

Movement-assisted dichogamy in *Atamisquea emarginata* (Capparaceae)

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Abstract. Various aspects of the reproductive biology of *Atamisquea emarginata* Miers ex Hook. et Arn. were studied in a population from Tucumán, northern Argentina. Flowering took place in late (austral) spring to early summer. The creamy white, entomophilous flowers were protandrous and lasted 3.5–4.5 days. A pleasant odor along with nectar and pollen attracted 36 mostly diurnal insect species of which 41.7% were Hymenoptera, 38.9% Lepidoptera and 19.4% Diptera. However, 75% from all recorded species were infrequent, and domestic bees made ca. 94% of all visits. One halictid bee, one sphecid wasp, one myzinid wasp, four small- to medium-sized butterflies and a hawkmoth completed the set of relatively frequent insect visitors. Pollen and stigma were presented in the same place within the flower, but interference was prevented by a movement-assisted, complete dichogamy mechanism in which the bending ability of the gynophore played a fundamental role. This form of dichogamy was previously unknown in the Capparaceae. In comparison with the known species of the closely allied genus *Capparis* L., *A. emarginata* has diurnal, smaller, longer-lasting flowers, that offer much smaller nectar amounts, and that attract a rather generalized array of non-hovering visitors, while *Capparis* behaves as a more crepuscular-biased sphingophile or ornithophile or chiropterophile. Low levels of seed set under bagging indicates dependence on insect visits and are partly congruent with an earlier report of self-incompatibility in *A. emarginata*. Pollen tubes arrived to ovules in 90.6% of the inspected flowers.

Fruit set of open-pollinated flowers was 43.6%–53.7%. Ninety-five percent of all ovules were regularly aborted in each fruiting ovary; thus, each fruit contained 1.2 developed seeds. Full-sized individuals were expected to produce ca. 10,700 potential offspring per year.

Key words: Movement-assisted dichogamy, *Atamisquea emarginata*, pollination, protandry, Capparaceae

Dichogamy, the temporal separation of male and female function in plants, is currently viewed as the evolutionary result of selection for avoidance of pollen-pistil interference, for avoidance of self-fertilization, and for synchrony of pollen discharge and stigma receptivity in the different flower types of diclinous species (Bertin and Newman 1993). In animal-pollinated plants there is an additional, conflicting selection for presentation of pollen and receptive surfaces at approximately the same position within a blossom, to promote precise between-flower transference of pollen (Lloyd and Webb 1986). This conflict might be solved by removal (either by abscission, movement or shriveling) of the sexual parts that are presented first. Removal of first-functioning sporophylls by some of these means has been recorded in ca. 5.6% of a comparative large sample of angiosperms with hermaphroditic

flowers (Bertin and Newman 1993), but apparently in only few of these cases movement-assisted dichogamy is associated with pollen dispatch and receipt at the same site. Our first objective was to contribute to the understanding of this poorly known dichogamy type, that presently includes a few, taxonomically unrelated taxa (Aizen and Basilio 1995, Lloyd and Webb 1986), by analyzing the floral mechanism of *Atamisquea emarginata* Miers ex Hook. et Arn.

The knowledge of the reproductive biology of *A. emarginata* is still fragmentary. Vogel (1968) indicated that, unlike co-occurring *Capparis* species (which are night-flowering and sphingophilous), *A. emarginata* behaves in Bolivia as a daytime flowering, melittophilous species. More recently Aizen and Feinsinger (1994a) found protandry and self-incompatibility in populations of *A. emarginata* of Tucumán Province, Argentina, and reported bees (largely *Apis mellifera*), wasps and moths as flower visitors. According to Aizen and Feinsinger (1994a), populations included in small forest fragments experienced diminished pollination quality and showed lower levels of fruit set in comparison to large fragments, which, among other factors, might be a consequence of fragmentation-related changes in the nature of the visiting assemblage. Our second objective was to address neglected or insufficiently known aspects of the reproductive biology of *A. emarginata*, including morphology of inflorescences, composition of the pollinator guild, breeding system, and maternal success.

Material and methods

Study site and plant material. *Atamisquea emarginata* is a 2–4 m high shrub growing in southern North America, north-central Argentina and adjacent parts of Bolivia and Chile (Gómez 1953, Wiggins 1980, Zuloaga and Morrone 1999). Over a century ago, Kuntze (1898) decided to subsume the monotypic genus *Atamisquea* Miers into *Capparis* L., giving rise to the binomial *Capparis atamisquea* O. Kuntze. Some authors followed

Kuntze's (1898) treatment (Hunziker 1984, and subsequent floristic works in Argentina) while others did not (Pax and Hoffmann 1936, Gómez 1953, Legname 1972, Wiggins 1980, Mabberley 1998). Some taxonomists currently working on Capparaceae at a global scale recognize *Atamisquea* as a distinct genus (H. Iltis and L. Kers, pers. comm. to D.M.), a view that we followed in this paper.

Field studies were carried out in November 1995/January 1996 near the El Cadillal reservoir in the vicinity of Ticucho, Tucumán Province, Argentina (26°9' S, 65°13' W), an area covered by dry thorn forest characteristic of the Chaco Serrano biogeographic region (Cabrera and Willink 1973, Cabrera 1976; for further information on the study area see Aizen and Feinsinger 1994a, 1994b). The site was included in continuous, nonfragmented forest. Within a population of ca. 50 reproductive individuals we established a 110 m long transect, in which mean distance to the nearest conspecific was 4.2 m (n = 24). Besides the 1–3 m high flowering individuals many smaller, nonreproductive plants of different sizes were observed. Ten individuals from the transect were selected for intensive study. Vouchers are kept at BAA (ARGENTINA. Tucumán: Ticucho, 27 Nov. 1995, D. Medan and G. Ponessa 771 and 772).

Reproductive phenology and pollination biology. We recorded the position of over 1300 flowers on representative branches of 12 individuals. Counts were made of flower number per reproductive short-shoot (n > 650), number of short-shoots per second-order branch (hereafter: branchlet) (n > 540), and number of branchlets per first-order shoot (hereafter: long branch). Intrafloral phenology was studied in sets of 5 individually-labeled flowers from five individuals. Morphological changes were recorded daily or twice a day for each set of flowers; moreover, additional flower buds and open flowers of different ages were dissected under a stereomicroscope to observe production of nectar and stigmatic status. Number of active flowers (i.e. those presenting pollen or stigmas) was recorded for 17 branches from several individuals. Stigmatic receptivity was assayed by applying a tiny drop of 40% H₂O₂ on stigmas (Zietsman and Botha 1992). Nectar was extracted with handmade capillaries. Ovule number was determined by dissecting 10 gynoecia under a stereomicroscope. Insect behavior was observed

under different weather conditions and at different times of the day and night (total time ca. 8 h). Representative individuals of most observed species were caught with nets when visiting plants on the transect and prepared for later identification. Additionally, six yellow traps 10–25 cm in diameter filled with water and a little detergent added were scattered along the transect and regularly monitored for fallen insects. Visitors were scored as very common, frequent, or scarce on the basis of six ten-minute censuses, extra-census field observations, and the number of caught specimens.

Breeding system and maternal success. To determine whether pollen transport by insects is necessary for fruit initiation, insects were excluded by enclosing branches with unopened buds with bridal veil. To separate insect from wind effects on pollination, additional branches were enclosed with cloth bags. Fruit set was also determined for unmanipulated flowering branches of known flower number. When selecting flowering branches care was taken that control and treatment branches were of similar size within a given individual. The exclusion treatments and controls involved 10 individuals. Both control and manipulated flowers were monitored until abscission or fruit initiation. To assess pollination quality under open-pollination conditions, 7–16 mature flowers from each of the 10 individuals were fixed in FAA (formaldehyde-glacial acetic acid-70% ethanol 1:1:9), gynoecia were dissected and soaked 36–48 h in 5% NaOH (weight:volume) at 40°C, gently brushed to remove the strongly autofluorescent peltate indument, mounted in 0.1% decolorized aniline blue, and viewed with a fluorescence microscope to assess pollen-tube growth. Estimates of flower number per plant were obtained by multiplying flower

number per long branch (see above) by number of long branches per plant ($n=3$ individuals). Number of mature fruits per long branch, and number of seeds per fruit, was determined in samples gathered from 20 individuals.

Results

Inflorescence, flower, and fruit morphology.

Flowers are borne on 1–5-flowered short-shoots (mean nr. flowers/short-shoot = 1.8), which are located in the axils of foliage leaves on 2–20 cm long, straight branchlets (besides these fertile short-shoots, nonfertile ones are found at some or all nodes of the branchlets). Thirty to sixty branchlets of decreasing length are borne on each 50–70 cm long branch (Figs. 1 and 2A). A small number of short-shoots are also directly located at the distal part of each long branch. Flowers are only present on long branches making up the peripheral area of the shrub crown. The mean flower number per long branch was 109 ± 57.1 s.d. ($n=12$), but only part of these flowers did release and receive pollen at a time (27.9 ± 20.2 , $n=17$ branches). The mean number of long branches per plant was 152.6 ($n=3$), therefore the total flower number per individual produced throughout the flowering period was 16,700.

Flowers are perfect, zygomorphic, when fully expanded, 12–15 mm in diameter and 10–12 mm long, on 5–7 mm long pedicels (Figs. 2 and 3). The 4-merous perianth consists of 2 median, concave sepals, 2 much

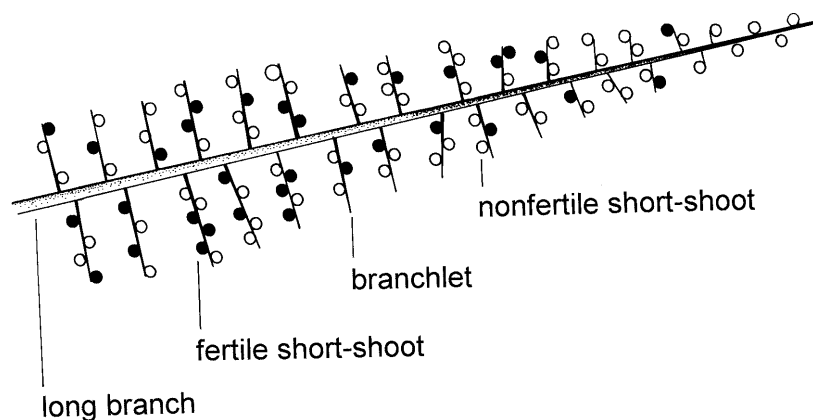


Fig. 1. Schematized long branch of *Atamisquea emarginata* showing the location of fertile and nonfertile short-shoots. Leaves not represented. Not to scale

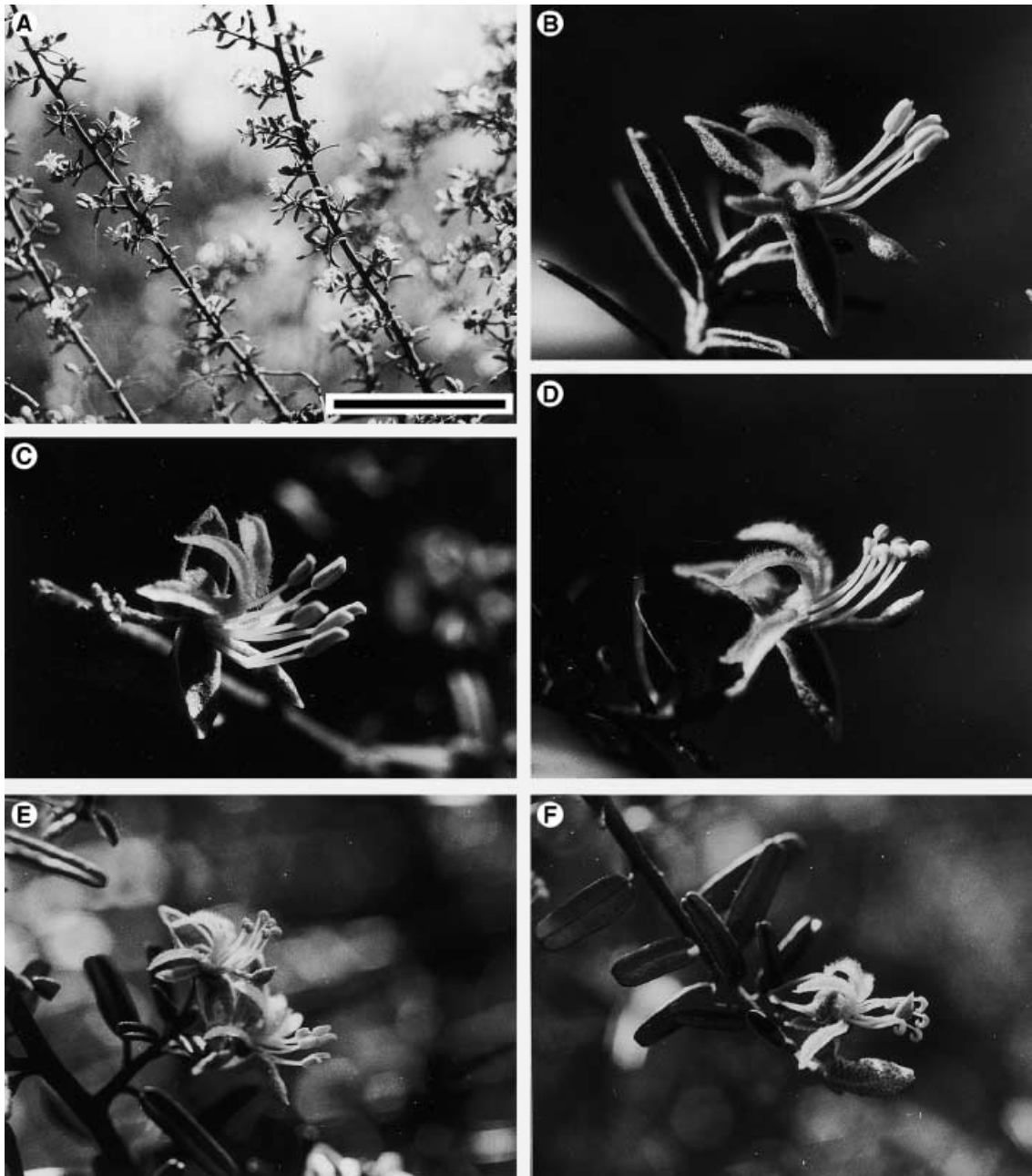


Fig. 2. *Atamisquea emarginata*. **A**, Partial view of peripheral crown showing long branches and branchlets, some of these with open flowers. **B–F** Flowers in different developmental stages (cf. Fig. 3). **B**, Early male-phase flower, note stamens still in a central bundle. **C**, Late male-phase flower. **D**, Early female-phase flower, note the curled anthers. **E**, Two flowers on the same branchlet, the upper one at early female- and the lower one at late male-phase. **F**, Late female-phase flower, note pistil emerging among the wilting stamens. Scale at **A** = 7 cm (valid also for **C–D**, = 8 mm, and for **E–F**, = 13 mm)

smaller lateral sepals, and 4 linear, reflexed, white-creamy petals. Six 10 mm long stamens alternate with 3 shorter, dorsal staminodes.

On top of the 6 mm long gynophore is the 2-carpellate gynoecium, with 23 ± 1.4 ovules on 2 parietal placentae and a sessile, punctiform

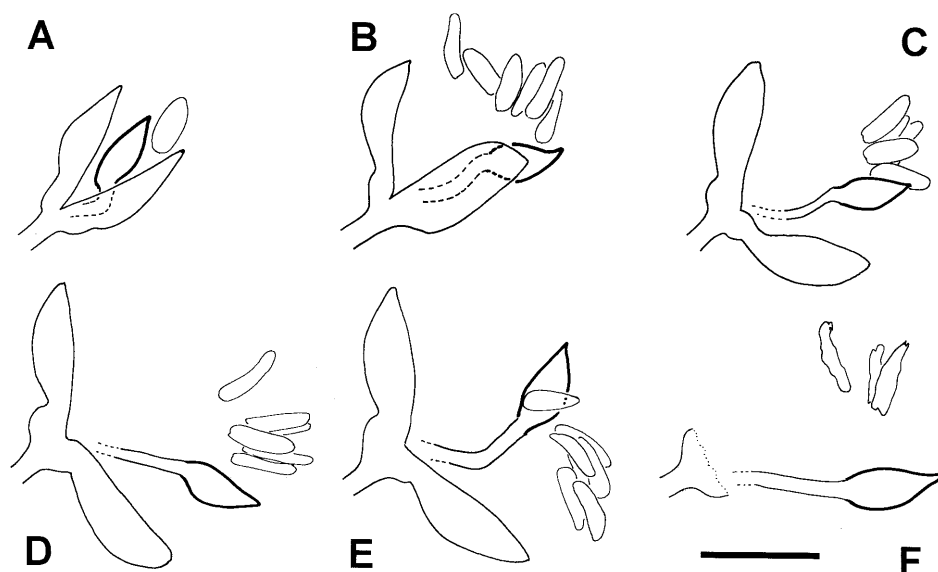


Fig. 3. Schematised median longisections of flowers of *Atamisquea emarginata* in different developmental stages (cf. Fig. 2). For the sake of clarity, only the median sepals, anthers, and the gynoeceum are shown. **A–C**, Early male-phase flowers. **D**, Late male-phase flower. **E**, Late female-phase flower. **F**, Postanthetic flower. Scale = 5 mm

stigma. The fruit is a 1–2-seeded, 5–8 mm long, ovoid berry.

Phenology and pollination biology. Flowering in the population under study extended from the second week of November to the third week of January, with a diffuse peak in December. Fruits were ripe by mid January.

The flowers open during the morning. Unfolding of sepals, petals and stamens takes about 6 h (Fig. 3A). The ensuing 1–1.5-day long male phase begins with anther opening, while the stamens (at first concentrated in a bundle, Figs. 2B, 3B, and 3C) spread away from the center of the flower and the petals become increasingly reflexed. At the same time, the gynophore tilts down and becomes straight, so removing the ovary from the anthers' position (Figs. 2C, 2E, and 3D). Minute amounts of nectar are already present at the base of the gynophore, being accessible at the junction of the dorsal and median petals at both sides of the flower (estimated standing crop = 0.1 $\mu\text{l}/\text{flower}$). A pleasant scent is perceptible at a distance of 2–3 m, and stigma receptivity tests give negative results. Visitors landing or hovering at the

flowers easily contact the pollen presented on the anthers, while the ovary tip remains out of the visitors' approach route. By the end of the male phase, most pollen has been removed. The usually 1-day long *female phase* starts with the shrivelling of the already empty anthers, which become C-shaped while the filaments wilt. Insect visits, nectar secretion and scent emission continue. The gynophore bends upwards, thus placing the ovary where the anthers stood before (Figs. 2D to 2F, and 3E). The stigma, which now (weakly) reacts with H_2O_2 , can be contacted by approaching visitors. By day 3.5–4.5 (or sooner if the weather is hot and dry) all perianth parts and stamens start to drop, nectar and scent disappear and the gynophore tilts down again (Fig. 3F), while the ovary (if ovules are fertilized) starts to enlarge.

A total of 36 insect species from 20 families were observed working flowers of *A. emarginata*, of which 41.7% were Hymenoptera, 38.9% Lepidoptera and 19.4% Diptera. Seventy-five percent of all recorded species were infrequent (Table 1). The domestic bee was by far the most frequent visitor, making up 168

from the 179 visits recorded through six 10-minute censuses. The predominance of domestic bees as visitors is also apparent from their high visitation rate (0.16 visits flower⁻¹ minute⁻¹), which means that bees alone could visit all active flowers in a typical long branch every 2.9 hours). One halictid bee, one sphecid wasp, one myzinid wasp, four small- to medium-sized butterflies and a hawkmoth completed the set of relatively frequent insect visitors.

These species fed on nectar or had a mixed nectar/pollen feeding habit, they did not discriminate between male- and female-phase flowers, and displayed a moderate to marked mobility, thus effecting geitonogamous and cross-pollinations. Because of their visitation frequency these 9 insect species are proposed here as putative pollinators (Table 1).

In addition to the observed flower visitors, twelve hymenopterans were recovered from

Table 1. Flower visitors to *Atamisquea emarginata*. + + + = very common, + + = frequent, + = scarce. Putative pollinators in **boldface**

Visitor species	Family	Order	Frequency
Apis mellifera	Apidae	Hymenoptera	+ + +
<i>Coelioxoides waltheriae</i>	Apidae	Hymenoptera	+
2 unidentified bumblebees	Apidae	Hymenoptera	+
1 unidentified anthophorid bee	Anthophoridae	Hymenoptera	+
Caenohalictus sp.	Halictidae	Hymenoptera	+ +
<i>Augochloropsis sp.</i>	Halictidae	Hymenoptera	+
<i>Epanthidium sp.</i>	Megachilidae	Hymenoptera	+
2 unidentified megachilid bees	Megachilidae	Hymenoptera	+
1 unidentified myzinid wasp	Myzinidae	Hymenoptera	+ +
<i>Notocyphus sp.</i>	Pompilidae	Hymenoptera	+
<i>Tachypompilus erubescens</i>	Pompilidae	Hymenoptera	+
Ammophila sp.	Sphecidae	Hymenoptera	+ +
<i>Prionyx striatum</i>	Sphecidae	Hymenoptera	+
<i>Monca cf. ornata</i>	Hesperiidae	Lepidoptera	+
<i>Hylephila phyleus</i>	Hesperiidae	Lepidoptera	+
<i>Pyrgus orcus</i>	Hesperiidae	Lepidoptera	+
1 unident. hesperiid butterfly	Hesperiidae	Lepidoptera	+
Strymon eurytulus	Lycaenidae	Lepidoptera	+ +
1 unident. lycaenid butterfly	Lycaenidae	Lepidoptera	+
<i>Heteropygas dogmini</i>	Noctuidae	Lepidoptera	+
1 unidentified noctuid moth	Noctuidae	Lepidoptera	+
Vanessa sp.	Nymphalidae	Lepidoptera	+ +
1 unidentified pyralid moth	Pyalidae	Lepidoptera	+
Adelotypa tinea	Riodinidae	Lepidoptera	+ +
Audre guttata	Riodinidae	Lepidoptera	+ +
<i>Euptychia cf. phares</i>	Satyridae	Lepidoptera	+
1 unidentified sphingid moth	Sphingidae	Lepidoptera	+ +
1 unidentified bombyliid fly	Bombyliidae	Diptera	+
1 unidentified empidid fly	Empididae	Diptera	+
1 unidentified muscid fly	Muscidae	Diptera	+
<i>Allograpta exotica</i>	Syrphidae	Diptera	+
<i>Allograpta obliqua</i>	Syrphidae	Diptera	+
1 unidentified syrphid fly	Syrphidae	Diptera	+
1 unidentified tachinid fly	Tachinidae	Diptera	+
Total	20	3	

water traps placed next to flowering individuals of *Atamisquea emarginata* [six wasp species: *Ancistrocerum* sp. (Eumenidae); *Anoplius* sp. (Pompilidae); *Liris* sp., *Sphex* sp., and *Bembecinus* sp. (Sphecidae); and *Polistes* sp. (Vespidae) and six bee species: [*Arhysosage flava*, *A. cf. ochracea*, and *Acamptopoeum* sp. (Andrenidae); *Diadasia* sp. (Apidae); and *Augochlorrella* sp. and *Leioproctus* sp. (Halictidae)]. These insects were occasionally seen flying among flowers of the focal species and may be infrequent visitors.

Breeding system and maternal success.

Mean fruit set in open-pollinated flowers (controls of the bagging experiment) was 43.6% (Table 2). Pollen-tubes arrived at ovules in 90.6% of the inspected flowers ($n = 128$ flowers from 10 individuals). Number of pollen tubes entering the ovary were not systematically recorded, but values of 10–15 tubes per ovary were common, and penetration of ovules by pollen tubes was often viewed.

Both bagging treatments significantly lowered fruit set (Table 2), which suggests that insect visits are very important for fruit initiation. However, some fruits were set under bagging, indicating that apomixis and/or automatic self-fertilization and/or wind transport of pollen may occur.

On average, a fruit of *A. emarginata* contained 1.2 ± 0.2 well-developed seeds ($n = 200$ fruits). On long branches exposed to natural pollination 58.6 ± 54.5 fruits/branch were set ($n = 20$ individuals). By relating this figure to the average number of flowers per

long branch (109 flowers/branch, see above) a fruit/flower ratio of 0.537 is obtained. To have a measure of fecundity, a seed-per-flower rate was calculated as flower/fruit ratio times mean seed set ($0.537 \text{ fruits/flower} \times 1.2 \text{ seeds/fruit} = 0.64 \text{ seeds/flower}$). A full-size *A. emarginata* individual produced an estimated 1.67×10^4 flowers; according to the calculated seed/flower rate, such a plant would produce ca. 10,700 potential offspring per year.

Discussion

Inflorescence morphology. This study seems to be the first morphological analysis of the shoot system of *Atamisquea*. The presence of distinct long branches, branchlets, and short-shoots has not been recognized before. Jacobs (1965) analyzed the inflorescence morphology of many Asian species of *Capparis* and addressed shoot morphology to some extent; he found heteroblasty in a number of taxa, as well as instances of reduction of axillary, flower-bearing shoots, but a pattern like that of *A. emarginata* was neither described nor illustrated. The presence of long-shoots as well as shorter, flower-bearing shoots was also recorded in *Capparis* by Troll (1969). The joint consideration of these data and of our results suggests that the occurrence of at least two types of shoots in the inflorescence area may be an architectural trait shared by *Capparis* and *Atamisquea*. The flowers have usually been described as axillary in *A. emarginata* (e.g. in floristic works like those by Legname 1972, Wiggins 1980). This is apparently the first time that the presence of one to several axillary flowers is explicitly related to the existence of short-shoots in the axils of foliage leaves in this species.

Movement-assisted dichogamy. Our results confirm the report on protandry in *A. emarginata* by Aizen and Feinsinger (1994a). A male phase precedes the somewhat shorter, apparently non-overlapping female phase. Since dichogamy is asynchronous (flowers in different functional stages coexist in the same long branch, and even in the same branchlet),

Table 2. Fruit set in manipulated and open-pollinated individuals of *Atamisquea emarginata*. Means with different superscript differ at $p < 0.001$ (Tukey t-test)

Treatment	Mean fruit set % (range)	Sample size (no. individuals/no. flowers)
Control	43.6 ^b (16.1–80.7)	9/407
Bagging (mesh)	3.8 ^a (0.0–9.1)	10/500
Bagging (cloth)	3.2 ^a (0.0–13.6)	10/503

interfloral interference is not avoided, and some degree of geitonogamous pollination must take place.

Dichogamy in *A. emarginata* is one of a two-part set of floral features enabling the presentation of pollen and stigma in exactly the same place of the flower. The second component lies in the gynophore's bending ability, by which the pistil is kept out of the approach way of flower visitors until the stigma becomes receptive. When this happens the ovary moves to the location where pollen has been presented. Proper stigma positioning seems also important because its tiny receptive surface will only collect few pollen grains. This fact underscores the risk of pollen-stigma interference: such a small stigma can also easily be saturated by "wrong" pollen.

Examples of this movement-assisted type of sequential, one-site presentation are known in *Alstroemeria* L. (Aizen and Basilio 1995), *Epilobium* L., and *Eryngium* L. (Lloyd and Webb 1986). This mechanism is also known from a number of species in Lamiales (Endress 1994: 349–350) but to our knowledge it has not previously been recorded in the Capparaceae. The usual presence of a gynophore in this family suggests that movements of floral parts may have a role in floral functioning of other genera. In fact, experiments by Hildebrand (1886) showed that stamen movements are possible in species of *Cleome* L. (Capparaceae), and that in this genus the gynophore may take different positions in different flowers. In the case of *Cleome* it is unclear whether Hildebrand (1886) faced an instance of floral dimorphism, or -rather- observed different phenological stages all flowers go through, without realizing that these stages made up a sequence.

Pollination syndrome and flower visitation. The flowers of *A. emarginata* seem to be moderately specialized entomophiles, offering easily accessible pollen and small amounts of nectar as rewards to visitors, and scent and color as advertisements. The dissected pattern of the corolla and androecium may contribute to the visual orientation of nectar-searching insects.

Nectarivorous visitors would at first sight be responsible for most successful pollen transfer, because nectar is secreted in both male- and female-phase flowers. Conversely, exclusive pollen-feeders are not expected to be important pollinators since pollen is no longer available in female-phase flowers (pollen-feeders could, however, pay some visits to female-phase flowers while exploring for pollen).

On a species diversity basis, the visitor assemblage is dominated by Hymenoptera and Lepidoptera. From a total of 36 insect species detected during our study, only nine bees, wasps, butterflies, and moths are likely pollinators because of their frequency, mobility, and feeding habit.

On an individual-abundance basis, the visiting assemblage to *A. emarginata* flowers is overwhelmingly dominated by the domestic bee, which made up 93.8% of all visits. This figure exceeds those recorded by Aizen and Feinsinger (1994b) in a similar habitat for *Prosopis nigra* (Gris.) Hieron. (82.3% of all visits) and *Cercidium australe* Johnst. (44.4%). The intensity of visitation by domestic bees is evident also in the rate of 0.06 visits flower⁻¹ minute⁻¹, a value intermediate between those reported for *P. nigra* (0.084 visits flower⁻¹ minute⁻¹) and *C. australe* (0.011 visits flower⁻¹ minute⁻¹) by Aizen and Feinsinger (1994b).

***Atamisquea* and *Capparis*.** As mentioned above, *Atamisquea* is closely related to *Capparis*, the largest genus in the family Capparaceae (250 spp., Mabberley 1998). In *Capparis*, the flowers while mostly perfect and zygomorphic, exhibit considerable diversity in perianth, androecium and nectary structure (Pax and Hoffmann 1936, Stoudt 1941, Jacobs 1965, Weberling and Uhlarz 1983, Erbar and Leins 1997). A handful of species have been studied in terms of their reproductive biology, including *C. frondosa* Jacq., *C. flexuosa* (L.)L., *C. micracantha* DC., *C. ovata* Desf., *C. pittieri* Standley, *C. retusa* Griseb., *C. spinosa* L., *C. tweediana* Eichl., and *C. verrucosa* Jacq. (Knuth 1905, therein the older literature; Mauritzon 1934, Vogel 1968, Silberbauer-

Gottsberger and Gottsberger 1975, Ruiz and Arroyo 1978, Bawa et al. 1985, Bullock 1985, Eisikowitch et al. 1986, Dafni et al. 1987, Petanidou et al. 1996, Bianchi and Gibbs 2000). In *Capparis*, the flowers are scented and anthesis seems mainly restricted to one night (daytime flowering being exceptional, see Jacobs 1965). Hummingbirds, hawkmoths, and probably bats dominate the visitor assemblages; they may exploit the easily accessible nectar, pollen, or both. Both protandry (Knuth 1905) and protogyny (Bianchi and Gibbs 2000) have been reported.

In comparison with the investigated *Capparis* species, *A. emarginata* has smaller and longer-lasting flowers, which are mainly active during daytime, with smaller amounts of nectar per flower (in the order of 0.1 μ l), and which offer support for non-hovering visitors. A primary assessment indicates that *Atamisquea* functions as a daytime generalist (a daytime melittophile in the view of Vogel, 1968), while *Capparis* behaves more as a crepuscular-biased sphingophile or ornithophile or chiropterophile, which offers much larger amounts of nectar per flower (11–70 μ l, Eisikowitch et al. 1986, Dafni et al. 1987, Petanidou et al. 1996).

Breeding system and maternal success. Exclusion of visitors led to a significant reduction of fruit set. However, some fruits were set in our bagging experiment (13.6% in one of the individuals of the cloth bagging treatment). Due to lack of pollen removal by insects in the bagged flowers, pollen is still available when the stigma becomes receptive; therefore, automatic self-pollination would be possible when the stamens wilt and curl down, while the gynophore bends and moves the ovary upwards. Therefore, our results do not unequivocally support an earlier report of self-incompatibility in *A. emarginata* (Aizen and Feinsinger 1994a). ‘Leakiness’ in the self-incompatibility mechanism has been observed in some species of the related genus *Capparis*, with isolated individuals producing up to 25% fruits from automatic selfing (Bianchi and Gibbs 2000). More studies at the individual

level are needed to characterize the breeding system of *A. emarginata*.

Fecundity in *A. emarginata* was rather high (fruit set = 43.6% and 53.7% in two independent measurements), which is in accordance with the previous report of 30%–50% by Aizen and Feinsinger (1994a) for populations included in continuous forest. Fruit set was apparently not primarily pollen-limited, since over 90% of the flowers received pollen in amount and quality enough to develop several pollen tubes down to the ovules.

In spite of over twenty ovules being available in each ovary, the mean number of seeds per fruit was only 1.2 in our sample, and never exceeded two seeds, in agreement with descriptions found throughout the floristic and systematic literature (from which it is evident that maximal seed number per fruit is fixed at 2). This indicates that the ‘surplus’ ovules, irrespective of the number of available pollen tubes, are systematically aborted. Single-seededness from multiovulate ovaries has been reported in many genera (see Seavey and Carter 1996 for references and possible ecological function).

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