

Original research

New records and floristic notes on the genus *Oenothera* (Onagraceae) in Morocco

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Abstract

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This study provides information on new and verified occurrences of *Oenothera* species in Morocco, emphasising the challenges of identification due to morphological similarities among taxa. For the first time, *Oenothera laciniata* is reported in the country, while the presence of *Oenothera indecora* and *Oenothera drummondii* is confirmed in the provinces of Kénitra and Tétouan, respectively. The latter species had previously been misidentified as *Oenothera biennis*. All three of these rare alien species were found in sandy or coastal habitats. Additionally, *Oenothera lindheimeri*, a species cultivated for ornamental purposes along roadsides, in public places, and in various gardens in several cities, occasionally escapes from cultivation. To facilitate accurate identification, this paper provides detailed morphological descriptions and illustrations of the species, a comparative analysis with closely related taxa and an updated dichotomous key for the genus *Oenothera* in Morocco.

Keywords: alien species, chorology, dichotomous key, flora, *Raimannia*.

INTRODUCTION

The strategic geographic position of Morocco, its ecological diversity and agricultural practices make it a hotspot for botanical discoveries. Several new species have been recorded in recent years, highlighting the dynamic nature of its plant biodiversity (Chambouleyron, 2023; Homrani Bakali & Susanna, 2022, 2024; Homrani Bakali & Chatelain, 2023; Homrani Bakali et al., 2024, 2025a, 2025b; Khamar et al., 2024; Giardi & Homrani Bakali, 2023; Léger et al., 2025).

The genus *Oenothera* L. (Onagraceae) comprises approximately 145 species divided into 18 sections,

positioning it as the second-largest genus within the family (Wagner et al., 2007). While *Oenothera* species are exclusively native to the Americas, many have been widely introduced across temperate and subtropical regions due to their horticultural appeal, adaptability to disturbed environments, and potential medicinal applications (Mihulka et al., 2006; Wagner et al., 2007; Ghasemian et al., 2017). Several species exhibit invasive tendencies, facilitated by their high reproductive output, broad environmental tolerance, and allelopathic potential (Mihulka et al., 2006).

In Morocco, *Oenothera* species are not native, but some were intentionally introduced as ornamental

plants, while others may have been introduced accidentally. The ‘*Flore pratique du Maroc*’ (Fennane et al., 2007) lists only two naturalised species: *Oenothera biennis* L. in Tétouan and *Oenothera stricta* Ledeb. ex Link following the earlier records in ‘*Catalogue des Plantes du Maroc*’ (Jahandiez & Maire, 1932). Additionally, Dobignard (2009) has reported *Oenothera indecora* subsp. *bonariensis* W.Dietr. (= *Oenothera indecora* Cambess) as new to the Kénitra province. Consequently, these three species have been listed as naturalised in the most recent edition of the ‘Moroccan Red Data Book’ (Fennane, 2021).

However, the taxonomic identity of the *Oenothera* population in Tétouan remains unresolved. Several authors have cited *Oenothera biennis* in the sandy soils of the region (Mas Guindal, 1932; Jahandiez & Maire, 1932; Hammada et al., 2011; Ouyahya, 2007; Fennane, 2021), whereas Dietrich & Wagner (1988) have identified *Oenothera drummondii* instead of *Oenothera biennis* in the dunes of Rio Martil. Given that Mas Guindal (1932) explicitly mentions Rio Martil, these records may refer to the same locality, with the discrepancy likely reflecting differences in identification rather than separate sites.

Despite the existing records, the distribution of *Oenothera* species in Morocco remains incompletely documented (Dobignard & Chatelain, 2010). New occurrences documented during recent fieldwork shed further light on their establishment and naturalisation in Moroccan ecosystems. The purpose of this paper is to clarify the identity of the *Oenothera* species found in Rio Martil (northeast of Tétouan) and to document and illustrate new records of other species throughout the country.

MATERIALS AND METHODS

Fieldwork was conducted between March 2023 and May 2025 in northern and central Morocco, along the Mediterranean Sea and Atlantic coasts and extending inland to Marrakech, in areas characterised by Mediterranean ecological conditions, including sandy and clayey soils and disturbed habitats. Geographical coordinates of all collection sites were recorded using a camera with a built-in GPS device, along with selected environmental data.

Specimens of *Oenothera* were collected during the flowering and fruiting stages to ensure accurate

identification. Voucher specimens were deposited at the RAB Herbarium. Diagnostic features, including leaf shape, floral structure, hypanthium length, and capsule morphology, were compared against descriptions provided in key floristic references (Wagner et al., 2007; Dietrich et al., 1997; Raven, 1979).

Photographs of fresh specimens and their habitats were taken for additional documentation. Existing records of *Oenothera* species, including herbarium specimens from collections (CCA, CORD, E, G, GH, K, L, LE, MA, MICH, MPU, NY, P, PH, R, RSA, SI, SP and US), were reviewed to validate species identification. Additionally, recent taxonomic treatments and phylogenetic studies of the genus *Oenothera* were consulted (Krakos et al., 2014; Overson et al., 2023). The distribution of *Oenothera* species in Morocco is also provided. Details of the Moroccan specimens examined, including the newly recorded material, are provided in Appendix I.

RESULTS

Recent surveys have revealed a new *Oenothera* species in the flora of Morocco. We present a detailed account of *Oenothera laciniata*, *Oenothera lindheimeri*, *Oenothera indecora*, and *Oenothera drummondii*. For each, we provide a morphological description, distribution data, and taxonomic notes.

Oenothera laciniata Hill, Syst. Veg., 12(App.): 64, pl. 10. 1767. Plants annual, erect to procumbent, 5–50 cm long, forming basal rosettes (Fig. 1). Leaves 2–15 × 0.5–3.5 cm, oblanceolate, deeply lobed to dentate, sometimes with reddish stems, sparsely to moderately strigillose, villous, and often glandular-puberulent. Inflorescence lax, simple or branched; flower buds nodding, later erect; floral tube 12–35 mm; petals yellow; sepals 0.5–1.5 cm, green to yellowish, often flushed with red. Style exserted, stigma lobes surrounded by anthers at anthesis. Capsules 2–5 cm, cylindrical, arising at an acute angle. Seeds 0.8–2 mm, brown, elliptic to rotund, distinctly pitted.

Distribution. *Oenothera laciniata* thrives in open, usually sandy, disturbed habitats across a broad range in North America, from North Dakota to Kansas, Oklahoma, and Texas, extending eastward to the Atlantic coast (Dietrich & Wagner,

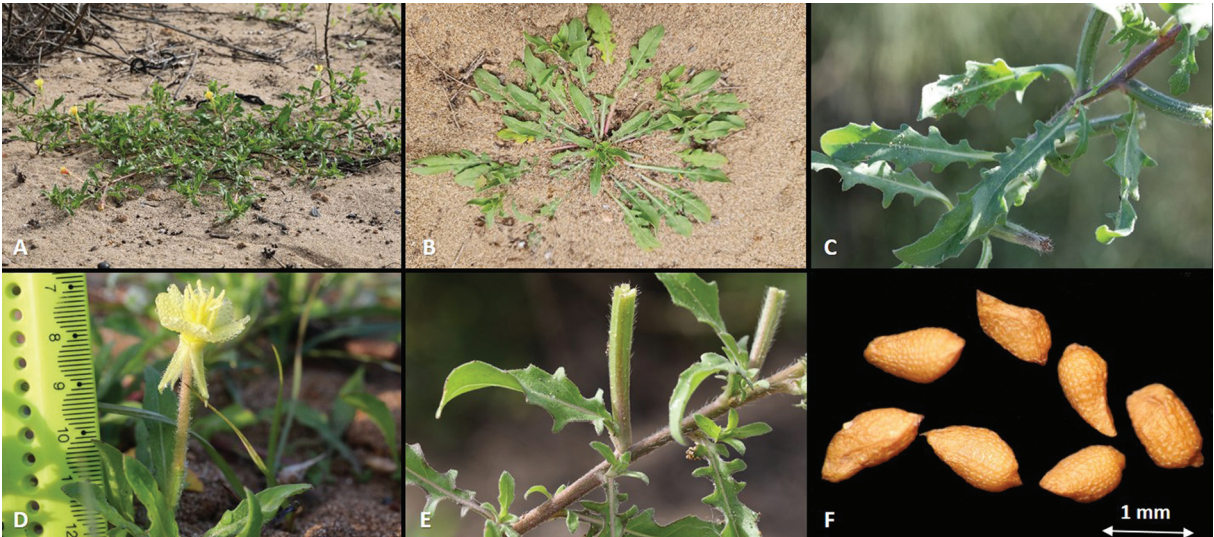


Fig. 1. *Oenothera laciniata* in Morocco. A – plant habit; B – basal rosette; C – cauline leaves; D – flower; E – capsule; F – seeds. Photographs by A. Homrani Bakali.

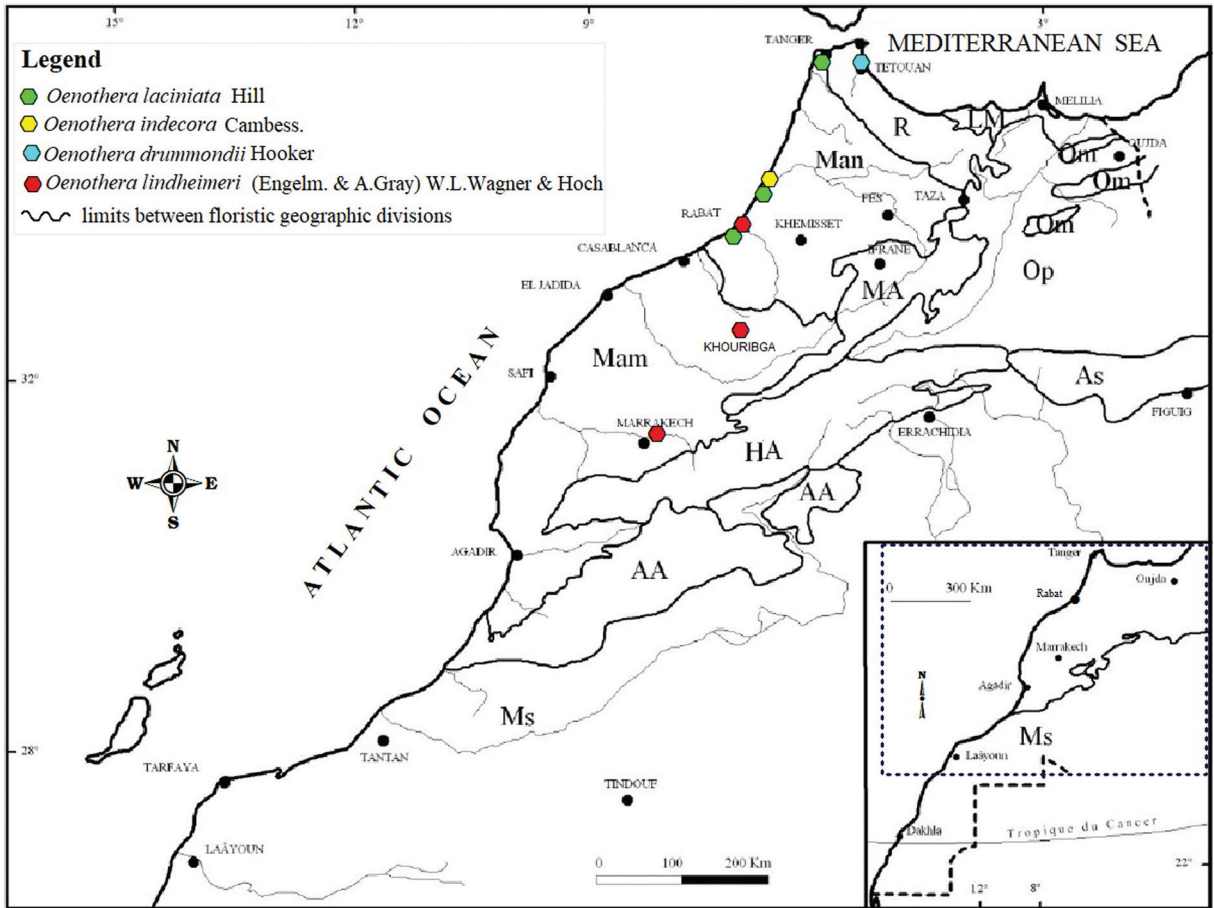


Fig. 2. Distribution map of *Oenothera* species in Morocco. The floristic and geographical divisions are adapted from Fennane & Ibn Tattou (1998), with the following abbreviations: HA – High Atlas Mountains; MA – Middle Atlas Mountains; R – Rif Mountains; AA – Anti-Atlas Mountains; Mam – Middle Atlantic Morocco; Man – North Atlantic Morocco; Ms – Moroccan Sahara; LM – Mediterranean Coast; Op – Eastern Plateaus; Om – Eastern Mountains; As – Saharan Atlas Mountains.

1988). Outside its native range, the species has been introduced and naturalised in many regions worldwide, including South America: Paraguay (Dietrich & Wagner, 1988), Europe: British Isles (Rostański, 1982), Belgium (Rostański & Verloove, 2015), France (MNHN, 2025), Spain (Flores et al., 2012), Greece (Korakaki et al., 2021), Austria, Germany, Italy, Lithuania, Sweden, and Norway (Rostański, 2006), Africa: Libya (Mahklouf, 2016) and South Africa (Jiarui et al., 2007), Asia: Iran (Amini & Zare, 2003), India (Nayar et al., 2012), China (Jiarui et al., 2007), Taiwan (Peng & Huang, 1986; Jiarui et al., 2007), and Japan (Osada, 1976), and Oceania: Australia (Jiarui et al., 2007).

The first Moroccan records of *Oenothera laciniata* come from the coast of Mehdiya (Appendix I), where the species occurs in disturbed, sandy sites. These areas, typically characterised by human activity and environmental disturbance, provide an ideal habitat for the species (Fig. 2).

Taxonomic notes. *Oenothera laciniata* is a highly variable species within sect. *Oenothera* subsect. *Raimannia* (Rose ex Britton & A. Brown) W. Dietrich, exhibiting different morphs across its range. It is autogamous and a permanent structural heterozygote, and one of the most widespread and naturalised species in the genus. The most common morphological features are the deeply divided leaves, and petals only 5–10 mm long. The occasional occurrence of larger petals is linked to putative hybridisation with species like *Oenothera mexicana* Spach, *Oenothera drummondii*, and *Oenothera grandis* Smyth. These morphological forms occur sympatrically and have evolved through complex interpopulational hybridisation (Dietrich & Wagner, 1988). It is the third most observed *Oenothera* species on iNaturalist (iNaturalist, 2025) and is recognised as a highly invasive plant worldwide.

Oenothera laciniata is closely related to several other species within the subsect. *Raimannia*, including *Oenothera drummondii*, *Oenothera humifusa* Nutt., *Oenothera grandis*, *Oenothera mexicana*, and *O. falfurriae* W. Dietr. & W.L. Wagner, but can be readily distinguished by a combination of floral and foliar characters. It has smaller petals (0.5–2.2 cm) compared with *Oenothera grandis* (2.5–4 cm) and a shorter style exertion (0.3–1.4 cm vs. 1.5–3 cm in *Oenothera grandis*). Its leaves are typically green, sparsely to moderately strigillose, and not revolute, in contrast to *Oeno-*

thera mexicana, which has greyish-green, densely strigillose leaves with revolute margins.

A key floral characteristic differentiating *Oenothera laciniata* from *Oenothera grandis* and *Oenothera falfurriae* is its stigma lobes, which remain surrounded by the anthers at anthesis, rather than being elevated above them as in *Oenothera falfurriae*. Furthermore, *Oenothera laciniata* has pollen fertility of approximately 50%, in contrast to *Oenothera drummondii* and *Oenothera falfurriae*, which have nearly 100% fertile pollen (Dietrich et al., 1997; Dietrich & Wagner, 1988).

Previously, two subspecies were recognised within *Oenothera laciniata* viz.: *Oenothera laciniata* subsp. *pubescens* (Willd. ex Spreng.) Munz and *Oenothera laciniata* subsp. *laciniata*. However, *Oenothera laciniata* subsp. *pubescens* has since been elevated to species rank as *Oenothera pubescens* Willd. ex Spreng. and is now classified within subsect. *Nutantigemma* (Dietrich & Wagner, 1987). This reclassification is based on its distinct morphological and genetic characteristics, as well as its unique geographical distribution in montane regions from the western United States to South America. This taxonomic revision reflects a broader distinction between subsect. *Nutantigemma* and *Raimannia* ser. *Raimannia*. *Oenothera* species in *Nutantigemma*, including *Oenothera pubescens*, are characterised by nodding buds and a downward-curved floral tube, whereas those in *Raimannia* ser. *Raimannia*, such as *Oenothera laciniata*, have an upward-curved floral tube (Dietrich et al., 1997). These differences highlight evolutionary divergence and ecological adaptations between the two groups. As a result of this taxonomic revision, *Oenothera laciniata* is now treated as a monotypic species. Additionally, *Oenothera laciniata* remains classified as a permanent structural heterozygote, with a haploid genome complex that differs only slightly from that of *Oenothera humifusa* (Dietrich & Wagner, 1988).

Oenothera indecora Cambess. in A.F.C.P. de Saint-Hilaire & al., Fl. Bras. Merid., 2: 268. 1830. Ascending to prostrate annual or biennial, up to 60 cm tall, with several basal branches, covered with fine, appressed to erect pubescence (Fig. 3). Leaves 1–6 cm long, sinuate-dentate, lanceolate or narrowly ovate, sessile. Inflorescence erect, buds also erect; flow-

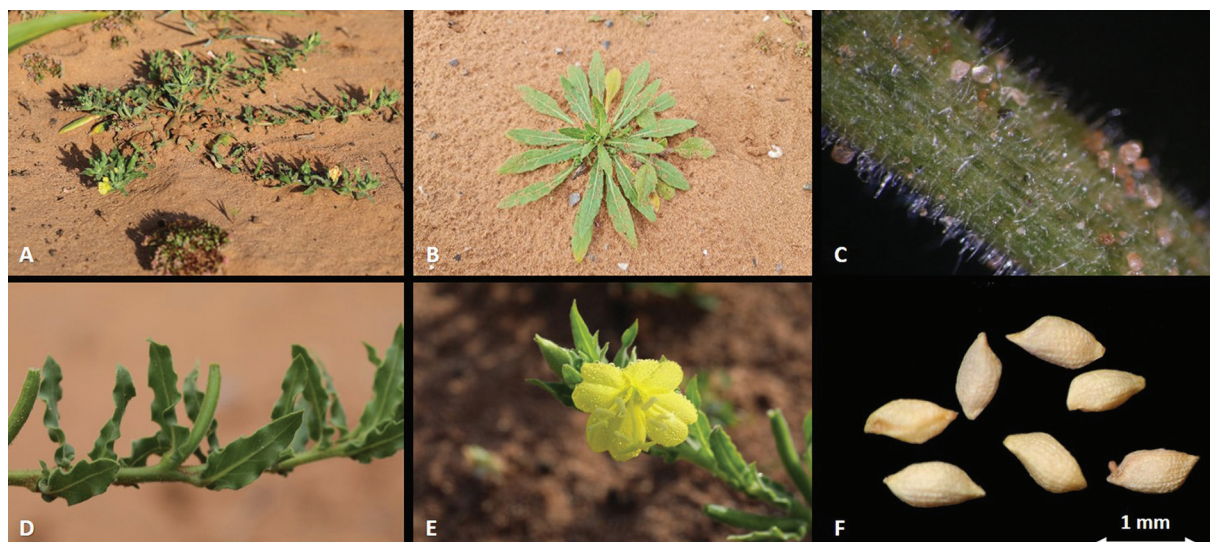


Fig. 3. *Oenothera indecora* in Morocco. A – plant habit; B – basal rosette; C – stem indumentum; D – cauline leaves and capsules; E – flower; F – seeds. Photographs by A. Homrani Bakali.

ers borne in the axils of much reduced leaves, opening near sunset. Floral tube 8–15 mm long. Sepals 5–6 mm long with ± 1 mm slender tips. Petals 3–6 mm long, bright yellow, fading reddish. Anthers ± 2 mm long; filaments 4–6 mm long. Style surrounded by anthers at anthesis; stigma with linear lobes 2–3 mm long. Capsule 15–22 $\times$ 1.5–2.0 mm, cylindric, subsessile, not winged. Seeds 0.7–1.3 mm long, light brown, obovoid, indistinctly and shallowly pitted.

Distribution. *Oenothera indecora* was first described from Brazil by Cambessedes (de Saint-Hilaire et al., 1830). Native to South America (Uruguay, Paraguay, Brazil, and Argentina (Dietrich, 1977)), it has expanded beyond its range and is now established in various tropical and subtropical regions. Outside its native range, the species occurs in Africa: Botswana, Rhodesia, South Africa (Frean et al., 1997), Tristan da Cunha (Dietrich, 1977), Namibia, Zimbabwe (Wagner et al., 2007; Crisafulli et al., 2013) and Morocco (Dobignard, 2009, based on a herbarium specimen collected in Kénitra in 1981 by Lewalle n° 9862, ex herb. LG, det. Lambinon, 1999), in Oceania: Australia (Dietrich, 1977) and New Zealand. In Asia, it is cited in Japan (Wagner et al., 2007) and Iran (Moradi & Mahdavi Fikajor, 2022), in Europe: the Netherlands, Hungary, France, Germany (Dietrich, 1977), Portugal (Dietrich, 1977, 2000; Crisafulli et al., 2013), Greece (Raus, 2006; DAISIE, 2008; Crisafulli et al., 2013), Belgium (Rostański & Verloove, 2015), Sweden (Rostański,

2006), Spain (Verloove & Sánchez Gullón, 2008), and Italy (Crisafulli et al., 2013). Additionally, it has been reported from the Atlantic islands of the Canary Islands and Madeira, as well as from Lesotho (Crisafulli et al., 2013). Our observations, therefore, do not represent a new record for Morocco, but rather confirm the earlier citation of Dobignard (2009), which is not reflected in several floristic databases such as APD and POWO, and has not been incorporated into the main Moroccan floras. *Oenothera indecora* has been found in the sandy soils of the city of Kénitra, located near the Forest of Maamora (Appendix I). This species thrives in the well-drained, sandy substrate typical of the area. Its presence near the Maamora Forest indicates its ability to colonise disturbed habitats and adapt to the local environmental conditions. By confirming the Kénitra locality, first documented in 1981, our record provides updated ecological information and supports the continued presence of the species in Morocco (Fig. 2). This confirmation is important because *Oenothera indecora* is considered a potentially invasive species due to its adaptability, rapid spread, and ability to outcompete native vegetation (Frean et al., 1997).

Taxonomic notes. *Oenothera indecora* belongs to the *Oenothera* sect. *Oenothera*, subsect. *Munzia* W. Dietr., series *Allochroa* W. Dietrich, a group of species distinguished by their cylindrical capsules, which are rarely enlarged in the upper third, sometimes somewhat pedunculate, and not fused with the

subtending bract (Dietrich, 1977). Originally, *Oenothera indecora* was subdivided into three subspecies: *Oenothera indecora* subsp. *indecora*, *Oenothera indecora* subsp. *boliviensis* W.Dietr., and *Oenothera indecora* subsp. *bonariensis* W.Dietr., based on differences in pubescence and flower size (Dietrich, 1977). Morphologically, *Oenothera indecora* subsp. *indecora* differs from subsp. *bonariensis* primarily in indumentum: subsp. *indecora* has a dense, villous indumentum composed of three hair types (long patent eglandular, medium patent glandular, and short appressed strigulose hairs), while subsp. *bonariensis* has a much shorter indumentum, appearing almost glabrous to the naked eye (Greuter & Raus, 2006). Therefore, these subspecific distinctions are considered insufficient for taxonomic recognition, because the subspecies intergrade extensively and show strongly overlapping geographic ranges; furthermore, subsp. *boliviensis* is known only from cultivated material, which further supports the inclusion of all entities within *Oenothera indecora* s. str. (Wagner et al., 2007).

Oenothera indecora is distinguished from other *Oenothera* species in Morocco by its small petals (0.5–1 cm) and short hypanthium (0.4–1.5 cm). It differs from *Oenothera drummondii* (petals 2–4.5 cm) and *Oenothera biennis* (1–3 cm) by its significantly smaller petals. Additionally, it can be separated from *Oenothera laciniata* by its sinuate-dentate leaves, in contrast to the deeply lobed leaves of the latter.

Oenothera drummondii Hooker, Bot. Mag., 61: t. 3361. 1834. Plant annual or perennial, erect to procumbent, 10–50 cm long, with thick taproots up to 2 cm, not forming rosettes (Fig. 4). Stems green, or reddish, simple or branched, strigillose or villous, often glandular-puberulent above. Leaves 1–14 cm × 0.4–2 cm, narrowly oblanceolate to elliptic, shallowly dentate to entire, greyish-green and strigillose. Bracts similar, sessile or shortly petiolate. Inflorescence lax, often branched; flower solitary, opening near sunset. Floral tube 2–5 cm long, strigillose to villous. Sepals 1.3–3.3 cm long, greenish to yellowish, flushed red. Petals 2–4.5 cm × 2.5–5.5 cm, yellow, broadly obovate. Filaments 1–2.3 cm; anthers 4–12 mm. Style exerted part 1.5–3.5 cm; stigma lobes 3–10 mm. Capsule cylindric, 2–5.5 cm × 2–5 mm, pubescent. Seeds 1.1–2 mm × 0.5–0.9 mm, ellipsoid, brown with darker flecks, surface pitted.

Distribution. *Oenothera drummondii* is widely distributed, naturally occurring in North America and Mexico and has been introduced in regions such as Australia, Europe, North Africa, and China (Wagner et al., 2007).

Over the past century, it has become naturalised in various regions worldwide, particularly in coastal environments. In Africa, the species has been reported in coastal areas of Egypt and South Africa (Castillo-Infante et al., 2021). In Europe, it has established populations along the Mediterranean coastlines, notably in Spain and France (Castillo-

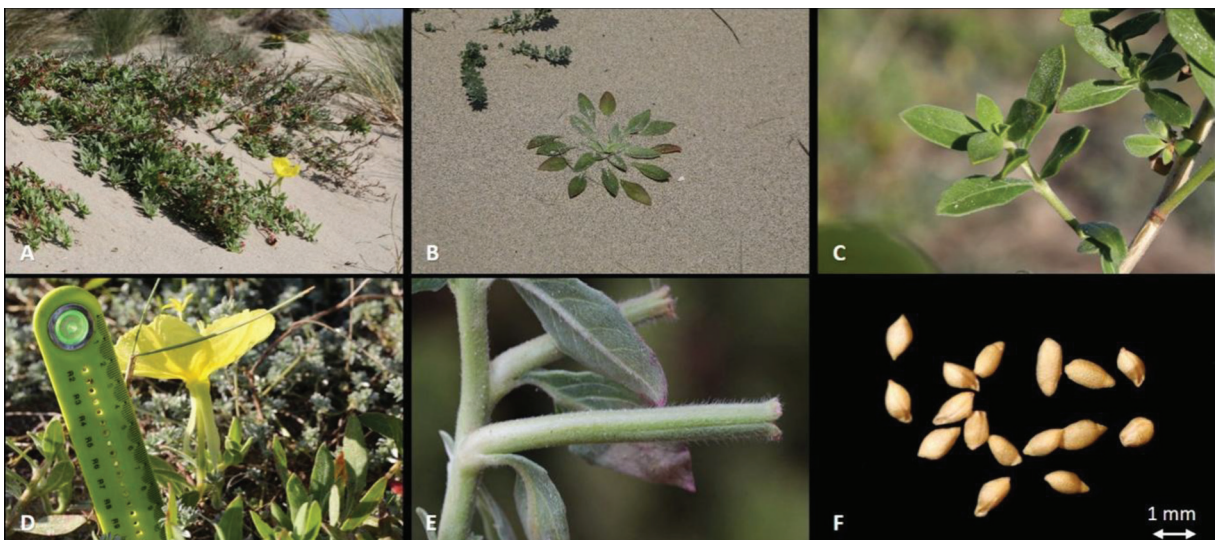


Fig. 4. *Oenothera drummondii* in Morocco. A – plant habit; B – basal (rosette) leaves; C – cauline leaves; D – flower; E – capsule; F – seeds. Photographs by A. Homrani Bakali.

Infante et al., 2021). In Asia, *Oenothera drummondii* has been introduced to countries such as Israel and China (Gallego-Fernández & García-Franco, 2021). In Oceania, it is widely naturalised in coastal districts of eastern and south-western Australia, including regions from southeastern Queensland to central and northern New South Wales, and parts of Western Australia (Lucid Central, 2005). It is also present on Lord Howe Island and has been recorded in New Zealand (Castillo-Infante et al., 2021). The species ability to colonise diverse coastal environments is attributed to its high self-compatibility and mixed reproductive systems, which facilitate establishment in new locations even with limited pollinator presence (Gallego-Fernández & García-Franco, 2021). Additionally, its seeds can be dispersed by marine currents, contributing to its spread along coastlines (Castillo-Infante et al., 2021).

According to Castillo-Infante et al. (2021), *Oenothera drummondii* poses a significant invasion risk in coastal ecosystems due to its high adaptability and competitive abilities. The species capacity for rapid growth, efficient seed dispersal via marine currents, and tolerance to salt spray enable it to outcompete native dune vegetation. Invasive populations of *Oenothera drummondii* can alter soil composition and disrupt plant-pollinator interactions, potentially reducing biodiversity in affected regions.

In Morocco, *Oenothera drummondii* has been found in the coastal dunes of Martil, located in the Tétouan province (Fig. 2; Appendix I). This species is well-suited to the sandy, salt-affected soils typical of coastal dune ecosystems. The open, sun-exposed environments of the dunes provide ideal conditions for *Oenothera drummondii*, allowing it to establish in these disturbed areas.

Taxonomic notes. In Morocco, it is important to point out that the Practical Flora of Morocco (Fennane et al., 2007) states that *Oenothera drummondii* was likely misidentified as *Oenothera biennis* because of an earlier mention of this latter species by Mas Guindal (1932) in Martil (northeast of Tétouan). Subsequent mentions of *Oenothera biennis* in the region by Jahandiez & Maire (1932), Ouyahya (2007), Hammada et al. (2011), and Fennane (2021) also appear questionable, as they rely on secondary sources rather than direct field observations or detailed surveys. Nonetheless, as previously stated,

our own field investigations in Martil and surrounding areas have confirmed the presence of *Oenothera drummondii*. Furthermore, an examination of the herbarium collections housed at the National Herbarium RAB revealed no specimens of *Oenothera biennis* from the Tétouan region. These findings support the conclusions of Fennane et al. (2007), namely that no specimens of *Oenothera biennis* have been seen.

Oenothera drummondii is distinguished within the subsect. *Raimannia* ser. *Raimannia* by its stiff, densely strigillose or villous stems and greyish-green, densely strigillose leaves, unlike the softer, more glandular puberulent stems of *Oenothera laciniata* and *Oenothera grandis*. It has the largest flowers in the series, with sepals 1.3–3.3 cm and petals 2–4.5 cm, whereas *Oenothera humifusa* and *Oenothera laciniata* have much smaller ones. Its stigma lobes are elevated above the anthers at anthesis, differing from *Oenothera laciniata* and *Oenothera humifusa*, where the stigma remains surrounded (Dietrich & Wagner, 1988).

Within its native range, *Oenothera drummondii* comprises two geographically distinct subspecies: subsp. *drummondii*, an annual, upright taxon of the Atlantic and Gulf coasts, and subsp. *thalassaphila* (Brandege) W. Dietr. & W.L. Wagner, a perennial with prostrate to ascending stems, restricted to the Pacific coast of Baja California (Dietrich & Wagner, 1988).

Oenothera lindheimeri (Engelm. & A.Gray) W.L.Wagner & Hoch, Systematic Botany Monographs, 83: 213. 2007. Perennial herb, forming a basal clump from a woody taproot, 50–150 cm tall (Fig. 5). Leaves are narrow, lance-shaped, 1–9 × 1–1.3 cm, with entire or faintly toothed margins. Lower cauline leaves are spatulate to oblong-oblancheolate, upper leaves are reduced and subentire. Inflorescence branched raceme or panicle, 20–60 cm long, with villous bracts 5–10 mm long. Flowers star-shaped, 2–3 cm wide; petals white to pink, 12–20 mm; sepals lance-linear, 12–15 mm, pilose, and glandular-pubescent. Hypanthium slender, reddish, 5–8 mm. Stamens eight, filaments 10–15 mm, anthers red. Style exerted pubescent at the base. Capsule sessile, four-angled, elliptic-oblong capsule 7–9 mm, containing 1–4 ovoid seeds (up to 2.3 × 1.5 mm).

Distribution. *Oenothera lindheimeri* is native to the southeastern United States, particularly Texas and Louisiana. However, it has been introduced to vari-



Fig. 5. *Oenothera lindheimeri* in Morocco. A – plant habit; B – cauline leaves; C – flowers; D – angular capsule. Photographs by A. Homrani Bakali.

ous regions outside its native range, including North America: Alabama, Europe: the Balearic Islands, Corsica, Germany, Great Britain, Greece, Italy, Portugal, and Spain, and Africa: the Cape Provinces, and the Northern Provinces of South Africa (POWO, 2025). In these introduced areas, it typically grows in disturbed habitats such as roadsides, fields, and rocky hillsides, adapting well to full sun exposure and well-drained soils. Its ability to thrive in diverse environments has led to its widespread cultivation and naturalisation worldwide (Lucid Central, 2025).

In Morocco, *Oenothera lindheimeri* has been introduced as an ornamental plant to decorate roadsides, public places and various gardens in several cities (Marrakech, Tangier, Rabat, Khouribga, Fig. 2; Appendix I). Although primarily cultivated as an ornamental, it occasionally escapes from gardens into adjacent ruderal habitats, raising questions about its potential for naturalisation (Fig. 6).

Taxonomic notes. *Oenothera lindheimeri* belongs to section *Gaura* W.L. Wagner & Hoch, which is distinguished from section *Oenothera* by several

key morphological traits. Species in section *Gaura* typically have flowers with a reduced or absent floral tube and white or pink petals. In contrast, section *Oenothera* species possess a well-developed floral tube and predominantly yellow petals. Additionally, the fruit of section *Gaura* is ovoid or club-shaped, differing from the elongated, cylindrical capsules found in section *Oenothera*. Seed morphology also varies, with section *Gaura* having ellipsoid to globose seeds with a regularly pitted surface, while section *Oenothera* has prismatic seeds with an irregularly pitted surface. These characteristics highlight the taxonomic and evolutionary distinctions between the two sections (Wagner et al., 2007, 2013).

DISCUSSION

Recent surveys have revealed a new *Oenothera* species in the flora of Morocco: *Oenothera laciniata*, recorded in the Kénitra region. This North American species is easily recognisable by its decumbent to ascending stems, deeply pinnatifid basal leaves, and



Fig. 6. Small plant of *Oenothera lindheimeri* escaped in Tangier, Morocco. Photograph by A. Homrani Bakali.

relatively small pale yellow flowers. Its establishment in coastal and disturbed areas in Kénitra represents a notable addition to the country's alien flora and merits further monitoring.

Additionally, *Oenothera lindheimeri* (= *Gaura lindheimeri*) has been documented in the city of Marrakech, notably as a garden escape.

Beyond these newly reported species, our recent investigations confirm that the *Oenothera* population found in Kénitra corresponds to *Oenothera indecora*. The subspecies *Oenothera indecora* subsp. *bonariensis*, cited by Dobignard (2009), is typically characterised by an erect growth habit with several lateral decumbent branches. Although the Kénitra population predominantly shows a decumbent habit, it shares key diagnostic traits of *Oenothera indecora*, including sinuate-dentate cauline leaves and a dense indumentum composed of three hair types (Raven, 1968).

This species could be mistaken for *Oenothera humifusa*, described from Florida, which is consistently decumbent and differs in having subentire leaves and silky, appressed pubescence, features that enable it

to thrive in sandy coastal environments (Wagner, 2021). The morphological characteristics observed in the Moroccan material, however, support the identification as *Oenothera indecora*.

In northern Morocco, the *Oenothera* population in Tétouan aligns with *Oenothera drummondii*, as previously described by Dietrich & Wagner (1988). Meanwhile, the presence of *Oenothera biennis* in the same region reported by Mas Guindal (1932), Hammada et al. (2011), Ouyahya (2007), and Fennane (2021) remains uncertain and requires additional fieldwork and specimen-based confirmation.

To enhance species identification, we present a dichotomous key to the *Oenothera* species of Morocco. This key is inspired by the taxonomic framework and diagnostic characters outlined in the works of Dietrich & Wagner (1988), Dietrich (1977, 2000), and Dietrich et al. (1997). We also included *Oenothera biennis* in the key, as it has been cited in Morocco, likely due to confusion with *Oenothera drummondii*. Note that the classification into subsections follows the Dietrich & Wagner (1988) system; this is retained here for consistency and ease of comparison.

Dichotomous key to the *Oenothera* species currently known in Morocco

1. Flowers star-shaped with white to pink petals; petals 12–20 mm long; fruit nut-like, indehiscent *Oenothera lindheimeri* (subsect. *Gaura*)
- Flowers not star-shaped, petals yellow or pale yellow; fruit a dehiscent capsule, seeds prismatic, angled, surface irregularly pitted *Oenothera biennis* (subsect. *Oenothera*)
2. Seeds ellipsoid to subglobose, not angled, surface usually regularly pitted, flower buds erect, floral tubes straight (never recurved or nodding) *Oenothera indecora* (subsect. *Munzia*)
- Flower buds nodding or floral tubes curved upward in the oldest buds (subsect. *Raimannia*) 3
3. Plants forming basal rosettes, floral tube 1.2–3.5 cm; petals 0.5–2.2 cm; stigma surrounded by the anthers at anthesis; seeds brown to light brown *Oenothera laciniata*
- Plants without basal rosettes, stems 10–50 cm; petals 2–4.5 cm; floral tube 2–5 cm; stigma elevated above anthers at anthesis; seeds brown with darker flecks *Oenothera drummondii*

This study highlights the increasing diversity and taxonomic complexity of the genus *Oenothera* in Morocco, resulting from recent discoveries and taxonomic revisions, as well as the confirmation of previously reported species occurrences. The new record of *Oenothera laciniata* in Morocco, along with the presence of *Oenothera lindheimeri* in cultivation and occasionally escaping, underscores the dynamic nature of alien plant introductions and the importance of continuous floristic monitoring. Our field investigations further clarify the status of *Oenothera* species in northern Morocco. In particular, the long-standing confusion between *Oenothera biennis* and *Oenothera drummondii* in the Martil-Tétouan region has now been resolved, as our observations confirm the presence of *Oenothera drummondii* and indicate that previous reports of *Oenothera biennis* likely resulted from misidentifications. Similarly, the confirmation of *Oenothera indecora* in Kénitra contributes to a more accurate understanding of species distributions within the country. Our integrative approach, combining field observations with literature-based comparisons, has enabled a clearer understanding of spe-

cies boundaries and distributions. The dichotomous key provided in this study aims to facilitate future field identification and to encourage further investigation and potential invasiveness of these species in Moroccan ecosystems.

Author contributions. AHB conceived and designed the study, conducted field surveys and investigations, carried out laboratory analyses (including morphological assessments), described the species, collected data, and made substantial contributions to drafting the manuscript. HK conducted field surveys and investigations, verified and confirmed species identification, developed a distribution map, contributed to the differentiation of morphological traits in species descriptions, and assisted in manuscript preparation. Both authors have read and approved the final version of the article.

REFERENCES

- Amini T., Zare H., 2003: *Oenothera sinuata* Linn. (Onagraceae), a new record for the flora of Iran. – Iranian Journal of Botany, 10: 41–43.
- Castillo-Infante F.R., Mendoza-González G., Rioja-Nieto R., Gallego-Fernández J.B., 2021: Range shifts in the worldwide expansion of *Oenothera drummondii* subsp. *drummondii*, a plant species of coastal dunes. – Diversity, 13: 603. <https://doi.org/10.3390/d13110603>
- Chambouleyron M., 2023: *Cotula australis*, a new alien species for the flora of Morocco and continental North Africa. – Acta Botanica Malacitana, 48: 147–149. <https://doi.org/10.24310/abm.v48i.16905>
- Crisafulli A., Picone R.M., Soldano A., 2013: *Oenothera indecora* (Onagraceae), a neophyte new to Italy. – Flora Mediterranea, 23: 87–92. <https://doi.org/10.7320/FIMedit23.087>
- de Saint-Hilaire A., De Jussieu A., Cambessedes J., 1830: Flora Brasiliae Meridionalis, 2. A. Belin, Paris.
- DAISIE European Invasive Alien Species Gateway, 2008: *Oenothera indecora* Cambess. DAISIE database. – <http://www.europe-aliens.org> [accessed 28 May 2025].
- Dietrich W., 1977: The South American species of *Oenothera* sect. *Oenothera* (Raimannia, Renneria; Onagraceae). – Annals of the

- Missouri Botanical Garden, 64(3): 425–626. <https://doi.org/10.2307/2395257>
- Dietrich W., 2000: *Oenothera* L. – In: Castroviejo S., Aedo C., Benedí C., Lainz M., Muñoz Garmendia F., Nieto Feliner G., Paiva J. (eds), *Flora Iberica*, 8: 90–100. Madrid.
- Dietrich W., Wagner W.L., 1987: New taxa of *Oenothera* L. sect. *Oenothera* (Onagraceae). – *Annals of the Missouri Botanical Garden*, 74(1): 144–150. <https://doi.org/10.2307/2399272>
- Dietrich W., Wagner W.L., 1988: Systematics of *Oenothera* section *Oenothera* subsection *Raimannia* and subsection *Nutantigemma* (Onagraceae). – *Systematic Botany Monographs*, 24: 1–91. <https://doi.org/10.2307/25027713>
- Dietrich W., Wagner W.L., Raven P.H., 1997: Systematics of *Oenothera* section *Oenothera* subsection *Oenothera* (Onagraceae). – *Systematic Botany Monographs*, 50: 12–34. <https://doi.org/10.2307/25027870>
- Dobignard A., 2009: Contributions à la connaissance de la flore du Maroc et de l’Afrique du Nord. Nouvelle série. 2. La flore du Nord-Maroc. – *Journal de Botanique*, 46–47: 3–136.
- Dobignard A., Chatelain C., 2010: Index Synonymique de la Flore d’Afrique du Nord, 1. Genève.
- Fennane M., 2021: Livre rouge de la flore vasculaire du Maroc. – *Travaux de l’Institut Scientifique, Série Botanique, Numéro Spécial*: 1–750.
- Fennane M., Ibn Tattou M., 1998: Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc. – *Bocconea*, 8: 5–243.
- Fennane M., Ibn Tattou M., Ouyahya A., El Oualidi J. (eds), 2007: Flore pratique du Maroc, Angiospermae (Leguminosae–Lentibulariaceae), 2. – *Travaux de l’Institut Scientifique, Série Botanique*, 38, Rabat.
- Flores F.M., Villalba M.C., Ripoll F.M., 2012: *Oenothera laciniata* Hill (Onagraceae) en la Comunidad Valenciana. – *Flora Montiberica*, 50: 8–14.
- Frean M., Balkwill K., Gold (née Anderson) C., Burt S., 1997: The expanding distributions and invasiveness of *Oenothera* in southern Africa. – *South African Journal of Botany*, 63(6): 449–458. [https://doi.org/10.1016/S0254-6299\(15\)30798-5](https://doi.org/10.1016/S0254-6299(15)30798-5)
- Gallego-Fernández J.B., García-Franco J.G., 2021: Floral traits variation in *Oenothera drummondii* subsp. *drummondii* across a wide latitudinal range of native and non-native populations. – *Flora*, 280: 151851. <https://doi.org/10.1016/j.flora.2021.151851>
- Ghasemian M., Owlia S., Owlia M.B., 2017: Review of *Oenothera biennis* as a natural product with multiple pharmacological properties. – *Chinese Journal of Integrative Medicine*, 25(4): 703–710. [https://doi.org/10.1016/S2221-1691\(17\)31117-6](https://doi.org/10.1016/S2221-1691(17)31117-6)
- Giardi L., Homrani Bakali A., 2023: *Maireana brevifolia* (Chenopodiaceae), an Australian xenophyte established recently in southeastern Morocco. – *Collectanea Botanica*, 42: e009. <https://doi.org/10.3989/collectbot.2023.v42.009>
- Greuter W., Raus T., 2006: Med-Checklist Notulae, 24. – *Willdenowia*, 36(2): 719–730. <https://doi.org/10.3372/wi.36.3620>
- Hammada S., Linares L., Cortes J., 2011: Biodiversité floristique des dunes littorales de l’Oued El Maleh (Martil) et du bas Tahaddart: résultats préliminaires. – *Travaux de l’Institut Scientifique, Série Générale*, 6: 45–50.
- Homrani Bakali A., Susanna A., 2022: *Centaurea achilleifolia* (Asteraceae), a new endemic species from the Oriental Middle Atlas of Morocco. – *Phytotaxa*, 542(1): 83–89. <https://doi.org/10.11646/phytotaxa.542.1.7>
- Homrani Bakali A., Chatelain C., 2023: *Phlomis lychnitidis* (Lamiaceae), an addition to the flora of Africa from Morocco. – *Collectanea Botanica*, 42: 1–7. <https://doi.org/10.3989/collectbot.2023.v42.004>
- Homrani Bakali A., Susanna A., 2024: *Rhaponticoides nuriae* (Asteraceae), a stunning new species from Morocco. – *Phytotaxa*, 659(1): 97–104. <https://doi.org/10.11646/phytotaxa.659.1.8>
- Homrani Bakali A., Léger J.F., Mombrial F., 2024: *Chorispora tenella* (Pall.) DC. (Brassicaceae), xenophyte naturalized in Morocco: comparison with similar-looking species. – *Flora Mediterranea*, 34: 113–119. <https://doi.org/10.7320/FIMedit34.113>
- Homrani Bakali A., Chambouleyron M., Léger J.F., 2025a: *Santolina razaneae* (Asteraceae), a new stepic species from Morocco. – *Phytotaxa*, 693(3): 235–244. <https://doi.org/10.11646/phytotaxa.693.3.4>
- Homrani Bakali A., Chatelain C., Khamar H., 2025b: New non-native species recorded in cumin crop in southeastern region of Morocco. – *Botany Letters*, 172(3): 320–339. <https://doi.org/10.1080/23818107.2025.2506559>
- iNaturalist, 2025: *Oenothera*. – <https://www.inaturalist>.

- [org/observations?iconic_taxa=Plantae&taxon_id=48626&view=species](#) [accessed 11 October 2025].
- Jahandiez E., Maire R., 1932: Catalogue des Plantes du Maroc (Spermatophytes et Ptéridophytes), 2. Dicotylédones Archichlamydées. Alger.
- Jiarui C., Hoch C.P., Wagner W.L., 2007: *Oenothera*. – Flora of China, 13: 423–426. Beijing, St. Louis.
- Khamar H., Dellahi Y., Homrani Bakali A., 2024: New records of three alien *Solanum* species in Morocco. – Check List, 20(2): 544–552. <https://doi.org/10.15560/20.2.544>
- Korakaki E., Legakis A., Katsanevakis S., Koulelis P.P., Avramidou E.V., Soulioti N., Petrakis P.V., 2021: Invasive alien species of Greece. – In: Pullaiah T., Ielmini M.R. (eds), Invasive Alien Species: Observations and Issues from Around the World. 3. Issues and Invasions in Europe: 125–189. Hoboken.
- Krakos K.N., Reece J.S., Raven P.H., 2014: Molecular phylogenetics and reproductive biology of *Oenothera* section *Kneiffia* (Onagraceae). – Systematic Botany, 39(2): 523–532. <https://doi.org/10.1600/036364414X680744>
- Léger J.F., Chambouleyron M., Herment P.C., Verloove F., Chatelain C., Mombrial F., Andrieu F., Homrani Bakali A., Tanji A., 2025: Contribution à la connaissance de la flore du Maroc, notamment de plantes exogènes naturalisées. – Carnets botaniques, 266: 1–38. <https://doi.org/10.34971/A41W-AC40>
- Lucid Central, 2025: *Oenothera lindheimeri*. Weeds of the World. – https://keyserver.lucidcentral.org/weeds/data/media/Html/oenothera_lindheimeri.htm [accessed 25 April 2025].
- Mahklouf M.H., 2016: A new record *Oenothera laciniata* Hill. for the flora of Libya. – International Journal of Modern Botany, 6(1): 6–9. <https://doi.org/10.5923/j.ijmb.20160601.02>
- Mas Guindal J., 1932: Notes sur la flore de Tétouan et de ses environs. – L'Hygiène Sociale, 77: 1–46.
- Mihulka S., Pyšek P., Martinková J., Jarošík V., 2006: Invasiveness of *Oenothera* congeners in Europe related to their historical residence time, cultivation frequency, and biological traits. – Preslia, 78: 287–305.
- MNHN, 2025: Muséum national d'Histoire naturelle *Oenothera laciniata* – INPN. – https://inpn.mnhn.fr/espece/cd_nom/109933 [accessed 23 March 2025].
- Moradi A., Mahdavi Fikajor E., 2022: A new record of an alien species *Oenothera indecora* (Onagraceae) for the flora of Iran. – Taxonomy and Biosystematics, 14(52): 97–106.
- Nayar E.R., Pradheep K., Bhandari D.C., 2012: *Oenothera laciniata* Hill (Onagraceae): an addition to the flora of north-western plains. – Indian Journal of Plant Genetic Resources, 25(2): 195–196.
- Ouyahya A., 2007: *Oenothera*. – In: Fennane M., Ibn Tattou M., Ouyahya A., El Oualidi J. (eds), Flore pratique du Maroc. 2. Angiospermae (Leguminosae–Lentibulariaceae). – Travaux de l'Institut Scientifique, Série Botanique, 38: 194. Rabat.
- Osada T., 1976: Coloured Illustrations of Naturalized Plants of Japan. Osaka.
- Overson R.P., Johnson M.G., Bechen L.L., Kinoshian S.P., Douglas N.A. et al., 2023: A phylogeny of the evening primrose family (Onagraceae) using a target enrichment approach with 303 nuclear loci. – BMC Ecology and Evolution, 23: 66. <https://doi.org/10.1186/s12862-023-02151-9>
- Peng C.-I., Huang S., 1986: *Oenothera laciniata*: a previously unrecorded species in Taiwan. – Botanical Bulletin of Academia Sinica, 27: 45–51.
- POWO, 2025: Plants of the World Online. *Oenothera lindheimeri*. Distribution. <https://powo.science.kew.org/taxon/77092955-1> [accessed 25 April 2025].
- Raus T., 2006: *Oenothera indecora* subsp. *indecora*. – In: Greuter W., Raus T. (eds), Med-Checklist Notulae, 24: 724–725. – Willdenowia, 36(2).
- Raven P.H., 1968: *Oenothera*. – In: Tutin T.G., Heywood Y.H., Burges N.A., Moore D.M., Valelentine D.H., Walters S.M., Webb D.A. (eds), Flora Europaea, 2: 306–308. London.
- Raven P.H., 1979: A survey of reproductive biology in Onagraceae. – New Zealand Journal of Botany, 17(4): 575–593. <https://doi.org/10.1080/0028825X.1979.10432572>
- Rostański K., 1982: The species of *Oenothera* L. in Britain. – Watsonia, 14: 1–34.
- Rostański K., 2006: The occurring of *Oenothera* species in Scandinavia. – Biodiversity: Research and Conservation, 1–2: 64–68.
- Rostański K., Verloove F., 2015: The genus *Oenothera* (Onagraceae) in Belgium. – Dumortiera, 106: 12–42.
- Verloove F., Sánchez Gullón E., 2008: New records of interesting xenophytes in the Iberian Peninsula. – Acta Botanica Malacitana, 33: 147–167.
- Wagner W.L., 2021: *Oenothera humifusa*. – In: Flora

- of North America North of Mexico, 10. – https://floranorthamerica.org/Oenothera_humifusa [accessed 30 September 2025].
- Wagner W.L., Hoch P.C., Raven P.H., 2007: Revised classification of the Onagraceae. – Systematic Botany Monographs, 83: 1–204.
- Wagner W.L., Krakos K.N., Hoch P.C., 2013: Taxonomic changes in *Oenothera* sections *Gaura* and *Calylophus* (Onagraceae). – PhytoKeys, 28: 61–72. <https://doi.org/10.3897/phytokeys.28.6143>

APPENDIX I

List of *Oenothera* herbarium specimens collected in Morocco

Oenothera laciniata

- Kénitra, Mehdiya city near the beach; 34.260697, –6.670685; 2–10 m a.s.l.; 14 November 2023; leg. A. Homrani Bakali (RAB114881);
- Rabat, Yacoub El Mansour, coastal road R322, sandy soil, 33.98374, –6.89366, 9 m a.s.l.; 21 June 2022; leg. H. Khamar (RAB114887);
- Tangier, Gueznaya rocade des deux mers, 35.723645, –5.893041, 25 m a.s.l.; 14 April 2024; leg. A. Homrani Bakali (RAB114884).

Oenothera indecora

- Kénitra, Rocade Sud near Maamora forest; 34.235735, –6.581347; 45–55 m a.s.l.; 17 March 2024; leg. A. Homrani Bakali (RAB114880).

Oenothera drummondii

- Tétouan, Martil coastal dunes near Oued el Maleh; 35.640594, –5.278682; 2–10 m a.s.l.; 14 March 2024; leg. A. Homrani Bakali (RAB114879).

Oenothera lindheimeri

- Tangier, city experimental station INRA and around garden city; 35.730270, –5.882203; 20–100 m a.s.l.; 10 July 2024; leg. A. Homrani Bakali (RAB114882; RAB114883);
- Rabat, Andalusian garden of the Kasbah of the Oudayas, 34.030195, –6.835389, 11 m a.s.l.; 12 April 2025; leg. H. Khamar (RAB114886);
- Khouribga, roadside 32.886744, –6.911472, 802 m a.s.l.; 20 April 2025; leg. H. Khamar (RAB114885).

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