midrib of the leaves and by petals being broader than long. *O. canovirens* is best differentiated from *O. depressa* by the flattened or slightly V-shaped bracts and leaves (without wrinkled margins), the chasmogamous flowers and by the complete or almost complete absence of hairs with a red bulbous base.

• *Oenothera deflexa* Gates, Philos. Trans., Ser. B 226: 332. 1936.

= *O. lipsiensis* Rostański & Gutte, Ber. Arbeitsgem. Sächs. Bot. n.s. 9: 69. 1971.
Figure 8.
Probable area of origin: North America.

Oenothera deflexa is, at present, perhaps the commonest species in Belgium. The first record dates from 1915 (Verloove 2006a) but it has only been spreading vigourously in recent decades (see current distribution map for Flanders in Verloove 2006c). This species was for a long time confused with *O. parviflora*, a species which does not resemble it at all, except that they both have small petals. *O. deflexa* resembles, for the most, *O. biennis* and *O. victorinii* (all with green sepals and flower buds, absence of hairs with red bulbous base, etc.). It differs from *O. biennis* by its much smaller petals that are not broader than long. *O. victorinii*, in turn, has petals, hypanthium and capsules that are slightly larger.

Gutte & Rostański (1971) described *Oenothera lipsiensis* from Germany as a new species. Later, it became evident that Gates had already earlier described the same species on the basis of American plant material (as *O. deflexa*) (Rostański 1985), the latter binomial evidently having priority.

Although this species is currently, without doubt, the most commonly found species in Belgium, it is elsewhere in Europe much less common. Rostański (2006) concluded that it was more or less widespread in Germany,



Figure 8. Oenothera deflexa*. Zwijnaarde (Gent), roadside, August 2014. This species is recognized by its small-sized petals and the absence of hairs with a red bulbous base.*

whereas in Sweden its occurrence was considered as very rare. According to field observations carried out by the second author, it is also to be found in the Netherlands and France, close to the Belgian frontiers.

At a sand storage area in the canal zone of Bruges, a hybrid with *Oenothera fallax* has also been found growing among the parental species. Likewise, in the port of Bruges and at several other locations, putative (unstabilized) hybrids of this species with *O. biennis* have also been collected.

• *Oenothera depressa* E. Greene, Pittonia 2: 216. 1891.
= *O. hungarica* (Borbás) Borbás, Magyar Bot. Lapok 2: 246. 1903.
= *O. salicifolia* Desf. ex G. Don, Gen. Hist. 2: 685. 1832, nom. inval.
Figure 9.
Probable area of origin: North America.

This species belongs, just as *Oenothera canovirens*, to the characteristic series *Devriesia* (see earlier). It differs mostly from the latter by the striking wavy edges of the leaves and bracts, the presence of numerous hairs with a red-bulbous base and the usually cleistogamous flowers. This combination of characteristics as well as the numerous white, eglandular hairs on the young fruits and the leaves that are velvety to the touch make it a striking and easy to recognize plant. In 2007, it was observed at an abandoned coal mining site in Hensies. An earlier Belgian record for Brussels (Jean 1975) now appears to be referable to *O. oakesiana*.

Just as with *Oenothera canovirens*, *O. depressa* easily forms hybrids with species from the series *Oenothera* and *Rugglesia*. At a coal mining spoil heap in Beringen-Mijn





Figure 9. Oenothera depressa*. Hensies (Les Sartis), abandoned coal mining site, July 2007. This species is softly grey-hairy throughout, its leaves have wavy margins and flowers are often cleistogamous.*

a reasonably large population of *O. paradoxa* is found, at least since 2001. This is a probable (stable) hybrid of *O. depressa* and *O. subterminalis* (or *O. parviflora*). It has striking flower buds that are only suffused with red for the uppermost third but for the remainder it is atypical and difficult to insert in the identification key. It is moreover unclear if (at least part of) the current concept of *O. paradoxa* is in agreement with the original concept of this species. [Compare for example Jäger & Werner (2005): "Stg. und Bstandachse nicht getupft" with Hudziok's original description (Hudziok 1968): "Caulis … rubropunctulatus …"] In addition to *O. paradoxa*, a probable hybrid of *O. deflexa* and *O. depressa* has recently been collected in Zeebrugge and Zwijnaarde.

In large parts of Central and Eastern Europe, *Oenothera depressa* is one of the most common species (e.g. Jehlík & Rostański 1979, Rostański *et al.* 1994, Zlatković *et al.* 1998, Rostański 2006). It is found especially in dried out riverbeds (e.g. Deschâtres 1954; sub *O. strigosa*) and similar habitats that are, for the most part, not found in Belgium. It is possible, that it has been overlooked along the River Maas, where it could find a suitable habitat. However, *O. depressa* obviously becomes much rarer towards Western Europe (compare also with Rostański 1982).

This species is often referred to as *Oenothera salicifolia* Desf. ex G. Don (1832). This is an invalid name since the epithet was already given to a different species by Lehmann (1824). The oldest valid name for this taxon appears to be *O. depressa*.

• *Oenothera ersteinensis* R. Linder & R. Jean, Bull. Soc. Bot. France 116: 523. 1970.

?= *O. perangusta* Gates, Canad. Field-Naturalist 64: 142. 1950.

Figure 10.

Probable area of origin: North America.

Oenothera ersteinensis is one of the relatively easy-to-identify species in Belgium. It is unmistakable due to its striking stem hairs: the thickened red hair base is not conical-shaped but cylindrical (much longer than broad) and often slightly curved. It is further characterized by its (usually) red striped sepals and flower buds, the relatively small petals and the (mostly) deep-red stem. Since 1971, it has, on two occasions, been collected in the vicinity of Liège (Ougrée and Chenée). However, it is most well known in the port of Antwerp where, since 2001, it has been found on a regular basis. At present (2014) it has become one of the most widely spread species in the port area. Also in the Kempen it is not rare at all (comm. R. Barendse).

Linder & Jean (1969) described *Oenothera ersteinensis* as a new species from northeastern France. Rostański

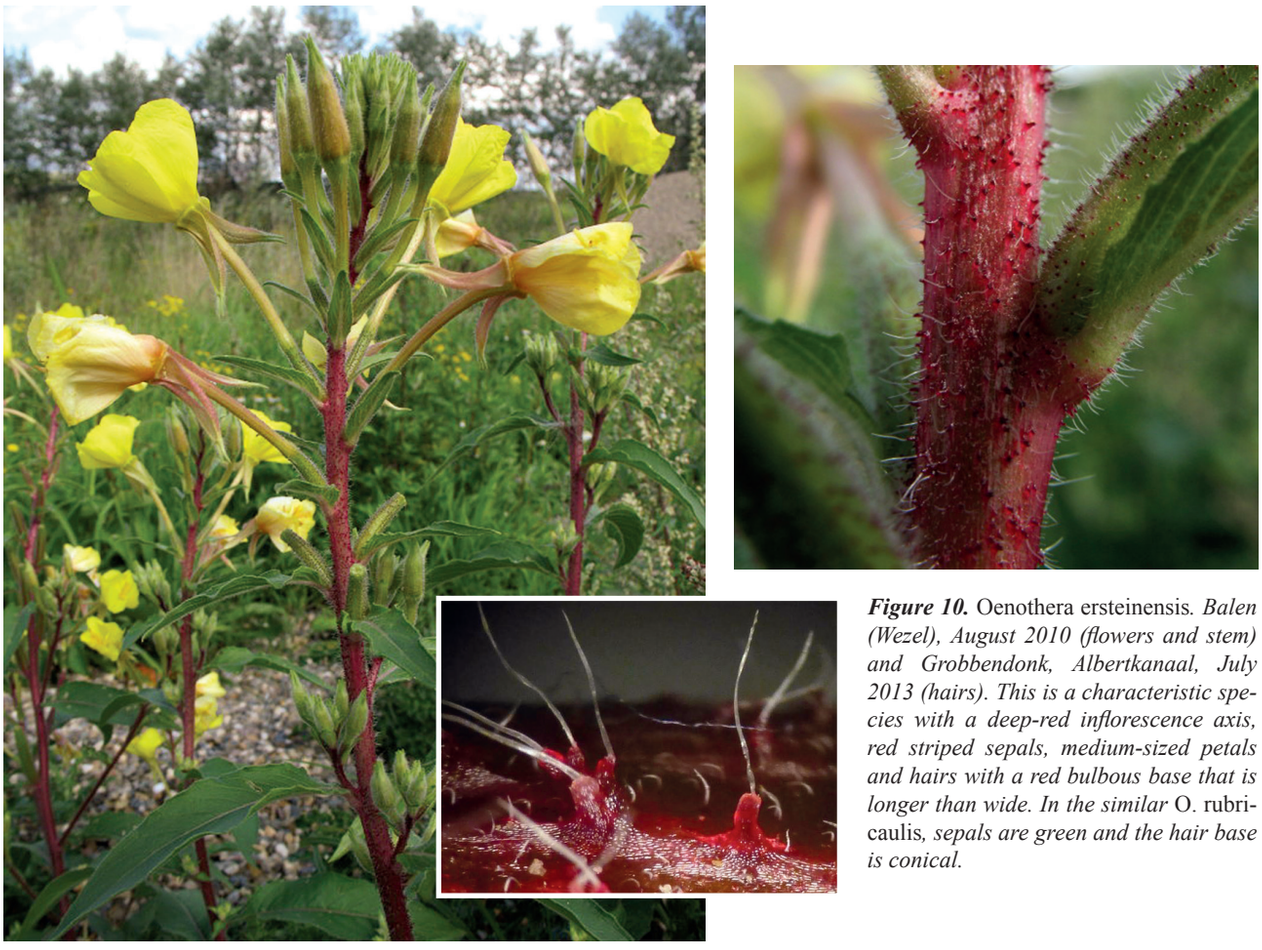


Figure 10. Oenothera ersteinensis. *Balen (Wezel), August 2010 (flowers and stem) and Grobbendonk, Albertkanaal, July 2013 (hairs). This is a characteristic species with a deep-red inflorescence axis, red striped sepals, medium-sized petals and hairs with a red bulbous base that is longer than wide. In the similar* O. rubricaulis*, sepals are green and the hair base is conical.*

(1985) commented that the species had already been earlier described by Gates on the basis of American plant material (as *O. perangusta*). Noteworthy, is that Dietrich *et al.* (1997) considered *O. perangusta* as a synonym for *O. oakesiana*, whilst *O. ersteinensis* was considered as belonging to *O. biennis*. Both are indeed probably distinct, the Belgian plants belonging to *O. ersteinensis*, not to *O. perangusta*. Also, in Rostański *et al.* (2010) both were eventually accepted as separate species.

• *Oenothera fallax* Renner emend. Rostański, Fragm. Flor. Geobot. 11: 507. 1965.
Figure 11.
Probable area of origin: Europe.

This stable hybrid of *Oenothera biennis* (♂) and *O. glazioviana* (♀) parentage is one of the strongest spreading species in Belgium (see also Wittig & Tokhtar 2003). It was already recorded at the end of the 19th century (valley of river Bocq) but its genuine naturalization probably started in the first half of the 20th century when it began to occur in coastal dunes where *O. glazioviana* and *O. biennis* were already naturalized. It is now locally common, especially at sites in the port of Antwerp and Ghent but also in numerous other localities throughout the country. After *O. biennis*, *O. fallax* is the most numerous species in the Rhine valley in Germany (Wittig *et al.* 1999).

Oenothera fallax is readily recognizable by its showy red-striped flower buds and its medium sized petals and cannot be confused with any other species. It is mostly found in populations with both parental species but is also found without them. Moreover, this hybridogenous species is also cultivated in gardens.

At a sand depot in the canal zone of Bruges, a (non-stabilized) hybrid has been found with *Oenothera deflexa*.

• *Oenothera fruticosa* L., Sp. Pl. 1: 346–347. 1753.
subsp. *glauca* (Michx.) Straley, Ann. Missouri Bot. Gard. 64(3): 403. 1977 [1978].
= *O. tetragona* Roth, nom. inval.
Probable area of origin: North America.

This ornamental was recorded only once, in 1998, near a waste recycling factory in Ghent. According to Dietrich (1999) this is one of the most frequently cultivated species but this does not seem to be the case in Belgium. It is a very attractive garden plant with its club shaped fruits, day flowering and for being a perennial (not biennial, the most typical life cycle found in the other taxa occurring in Belgium). For a long time, *O. fruticosa* was accommodated in a distinct genus (*Kneiffia* Spach).

This taxon has long been referred to as *Oenothera tetragona*, an invalid name. The correct name, according to Wagner (2014), is *O. fruticosa* subsp. *glauca*.

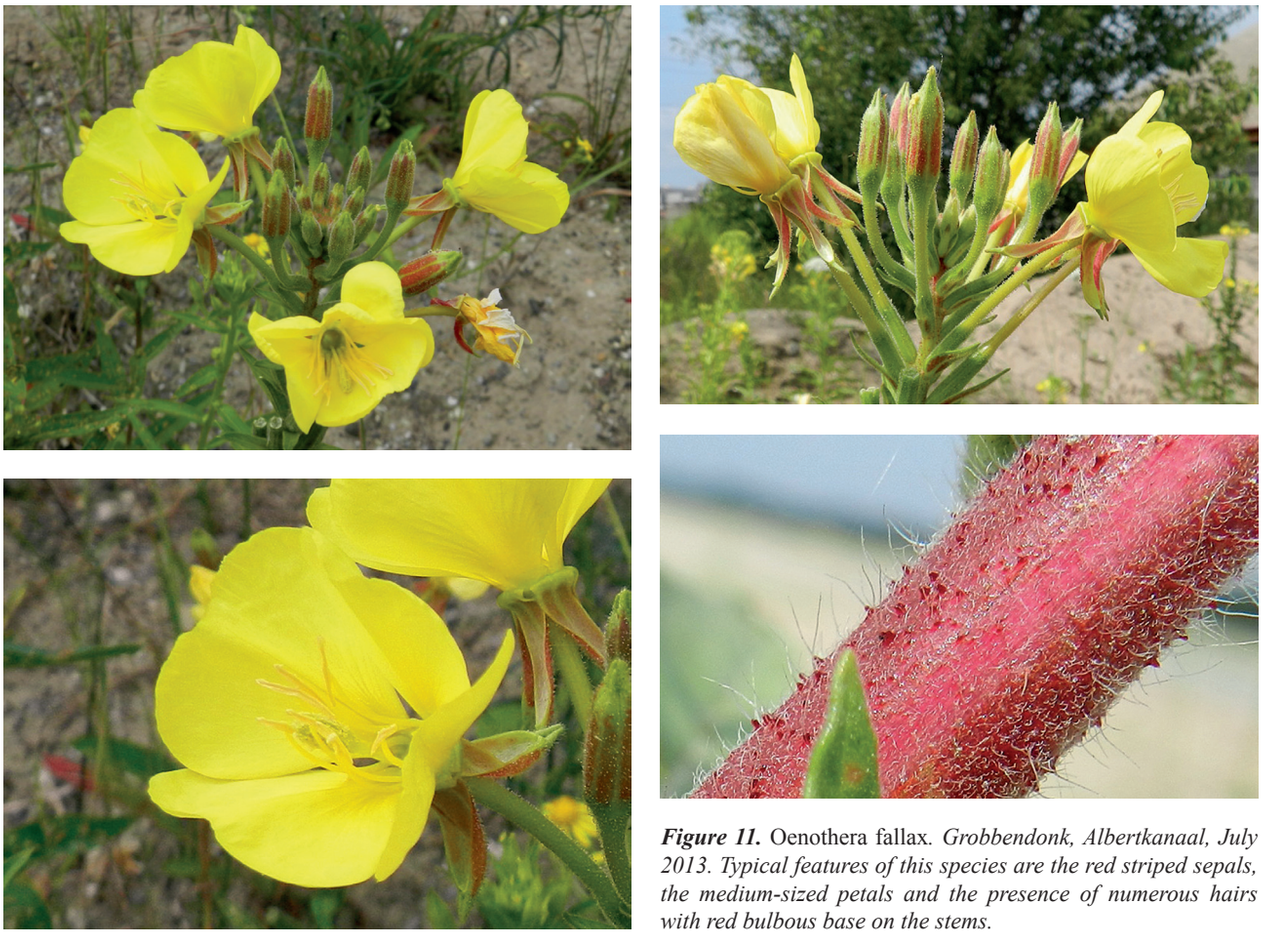


Figure 11. Oenothera fallax. *Grobbendonk, Albertkanaal, July 2013. Typical features of this species are the red striped sepals, the medium-sized petals and the presence of numerous hairs with red bulbous base on the stems.*







Figure 12. Oenothera glazioviana*. Kortrijk, August 2014. Very characteristic species with large petals, sepals that are suffused with red and stems that are red punctate. Compared with* O. hirsutissima*, leaves are wider, less hairy and with distinctly wavy margins.*

• *Oenothera glazioviana* Micheli, Fl. Bras. 13(2): 178-179. 1875.

= *O. erythrosepala* Borbás, Magyar Bot. Lapok 2: 245. 1903.

Figure 12.

Probable area of origin: Europe.

Oenothera glazioviana is one of the few genuinely established species in Belgium. Initially published as *O. lamarckiana* (misapplied), subsequently as *O. erythrosepala* (synonym), this species was already well-established in the first half of the 20th century according to Goffart (1945), especially in the coastal dunes: "se propage au littoral où il abonde dans les dunes (…)". In 1920, it was already found in the vicinity of the coastal towns of Koksijde and Nieuwpoort. It appears that it is still spreading, as shown on the distribution map for Flanders in Verloove (2006d), with a concentration of its expansion clearly located on the Belgian coast. In Belgium it can only be confused with *O. hirsutissima* (see earlier), *O. rubricalyx* (see further) and *O. oehlkersii*, all with large petals and with stigma branches elevated high above the anthers. From the latter it is best differentiated by the presence of hairs with red bulbous base on the stems and the sepals that are suffused with red.

Oenothera glazioviana probably arose in Europe as a result of hybridization or mutation. It is unknown in North America, at least as a wild species.

• *Oenothera hirsutissima* (A. Gray ex S. Watson) de Vries, Mutationstheorie 1: 327. 1901.

≡ *O. elata* Kunth subsp. *hirsutissima* (A. Gray ex S. Watson) W. Dietrich.

Figure 13.

Probable area of origin: North America, Mexico.

Oenothera hirsutissima is a rare and ephemeral species in Belgium. Up to the present it has always been found on sand: in 1961 in the sand dunes near to Nieuwpoort (Belgian coast) and, more recently, at a sand storage area alongside the canal zone of Bruges (between 2004 and 2007) and at a sand raised site located at the Kluizendok in the Ghent port area (2007). This species most resembles *O. glazioviana* (large petals, stigma branches elevated high above the anthers, presence of hairs with red bulbous base, etc.). It is nevertheless differentiated by the typical appressed whitish hairs (absence of glandular hairs) on young leaves and capsules and the narrower, nearly entire leaves that are velvety to the touch. At the site in Bruges it has been observed that *O. hirsutissima* gradually dimin-





Figure 13. Oenothera hirsutissima. *Brugge, E-side of Boudewijnkanaal, sand storage area, July 2007. This species is much reminiscent of* O. glazioviana *but it has softly hairy upper leaf surfaces. Its petals often turn orangish.*

ished, apparently as a result of introgression or hybridization with the accompanying species (especially *O. biennis*, *O. deflexa*, *O. fallax* and *O. glazioviana*).

Oenothera hirsutissima is possibly overlooked in Europe. This species is also cultivated but is probably not fully hardy in Western Europe (Dietrich 1999). Also in Germany, it was recently found in the wild (Rostański & Meierott 2006).

The systematic position of *O. elata*, *O. hirsutissima* and *O. hookeri* Torr. & A. Gray, the latter two considered as subspecies of the former by Dietrich *et al.* (1997), is very unclear. Rostański (1985) assigned *O. elata* s.str. to the series *Devriesia*, whilst he included both other taxa in the series *Linderia*. From this complex *O. hirsutissima* is the most widely spread taxon (Dietrich *et al.* 1997).

• *Oenothera issleri* Renner ex Rostański, Fragm. Florist. Geobot. 11: 514. 1965.

Figure 14.

Probable area of origin: Europe.

Oenothera issleri is a very rare and ephemeral species in Belgium and has been collected only twice so far. It was seen along a railway track in Jambes (Namur) in 1955 and more recently, in 2014, on bare sandy ground in an



Figure 14. Oenothera issleri. *Beveren (Verrebroek), bare sandy area, August 2014. Typical features of this species are its oblique stem and flower buds with sepal tips with V-shaped sinus.*



Figure 15. Oenothera lindheimeri. *Vlissingen (Netherlands), dry grassland, September 2009. Unmistakable by its zygomorphic flowers and previously accommodated in a separate genus (*Gaura*).*



industrial area in Verrebroek (Beveren). It is a stable hybrid of *O. biennis* and *O. oakesiana* parentage (series *Oenothera* and *Rugglesia* respectively). *Oenothera issleri* is also known from a single population on a coal mining spoil heap in northwestern France, relatively close to the Belgian frontiers (Jean & Delay 2008).



Figure 16. Oenothera nuda. *Blaton, sand pit, July 2007. Fairly characteristic in being virtually glabrous throughout.*

• *Oenothera lindheimeri* (Engelm. & A. Gray) W.L. Wagner & Hoch, Syst. Bot. Monogr. 83: 213. 2007.

≡ *Gaura lindheimeri* Engelm. & A. Gray, Boston J. Nat. Hist. 5: 217. 1845.

Figure 15.

Probable area of origin: North America.

Oenothera lindheimeri is at present often cultivated as an ornamental in Belgium ('prachtkaars'). It is unmistakable with its numerous white (or rose) flowers borne on an inflorescence, which is long and drawn out. In recent years it has, now and then, been found on waste ground or levelled soil, often in places where garden waste has been disposed. In Vlissingen (the Netherlands) it has been recorded in dry grassland in the port area, close to the railway station where it persists in small number since its initial discovery in 2009.

This species was until recently included in the genus *Gaura* but molecular phylogenetic analysis has demonstrated that this genus is better included in *Oenothera* (Wagner *et al.* 2007).

• *Oenothera nuda* Renner ex Rostański, Nordic J. Bot. 27(2): 138 (-139). 2009.

Figure 16.

Probable area of origin: Europe.

Oenothera nuda is distinctive with its stem, floral tube, capsule and inflorescence that are virtually glabrous. For the rest, it is particularly reminiscent of *O. biennis*. This species has been found earlier on a few occasions in Wallonia (Houx and Huy). More recently, *O. nuda* has also been collected from a sand pit near to Blaton and at an abandoned coal mining site in Hensies.



Figure 17. Oenothera oehlkersii. *Brugge, rough ground, August 2014. This species is much reminiscent of* O. glazioviana *but it has green sepals and stems.*

• *Oenothera oehlkersii* Kappus ex Rostański, Feddes Repert. 96 : 9. 1985.

Figure 17.
Probable area of origin: Europe.

Oenothera oehlkersii is a striking hybridogenous species which cannot be confused with any other species in Belgium. It resembles for the most *O. glazioviana* (large petals, stigma branches elevated high above the anthers, etc.). It differs from the latter by its uniformly green sepals and flower buds and by the total absence of hairs with a red bulbous base.

Oenothera oehlkersii was already collected in Liège in 1884 but all of the remaining finds are (very) recent. Since 2001, this species has been found fairly often (e.g. in Balegem, Bruges, Ghent, leper, Mouscron, Roeselare, Zonhoven, Zwijnaarde), sometimes in large amounts (for example, at an old dumping site alongside the E40 motorway in the vicinity of Zwijnaarde). Currently, it is a fairly regularly found species, partially due to the fact that it is easy to identify. *O. oehlkersii* has been claimed as a hybrid of *O. glazioviana* and *O. suaveolens* Desf. parentage. However, the presence of a long style is a recessive character that rather suggests a mutant (translocation) of *O. glazioviana*, not a hybrid (comm. R. Jean, January 2009).

• *Oenothera parviflora* L., Syst. Nat. (ed. 10) 2: 998. 1759.

Probable area of origin: North America.

In Belgium, *Oenothera parviflora* is rare and declining. Nearly all references cited in the literature are in fact referable to *O. deflexa* (see earlier). *O. parviflora* belongs (along with *O. subterminalis*) to the series *Rugglesia*. This group is characterized by a slight to clearly curved inflorescence just before flowering and the sepal points which are separated from the base. Unfortunately, both characteristics are only really clear in fresh material. Moreover, this species is also differentiated from *O. deflexa* by the frequent presence of hairs with a red bulbous base. *O. parviflora* has, since 1884, been collected on 15 occasions, especially around Brussels. The majority of the finds date from the 1950s and 1960s. Yet more recently, it has also been collected in Halle (near to Brussels) (1978), Heist-aan-Zee (Belgian coast) (2000) and Jemeppe-sur Meuse (1984).

• *Oenothera pycnocarpa* Atkinson & Bartlett in Bartlett, Rhodora 15: 83. 1913.

= *O. chicaginensis* de Vries ex Renner & Cleland, Z. Indukt. Abstammungs- Vererbungsl. 66: 275. 1933.
Figure 18.
Probable area of origin: North America.

This species is a recent newcomer to Belgium (the oldest finding dates from 1992 in Queue-du-Bois). It was regularly found, especially since 2007, at several different sites in the port of Antwerp as at a demolition site in the port of Bruges. The largest population (at least 1000 plants) was, also in 2007, discovered at an excavated coal mining spoil heap in Gilly near to Charleroi. At this site it appeared that *Oenothera pycnocarpa* was more or less established; however, three years after its discovery it completely disappeared, despite its habitat remaining unchanged (comm. M. Lannoy, August 2014). This species bears some resemblance to *O. biennis* (medium sized petals, green sepals) but differs from it by the presence of hairs with a red bulbous base, the stem which in the lower half is colored red (also often peach-colored) and in the upper half green, at least at the beginning of flowering. Moreover, *O. pycnocarpa* flowers rather late, from the second half of July to the beginning of August.

In the west of Germany it is the 3rd most numerous species (e.g. Wittig *et al.* 1999, Wittig & Tokhtar 2003). Bearing this in mind, it is possible that it has been overlooked in the east of Belgium.

• *Oenothera rosea* L'Hér. ex Ait., Hort. Kew. 2: 3. 1789.

Probable area of origin: Central America.

This unmistakable species, which at first sight resembles more an *Epilobium* (on behalf of its relatively small, rose coloured petals), was collected on several occasions in the 19th century in Wallonia. Around 2000, it was also observed at an abandoned coal mining site near to Saint Ghislain, where it did not persist (comm. P. Dupriez).



Figure 18. Oenothera pycnocarpa*. Brugge, industrial area, demolition site, August 2007. This species is related to* O. biennis *but differs from it by its red-punctate stem that is always reddish in the lower half.*





Figure 19. Oenothera rubricalyx. *Rekkem, LAR-transportzone, grassland, July 2014. This species differs from* O. glazioviana *by its entirely blood red sepals.*



In the extreme Southwest of France, *Oenothera rosea* is commonly naturalized.

• *Oenothera royfraseri* Gates, Philos. Trans., Ser. B 226: 285, fig. 30, 31. 1936.

= *O. turoviensis* Rostański, Fragm. Florist. Geobot. 11: 514. 1965.
Probable area of origin: North America.

In common with other species, including *Oenothera deflexa* and *O. parviflora*, this species also has small petals. It can be differentiated from *O. deflexa* by the presence of hairs with a red bulbous base on the stem. By the absence of a curved inflorescence as well as the basally contiguous sepal tips it can be differentiated from *O. parviflora*.

Oenothera royfraseri was found in large numbers at a demolition site in the port of Antwerp in 2007 but not confirmed subsequently.

• *Oenothera rubricalyx* Gates, Rep. (Annual) Missouri Bot. Gard. 20: 133. 1909.

≡ *O. glazioviana* f. *rubricalyx* (Gates) Lambinon, Nouv. Fl. Belg., Grand-Duché Luxemb., Nord France, 5th ed.: 1048. 2004.
Figure 19.
Probable area of origin: North America.

A beautiful population of this species was discovered in dry grassland (former sand raised site) in the Lauwe/Aalbeke/Rekkem transport zone (LAR) in 2014. The species occurs in fairly large amounts and looks more or less established.

Oenothera rubricalyx is a mutant of *O. glazioviana* with entirely deep red sepals. It is striking and garden worthy. It seems to be rare in the wild in Europe and was previously only reported from coastal dunes near Etaples in northwestern France (Rostański *et al.* 1994, Lambinon & Verloove 2012).

• *Oenothera rubricaulis* Klebahn, Jahrb. Hamburg. Wiss. Anst. 31: 12. 1914.

Figure 20.
Probable area of origin: Europe.

Although this species was already collected in 1887 (Antwerp) it has only become more or less widespread in recent years. Especially around the city of Ghent (e.g. in the port area, where it has been observed at least since 1985 and where it is firmly established now) *Oenothera rubricaulis* has become a reasonably common species. Recently, it has also been seen more often around Antwerp. It differs from most other species by its small to medium sized petals and the deep red inflorescence axis. It is similar to *O. ersteinensis*; however, the latter has red-bulbous hairs with a cylindrical (not conical) base and mostly red-striped sepals. However, *O. rubricaulis* most resembles *O. rubricauloides* (see under).

Elsewhere in Europe, *Oenothera rubricaulis* is also a rapidly expanding species. It is even the second most numerous *Oenothera* species in Scandinavia (Rostański 2006) and in Eastern Europe, it is considered – along with *O. biennis* and *O. depressa* – the species with the highest invasion rate (Tokhtar & Groshenko 2014).

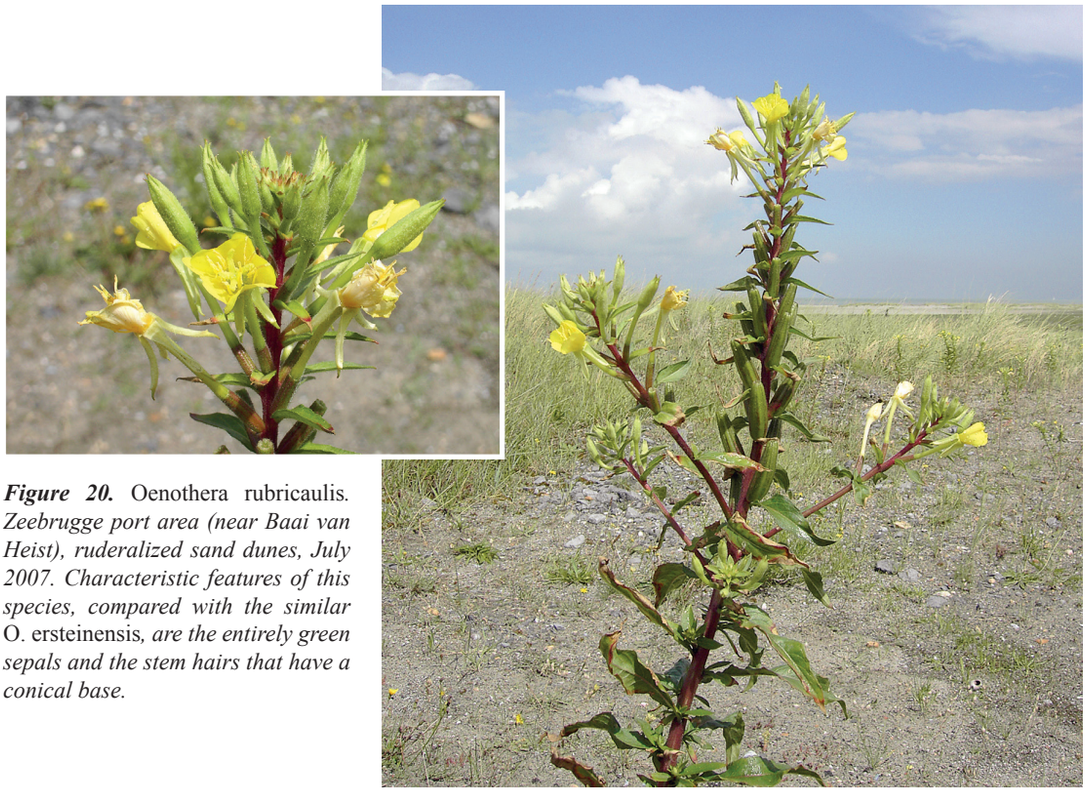


Figure 20. Oenothera rubricaulis. *Zeebrugge port area (near Baai van Heist), ruderalized sand dunes, July 2007. Characteristic features of this species, compared with the similar* O. ersteinensis*, are the entirely green sepals and the stem hairs that have a conical base.*

• *Oenothera rubricauloides* Rostański, Ann. Bot. Fenn. 44: 395. 2007.

= *O. rubricaulis* var. *longistylis* Gutte & Rostański, Ber. Arbeitsgem. Sächs. Bot. 11: 187. 1981.
Probable area of origin: Europe.

This hybridogenous species was collected in 2007 on two occasions around Ghent, each time at locations where (among others) *Oenothera glazioviana* as well as *O. rubricaulis* were found. Rostański (2007), who recently described this taxon, did not cover its possible relationship. A cross between the two mentioned species appears quite possible: *O. rubricauloides* is in all floral characteristics more or less intermediate between both and the stigma branches are somewhat elevated above the anthers (hence the variety name if considered an infraspecific taxon of *O. rubricaulis*). Alternatively, Rostański & Karlsson (2010) suggested a hybrid formula *O. muricata* × *O. biennis*.

In Scandinavia this taxon is reasonably widespread and for this reason it is considered as an independent species.

• *Oenothera stricta* Ledeb. ex Link, Enum. Hort. Berol. Alt. 1: 377. 1821.

Probable area of origin: South America.

At the end of the 19th century (at least between 1878 and 1900), *Oenothera stricta* was more or less established at the old city walls of Antwerp ("station abondante"). Now and then it was also collected elsewhere (e.g. De Panne, Fleurus, Wilsele, etc.) but perhaps always as an ephemeral alien. In the 20th century only two collections are forthcoming: Bellecourt (around 1950) and Angleur (1984). Elsewhere in Europe, *O. stricta* is, in many places, established, mostly in coastal sand dunes (e.g. France, Great Britain, Portugal, etc.). It obviously is confined to the climatologically milder parts of Europe and may perhaps be not fully hardy in Belgium.

Typical for this species are its nearly hemispherical seeds, the capsules which are gradually narrowing towards base and the petals which are turning reddish or pinkish after flowering.

• *Oenothera subterminalis* Gates, Philos. Trans., Ser. B 226: 278, Fig. 26, 27. 1936.

= *O. silesiaca* Renner, Ber. Deutsch. Bot. Ges. 9: 455. 1942.
Figure 21.
Probable area of origin: North America.

Just like *Oenothera parviflora*, this species belongs to the series *Rugglesia* and thus combines the drooping tip of the inflorescence (just before flowering) with the sepal tips which are separated from the very base. The petals are mostly larger, the stem has a deeper red color and sepal tips are longer (see key).

Oenothera subterminalis is one of the characteristic species found in the coal mining basins of northwest France. Strangely, it is virtually absent at identical habitats found just over the border in Belgium (Borinage) (see also Jean 1975). In 1979, it was collected on a single occasion at a spoil heap in Châtelineau. In 2004, it was also collected near the Zeebrugge port area (Baai van Heist) together with *O. wratislaviensis*, its possible hybrid with *O. canovirens* (see earlier).



Figure 21. Oenothera subterminalis. *Hénin-Beaumont (France), coal mining spoil heap, July 2009. This species has narrowly lanceolate leaves, a deep red stem and relatively small petals. Before flowering its inflorescence axis is slightly curved.*

This species was described by Renner on the basis of European material (as *Oenothera silesiaca*). As in similar cases, later it appeared that it was already earlier described in America (as *O. subterminalis*) (Rostański 1985), although both may be distinct as well (comm. R. Jean, August 2014).

• *Oenothera victorinii* Gates & Catches., J. Linn. Soc., Bot. 49: 182. 1933.

= *O. nissensis* Rostański, Fragm. Florist. Geobot. 11: 508. 1965.
= *O. rostanskii* Jehlík, Folia Geobot. Phytotax. 20(4): 439. 1985.
Figure 22.
Probable area of origin: North America.

Oenothera victorinii mostly resembles *O. biennis* and *O. deflexa* (see earlier). This species was only collected in Belgium for the first time in 1992 (Lasne). In the last few years it has certainly been observed more often, for





Figure 22. Oenothera victorinii. *Osłowo, Podlaskie region, Siemiatycze commune (Poland), July 2011. This species much resembles* O. deflexa *but it has slightly larger petals.*



Figure 23. Oenothera villosa. *Brugge, E-side of Boudewijnkanaal, sand storage area, July 2014. This species shares the soft greyish pubescence with* O. depressa *but its stem is hardly (or not at all) red-punctate, leaf margins are not crispate and flowers are chasmogamous.*





instance in Gentbrugge (1998-2004) and Roeselare. At both sites it persisted over the course of several years but eventually disappeared. It was also recently collected at several locations around Antwerp.

Just as with the previous species, it turned out only recently that this species was already earlier known in North America and thus was needlessly described from Europe (Rostański 1985).

• *Oenothera villosa* Thunb., Prodr. Pl. Cap. 1: 75. 1794.

Figure 23.

Probable area of origin: North America.

Oenothera villosa was discovered in 2007 in a sand storage area alongside the Boudewijnkanaal in Bruges and regularly confirmed subsequently (ca. 5-10 plants still present in 2014).

This species from section *Devriesia* is much reminiscent of *Oenothera canovirens* (both with a velvety leaf indumentum, flat leaf margins, hairs with red bulbous bases absent or scarce on the stem, etc.). It is distinguished from the latter by its capsule teeth that are truncate to nearly round at apex instead of emarginate.

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Appendix: overview of specimens examined

In this overview all species of *Oenothera* ever recorded in Belgium (including those recorded exclusively prior to 1950) are alphabetically listed. Records are provided chronologically per province. Records from the current provinces Flemish Brabant and Walloon Brabant are grouped together.

Oenothera affinis

• Liège: Vovegnez, graviers, 09.1909, P. Halin s.n. (LG); Vovegnez (Wegnez), berge de la Vesdre, 12.09.1909, M. Halin s.n. (BR).

Oenothera angustissima

= *O. rubricuspis* Renner ex Rostański

• Brabant: Héverlé, talus, 08.1864, O. De Dieudonné s.n. (BR); Tirlemont, talus du chemin de fer, 08.08.1864, H. Vandenborn s.n. (LG); Dieghem, vias ferreas, 1877, C. Baguet s.n. (BR); entre Groenendael et La Hulpe, ligne du chemin de fer, 08.1877, O. Hecking s.n. (BR);
• Limburg: St-Trond, talus du chemin de fer, 30.07.1860, H. Vandenborn s.n. (LG); St-Trond, bord de chemin, 24.07.1861, A. Thielens s.n. (BR); St-Trond, 07.1862, A. Thielens s.n. (LG); St-Trond, talus du chemin de fer, 05.08.1862, H. Vandenborn s.n. (BR); St-Trond, 1864, Vandenborn s.n. (BR); St-Trond, talus du chemin de fer, 08.08.1864, Vandenborn s.n. (BR, LG); St-Trond, talus du chemin de fer, 22.07.1865, H. Vandenborn s.n. (LG); St-Trond, talus du chemin de fer, 22.07.1865, H. van Heurck & A. Martinis s.n. (BR, GENT); St-Trond, talus du chemin de fer, 08.1867, H. Vandenborn s.n. (BR); St-Trond, bords des chemins, cette plante n'existe en Belgique que sur les talus d'un chemin de fer à St-Trond, où elle tend à se naturaliser, 05.08.1867, A. Thielens & A. Devos s.n. (BR, GENT, LG); St-Trond, talus du chemin de fer, 1869, J.-E. Bommer s.n. (BR); St-Trond, 10.1870, P. de Chestret 154 (BR); St-Trond, fortifications, 07.1884, P.J. Delrez s.n. (LG).

Oenothera biennis

• Antwerp: Anvers, endroits frais, bassin de natation, 06.1855, Tosquinet s.n. (BR); Anvers, Kiel, digue de l'Escaut, 08.1860, A. Vanheurck s.n. (LG); Tongerlo, sous les murs de l'abbaye, 07.1862, Carnoy s.n. (BR); Tongerloo, 07.1863, A. Thielens s.n. (BR); Lierre, bords des chemins, 11.07.1874, L. Piré s.n. (BR); Anvers, fortifications près de la porte de Wilrijk, 23.06.1878, H. Vandenbroeck s.n. (BR); Calmpthout, terrain inculte, 08.07.1882, J. Hennen s.n. (BR); Brasschaet, au Peerdsbosch, station de Vieux Dieu, 07.1896, J. Spas s.n. (BR); Anvers, fortifications à Berchem, 07.1900, R. Godding s.n. (BR); Wilryck, fortise 6, 09.1903, C. Picquet s.n. (BR); Emblehem-sas, helling van den aquaduc, 06.07.1913, E. van Rompaey GIII/1436.1 (BR); Herenthals, colline, 25.07.1920, V. Lambert s.n. (BR); St. Anna, chemin (naturalisé), 15.08.1934, G. De Gottal s.n. (BR); Antwerpen, Zuidervesting, grazige plaats, 17.08.1942, Frison s.n. (GENT); Malines, Coloma, talus du chemin de fer, 15.07.1949, N. Cnops 49.118 (BR); Deurne, op droge grond, 19.07.1951, H. Mervielde s.n. (BR); Brecht, le long de voie ferrée, 07.1953, J. Plancke 104 (BR); Kruisschans, zandgrond, 12.07.1953, E. Jacques 341 (BR) ; Rijmenam (IFBL D5.31.24), zandig terrein, 13.07.1956, A. Jans 127/56 (BR); Postel, Moeren, rudéral, bord de route, 02.09.1956, A. Lawalrée 8078 (BR); Postel, chemin sablonneux près de la tourbière de Postel, 21.09.1956, J. Lambinon (LG); Antwerpen-West, zandgrond, 11.07.1957, Léothade De Ruyver s.n. (BR); Sint-Anna (IFBL C4.26.14), opgespoten gronden, 28.06.1959, E. van Rompaey GIII/1436.1 (BR); Postel, digue d'un étang, 03.08.1965, A. Lawalrée 13185 (BR); Mol-Postel, langs waterkant, 03.08.1965, S. Peeters 123 (BR); Mol-Maat, langs het kanaal aan sluis, 08.1967, H.G. Rabijns 1465 (BR); Turnhout, weg naar Baarle-Hertog, grazige ruigte, niet afgemaaide plaats, 04.08.1974, J. Aerts 74/57 (GENT); Turnhout, Kempenlaan, tussen Gierledreef en Antwerpsesteenweg, opgehoogde braakliggende grond langs de weg, 09.07.1976, J. Aerts 76/38 (GENT);
• Brabant: Kessel-Loo, chemin de fer (talus), 07.1855, C. Baguet s.n. (BR); près de Bruxelles, naturalisé à Groenendaal, 08.1856, Martinis s.n. (BR); Groenendael, 18.07.1861, L. Piré s.n. (BR); Uccle, sur les hauteurs, 09.1862, L. Van Den Borren s.n. (BR); Betekom, bords du Demer, 20.07.1863, C. Baguet s.n. (BR); Louvain, parc, talus du chemin de fer, 07.1865, C. Baguet s.n. (BR); Forest, talus sablonneux, 06.07.1866, L. & V. Coomans s.n. (BR); Auderghem, 1868 (BR); Forest, champ sablonneux, L. & V. Coomans s.n. (BR); Forest, lieux incultes, 25.07.1875, A. Gravis s.n. (LG); St. Josse-ten-Noode, talus du chemin de fer, 18.06.1883, L. Guelton s.n. (BR); Ottignies, 05.1885, H. Vindevogel s.n. (BR); Louvain, talus du chemin de fer, 02.06.1887, A. Busschodts s.n. (BR); Parck, talus du chemin de fer, près de l'abbaye, 06.1888, C. Piquet s.n. (BR); Blauwput, 29.08.1894, E. Michel s.n. (BR); Wilsele, lieux incultes, 07.1896, C. Baguet s.n. (BR); Uccle (Crabbegat), 06.09.1918, F. Stockmans s.n. (BR); Forest, derrière le Parc Duden, carrières de sable, 10.09.1919, F. Stockmans s.n.

(BR); entre Vilvorde et Haeren, talus du chemin de fer, <1920, Vermoesen & Guns s.n. (BR); Louvain, talus du chemin de fer entre les 2 lignes de Malines et d'Aerschot, 30.08.1920, Vermoesen s.n. (BR); Louvain, Blauwput, voie du chemin de fer vers Malines, 30.08.1920, Vermoesen s.n. (BR); Etterbeek-Cinquentenaire, cendrée de la station, 14.07.1923, E. Michel s.n. (BR); Haeren, talus le long des voies du chemin de fer de l'état, 26.09.1923, V. Lambert s.n. (BR); Uccle, <1929, J. Henry s.n. (BR); Vilvorde, remblai du chemin de fer, 02.07.1930, De Vits s.n. (BR); Vilvorde, remblai du chemin de fer, 28.07.1930, V. Lambert s.n. (BR, LG); Louvain, canal, 07.07.1933, R. Mosseray & F. Vandevelde s.n. (BR); Aarschot, terrain inculte le long du chemin de fer de ceinture Anvers-Diest, 29.07.1937, E. Michiels s.n. (BR); Parc (lez Louvain), talus de la tranchée de la voie ferrée, 07.07.1941, A. Lawalrée 720 (BR); Genval, décombres, 29.06.1946, J.-E. Rogister s.n. (BR); Schaarbeek, gare de formation, 07.1947, E. Michel s.n. (BR); Bruxelles, jonction nord-midi, décombres, 08.1947, E. Michel s.n. (BR); Woluwé, bois, 06.07.1950, M. Couteaux s.n. (BR); entre Oud-Heverlee (gare) et Corbeek-Dijle, décombres au bord du chemin, 01.07.1951, A. Lawalrée 3619 (BR); Kessel-Lo, Blauwput, puinen, 12.07.1951, J. Pelgrims s.n. (BR); Anderlecht, décombres, 08.1954, s.c. (BR); Heverlee, wegkant, 01.11.1954, M.-T. De Roo s.n. (BR); Auderghem, coin du Boulevard du Souverain et de l'Avenue Hermann-Debroux, terre remuée cette année pour les travaux du viaduc-autoroute, 23.09.1973, A. Lawalrée 18221 (BR);

• East Flanders: Aeltere (Aalter), Craenepoel, s.d., s.c. (GENT); Aeltere, sapinières, 1851, Coemans s.n. (BR) + Gand, chemin de remblais dans les prés aux moines (semences probablement apportées avec les décombres), 1851, Coemans s.n. (BR); Gand St.-Pierre, 08.1854, Scheidweiler s.n. (BR); Tronchiennes (Drongen), 07.1855, s.c. (GENT); Gand, 1871, s.c. (BR); Bellem, station, 07.1873, E. Vandermeersch s.n. (GENT); Bellem, bois (coupes), naturalisé, 19.07.1883, L. Magnel s.n. (BR); Waasmunster, Uilenkasteel, 21.07.1903, Guns s.n. (BR); Assels, oostzijde spoorweg, 15.09.1931, s.c. (GENT); Sint-Amandsberg, spoorberm, 23.07.1966, J. Van Den Haute 164 (BR); Gent, even voorbij Meulestedebrug, driehoekig terrein tegenover Café "Les Routiers", kruidenrijke vegetatie met Malva sylvestris, 06.07.1974, E. Robbrecht 638 (BR); Gent, RUG, Plantentuin Maton, K.L. Ledeganckstraat 35, braakliggend terrein, zonnig, droog, opgehoopt, 05.08.1976, H. Viane 62 (GENT); Sint-Denijs-Westrem, station, in verwaarloosd terrein, vroeger opslagplaats van goederen en kolen, 03.08.1978, D. Duytschaever 60-61 (GENT); Zelzate, weg Gent-Zelzate via Linkeroever, graafwerken ten N van executieoord Rieme (IFBL C3.33.34), ruigte, 17.09.1982, E. Robbrecht 2530 (BR); Appels (IFBL D3.28.24), gestorte grond rand weg, 16.09.1992, K. Thielemans s.n. (BR); Harbour of Ghent, Singel near Farmanstraat (IFBL D3.13.11), ruderal gravelly road verge, 24.06.2000, F. Verloove 4409 (BR); Gent, Hundelgemsesteenweg near river Schelde (IFBL D3.23.33), waste ground, 27.06.2004, F. Verloove 5714 (BR); Belzele (N-Gent), N of Ringvaart near junction with Brugse Vaart (IFBL D3.11.21), stony border of canal, common, 24.06.2007, F. Verloove 6777 (BR); Kerkbrugge (N-Gent) (IFBL C3.52.24 + 53.13), former railway yard, 24.06.2007, F. Verloove 6778 (BR);

• Hainaut: Braine-le-Comte, tunnel, 05.07.1949, S. Depasse 88/22 (BR); Quivrain, railway yard, gravelly soil, 04.07.2004, F. Verloove 5726 (BR); Frameries, bas du terril du PASS, 08.2006, D. Geerinck-Coutrez 9701 (BR); Dour, La Grande Machine à Feu (terril) (IFBL G3.53.12-21), coal mine heap, 07.07.2007, F. Verloove 6872 (BR); Mons, Mont Ostène, terril du Pass (IFBL G3.45.41), terril, zone en combustion, 25.07.2007, F. Verloove 6866 (BR);

• Liège: Rochefort, s.d., F. Crépin s.n. (BR); Tilff, 06.1871, H. Donckier s.n. (LG); Fraipont, rocailles au bord de la Vesdre, 1872, s.c. (GENT); entre Trooz et Fraipont, lieu rocailleux, 1872, Strail s.n. (BR); Ougrée, bord de la Meuse, 30.06.1872, J.-L. Wathelet s.n. (BR); entre Limbourg et [...], le long de la […], 08.1874, O. De Dieudonné s.n. (BR); environs de Visé, 1876, A. Hardy s.n. (BR); Flaire, 09.09.1883, P.J. Delrez 450 (LG; mixed collection with O. cruciata); Soiron, […], 09.09.1883, P. Delrez s.n. (LG); Modave, jardin, 04.08.1884, G. Evrard s.n. (BR); Esneux, 1888, C. Sladden s.n. (BR); Val-Dieu (Charneux), bord d'un chemin, 07.1890, M. Halin s.n. (BR); Tilff, bords de l'Ourthe (il n'y en avait que 2 ou 3 pieds, j'ai remarqué qu'il était plus abondant près d'Esneux), 26.06.1892, C. Sladden s.n. (BR); Comblain-au-Pont, 29.07.1902, H. de Luesemans s.n. (BR, LG); Lambermont, 1905, P. Doubleman s.n. (LG); Esneux, sous la Roche aux Faucons, sentier broussailleux, 10.07.1906, A. Maréchal s.n. (LG); Vovegnez (Wegnez), berge de la Vesdre, 07.1907, M. Halin s.n. (BR); Seraing, décombres, 09.08.1907, H. Henin s.n. (LG); Val-Benoit, terrain vague, 13.07.1908, M. Halin s.n. (BR); Theux, 13.07.1908, s.c. (BR); Liège, 08.1908, P. Doubleman s.n. (LG); Vierset-Barse, gare de Régissa, 08.07.1919, A. Charlet s.n. (LG); Vesdre, 12.09.1920, A. Visé s.n. (LG); Ensival, Vesdre, 07.1940, A. Visé s.n. (LG); Fond des Cris (Chaudfontaine), 09.1946, L. Renard s.n. (LG); Tilff, quai Ste. Anne, sentier longeant la rive droite de l'Ourthe, 18.08.1962, A. Lawalrée 11711 (BR);

• Limburg: Hasselt, derrière le cimetière, 1877, O. Geraets s.n. (BR); Wychmael (Beverloo), 16.07.1911, M. Guns s.n. (BR); Curange-Hasselt, voies du chemin de fer, aux environs des ateliers de réparation, assez répandu, 07.08.1920, Vermoessen s.n. (BR); Leopoldsburg, sables, 07.1956, J. Lebeau s.n. (BR); Genk (IFBL D7.51.22), port, 26.08.1956, A. Lawalrée 8032, 8034 (BR); Genk-Waterschei, déblais d'usine, 21.07.1958, A. Lawalrée 10159 (BR); Bree ('t Hasselt), langs brug, oever Zuid-Willemsvaart, 17.07.1962, J. Pelgrims 1454 (BR); Leopoldsburg, langs een weg, 07.1967, H.G. Rabijns 1462 (BR); Zolder, <1998, L. Janssen s.n. (BR);

• Luxembourg: Orval, abbaye, 26.07.1856, Gravet s.n. (BR); Forêt d'Orval, coteau, 08.1882, E. Chapuis s.n. (LG); Virton, à la grande route vers Rabais, 08.08.1949, A. Lawalrée 2417 (BR); Lahage, halte, près de la halte de la voie ferrée, 04.07.1963, A. Lawalrée 12499 (BR); limite des communes Mirwart, Arville et Smuid, bord de la voie ferrée, 09.09.1964, A. Lawalrée 12864 (BR); Buzenol, gare, 27.07.1968, M. Lambert s.n. (LG); entre Orval et […], route, 24.07.1974, D. Geerinck 782 (BR);

• Namur: Anseremme, bords de la Lesse, 07.1867, C.L. Guilmot s.n. (BR); Han, bois à l'entrée de la grotte, 06.1882, P. de Chestret s.n. (BR); Eprave, abondant à la lisière d'un bois, 07.1886, F. Pietquin s.n. (BR); Belvaux, 1889, H. Verheggen s.n. (BR); La Plante, naturalisé, 06.1890, Leclerc s.n. (BR); Belvaux, coteau près du Gouffre de Belvaux, 09.1936, O. Gras s.n. (BR); Eprave, route de Han, 08.1938, O. Gras s.n. (BR); Anseremme, décombres, 06.09.1942, O. Gras s.n. (BR); Houyet, talus du chemin de fer vers Hout, 07.1943, J. Legrain s.n. (BR); Durnal, Pipeti, Vallée du Bocq, rive droite, talus dans une chênaie silicicole, 17.07.1977, E. Sérusiaux 77/B/434 (LG); Namur, chemin du Pont de Bricques à Jambes (IFBL G5.47.11), 10.07.1986, D. Geerinck 3728 (BR); environs de Sosoye, long de l'ancienne voie ferrée, ballast de la voie ferrée, 13.10.1990, D. Geerinck 1569 (BR); vallée de la Molignée, près de l'abbaye de Maredsous, ballast de la voie ferrée, 13.10.1990, G. Bruynseels 1662 (BR);

• West Flanders: Nieuport-Bains, lieux incultes, 23.07.1892, C. Baguet s.n. (BR); La Panne, lieux incultes, 27.07.1892, C. Baguet s.n. (BR); Duinbergen, dunes, 07.1929, E. Dewildeman s.n. (BR); Wenduine, 07.1946, L. Renard s.n. (LG); Comines, bord de la Lys, 28.06.1947, J. Baily s.n. (BR); Adinkerke, sable au bord d'une avenue, 03.09.1954, J.-L. De Sloover 2581 (BR); De Panne, dunes, 08.1956, J. Lebeau s.n. (BR); Avekapelle (IFBL D1.11.11), braakliggende akker, 06.10.1997, H. Ruysseveldt 2007 (BR); Gits (IFBL D1.38.13), ruigte bij het station, 27.08.1987, F. Verloove 6 (BR); Nieuwpoort (IFBL C1.41.11), open plek gefixeerd duin, 07.08.1995, H. Ruysseveldt s.n. (BR); Waregem (Eertbrugge) (IFBL E2.26.13), grazige vegetatie berm, brug over autosnelweg, 24.06.2003, H. Ruysseveldt 3459 (BR); Brugge, E-side of Boudewijnkanaal (IFBL C2.11.24), sand deposit, 08.08.2007, F. Verloove 6853 (BR).

Oenothera cambrica* var. *cambrica

• East Flanders: Zwijnaarde (Gent), Ringvaart (W-side), close to E40 motorway (IFBL D3.32.21), worked-up roadside, 17.08.2014, F. Verloove 10953 (BR).

• West Flanders: Roeselare, Bruggesteenweg x Leopold III-laan (IFBL D1.48.31), ruderal area, 21.07.2001, F. Verloove 4993 (priv. herb. F. Verloove).

• ***Oenothera cambrica* var. *impunctata***

• East Flanders: Zwijnaarde (Z-Gent) (IFBL D3.32.24), road verge, along river Schelde, one specimen, 10.07.2007, F. Verloove 6809 (priv. herb. F. Verloove).

Oenothera canovirens

• Antwerp: St.-Anna (IFBL C4.26.14), opgespoten gronden, 28.06.1959, E. Van Rompaey 1436-2 (BR);
• Liège: Entre Ensival et Pepinster, graviers de la Vesdre, 09.1901, P. Halin s.n. (LG).

Oenothera cruciata

• Brabant: Forest, 06.1870, Coomans s.n. (BR);
• Liège: Flère, Gomélèvai, 09.09.1883, P. Delrez 450 (LG; mixed collection with O. biennis).

Oenothera deflexa

• Antwerp: Anvers-Ouest (rive gauche), 18.08.1955, L. De Ruyver s.n. (BR); Koersel, bord d'un sentier, 23.09.1962, E. Hostie s.n. (GENT); Balen-Nete, route de Postel, bord de la route, 03.08.1965, A. Lawalrée 13157 (BR); Antwerpen-Noord (IFBL C4.16.33), opgespoten gronden ten W van Oosterweel, 04.08.1965, E. Van Rompaey 1436-2 (BR); Hoboken, langs weg, 05.10.1965, M. Van den Wijngaert s.n. (BR); Turnhout, Dombergstraat, tussen Watertappingstraat en pannenfabriek Tuca, inz. noordelijke boord van de weg, 22.09.1969, J. Aerts s.n. (GENT); Turnhout, kanaal, noordelijke oever nabij de grens Turnhout-Beerse, 25.07.1974, J. Aerts 74/48 (GENT); Mechelen-Battel, oude Gentse Steenweg nabij Heffen, Heembeemd (IFBL D4.27.13), verwilderd langwerpig perceel, droog, spoorwegsintels, 14.08.1974, L. Vanhecke 4260 (BR); Lillo (IFBL B4.54.21), opgespoten gebied langs de Galgeschoor, droge open zandgrond, pioniersbegroeiing, 11.09.1974, L. Vanhecke 4318 (BR); Turnhout, Everdongenlaan, enkele meters ten zuiden van de brug over de Aa, op de rand van de weg, 09.07.1976, J. Aerts 76/37 (GENT); Turnhout, kanaal, noordelijke dijk, nabij de grens met Beerse, op de oever van het kanaal, 22.07.1976, J. Aerts 76/48 (BR, GENT); Turnhout, werf De Clercq (IFBL B5.48.11), tussen steenslag, 1 eks., 22.07.1979, A. Vermeijen 79/75 (BR); Mechelen, Mechels Veld, terrain vague près Du Pont de Nemours, 06.07.1980, R. Wechuysen 1023 (BR); Turnhout, Nieuwe Kaai (IFBL B5.47.42), wegenbouw Van Gorp, aardhopen grondwerken, 05.09.1981, J. Aerts 81/79 (GENT); Burcht (comm. actuelle Zwijndrecht) (IFBL C4.25.44), terrain vague sablo-argileux près de l'Escaut, 24.09.1990, J. Lambinon 90/B/504 (BR, LG); Harbour of Antwerp, between 4e and 5e Havendok (IFBL C4.16.32), road verge, along railway track, 1 ex., 29.07.2007, F. Verloove 6870 (BR);
• Brabant: Anderlecht, talus de la voie ferrée à la Petite Ile, 09.1938, G. André s.n. (BR); Evere, terrains vagues, 17.09.1944, E. Hostie s.n. (GENT); Evere, Kerkebeek, puinen van verwoeste huizen bij de kerk, 23.10.1948, E. Michiels s.n. (BR); Jette-Diegem, woest terrein bij den Paelboschwegel, 23.07.1949, E. Michiels s.n. (BR); Kessel-Lo, Blauwput, stort van puinen, 28.08.1951, J. Pelgrims s.n. (BR); Anderlecht, remblai chemin de fer, 09.1951, A. Lefebvre s.n. (BR); Nodebais, décombres, 27.09.1954, L. Muyldermans 858 (BR); Leuven, Keizersberg, wegkant, 15.10.1954, M.-T. De Roo s.n. (BR); Kessel-Lo, Martelarenlaan, braakliggend terrein langs de spoorweg, 25.07.1955, J. Pelgrims 109 (BR, GENT, LG); Hofstade, prairie boissée près grand lac, sol sablonneux, 24.09.1955, R. Wilczek 1532 (BR); Auderghem, Parc des Princes, Avenue Leemans, terrain vague, 22.07.1960, A. Lawalrée 11030, 11032 (BR); Kessel-Loo, terrain vague, 31.07.1962, J. Bouharmont 1383 (BR); Ixelles (Boondael), Chaussée de Boitsfort, le long du chemin de fer, plante très abondante partout, 08.1965, L. Dubois 1647 (BR); Auderghem, à l'angle de l'Avenue Hermann-Debroux et du Boulevard du Souverain, terre remuée il y a quelques mois à peine lors de la construction de l'autoroute en viaduc, une colonie abondante et uniforme, 23.09.1973, A. Lawalrée 18225 (Soc. Ech. Pl. Vasc. Eur. Bass. Médit.: BR, GENT, LG); Auderghem, Rue de la Vignette (IFBL E4.36.24), terrain rudéralisé sur sable, 08.1977, D. Geerinck-Coutrez 1686 (BR); Kessel-Lo, Koning Albertlaan, straatberm, 08.08.1978, s.c. (BR); Haacht, station Wespelaar-Tildonk, rond « La Corbeille » (IFBL D5.42.41), 20.07.1980, R. Wechuysen 1060 (BR); Uccle, Rue de Bourdon, terrain sableux pauvre, pelouse ouverte et rase, 01.08.1980, M. Tanghe s.n. (BR); Anderlecht, Rue Bollinckx, sur terre de remblai, limoneuse, mêlée, 23.07.1981, M. Tanghe s.n. (BR); Strombeek-Bever, chantier du Ring de Bruxelles, croisement avec le chemin Meise-Heysel, buttes de sol amené, groupement riche en annuelles, 23.09.1981, E. Robbrecht 1592 (Soc. Ech. Pl. Vasc. Eur. Bass. Médit.: BR, GENT); Boitsfort, Avenue de la Forestière (International School), pelouse à saules, 04.10.1982, M. Tanghe s.n. (BR); Watermael-Boitsfort, terrain rudéralisé dans le quartier des Pêcheries, 09.1984, D. Geerinck-Coutrez 3380 (BR); Woluwe-Saint-Lambert (IFBL E4.27.31), prairie près du Cora, 08.1987, D. Geerinck-Coutrez 4372 (BR); Diest (IFBL D6.31.44), oud stort langs de Demer, 07.07.1990, E. Jacques 17572 (BR); Watermael-Boitsfort (IFBL E4.46.42), terrain rudéralisé de la Foresterie, 08.1992, D. Geerinck-Coutrez 6716 (BR, LG); Wemmel, Allée des Peupliers, fasciatie, 1995, Verheyden s.n. (BR);
• East Flanders: Langerbrugge, 1932, […] (GENT); Denderleeuw, Grote Steenweg, op uiterwaarden, zandgrond, 22.08.1971, J. Van den Haute 605 (BR); Eke (IFBL D3.41.14), 14.07.1973, D. Duytschaever 7 (GENT); Oudegem, spoorwegbrug over de Dender, berm van de spoorwegbrug (grazig en kruidenrijk), 18.07.1976, E. Robbrecht 1055 (BR, GENT); Denderleeuw (IFBL E3.28.21), recent opgehoogd terrein, 07.08.1976, H. Ruysseveldt 1504 (BR); Welle-Wellemeersen (IFBL E3.18.23), braakliggende akker, 11.09.1980, H. Ruysseveldt 1503 (BR); Gent, westzijde Handelsdok, bij douane (IFBL D3.12.44), grazige braakliggende terreinen (opgevuld voormalig dok), 10.1987, E. Robbrecht 3539 (BR); Appels (IFBL D3.28.24), grazige wegkant op dijk, 15.07.1992, A. Van Den Bergh s.n. (BR); Asbeek (IFBL E4.12.14), braakliggende akker, 22.07.1992, W. De Schrijver s.n. (BR); Denderleeuw (IFBL E3.28.21), verruigd hooiland, 14.07.1993, H. Ruysseveldt s.n. (BR); Bornem (Mariekerke) (IFBL D4.12.44), bij een klein kanaal naar de Schelde, 06.09.1998, D. Geerinck-Coutrez 9319 (BR); Harbour of Ghent, Singel near Farmanstraat (IFBL D3.13.11), ruderal gravelly road verge, 24.06.2000, F. Verloove 4410 (BR); Gent, border of river Schelde at Gentbruggebrug (IFBL D3.23.13), demolition area of former steel-factory, abundant, 08.07.2002, F. Verloove 5120 (priv. herb. F. Verloove); Gent, river Schelde near Rijmstraat, crack in pavement, 27.06.2004, F. Verloove 5715 (BR); Gent, Voorhavenlaan (IFBL D3.12.24), ruderal area, 27.06.2004, F. Verloove 5716 (BR); Zwijnaarde (Z-Gent) (IFBL D3.32.24), former dump site near river Schelde and E40 motorway, 10.07.2007, F. Verloove 6873 (BR); Zwijnaarde (Z-Gent), border of river Schelde (IFBL D3.32.24), ruderal road verge, 10.07.2007, F. Verloove 6874 (BR); Harbour of Ghent, S-side of Kluizendok (IFBL C3.43), artificial sandscape, 10.07.2007, F. Verloove 6875 (BR); Zwijnaarde (Z-Gent), border of river Schelde (IFBL D3.32.24), road verge, 10.07.2007, F. Verloove 6876 (BR);
• Hainaut: Marchiennes-au-Pont, cendrées le long de la voie ferrée, 08.1949, J. Duvigneaud s.n. (BR); Mons, bord d'un chemin, 10.1949, F. Buxant s.n. (BR); Jamioulx, talus chemin de fer, 08.1954, J. Lebeau s.n. (BR); Viesville, terrain vague, 29.07.1956, P. Demalsy s.n. (BR); Soignies, carrière de Perlonjour, chantier, 19.07.1969, A. Lawalrée 15859 (BR); Chapelle-lez-Herlaimont, terril n° 7, pente schisteuse, M. Tanghe s.n., 13.08.1970 (BR); Cuesmes, terrain rudéral, 03.10.1976, C. Vanden Berghen s.n. (BR); Baudour, 24.07.1983, S. Depasse 88/102 (BR); Soignies (IFBL F3.58.32), terrain rudéralisé sur la pierre blanc de la carrière de Hainaut, 14.09.1985, D. Geerinck-Coutrez 3618 (BR); Boussu, terril Saint-Antoine, coalmine heap, 04.07.2004, F. Verloove 5719 (BR); Quivrain, railway yard, gravelly area, 04.07.2004, F. Verloove 5727 (BR); Blaton, réserve naturelle « La Grande Bruyère » (IFBL G3.21.41), ancienne sablière, très commun, 25.07.2007,

F. Verloove 6869 (BR); Quiévrain, gare (IFBL G3.41.44), along railway track, 12.07.2007, F. Verloove 6877 (BR); Hensies (Les Sartis) (IFBL G3.31.44), coal mine heap, 12.07.2007, F. Verloove 6879 (BR); Hornu, terril du Sept (IFBL G3.44.31), coal mine heap, 25.07.2007, F. Verloove 6867 (BR);

• Liège: Dison, terrain vague, 06.1915, P. Doubleman s.n. (LG); Vierset-Barse, gare de Régissa, 08.07.1919, A. Charlet s.n. (BR); Ensival, Vesdre, 07.1940, A. Visé (BR); Chaudfontaine, carrières, 16.08.1943, A. Isaäcson s.n. (BR); Fond de Cris (Chaudfontaine), terrain vague, 16.08.1943, A. Visé s.n. (LG); Vallée de la Vesdre, bord de la route Liège-Verviers, 26.09.1960, N. Cnops 60.163 (BR); Angleur, rive gauche de l'Ourthe, en aval de l'île Rousseau, terres remaniées, 29.08.1973, J. Duvigneaud 73/B/1131; Ougrée, ancien crassier des usines métallurgiques, bois Saint-Laurent, 22.07.1974, J. Duvigneaud 74/B/953 (LG); Angleur, graviers déversés dans la plaine alluviale de l'Ourthe, 30.07.1974, J. Duvigneaud 74/B/1013 (LG); Amay, graviers le long de la Meuse, 30.09.1975, W. Bellotte 75/707 (LG); Angleur, rive gauche de l'Ourthe, 20.10.1975, Hechtermans & Monfort 75/752 (LG); Herstal (IFBL F7.24.33), décombres d'une vieille usine au nord de la gare, 09.08.1980, R. Wechuysen 1118 (BR); Jemeppe-sur-Meuse, terril houiller du Bas Laveu, friche en bordure d'une zone en combustion, 25.08.1984, J. Lambinon 84/B/640 (LG); Hamoir (IFBL G7.42.32), au S de l'agglomération, le long de la vallée de l'Ourthe, rive gauche, site rudéral, 13.08.1985, A. Lawalrée 25745 (BR); Angleur (IFBL F7.43.22), pied du remblais du chemin de fer près de l'ancienne gare, 27.07.1986, J. Lambinon 86/B/208 (LG); Angleur (IFBL F7.43.21), pied de mur près du canal de l'Ourthe, à proximité du Pont Marcotty, 03.08.1988, J. Lambinon 88/B/265 (LG); Queue-du-Bois, parking usine Aldi, 04.09.1992, J. Beaujean 92/86 (LG); Chênée, décombres au Piedrou, 30.09.1992, J. Beaujean 92/131 (LG);

• Limburg: Genk, Waterschei, Horenszee, bord de route, 26.08.1956, A. Lawalrée 8010 (BR); Hasselt, rudéral, 07.1960, L. Delvosalle s.n. (BR); Stokrooi, langs kanaal, 08.07.1960, H. Vannerom s.n. (BR); Genk, aan de spoorweg van de Kolenhaven, 21.07.1967, J. Rammeloo 309 (GENT); Genk-Langerloo, zandige wegberm, 22.07.1967, L. Vanhecke 67/4 (BR); Genk, terrain vague, 02.08.1979, P. Claes s.n. (LG);

• Luxembourg: entre Chantemelle et Châtillon, dans une sablonnière, 13.08.1968, V. d'Ansembourg 3737 (BR); Forrières, bord de la voie ferrée vers Jemelle, association rudérale, plusieurs petites colonies, au total +/- 50 pieds, 04.09.1998, A. Lawalrée 26229 (BR);

• Namur: Namur, terrain vague, 22.09.1954, J.-L. De Sloover 2581 (BR); Jambes, bord de la voie ferrée près des usines Materne, 09.1955, J. Lambinon s.n. (LG); Lustin, bord de la voie ferrée près de la gare, 04.09.1956, J. Lambinon s.n. (LG); Godinne (îles), colonisatrice de pierres, 06.08.1972, E. Sérusiaux 72/B/38 (LG); Dorinne, rive gauche du Bocq (IFBL H5.28.14), ancienne carrière de Famennien, 20.08.1978, J. Duvigneaud 78B603 (BR); Rochefort, carrière abandonnée, 28.08.1978, B. Bastin s.n. (BR); Namèche (IFBL G6.31.13), friche, 09.08.1983, J. Saintenoy-Simon s.n. (BR); Noville-sur-Méhaigne (IFBL F5.47.14), gare désaffectée, 10.08.1983, J. Saintenoy-Simon s.n. (BR); Grands Malades (IFBL G5.37.14), friche, 21.08.1983, J. Saintenoy-Simon s.n. (BR);

• West Flanders: Brugge, Sint-Michiels, spoorwegberm, 29.07.1973, R. Viane 93 (GENT); bos van Houthulst, ruigte, 11.09.1977, L. Vanhercke s.n. (BR); Haven Roeselare, Beurtkaai (IFBL D1.48.43), wegberm, achter een bermmarkering, 04.07.1992, F. Verloove 383 (BR); Rekkem (IFBL E1.58.22), wand greppel langs maïsveld, 29.07.2000, H. Ruysseveldt 2643 (BR); Roeselare, near the railway station (IFBL D1.48.34), railroadbank, several specimens, established, 12.07.2001, F. Verloove 4992 (priv. herb. F. Verloove); Zedelgem, ongebruikte spoorweg, 11.09.2001, H. Ruysseveldt 3009 (BR); Ingelmunster, railway track, 03.07.2004, F. Verloove 5717 (BR); Kortemark, railway yard, gravelly area, common, 08.07.2004, F. Verloove 5721 (BR); Rumbeke-Roeselare (IFBL D1.58.32), former clay-pit Ostyn, dump area, 18.07.2004, F. Verloove 5731 (BR); Brugge, port (IFBL C2.22.11), ruderal area, gravelly soil, 28.06.2007, F. Verloove 6878 (BR, LG) (hybrid); Zeebrugge (port-area), SE of Distrigas-plant, A. Ronsestraat (IFBL B2.42), sandy ruderal area, +/- 10 ex., 18.07.2007, F. Verloove 6859 (BR); Heist, Baai van Heist (IFBL B2.32.33), seadunes, +/- ruderalized, 18.07.2007, F. Verloove 6860 (BR); Brugge, Pathoekeweg, W of Nijverheidsdok (IFBL C2.21.22), ruderal area (demolition site), small population of uniform plants, 08.08.2007, F. Verloove 6856 (BR).

Oenothera depressa

• Hainaut: Hensies, Les Sartis (IFBL G3.31.44), coal mine heap, scattered specimens, 12.07.2007, F. Verloove 6801 (priv. herb. F. Verloove, BR);

• Liège: Horto Leod., 1828, R. Courtois s.n. (LG).

Oenothera ersteinensis

• Antwerp: Harbour of Antwerp, Eerste Havendok (IFBL C4.16.42), sandy, worked-up road verge, nice population, >100 specimens, 22.07.2001, F. Verloove 4991 (priv. herb. F. Verloove, BR, LG); Harbour of Antwerp, SW-side of Hansadok (IFBL C4.15.23), along railway track, 2 ex., 29.07.2007, F. Verloove 6831 (priv. herb. F. Verloove); Retie (IFBL C6.13.21), omgewerkte berm, 08.07.2009, R. Barendse s.n. (BR); Brecht, Groot Schietveld (Brechtse Baan) (IFBL B4.48.24), zandige braakgrond bij ingang schietstand, talrijk, 11.07.2010, F. Verloove 8131 (BR); Antwerp (Luchtbal) (IFBL C4.17.13), ground heaps, by railway track, 03.08.2014, F. Verloove 10951 (BR);

• Liège: Ougrée-Sart Tilman, domaine universitaire, en bordure de la route près de l'Institut de Botanique, 13.08.1971, P. Auquier 1566 (BR); Chenée, décombres au […], 30.09.1992, J. Beaujean 92/131 (BR);

• Limburg: Lommel-Balendijk (IFBL C6.25.24), in redelijke hoeveelheid (met O. glazioviana, O. biennis), 07.08.2010, R. Barendse s.n. (BR).

Oenothera fallax

• Antwerp: Harbour of Antwerp, SW-side of Delwaidedok (IFBL B4.45.33), sandy border of a railway-track, numerous specimens, 22.07.2000, F. Verloove 4627 (priv.herb. F. Verloove);

• Brabant: Bruxelles, chantiers de la jonction Nord-Midi, 09.1951, A. Lawalrée 3790 (BR); Bruxelles, chantier de la jonction Nord-Midi, association rudérale, 04.08.1956, A. Lawalrée 7775 (Soc. Fr. Ech. Pl. Vasc. n° 2982; BR); Auderghem, Avenue Chaudron, terrain vague, remblai, 11.07.1958, A. Lawalrée 10037 (BR); Rijmenam (IFBL D5.31.22), langs de baan aan 't Zwart Water, 16.08.1967, N. Cnops 67.567 (BR); Sint-Jans-Molenbeek, braakliggend terrein, 22.06.1971, J. Loots 105 (BR; mixed with O. glazioviana); Haeren, près de Bruxelles, gare de triage, talus rudéralisé, 29.08.1987, G. Bruynseels 1257 (BR);

• East Flanders: Haven van Gent, Gent-Zelzate via Linkeroever, graafwerken ten N van executieoord Rieme (IFBL C3.33.34), ruigte, 17.09.1982, E. Robbrecht 2529 (BR); Port of Ghent, Farmanstraat near Kennedylaan (IFBL D3.13.13), roadsides, railways and rough places, ca. 15 individuals in old railway bed, 19.08.1986, E. Robbrecht 3122 (BR); Zwijnaarde (Z-Gent), langs Ringvaart (IFBL D3.32.24), voormalige zandopspuiting, enkele planten met O. biennis, 23.06.2001, F. Verloove 4822 (BR); Sint-Denijs-Westrem, oprit E40 richting Oostende, zandig braakliggend terrein, talrijk, 21.06.2004, F. Verloove 5655 (BR);

• Hainaut: Dour, terril Grande Machine à Feu, coalmine heap, 04.07.2004, F. Verloove 5720 (BR); Hensies (Les Sartis) (IFBL G3.31.44), coalmine heap, 04.07.2004, F. Verloove 5718, 5722, 5723 & 5725 (BR);

• Liège: Neupré, Rotheux-Rimière, jonction des routes de Marche et d'Esneux, bord rudéralisé de la route, 20.07.1979, P. Auquier 5069 (LG);

• Limburg: Waterschei, ancien […], près de […], 09.1956, J. Lambinon s.n. (BR);

• Namur: vallée du Bocq, bords des eaux, 08.1889, Dens s.n. (BR); between Freyr and Waulsort along the river Meuse, 06.09.1991, R. Govaerts 33 (BR);

• West Flanders: Middelkerke, dune, 25.07.1934, P. [...] s.n. (BR); Le Coq, wegkanten, 14.08.1939, L. Standaert s.n. (BR); Koksijde, dans les dunes, très répandue partout, 07.1966, L. Dubois 1646 (BR); Koksijde, près du moulin, 20.08.1970, R. Boutique 808 (BR); St-Idesbald, dune rudéralisée, 28.07.1974, B. Bastin s.n. (BR); Knokke, Duinbergen, restje duin tussen villa's langs Kon. baan, 01.11.1978, R. Viane 697 (GENT); Knokke-Heist, dunes rudéralisées, 07.1982, D. Geerinck-Coutrez 688 (BR); Nieuwpoort (IFBL C1.41.11), open plekjes gefixeerd duin, 07.08.1995, H. Ruysseveldt s.n. (BR); Wervik (IFBL E1.46.24), tussen resten afgebroken fabrieksgebouw, 01.08.2000, H. Ruysseveldt 2647 (BR); Brugge, Pathoekeweg, W of Nijverheidsdok (IFBL C2.21.22), ruderal area (demolition site), 1 ex., 08.08.2007, F. Verloove 6855 (BR).

Oenothera fruticosa* subsp. *glauca

• East Flanders: Gent-West, Vinderhoute, Vinderhoutse Meersen (IFBL D3.11.22), ruderale inrijlaan van een afvalverwerkend bedrijf langs de R4, samen met andere tuinvluchtelingen, 05.07.1998, F. Verloove 3381 (BR).

Oenothera glazioviana

• Antwerp: Hoboken, braakland aan de staalgieterij, 02.07.1937, E. Frison s.n. (GENT); Wildert, barre grond, zand, 01.08.1953, E. Jacques 354 (BR); Essen, 't Hoefken, adventief in Arnosereto-Scleranthetum, 09.10.1956, J. Traets 520 (BR); Duffel (IFBL D4.18.13), op spoorwegdam, 02.09.1957, N. Cnops 57.313 (BR); Antwerpen (IFBL C4.36.23), afgegraven vestingwal, ruigte, 18.08.1967, E. Van Rompaey GIII/1435-1 (BR); Antwerpen (IFBL C4.36.23), afgegraven vestingwal, ruigte, 21.08.1967, E. Van Rompaey GIII/1435-1 (GENT); Duffel, bord de la route Lierre-Malines, à l'ouest de la voie ferrée Anvers-Malines (IFBL D4.18.13), talus, 02.07.1970, A. Lawalrée 16128 (BR); Turnhout, Smalvoortstraat (IFBL B5.47.32), bouwwerf, 21.07.1979, J. Aerts 79/25 (GENT); 's Gravenwezel, oude baan (IFBL C4.28.22), aan de voet van de oprit van de brug over het Albertkanaal, zandige wegkant, 21.07.1986, E. Jacques 15852 (BR); Haven van Antwerpen, N-Delwaidedok (IFBL B4.45.13), spoorwegemplacement, 08.10.2001, E. Molenaar s.n. (BR);
• Brabant: Park-Heverlee, spoorweg naar Waver, 01.08.1909, E. Michiels s.n. (BR); Keerbergen, marécage, 12.08.1920, E. Hostie s.n. (GENT); Wilsele, talus du chemin de fer, 19.07.1923, J. Lebrun s.n. (BR); Uccle, sablière, 07.1928, J. Lebrun 2680 (BR); Aarschot, woest terrein achter het station, 30.07.1937, E. Michiels s.n. (BR); Louvain, Mont-César, pelouses, 29.09.1940, A. Lawalrée 525 (BR); Aarschot, woest terrein achter het station, 02.07.1941, E. Michiels s.n. (BR); Uccle, talus de la voie ferrée, 18.07.1951, G. André s.n. (BR); Bruxelles, chantier jonction Nord-Midi, rudéral, 04.08.1956, A. Lawalrée 7779 (BR); Kessel-Loo, terrain vague, 31.07.1962, J. Bouharmont 1382 (BR); Kessel-Lo, spoorwegberm, 18.06.1964, J. Pelgrims 1822 (BR); Sint-Jans-Molenbeek, braakliggend terrein, 22.06.1971, J. Loots 105 (BR; mixed with O. fallax); Auderghem, Jardin Massart, grande parcelle expérimentale, 03.08.1976, M. Tanghe s.n. (BR); Auderghem, Chaussée de Wavre (IFBL E4.37), bord de route, 07.1977, D. Geerinck-Coutrez 1591 (BR); près de Haren, gare de formation, terrain rudéralisé, 01.09.1987, G. Bruynseels 1247, 1552 (BR); Ramsberg (ten E van Tienen) (IFBL E6.21.21), stortplaats tussen maïsakkers en laagstamboomgaarden, 02.10.2002, L. Vanhecke s.n. (BR);
• East Flanders: Haven van Gent, Gent-Zelzate via Linkeroever, graafwerken ten N van executieoord Rieme (IFBL C3.33.34), ruigte, 17.09.1982, E. Robbrecht 2528 (BR); Haven van Gent, Gent-Zelzate via Linkeroever (km 7.0), bij executieoord (IFBL C3.33.44), grote zandhopen, 16.08.1984, E. Robbrecht 2829 (BR); Gent, Dampoort, railway yard, now demolished, 10.07.2004, F. Verloove 5728 (BR);
• Hainaut: Montigny-sur-Sambre, colonise certains terrils de charbonnages, 05.08.1930, Culot s.n. (BR); Jamioulx, le long du chemin de fer, terrain vague, 07.1954, J. Lebeau s.n. (BR) ; Beauvechain, friche, 01.10.1954, L. Muyldermans 841 (BR);
• Liège: Visé, bord de la Meuse, 08.1868, E. Marchal s.n. (BR); Vierset, bois de Faqueval, 08.1889, A. Charlet s.n. (LG); Lambermont, décombres, 07.1908, P. Halin s.n. (LG); Theux (Hodbomont), 09.08.1948, J.-M. Warlet 538-2584 (BR); Angleur, domaine universitaire du Sart Tilman, le long de la route axiale, bord de la route, accotements remués, 06.07.1971, A. Lawalrée 16675 (BR); Ougrée, Sart Tilman, domaine universitaire, en bordure de la route près de l'Institut Botanique, 13.08.1971, P. Auquier 1566 (LG); Angleur, talus en bord de route, 04.07.1973, J. Beaujean 167 (LG); Tilff, route aux abords du château de Colonster, bord de route, 09.08.1973, J. Duvigneaud s.n. (LG); Jupille-sur-Meuse, bord de route, 14.09.1979, J. Beaujean 79/146 (LG); Ben-Ahin (IFBL G6.24.14), milieu rudéralisé, 01.09.1983, J. Rousselle s.n. (LG); Gué (?) [Ben-Ahin], IFBL G6.24.14, terrain vague, 01.09.1983, J. Saintenoy-Simon s.n. (BR);
• Limburg: Bokrijk, deux pieds dans un lieu cultivé, 28.07.1889, H. Dupont s.n. (LG); Berlingen, bij 't Kasteel van Rullingen, grasboord, 02.08.1934, E. Michiels s.n. (BR); Genk (IFBL D7.51.22), port, 26.08.1956, A. Lawalrée 8033 (BR); Waterschei, ancien crassier près d'un charbonnage, 09.1956, J. Lambinon s.n. (LG); Wellen, wegboord, 18.07.1958, E. Michiels s.n. (BR); Beringen, vaartkant, 27.08.1959, E. Jacques 3939 (BR) ; Beringen, langs een weg aan de mijnterril, 07.1967, H.G. Rabijns 1464 (BR); Genk, aan de spoorweg van de kolenhaven, 21.07.1967, J. Rammeloo 310 (GENT); Genk, Kolenhaven, langs de spoorlijnen, abondant in droge zandige vegetatie, 22.07.1967, H. Stieperaere s.n. (GENT); Genk, terrains vagues, 17.08.1980, P. Claes s.n. (LG); Lanaken (Neerharen), Hochter Bampd (IFBL E7.15.11), grindbank langs de Maas, 02.10.2010, F. Verloove 8289 (BR) ;
• Luxembourg: Poncelle (Tintigny), prairie aride (sable), assez abondant, 20.08.1945, V. d'Ansembourg 599 (BR); Buzenol, jardin près de la voie ferrée, 08.1949, J. Duvigneaud s.n. (BR) ; Poncelle, terrain sec, 13.09.1946, J. Legrain s.n. (BR); Torgny, 20.09.1959, A. Louette s.n. (LG);
• Namur: Lustin, bord de la voie ferrée, 04.09.1956, J. Lambinon s.n. (BR); Andenne, dans des décombres, 1962, F. Siebertz s.n. (LG);
• West Flanders: Nieuport, ruines, 1920, A. Navez s.n. (BR); Houthulst, forêt, 01.07.1920, Guns s.n. (BR); Coxyde, dunes, 10.08.1920, L. Magnel s.n. (BR); Clemskerke, pâturages, 31.08.1923, A. Isaacson s.n. (BR); Westende, bord de la route, 07.09.1924, J. Lebrun s.n. (BR); Koksijde, dunes fixées, 20.08.1928, A. Maréchal s.n. (LG); Duinbergen, 08.1931, E. Dewildeman s.n. (BR); Middelkerke, 07.1946, J. Duvigneaud s.n. (BR); Wenduine, 07.1946, L. Renard s.n. (LG); Ostende, partout, 06.07.1947, A. Visé s.n. (BR); St-Idesbald, dunes voisinages des villas, 02.09.1947, V. d'Ansembourg 1025 (BR); Oostduinkerke, 08.1948, L. Renard s.n. (LG); Groenendijk, dunes herbeuses, 12.08.1949, A. Maréchal s.n. (LG); Koksijde, duinen, 14.07.1952, J. Pelgrims s.n. (BR); St-Idesbald, dunes rudéralisées, 15.08.1953, J. Duvigneaud s.n. (BR); Koksijde, ten W van de Normandie, rand weg, 17.07.1957, E. Jacques 3080 (BR) ; Coxyde (Saint-Idesbald), dunes, 06.07.1958, A. Lawalrée 9991 (BR); Coxyde-Bains, près du moulin, dunes rudéralisées, 16.07.1960, A. Lawalrée 11078 (BR); Nieuport, dunes, 10.1961, P. Auquier 462 (LG); Le Coq, dunes, 05.08.1962, J.-E. Rogister s.n. (BR); Nieuport, sables +/- rudéralisés, 07.1963, L. Delvosalle s.n. (BR); Sint-Idesbald, dunes près de la localité balnéaire, 08.07.1965, A. Lawalrée 13112 (BR); Koksijde, dans les dunes, très répandue partout, 07.1966, L. Dubois 1648 (BR); De Panne, droge wegkant aan het standbeeld Leopold I, 29.07.1967, E. Robbrecht 67.13 (BR); Saint-Idesbald (sud du village), panne rudéralisée, 09.07.1968, P. Auquier 1142 (LG); Koksijde, Doornpanne, begroeide duinpanne, 10.07.1973, M. Lejeune 84 (BR) ; Hoeke, Steenoven, wegberm in zware kleigrond, 15.07.1973, R. Viane 94 (GENT); Oostduinkerke, duinen, 07.07.1974, J. Loots 571 (BR); De Panne, verkaveling "Westhoek", zuidelijke weg (IFBL C0.56.41), verruigde Salix repens-Rosa pimpinell.-zoom aan de rand van Ligustrum-struweel met Euonymus europaeus, 03.09.1977, P. Goetghebeur 2790 (GENT); De Panne (IFBL C0.56.44), dunes, 01.11.1978, P. Sotiaux s.n. (BR); Coxyde, dunes rudéralisées, 20.09.1979, W. Debaisieux s.n. (LG); Koksijde, wegkant, 23.07.1980, R. Vanquathem 110 (BR); Oost-

duinkerke, Doornpanne, dépression dunaire, 14.10.1982, M. Tanghe s.n. (BR); Coxyde, dune rudéralisée, 27.07.1983, J. Beaujean 83/10 (LG); Heist-Duinbergen, Zeegrasstraat (IFBL B2.32.43), in verruigde duinen, braakland, 21.08.1983, J. Van Den Haute 1455 (BR); Nieuwpoort-Bad, duinen, 08.09.1984, J. Loots 1066 (BR); Oostende, Fort Napoleon (C1.14.42), talus sablonneux en contrebas de dunes rudéralisées, 09.1991, R. Fabri 1524 (Soc. Ech. Pl. Vasc. Eur. Occ. Bassin. Médit. n°15322: BR, LG); Diksmuide, industrieterrein (IFBL D1.23.32), droge grond, 21.06.1992, F. Verloove 286 (BR); Kortemark (IFBL D1.26.42), spoorwegemplacement, op grintpuin, 24.06.1992, F. Verloove 311 (BR); N382 tussen Roeselare en Izegem, ter hoogte van kanaal naar Leie te Kachtem (IFBL D2.51.13), wegberm, onder de vangrail, 18.07.1998, F. Verloove 3184 (BR); Adinkerke, road towards Bray-Dunes (IFBL D0.16.11), seadunes, near railway-track, locally abundant, 26.06.2000, F. Verloove 4624 (priv.herb. F. Verloove); N382 Roeselare-Izegem, near drive-in E403 (IFBL D2.51.11), ruderal area, levelled soil (former dumping place), 09.07.2000, F. Verloove 4626 (priv.herb. F. Verloove).

Oenothera hirsutissima

• East Flanders: Harbour of Ghent, S-side of Kluizendok (IFBL C3.43), artificial sandscape, few specimens, 24.06.2007, F. Verloove 6769 (priv. herb. F. Verloove);
• West Flanders: Nieuport, dunes, 10.1961, P. Auquier 462 (BR); Brugge, E-side of Boudewijnkanaal, sand depot, 17.07.2004, F. Verloove 5734, 5735 & 5736 (priv.herb. F. Verloove, BR); Brugge, E-side of Boudewijnkanaal (IFBL C2.11.24), sandy ruderal area, few specimens, known since several years (+ hybrids with several other taxa), 28.06.2007, F. Verloove 6768 (priv. herb. F. Verloove); Brugge, E-side of Boudewijnkanaal (IFBL C2.11.24), sand deposit, 18.07.2007, F. Verloove 6863 (BR) (hybrid); Brugge, E-side of Boudewijnkanaal (IFBL C2.11.24), sand deposit, 18.07.2007, F. Verloove 6865 (BR) (hybrid).

Oenothera indecora

• Brabant: Corbeek-Loo, champ de trèfles, 08.1895, C. Baguet s.n. (BR).

Oenothera issleri

• East Flanders: Vrasene, Aven Ackers (industrial area) (IFBL C4.13.31), bare sandy area, 31.08.2014, F. Verloove 11203 (BR).
• Namur: Jambes, Materne, bord de la voie ferrée, 09.1955, J. Lambinon s.n. (BR).

Oenothera laciniata

• Brabant: Wilsele, lieux incultes, 07.1893, C. Baguet s.n. (BR); Wilsele, dépendances de l'usine Bodart, 07.1894, C. Baguet s.n. (BR, GENT, LG); Schaarbeek, environs de la gare, 1907, A. Isaacson s.n. (BR); Anderlecht, immondices, 05.07.1920, E. Michel s.n. (BR);
• Liège: Juslenville, voie ferrée, 27.09.1903, M. Halin s.n. (BR); Vovegnez, graviers, 12.09.1909, P. Halin s.n. (LG); Vovegnez, berge de la Vesdre, 12.09.1909, M. Halin s.n. (BR); Liège, subspontané dans le jardin du collecteur, 1924, A. Maréchal s.n. (BR);
• West Flanders: Coxyde, entre les fils de fer barbelés au pied du Hoogenblikker près du nouveau chemin empierré vers Oostduinkerke, un seul pied, 28.09.1919, L. Magnel s.n. (BR).

Oenothera nuda

• Hainaut: Hensies, Les Sartis (IFBL G3.31.44), coal mine heap, 12.07.2007, F. Verloove 6880 (BR) (hybrid); Blaton, sablière le long du canal (IFBL G3.21.42), sur sable, 25.07.2007, F. Verloove 6868 (priv. herb. F. Verloove);
• Liège: Huy, terrain vague, 16.08.1956, A. Lawalrée 7784 (BR);
• Namur: Houx, taillis, 01.10.1933, R. Mosseray s.n. (BR).

Oenothera oakesiana

• Brabant: Bruxelles, travaux de la jonction Nord-Midi, 26.06.1945, A. Lawalrée 1303 (BR);
• Liège: Val-Benoit, décombres, 12.07.1923, A. Maréchal s.n. (LG);
• Limburg: St-Trond, bords de chemin, 05.08.1867, A. Thielens (BR).

Oenothera oehlkersii

• East Flanders: Gent, Sneppebrug (IFBL D3.22.13), road verge, near railway track (disturbed soil), 24.06.2007, F. Verloove 6774 (BR); Zwijnaarde (Z-Gent) (IFBL D3.32.24), voormalige stortplaats langs de E40, 10.07.2007, F. Verloove 6810 (BR, LG);
• Liège: Angleur, fortifications, 07.1884, P.J. Delrez s.n. (BR);
• West Flanders: Roeselare, Bruggesteenweg (IFBL D1.48.13), demolition area of former Coca-Cola-factory, several specimens, 21.07.2001, F. Verloove 4994 (priv. herb. F. Verloove, BR); Rumbeke-Roeselare, former clay-pit Ostyn, dump, 18.07.2004, F. Verloove 5732 (BR); Ieper, railway yard, gravelly area, 27.07.2004, F. Verloove 5730 (BR).

Oenothera paradoxa

• Limburg: Beringen-Mijn (IFBL D6.15.13), S-side of coal mine heap, common, 08.07.2001, F. Verloove 4848 (priv. herb. F. Verloove); Beringen-Mijn (IFBL D6.15.31), coal mine heap, common, 01.07.2007, F. Verloove 6812 (priv. herb. F. Verloove).

Oenothera parviflora

• Brabant: Dieghem, talus du chemin de fer, 1884, A. Douret s.n. (BR); Bruxelles-Nord, chantier de la jonction Nord-Midi, secteur Botanique, 21.06.1947, A. Lawalrée 1627 (BR); Bruxelles, plaine de l'Exposition de 1935, à 100 m du Planetarium, 08.08.1948, E. Michel s.n. (BR); Bruxelles, chantier jonction, 19.08.1958, M. Coûteaux 742 (BR); Bruxelles, terrain vague, 19.09.1972, A. Lawalrée 17972 (BR); Halle, gare, 02.09.1978, S. Depasse 88/85 (BR);
• Hainaut: Viesville, près du canal, rudéralia, 10.08.1955, A. Lawalrée 6870 (BR); Braine-le-Comte, talus SNCB, 22.07.1957, S. Depasse 88/26 (BR); Tertre, 05.08.1967, S. Depasse 88/69 (BR);
• Liège: Jemeppe-sur-Meuse, terril houillers du Bas Laveu, friche en bordure d'une zone en combustion, 25.08.1984, J. Lambinon 84/B/640 (BR);
• Luxembourg: Halte de Rossart, chantier de bois, 30.08.1965, V. d'Ansembourg 3372 (BR);
• West Flanders: Baai van Heist (O-Zeebrugge) (IFBL B2.32.33), ruderal sandy area, near the sea, abundant, 08.09.2000, F. Verloove 4623 (priv.herb. F. Verloove).

Oenothera perennis

• Antwerp: Capellenbosch, zandgrond, 20.06.1943, L. Standaert s.n. (BR).

Oenothera pycnocarpa

• Antwerp: Harbour of Antwerp, S-side of 5th Havendok (IFBL C4.16.33), road verge, talus, few specimens, 29.07.2007, F. Verloove 6834 (BR); Harbour of Antwerp, SW-side of Hansadok (IFBL C4.15.23), along railway track, 1 ex., 29.07.2007, F. Verloove 6835 (BR); Waaslandhaven, Kallo, Sint-Jansweg (IFBL C4.14.12), ruderal sandy area, in front of Sagrex sand storage, very numerous, 27.07.2014, F. Verloove 10925 (BR);
• Hainaut: Gilly, au NO du cimetière (IFBL G4.48.11), le long d'une route, creusée dans les flancs d'un ancien terril, peuplement très important (1000 pieds au moins), 07.2007, M. Lannoy s.n. (priv. herb. F. Verloove 6854, BR, LG);
• Liège: Queue-du-Bois, parking usine Aldi, 04.09.1992, J. Beaujean 92/86 (BR);
• West Flanders: Brugge, Pathoekeweg, W of Nijverheidsdok (IFBL C2.21.22), waste ground (demolition area), locally abundant, 08.08.2007, F. Verloove 6852 (priv. herb. F. Verloove, BR).

Oenothera rosea

• Hainaut: Ath (Tournai), s.d., Ronday s.n. (BR); Ath, 1874, Ronday s.n. (BR);

• Liège: Vervian, Leodis, sponte in oleraciis, s.d., R. Courtois s.n. (LG).

Oenothera royfraseri

• Antwerp: Harbour of Antwerp, angle of Amerika- and Albertdok (IFBL C4.16.41), ruderal area, bare and gravelly, very common, 29.07.2007, F. Verloove 6833 (priv. herb. F. Verloove).

Oenothera rubricalyx

• West Flanders: Rekkem, LAR-transportzone (IFBL E2.41.32), grassland, several populations, 11.07.2014, F. Verloove 10892 (BR).

Oenothera rubricaulis

• Antwerp: […], bords de chemin, 07.1887, P. Halin s.n. (BR); Harbour of Antwerp, S-side of Delwaidedok, railway track, 15.08.2004, F. Verloove 5748 (BR);
• Brabant: Aarschot, woest terrein achter het station, 06.07.1939, E. Michiels s.n. (BR);
• East Flanders: Haven van Gent, Meulestedekaai, aan Meulestedebrug (IFBL D3.12.22), kanaalberm met naakte min of meer dichtgeslagen zandbodem, massale populatie, 05.07.1985, E. Robbrecht 2929 (BR); Gent, spoorwegberm tussen Ringvaart en Watersportbaan (IFBL D3.21.24 + D3.22.13), grindrijk terrein, zeer talrijk, 09.10.2005, F. Verloove 6230 (BR); Gent-West, Ringvaart x railway track (IFBL D3.21.24), railway track, formerly a massive population, now partly demolished after infrastructural works, 24.06.2007, F. Verloove 6775 (BR); Harbour of Ghent, Singel (E of Grootdok) (IFBL D3.13.11), ruderal area, abundant, 24.06.2007, F. Verloove 6779 (BR);
• West Flanders: Heist, Baai van Heist (IFBL B2.32.33), seadunes, +/- ruderalized, 18.07.2007, F. Verloove 6861 (BR).

Oenothera rubricauloides

• East Flanders: Gent-West, Ringvaart x railway track (IFBL D3.21.24), railway track, 24.06.2007, F. Verloove 6776 (BR); Zwijnaarde (Z-Gent) (IFBL D3.32.24), former dump site, 10.07.2007, F. Verloove 6811 (priv. herb. F. Verloove).

Oenothera speciosa

• Hainaut: Saint-Ghislain, s.d., Van Bastelaer s.n. (BR).

Oenothera stricta

• Antwerp: Anvers, fortifications près de la porte de Wilrijk, 23.05 & 23.06.1878, H. Vandenbrouck s.n. (BR); Anvers, fortifications, station abondante, 23.06.1878, H. Vandenbrouck s.n. (BR); Anvers, fortifications, 08.1882, H. Vandenbrouck s.n. (BR); Anvers, remparts, 31.08.1882, J. Hennen s.n. (BR); Anvers, fortifications, 07.1884, P.J. Delrez 451 (LG); Anvers, remparts, 29.07.1884, J. Hennen s.n. (BR); Anvers, remparts, 07.1887, J. Hennen s.n. (BR, LG); Anvers, fortifications à Berchem, 07.1900, R. Godding s.n. (BR);
• Brabant: Wilsele, lieux incultes, 07.1893, C. Baguet s.n. (BR);
• Hainaut: Saint-Amand-lez-Fleurus (IFBL G5.21), 06.1883, Grosse s.n. (BR); Bellecourt (IFBL G4.23), sur les talus du chemin de fer, plante naturalisée, <1951, A. Briart s.n. (BR);
• Liège: Angleur, friche en bordure d'une zone en combustion, 25.08.1984, J. Lambinon 84/B/640 (LG);
• West Flanders: La Panne, 05.06.1881, W. Rouseau s.n. (BR).

Oenothera subterminalis

• Hainaut: Châtelineau, Châtelet, terril, face sud SW, 11.06.1979, J-C Moniquet s.n. (BR);
• West Flanders: Heist, Baai van Heist, seadunes, +/- ruderalized, 02.08.2004, F. Verloove 5738 (BR).

Oenothera victorinii

• Antwerp: Harbour of Antwerp, right bank of river Schelde, SW of 5th Havendok (IFBL C4.15.43), worked up road verge, several specimens, 29.07.2007, F. Verloove 6830 (BR);
• Brabant: Lasne, rue du Double Ecot, carrière abandonnée, 12.07.1992, F. Billiet & B. Jadin 2331 (BR);
• East Flanders: Gentbrugge, Hundelgemsesteenweg (IFBL D3.23.33), braakgrond, nabij de oevers van de Schelde, 02.08.1998, F. Verloove 3357 (BR); Gent, Hundelgemsesteenweg near river Schelde (IFBL D3.23.33), ruderal area, 10.07.2004, F. Verloove 5729 (BR);
• West Flanders: N382 Roeselare-Izegem, near drive-in E403 (IFBL D2.51.11), ruderal area, levelled soil (former dumping place), several specimens, along with O. glazioviana, 09.07.2000, F. Verloove 4625 (priv. herb. F. Verloove); Roeselare, N382 at drive-in E403 (A17) (IFBL D2.51.11), levelled soil, persistent, first recorded in 2000, 13.07.2001, F. Verloove 4996 (LG).

Oenothera villosa

• West Flanders: Brugge, E-side of Boudewijnkanaal (IFBL C2.11.42), sand deposit Hanson, one specimen, 18.07.2007, F. Verloove 6816 (priv. herb. F. Verloove); Brugge, E-side of Boudewijnkanaal (IFBL C2.11.42), sand storage, +/- 5 specimens, 21.07.2014, F. Verloove 10917 (priv. herb. F. Verloove, BR).

Oenothera wratislaviensis

• Antwerp: Harbour of Antwerp, S-side of 5th Havendok (IFBL C4.16.33), road verge, talus, abundant, 29.07.2007, F. Verloove 6832 (priv. herb. F. Verloove);
• Hainaut: Hensies, Les Sartis (IFBL G3.31.44), coalmine heap, 04.07.2004, F. Verloove 5724 (priv. herb. F. Verloove);
• West Flanders: Heist, Baai van Heist, sandy grassland near the sea, 17.07.2004, F. Verloove 5733 (priv. herb. F. Verloove, BR).

Non-stabilized hybrids

Cf. *Oenothera biennis* × *O. deflexa*

• Antwerp: Harbour of Antwerp, Vosseschijnstraat, E of 2e Havendok (IFBL C4.16.42), railway track, 29.07.2007, F. Verloove 6871 (BR);
• East Flanders: Gent, Leon Tertzweillaan (IFBL D3.23.13), omgewoelde, eroderende, zandige, grintrijke spoorwegberm, pioniervegetatie met veel adventieven, 06.09.1977, P. Goetghebeur 2802 (GENT); Handzame (IFBL D1.26.33), hoop gestorte grond langs wegkant, 28.08.1999, H. Ruysseveldt 2389 (BR);
• West Flanders: Brugge, harbour, E of Groot Handelsdok (IFBL C2.22.11), former railway track + ruderal area, 18.07.2007, F. Verloove 6864 (BR).

Oenothera biennis* × *O. glazioviana

• Luxembourg: Buzenol, coupe dans le bois de la Ferme de Buzenol, le long du ruisseau, 08.1949, J. Duvigneaud s.n. (BR).

Cf. *Oenothera deflexa* × *O. fallax*

• West Flanders: Brugge, E-side of Boudewijnkanaal (IFBL C2.11.24), sand deposit, 08.08.2007, F. Verloove 6857 (BR).

Cf. *Oenothera depressa* × *O. deflexa*

• East Flanders: Zwijnaarde (Z-Gent) (IFBL D3.32.24), entrance of former dump area, one specimen, 10.07.2007, F. Verloove 6808 (priv. herb. F. Verloove);
• West Flanders: Zeebrugge (port-area), N of Verbindingsdok (IFBL B2.41.42), artificial sandscape near Tropicana-plant, 18.07.2007, F. Verloove 6858 (BR); Zeebrugge-Strand, W-side of port (IFBL B2.41.24), sandy ruderal soil, near railway station, 2 ex., 08.08.2007, F. Verloove 6851 (BR).