A new natural hybrid in *Argemone* (Papaveraceae)

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Abstract

*Argemone × hybridra* is described as a natural hybrid of *A. mexicana* and *A. ochroleuca*, based on a collection from La Palma (Canary Islands, Spain), where both parents are found growing in close proximity. This hybrid may be more widespread but overlooked. Distinguishing features of all three taxa are thoroughly discussed and illustrated.

Key words: Hybridization, Invasive species, Macaronesia, Neotropical flora

Introduction

*Argemone* Linnaeus (1753: 508) (Papaveraceae—Papaveroideae) is a New World genus distributed in North and South America, Hawaii and the West Indies (Ownbey 1958, Ownbey 1961). Its center of diversity lies in the dry and warm areas in the southwestern United States and adjacent parts of Mexico (Schwarzbach & Kadereit 1999). The taxonomy of the genus is controversial and species number ranges between 24 (Schwarzbach & Kadereit l.c.) and 32 (Ownbey 1997). Only few species are economically important, either as ornamentals or as medicinal plants, or as agricultural or environmental weeds. Probably most widespread are *Argemone mexicana* Linnaeus (1753: 508) and *A. ochroleuca* Sweet (1828: 242), the latter sometimes treated as an infraspecific taxon of *A. mexicana* or even as a mere synonym (e.g. Euro+Med 2016). Both are now found in many temperate and (sub-) tropical regions across the world. Much less frequent are the Chilean endemic *A. subfusiformis* Ownbey (1961: 97) that locally naturalized as a weed in parts of Australia (Green 1994) and the North American *A. albiflora* Hornemann (1815: 489) that was recently found in Morocco (Faucheux 2011).

Most of the herbaceous species of *Argemone* can hybridize, but the F₁ plants are sterile when the parents differ in ploidy level, and the F₂ generation, when formed, consists mainly of plants of low vigor (Ownbey 1997). Hybrids between two of the aforementioned weedy species (*A. mexicana* and *A. ochroleuca*) have been raised artificially (Grover 1970, Malik & Grover 1973) but are also sometimes found in the wild (e.g. Malhotra 1960, Viveiros & Pereira 1970, Chaturvedi et al. 1999, pers. obs. first author). According to these authors the incidence of such hybrids in mixed populations can range between 1% and 5%. Surprisingly, this hybrid appears to have never been formally described and an appropriate binomial is lacking. Since both parental species are increasingly common and often sympatrically occurring weeds, and hybridization does not seem to be an exceptional event, it seems useful to provide a binomial for this hybrid. Moreover, it has been shown that natural hybridization processes may produce genotypes that establish new evolutionary lineages (Arnold & Hodges 1995).

On the island of La Palma, Canary Islands (Spain) *Argemone mexicana* and *A. ochroleuca* are widely naturalized and invasive species. In two mixed populations, sterile plants with intermediate characters have recently been encountered that obviously belong to the hybrid of these two species. In this paper the new hybrid *Argemone × hybridra* is formally described. Features distinguishing it from both parent species are provided and copiously illustrated.

Material and methods

Specimens of *Argemone mexicana*, *A. ochroleuca* and their putative hybrid were collected from La Palma, Canary Islands (Spain) in 2014. Voucher specimens of all taxa are deposited in the herbarium of the Botanic Garden of Meise,
Belgium (BR) as well as in the private herbarium of the first author. The presence of “minigrains” (i.e., pollen grains of less than half the length of normal pollen grains; see Chaturvedi et al. 1999) in the pollen mass was assessed using light microscopy without any staining.


Results and discussion

*Argemone × hybrida* R.Otto & Verloove, *hybr. nov.* (Figs. 1–5)

(*A. mexicana* L. × *A. ochroleuca* Sweet)

Diagnosis:—Intermediate in morphology between *Argemone mexicana* and *A. ochroleuca*, but usually more vigorous. It differs from both parents by the slightly larger petals, 35–45 × (25–)30–35(–40) mm which are paler than in the former but darker than in the latter (lemon to light yellow); the larger flower buds, 13–19(–22) × 8–12 mm; the smaller capsules, 15–23 × 7–10 mm; and its complete sterility. The pollen mass of the hybrids contains “minigrains” (13–19 μm) unlike the pollen of both parents.

Type:—SPAIN. Canary Islands: La Palma, Sta. Cruz de La Palma, Barranco de las Nieves parallel to Avenida de las Nieves, dry gravelly exposed riverbed, in open ruderal vegetation, several specimens among *A. mexicana* and *A. ochroleuca*, 41 m, 28.68926º N, 17.765060º W, 4 August 2014, *R. Otto* 21182 (holotype: BR!; isotype: priv. herb. *R. Otto*!).

Description:—Plants annual (?) or more often short-lived perennial, with latex bright yellow; flowering abundantly all year round. Stems glaucous, leafy, sparingly prickly, moderately to richly branched from base and distally, 50–100 cm tall, lower branches often very long and spreading, vigorous specimens well over 100 cm wide and tall, squarrose with decumbent basal branches and basal stem diameter up to 20 mm or more, older plants produce new branches basally. Leaf blades bluish-green, conspicuously white-blush mottled over veins, adaxially nearly unarmed, abaxially sparsely prickly on the veins, pinnately divided to more than halfway, lobes broadly dentate, the tooth ending in strong spines, the middle and upper leaves usually clearly clasping the stem. Inflorescences: buds oblong, ca.1.5 times longer than wide, 13–19(–22) × 8–12 mm; sepals 3, ovovate, 3–7 prickles per sepal, horns terete, unarmed, up to 14 mm long (including...
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apical spine); flowers (6–)7–8(--9) cm wide, subtended by (1–)2(–3) foliaceous bracts; petals 6, lemon to light yellow, obovate, up to 3.5–4.5 cm long and (2.5–)3–3.5(–4) cm wide; stamens 40–70, filaments yellow, up to 11 mm long; anthers bright yellow, oblong, open, 1.5–2.5 mm long, curved after flowering; pollen contains ca. 7% of “minigrains”, 13–19 μm in diameter; pistil 4–6-carpellate; ovary ovate, 9–11× 5–6 mm, covered with adpressed and pointed stramineous spines with darker base, to 6 mm long; stigma purple-red to purple-brownish, 3–5 mm wide, 1.5–2.5 mm high, dissected, lobes moderately to strongly spreading, the pale bluish non-receptive area of the stigma visible. Capsules erect, oblong, 15–23 × 7–10 mm (incl. stigma and excl. prickles), slightly grooved on sutures, dehiscing on top or indehiscent, with numerous striking stramineous prickles with expanded glaucous base, these adpressed or erect-patent, variable in size, longest prickles 5–10 mm long, style and stigma persistent, only aborted seeds present.

Argemone × hybrida is intermediate between its parents in nearly all vegetative and floral characters. The most important diagnostic features among Argemone mexicana, A. ochroleuca and A. × hybrida are summarized in Table 1 and illustrated in Fig. 4.

TABLE 1. Diagnostic features among Argemone mexicana, A. ochroleuca and A. × hybrida. Data for A. mexicana and A. ochroleuca based on own observations as well as modified from Karnavat & Malik (2010), Ownbey (1958), Ownbey (1997) and Sudhakar et al. (2008); chromosome numbers and pollen size based on Chaturvedi et al. (1999); data for A. × hybrida based on own observations and Karnavat & Malik (2010). Features that are variable in both parent species (e.g. leaf shape and degree of spinyness of leaves, stems, branches and sepals, and number of stamens) are difficult to quantify and/or overlapping and therefore not taken into account.

<table>
<thead>
<tr>
<th>Feature</th>
<th>A. mexicana (2n = 28)</th>
<th>A. × hybrida (2n = 42)</th>
<th>A. ochroleuca (2n = 56)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stigma</strong></td>
<td>1.5–4 mm wide, 1–2 mm high, shallowly dissected, the lobes pressed against each other and tightly appressed to the style, non-receptive areas between the lobes are usually completely hidden by the receptive surfaces</td>
<td>3–5 mm wide, 1.5–2.5 mm high, somewhat intermediate in shape, but mostly more similar to A. ochroleuca with lobes moderately to strongly spreading, the non-receptive pale bluish area between them visible</td>
<td>2–4 mm wide, 1–1.5 mm high, deeply dissected, the lobes narrow, widely spreading, the non-receptive area between them ± bluish and clearly visible</td>
</tr>
<tr>
<td><strong>Style</strong></td>
<td>0–1 mm in fruit</td>
<td>0.5–1.5 mm in fruit</td>
<td>1–3 mm in fruit</td>
</tr>
<tr>
<td><strong>Petals</strong></td>
<td>6, bright yellow, obovate, flower diameter (4–)5–6(7) cm</td>
<td>6, lemon to light yellow, obovate, flower diameter (6–)7–8(--9) cm</td>
<td>somewhat variable in all features, i.e. 6–7 (rarely to 9), lemon yellow to whitish, pale yellowish on fading, oblanceolate-obovate to narrowly elliptical, flower diameter 3–6–(–7) cm</td>
</tr>
<tr>
<td><strong>Flower buds</strong></td>
<td>body slightly longer than wide (subglobose), 10–16(–18) × 9–15 mm, sepal horns 5–10 mm including apical spine</td>
<td>body significantly larger than the bodies of both parental species, c. 1.5 times longer than wide (oblong), 13–19(–22) × 8–12 mm, sepal horns up to 14 mm including apical spine</td>
<td>body c. 1.5–2 times longer than wide (oblong), 8–12(–18) × 4–8(–11) mm, sepal horns 5–12 mm including apical spine</td>
</tr>
<tr>
<td><strong>Capsules</strong></td>
<td>oblong to broadly ellipsoid, 25–45 × 12–20 mm (incl. stigma and excl. prickles), prickles somewhat variable in size, the longest up to 6–10 mm or unarmed in F. leiocarpa (Greene) Ownbey (1958: 37), erect to laterally protruding, straight or slightly outwardly curved, dry capsules turning light-brown</td>
<td>± oblong, 15–23 × 7–10 mm (incl. stigma and excl. prickles), prickles not bent, ± adpressed or erect-patent, variable in size, the longest 5–10 mm, dry capsules intermediate brown or glaucous, prickles crowded next to each other because of the small capsule size, prickles therefore striking</td>
<td>ovoid-ellipsoid, 20–50 × 10–18 mm (incl. stigma and excl. prickles), prickles somewhat variable in size, longest up to 8–12 mm, erect to strongly laterally protruding, straight or sometimes strongly curved, capsules turning light-brown and remaining often slightly tinged with bluish-white and with a more clear blue-white strip between the ribs</td>
</tr>
</tbody>
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TABLE 1. (Continued)

<table>
<thead>
<tr>
<th></th>
<th>A. mexicana (2n = 28)</th>
<th>A. × hybrida (2n = 42)</th>
<th>A. ochroleuca (2n = 56)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leaf color</strong></td>
<td>green to slightly bluish green, somewhat mottled whitish-blue over veins</td>
<td>intermediate, the glaucous color and the mottled appearance sometimes reduced with age (especially in lower parts of plants)</td>
<td>conspicuously glaucous, mottled white bluish over veins, distinct variegated appearance</td>
</tr>
<tr>
<td><strong>Stem</strong></td>
<td>2.5–8(–10) dm tall, typically branching from near the base</td>
<td>5–10 dm tall, typically abundantly branching from base and also distally; lower branches often long and spreading; vigorous specimens to well over 100 × 100 cm and with stem base 20 mm across or more</td>
<td>3–10 dm tall, mostly growing upright, typically branching distally</td>
</tr>
<tr>
<td><strong>Life form</strong></td>
<td>annual</td>
<td>annual (?) or short lived perennial</td>
<td>annual or short lived perennial</td>
</tr>
<tr>
<td><strong>Seeds</strong></td>
<td>1.6–2 mm, globular</td>
<td>only aborted seeds present</td>
<td>1.5–2 mm, globular</td>
</tr>
<tr>
<td><strong>Pollen size (P×E) and range</strong></td>
<td>24 × 27 μm (23–27 × 24–28 μm); “minigrains” absent</td>
<td>wide variation in pollen size: 27–43 × 29–38 μm; “minigrains” present, 13–19 μm</td>
<td>39 × 33 μm (34–40 × 29–35 μm), “minigrains” absent</td>
</tr>
</tbody>
</table>

The presence of “minigrains” is (beside other pollen anomalies) a particularly characteristic feature of the hybrid, since these are always absent in A. mexicana and A. ochroleuca (see Chaturvedi et al. 1999). These “minigrains” have the appearance of normally developed pollen grains, but they are less than half the length of the normal grains. According to our own counts “minigrains” represent ca. 7% of the pollen mass.

**Distribution:**—Potentially naturally occurring in parts of Mexico where both parents grow sympatrically (e.g. in the states Guerrero, San Luis Potosi, Tamaulipas and Vera Cruz; Ownbey 1958). Since both species have widely been introduced in temperate and (sub-) tropical areas worldwide, their hybrid potentially is relatively widespread but overlooked. However, natural hybrids seem to have been rarely reported and are even absent from the native area. To our knowledge they have only been reported so far from the Indian subcontinent (e.g. Malhotra 1960, Chaturvedi et al. 1999) and Mozambique (Viveiros & Pereira 1970).

In the Canary Islands both Argemone mexicana and A. ochroleuca are considered invasive species (Acebes Gínovés et al. 2009). Both compete with and possibly displace indigenous pioneer species, thus threatening biodiversity, especially in riparian habitats (see also Van der Westhuizen & Mpedi 2011). Although occupying the same type of habitats and often growing in close proximity, natural hybrids had not yet been reported so far from Europe and Macaronesia.

**Notes:**—Argemone × hybrida was found in two locations in the municipality of Sta. Cruz de La Palma on the island of La Palma (Canary Islands, Spain). Both places are relatively near to one another (approximately one kilometer apart at flight distance) but geographically completely separated by mountain, ravine and urban areas. In 2014 several individuals were found that clearly showed an intermediate morphology, compared with both putative parents that were found in the same localities. The most striking features of these hybrids were the intermediate petal color (light yellow) and the smaller, empty capsules (complete sterility). In addition, these plants were often noticeable bigger than either parent, more richly and profusely branched and more abundantly flowering (doubtlessly as a result of hybrid vigor).
FIGURE 2. *Argemone × hybrida* (holotype), Sta. Cruz de La Palma, part of flowering and fruiting shoot (big picture), two buds and young fruit (small picture), priv. herb. RO 21182, August 2014 (Photograph: R. Otto).
In the first locality, about 45 individuals were found along a stretch of ca. 1.2 km in the exposed river bed of the Barranco de las Nieves, just before the river mouth. The riverbed is dry for most of the year. Water runs through the barranco very irregularly after heavy precipitation but then sometimes very strongly so. The stretch that runs through the town is mostly bordered by concrete sidewalls with access ramps in its lower part. The substrate in the barranco is sandy and gravelly. Parts of the area are sometimes transformed into a large unsurfaced parking place, after removal of all aboveground vegetation, scree and scrap, levelling the terrain. Thus, the area is frequently disturbed, permanently creating an open, sun-exposed area suitable for the establishment of thermophilous vegetation. The Argemone taxa are associated with native species like Bosea yervamora L., Hyparrhenia sinaica (Delile) Llauradó ex G.López, Kleinia neriifolia Haw., Lavandula canariensis Mill., Rumex lunaria L., etc. Many of the other accompanying species are of Mediterranean origin and/or cosmopolitan or pantropical weeds such as Ageratina adenophora (Spreng.), Ageratum conyzoides L., Atriplex hortensis L., Bidens pilosa L., Chenopodium album L., Chenopodium murale L., Datura stramonium L., Glaucescentia flavum Crantz, Erigeron bonariensis L., Erigeron sumatrensis Retz., Hirschfeldia incana (L.) Lagr.-Foss., Solanum nigrum L. subsp. nigrum, etc. The locality is also invaded by exotic species, mainly escapes from cultivation, e.g. Abutilon grandifolium (Willd.) Sw., Datura innoxia Mill., Dysphania anthemum (L.) Mosyakin & Clemants, Leonotis nepetifolia (L.) R.Br., Lycopersicon esculentum Mill., Malvastrum coromandelianum (L.) Garcke subsp. coromandelianum, Nicotiana glauca Graham, Pennisetum setaceum (Forssk.) Chiov., Ricinus communis L., Sida rhombifolia L. var. canariensis (Willd.) Griseb., Tagetes minuta L. and Waltheria indica L. Erodium neudatifolium Delile ex Godr. is an accompanying species of Saharan-Arabian distribution.

In the second location three hybrid individuals were detected among the parent species. They were found on a narrow, disturbed urban slope between Carretera del Galión and Calle Teneguía, on bare ground (maybe a former lawn) and sun-exposed. Common companion plants were, among others, Amaranthus hybridus L. s.str., Amaranthus viridis L., Avena barbata Pott ex Link, Bidens pilosa L., Chenopodium album L., Chenopodium murale L., Datura stramonium L., Glaucescentia flavum Crantz, Erigeron bonariensis L., Erigeron sumatrensis Retz., Hirschfeldia incana (L.) Lagr.-Foss., Solanum nigrum L. subsp. nigrum, etc. The locality is also invaded by exotic species, mainly escapes from cultivation, e.g. Abutilon grandifolium (Willd.) Sw., Datura innoxia Mill., Dysphania anthemum (L.) Mosyakin & Clemants, Leonotis nepetifolia (L.) R.Br., Lycopersicon esculentum Mill., Malvastrum coromandelianum (L.) Garcke subsp. coromandelianum, Nicotiana glauca Graham, Pennisetum setaceum (Forssk.) Chiov., Ricinus communis L., Sida rhombifolia L. var. canariensis (Willd.) Griseb., Tagetes minuta L. and Waltheria indica L. Erodium neudatifolium Delile ex Godr. is an accompanying species of Saharan-Arabian distribution.

FIGURE 4. Important differentiating features between *Argemone mexicana* (left), *A. × hybrida* (middle) and *A. ochroleuca* (right), Sta. Cruz de La Palma, August 2014 (Photograph: R. Otto).
FIGURE 5. *Argemone × hybrida*, Sta. Cruz de La Palma, three vigorous individuals: overall view of a single plant (above), stem base (left) and newly sprouting stem base with dead basal branches (right), August 2014 (Photograph: R. Otto).
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