

F10-1-A-052-MA

F01-1-A-052

2002

40002,2

CLAVES TAXONÓMICAS 01

- 3' Mature fr and ovary oblong or ovate, gen not tapered to a beak, not striped green, prickles $\pm$ dense, stiff;
seeds gen > 6 , ovate or oblong, sometimes flat at 1 end; SNF, SW, D *M. horridus*
4. Corolla deeply cup-shaped; seeds very flat at 1 end; c&s SNF, Teh *M. macrocarpus*
4' Corolla shallowly cup-shaped; seeds not very flat at either end; SW, DSon var. *macrocarpus*
5. Staminate fls 8–13 mm wide; seeds 15–20 mm; mainland var. *major*
5' Staminate fls 14–30 mm wide; seeds 20–33 mm; Chl

M. fabaceus (Naudin) E. Greene (p. 543) CALIFORNIA MAN-ROOT
Herbage gen not glaucous. FL: corolla rotate, yellowish green,
cream-colored or (esp inland) white. FR 4–5 cm, $\pm$ round; prickles
sparse to dense, < 12 mm, $\pm$ stiff, unhooked. SEEDS 2–4, 18–24
mm, ovate to oblong, $\pm$ flat on sides or not. $2n=32$. Streamsides,
washes, shrubby and open areas; < 1600 m. CA-FP (exc n NW, n
CaR). Highly variable; pls outside SnFrB and CCo are assignable
to var. *agrestis* (E. Greene) K.M. Stocking (fr prickles flexible, < 5
mm; seeds gen 2–3, not flat on sides), which intergrades $\pm$ com-
pletely with the pls considered var. *f.*; more study needed. $\oplus$ DRN:
7,8–10,14–24; INV.

M. horridus (Congdon) Dunn (p. 543) Herbage not glaucous.
FL: corolla deeply cup-shaped, white. FR 9–20 cm, oblong,
rounded at both ends; prickles dense, stiff. SEEDS gen 6–16(24),
26–32 mm, oblong or ovate, very flat at 1 end. Shrubby and open
areas; < 1000 m. c&s SNF, Teh.

M. macrocarpus (E. Greene) E. Greene (p. 543) Herbage not
glaucous. FL: corolla shallowly cup-shaped, white. FR 5–12 cm,
oblong, gen rounded at both ends (sometimes with sharp beak);
prickles $\pm$ dense, stiff. SEEDS gen 4–12(24), 13–33 mm, $\pm$ round,

oblong, or ovate, angled at tip or not. $2n=32,64$. Washes, shrubby
or open areas; < 900 m, SW, DSon; Baja CA.

var. *macrocarpus* FL: staminate 8–13 mm wide. SEED 13–
20 mm. Habitats of sp. SW mainland, DSon; Baja CA.

var. *major* (Dunn) K.M. Stocking FL: staminate 14–30 mm
wide. SEED 20–33 mm. Habitats of sp. Chl. Larger, but much
like var. *macrocarpus*; more study warranted.

M. oreganus (Torrey & A. Gray) Howell (p. 543) COAST MAN-
ROOT Herbage not glaucous. FL: corolla deeply cup-shaped,
white. FR 4–8 cm, ovate, tapered to a beak, gen striped dark green;
prickles sparse to dense (gen 0 at tip), flexible. SEEDS gen 3–6,
16–22 mm, disc-shaped, $\pm$ flat. $2n=32$. Shrubby or open areas,
forest edges; < 1800 m. NW, SnFrB; to B.C.

M. watsonii (Cogn.) E. Greene (p. 543) Herbage glaucous. FL:
corolla deeply cup-shaped, white. FR 2–3.5 cm, $\pm$ round, often
striped dark green; prickles ± 0 to dense, flexible, often hooked.
SEEDS 1–4, 11–14 mm, $\pm$ round. Shrubby areas, forest edges; $<$
1200 m. NCoRI, CaRF, n SNF, ScV.

CUSCUTACEAE DODDER FAMILY

Tania Beliz

Ann, parasitic vine. ST twining, $\pm$ thread-like, yellow-green to bright orange, gen glabrous. LVS 0 or scale-like, ± 2 mm, gen
triangular to lanceolate. INFL: cyme or cluster (rarely fls solitary), gen head- or spike-like, axillary, sometimes bracted. FL
bisexual, radial; calyx gen persistent, lobes gen 4–5, gen overlapped; corolla gen deciduous, < 6 mm, mostly white, tube gen
appendaged opposite stamens, lobes 4–5; stamens 4–5, alternate corolla lobes; ovary superior, chambers 2(3), 2-ovuled,
styles gen 2, stigma gen 1 per style, gen $\pm$ head-like. FR: capsule (circumscissile or irregularly dehiscent) or berry-like. 1
genus, ± 150 spp.: esp Am trop; some crop pests. Sometimes incl in Convolvulaceae.

CUSCUTA DODDER

The only genus (Arabic: ancient name)

1. Corolla appendages 0–0.1 mm *C. californica*
2. Ovary and fr conic, top acute var. *apiculata*
2' Ovary and fr obovoid, top depressed var. *papillosa*
3. Perianth papillate
3' Perianth not papillate var. *breviflora*
4. Corolla bulged out between stamens var. *californica*
4' Corolla not bulged out between stamens
1' Corolla appendages 0.7–2.5 mm *C. approximata*
5. Stigma cylindric
5' Stigma $\pm$ head-like
6. Corolla shallowly bell- to urn-shaped, tube $\pm$ shorter than wide *C. denticulata*
7. Corolla appendage divisions gen 0–few, knob-like
7' Corolla appendage divisions few–many, finger-like *C. pentagona*
8. Ovary and fr top unthickened *C. indecora*
8' Ovary and fr top thickened var. *indecora*
9. Pedicel and calyx not papillate var. *neuropetalata*
9' Pedicel and calyx $\pm$ papillate
6. Corolla funnel- or bell-shaped, tube longer than wide *C. subinclusa*
10. Anthers sessile; corolla lobes $<$ tube
10' Anthers on filaments; corolla lobes $<$ to $>$ tube
11. Perianth parts obtuse, gland-dotted, not papillate; corolla appendage divisions few, scattered, finger-like,
near streams, rivers, lakes *C. cephalanthi*

11' Perianth parts acute, sometimes papillate and gland-dotted; corolla appendage divisions many, finger- or knob-like; salty marshes, flats, or ponds, vernal pools

12. Corolla appendages 0.7–1.2 mm, divisions finger-like; vernal pools *C. howelliana*
 12' Corolla appendages 1.2–1.5 mm, divisions knob-like; salty marshes, flats, ponds *C. salina*
 13. Perianth papillate; fl $\pm$ 3 mm var. *papillata*
 13' Perianth not papillate; fl 2–4.5 mm var. *major*
 14. Fl 3–4.5 mm; coastal salt marshes var. *salina*
 14' Fl 2–3 mm; inland salt flats

C. approximata Bab. (p. 543) INFL head-like; pedicels 0–0.5 mm. FL: calyx gen 2–2.5 mm, lobes 4, 1–1.5 mm; corolla 2–4 mm, shallowly bell-shaped (urn-like in fr), lobes 5, spreading to ascending, each with a fleshy keel, appendages 1.5–2 mm, divisions gen knob-like; filaments 0.3–0.7 mm, anthers $\pm$ 0.5 mm; ovary 1–1.5 mm, obovoid, top depressed, style $\pm$ 0.4 mm, stigma cylindric. $n=14$. Uncommon. On alfalfa, other crops; gen < 1500 m. NCoR, GV, MP; to UT; native to Old World. [*C. epithymum* Murray; var. *urceolata* (Kunze) Yuncker misapplied]

C. californica Hook. & Arn. INFL spike-like. FL 2.6–4 mm; calyx persistent, lobes 5, spreading to recurved, lanceolate, acute to acuminate, 0.5–1 $\times$ corolla tube; corolla persistent, shallowly bell-shaped, gland-dotted, lobes 5, $\pm$ 3–6 mm, reflexed to spreading, lanceolate, acute, appendages 0–0.1 mm; filaments 0.7–1.4 mm, anthers 0.2–1.1 mm; ovary 1–2 mm, gen obovoid, gland-dotted, top gen depressed; styles 0.7–3 mm. FR 1.5–2 mm, enveloped by perianth, gen obovoid; top gen depressed. On herbs and shrubs on roadsides, chaparral, grassland, yellow-pine forest; gen < 2500 m. CA-FP, DSon; to WA, Colorado, Mex.

var. *apiculata* Engelm. FL: corolla not papillate; ovary (and fr) conic, top acute. On herbs; probably < 500 m. e DSon (near Colorado River).

var. *breviflora* Engelm. FL: corolla bulged out between stamens, not papillate; ovary (and fr) obovoid, depressed. On herbs, habitats of sp. CA-FP; to WA, Colorado, Mex. [*C. brachycalyx* (Yuncker) Yuncker incl var. *apodanthera* (Yuncker) Yuncker; *C. occidentalis* Millsp.; *C. suksdorfii* Yuncker incl var. *subpedicellata* Yuncker]

var. *californica* (p. 543) FL: corolla not bulged between stamens, not papillate; ovary (and fr) obovoid, depressed. Habitats of sp. CA-FP; to WA, NV, Baja CA.

var. *papillosa* Yuncker FL: perianth (and pedicel, receptacle) papillate; ovary (and fr) obovoid, depressed. $n=14$. On herbs and shrubs in chaparral; < 1500 m. SNF, GV, SCoRO, SCo.

C. cephalanthi Engelm. (p. 543) INFL head- or spike-like; pedicels 0–1.2 mm. FL 3–4 mm; perianth parts obtuse, gland-dotted, not papillate; calyx appressed, lobes 3–5, gen free, 1–2 mm, unequal, margins irregular; corolla sometimes persistent, 2–4 mm, funnel-shaped, tube longer than wide, lobes 3–4, spreading to erect, 0.6–1.3 mm, unequal, appendages 1.3–2 mm, divisions few, scattered, finger-like; filaments 0.2–0.6 mm, anthers 0.4–0.7 mm; ovary 0.9–2 mm, $\pm$ spheric to ovoid, top depressed or not, thickened or not. FR sometimes asymmetric; top as ovary. $2n=60$. Uncommon. On herbs, near streams, rivers, lakes; probably < 3000 m. KR, CaR, Wn; to WA, e US, Mex.

C. denticulata Engelm. INFL loose, spike-like, few-fl'd; pedicels 0–3.3 mm. FL 2–4 mm; calyx persistent, lobes 5, 0.3–1.5 mm, finely toothed, acute to obtuse; corolla gen persistent, 2–3 mm, shallowly bell- to urn-shaped, tube gen shorter than wide, lobes 5, becoming reflexed, tube, widely ovate, obtuse, appendages 0.7–1.4 mm, divisions 0–few, knob-like; ovary $\pm$ 1–2 mm, conic, top acute. On herbs or esp shrubs in creosote-bush scrub, Joshua-tree woodland; gen < 1300 m. D; to UT, AZ, Baja CA. Pls with acute calyx lobes have been called *C. veatchii* Brandegee.

C. howelliana Rubtsoff BOGGS LAKE DODDER INFL spike- or head-like; pedicels gen 0. FL: perianth parts papillate, acute; calyx 1.5–3 mm, lobes 4–5, not overlapped, loose around corolla tube, 1–1.4 mm, partly divided, triangular, tips spreading, acute to acuminate; corolla gen persistent, funnel-shaped, tube longer than wide,

lobes 4–5, sometimes spreading, 1–1.5 mm, triangular, acute to acuminate, appendages many, 0.7–1.2 mm, divisions finger-like; filaments 0.1–0.5 mm, anthers 0.6–1.1 mm; ovary 0.5–1 mm, $\pm$ obovoid, top depressed, thickening inconspicuous. UNCOMMON. Esp on *Eryngium* in vernal pools; < 100 m. NCoR, CaR, n SNF, GV.

C. indecora Choisy (p. 543) INFL spike- or panicle-like; pedicels 0–4.4 mm. FL 3–5 mm; calyx 1–2 mm, lobes 5, not overlapped, $\pm$ 1/2 corolla tube, acute; corolla gen persistent, 3–4.5 mm, shallowly bell-shaped, tube gen shorter than wide, lobes 5, < tube, triangular, erect, tips incurved, appendages 1.5–2.5 mm, divisions many, finger-like; ovary 2–3 mm, ovoid-spheric, top with thickening, styles 3–4 mm. FR sometimes gland-dot-lined; top as ovary. Common. On herbs, often in moist fields, roadsides; probably < 1500 m. NCo, NCoR, SN, GV, D; to c&se US, Mex; also Caribbean, S.Am.

var. *indecora* INFL: pedicel and calyx not papillate. $n=15$. Habitats and range of sp. [*C. jepsonii* Yuncker; *C. suaveolens* Ser. misapplied]

var. *neuropetala* (Engelm.) Hitchc. INFL: pedicel and calyx $\pm$ papillate. Common. Habitats of sp. SNF, GV, D.

C. pentagona Engelm. (p. 543) INFL: pedicels 0.8–1 mm. FL: calyx $\pm$ 1–2 mm, lobes 4–5, 0.6–1.3 mm, ovate to round, gland-dotted; corolla $\pm$ 2–3 mm, shallowly bell-shaped, tube gen wider than long, lobes 4–5, erect, 0.9–1.3 mm, tips incurved to reflexed, acute, often papillate outside, appendages $\pm$ 1–2 mm, curved over ovary, divisions few-many, finger-like; filaments 0.3–0.8 mm, anthers 0.3–0.6 mm; ovary 1–1.6 mm, $\pm$ spheric, unthickened, top depressed, styles 0.4–0.5 mm. FR 1–3.6 mm, $\pm$ spheric; top as ovary. Common. On herbs and shrubs on roadsides; < 500 m. NCo, SNF, GV, CCo, SCo; to se US, Caribbean, n Mex. [*C. campestris* Yuncker]

C. salina Engelm. (p. 543) INFL spike-like; pedicels 0–2.5 mm. FL 2–4.5 mm; perianth parts $\pm$ acute, gland-dotted; calyx 1.3–2.7 mm, lobes 5, erect to spreading, triangular-lanceolate; corolla 3–5 mm, bell-shaped, tube longer than wide, lobes 5, erect to spreading, lanceolate, appendages 1.2–1.5 mm, divisions many, knob-like; filaments 0.1–0.7 mm, anthers 0.4–0.7 mm; ovary 1–3 mm, gland-dotted, thickening at top more conspicuous in fr, styles 0.4–1 mm. Common. On herbs in salty marshes, flats, ponds; gen < 100 m. NCo, KR, GV, CCo, SnFrB, SCo; to B.C., UT, AZ, Baja CA.

var. *major* Yuncker FL 3–4.5 mm; perianth not papillate. Gen on *Salicornia* in salt marshes; gen < $\pm$ 100 m. NCo, CCo, SCo; to B.C.

var. *papillata* Yuncker FL $\pm$ 3 mm; perianth (and sometimes ovary) papillate. Uncommon. Salt flats, saline ponds; gen < 100 m. NCo; to UT, AZ.

var. *salina* FL 2–3 mm; perianth not papillate. Inland salt flats; gen < $\pm$ 100 m. Range of sp. (exc coast).

C. subinclusa Durand & Hilg. INFL spike- or head-like; pedicels 0–1 mm. FL: calyx persistent, 2–3.4 mm, lobes (4)5, $\pm$ 1.5–2.5 mm, lanceolate, acute to acuminate; corolla $\pm$ 4.5–5.5 mm, funnel-shaped, tube longer than wide, lobes spreading, 1–1.5 mm, < tube, triangular, tip often papillate outside, appendages 1.6–2.1 mm, spoon-shaped, divisions short, knob- to finger-like; anthers sessile, $\pm$ 1–2 mm; ovary 1–1.5 mm, obovoid to elliptic, top thickened, styles 1.1–1.5 mm. Common. Gen on shrubs, in forests near streams, rivers; < 1600 m. NCoR, SN, GV, SnFrB, SCoR, SNE.

ssp. *parishii* Pl 15–26 cm. INFL 5–14 cm. FL: calyx lobes 10–16 mm; corolla 20–25 mm, lips 6–8 mm, spreading; anthers glabrous or hairy; stigma lobes wide, spreading. $2n=48$. Uncommon. Openings in chaparral, scrub, gen on shrubs; < 2800 m. s SNH, Teh, SW, W&I, DMtns; Baja CA. [*O. californica* var. *p.* Jepson] Separation from *O. ludoviciana* Nutt. var. *arenosa* (Suksd.) Cronq. blurred in GB.

O. pinorum Hook. (p. 813) Pl 10–30 cm, glandular-puberulent aboveground. ST slender above; base gen enlarged, with many overlapping bracts; root attachment roundish, coral-like. INFL at first dense, gen becoming open; lower pedicels 2–6 mm, upper 0. FL: calyx 5–8 mm, lobes $\pm$ tube, triangular-acuminate; corolla 12–20, yellowish, hairy in a ring at stamen bases, lips erect, lobes tinged pale purple; anthers glabrous or sparsely hairy; stigma lobes 2, recurved. $2n=48$. Uncommon. Rocky, open forest slopes, on *Holodiscus* spp. (not known on conifers); < 2100 m. NW, CaRH, SnFrB; to WA, ID; NM.

O. ramosa L. Pl 10–60 cm, yellowish, glandular-puberulent. ST: branches many from near base, slender. INFL open; lower pedicels short, upper 0. FL: calyx divided more deeply on top, lobes gen 4; corolla 10–15 mm, tube whitish, throat and lobes pale blue or lilac; anthers gen glabrous; stigma 2-lobed. $2n=24$. Near fields; < 50 m. n SNJV, SnFrB, SCoRI, SCo; native of Eur. NOXIOUS (controlled) weed on tomatoes; may persist.

O. uniflora L. (p. 813) NAKED BROOM-RAPE ST 0.5–5 cm. INFL: gen raceme; fls gen 1–3; bracts gen < 6, gen glabrous; pedicels 3–12 cm, scapose; bractlets 0. FL: calyx lobes gen 4–8 mm, > tube, narrowly triangular; corolla 12–35 mm, $\pm$ horizontal, purplish to yellowish, lobes gen rounded, finely ciliate; anthers gen hairy; stigma lobes 2, margins recurved. $2n=36, 48, \pm 70$. Gen moist places, on herbs, esp *Sedum*, Saxifragaceae, Asteraceae; < 3100 m. NW, CaR, SN, ScV (Sutter Buttes), CW, SCo, n ChI, Wn; to Yukon, e N.Am. [var. *minuta* (Suksd.) D.B. Achey; var. *sedi* (Suksd.) D.B. Achey; ssp. *occidentalis* (E. Greene) Ferris] Variable. Pls < 20 cm, with deep violet corollas 25–35 mm, of n&c CA to Can have been called var. *purpurea* (A.A. Heller) D.B. Achey.

O. valida Jepson Pl 6–35 cm, dark purplish, glandular-puberulent. ST gen 1; branches (if any) slender to stout, base gen not. INFL 2–3 cm wide. FL: calyx 5–11 mm, lobes $\pm$ ear-triangular; corolla 12–18 mm, lips 3–5 mm, acute; anthers glabrous or hairy; stigma bowl-shaped. Rocky soils in chaparral, on shrubs; < 2000 m. n SNGB.

ssp. *howellii* Heckard & L.T. Collins HOWELLII Pl 6–20 cm; glandular hair stalks 0.2–0.4 mm, gen slender, gen enlarged at base. FL: corolla 14–18 mm, outside at sinuses, hairs 0.4–0.7 mm; folds of lower throat gen present; filament base and anther hairy. $2n=48$. UNCOMMON. In and serpentine slopes, open chaparral, gen on rocky slopes; 1700 m. s NCoRH, c&s NCoRI.

ssp. *valida* (p. 813) ROCK CREEK BROOM-RAPE Pl 6–20 cm; glandular hair stalks $\pm$ 0.1 mm, gen slender, gen enlarged at base. FL: corolla 12–14 mm, sparsely hairy at sinuses, hairs $\pm$ 0.1 mm; folds of lower throat glabrous; base and anther glabrous. $2n=48$. RARE. Decomposed in various chaparral shrubs; 1250–2000 m. c WTR (Clappan) SNGB.

O. vallicola (Jepson) Heckard (p. 813) Pl 8–40 cm, pinkish, glandular-puberulent. ST stout; base gen thickened, branched at base and above. INFL > 4 cm, sometimes branched from base into raceme-like units; bracts narrowly triangular, 3–5, inconspicuous; pedicels short. FL: calyx 8–15 mm, pinkish; corolla 17–30 mm, yellowish to pinkish, per lobes triangular with pointed tip, veins gen reddish; anthers hairy; stigma 2-lobed, margins recurved. $2n=48$. Common. Woodlands, forest openings, gen on *Sambucus* < 3000 m. NCoR, CaRF, GV, CW, SCo (Los Angeles Co.). [var. *californica* & *claremontensis* Munz misapplied] Separate from *O. californica* ssp. *jepsonii*.

OXALIDACEAE OXALIS FAMILY

Robert Ornduff

Ann to tree. LVS compound (palmate, pinnate, or llet 1), alternate, often $\pm$ basal in rosettes or in clusters at st or root tips, gen petioled; stipules gen 0; lflets gen sessile. INFL: cyme, sometimes umbel- or raceme-like, or fls solitary, gen axils; peduncle bracted. FL gen bisexual, radial; sepals 5, free or fused at base; petals 5, free or fused above base; stamens 10, fused below, of 2 lengths; pistil 1, ovary superior, chambers 3–5, placentas axile, styles 1–5, gen $\pm$ free. FR: gen sili-
sule, loculicidal. SEEDS gen with aril. 8 genera, 575 spp.: esp temp. Often heterostylous.

OXALIS

Ann, per, shrub; roots fibrous or woody; bulbs, tubers, or rhizomes often present. ST sometimes 0 or very short. LF perianth stipules 0 or small; lflets 3, gen $\pm$ obcordate in CA, gen entire, gen green. FL: petals clawed; stamens 10; ovary chambers 3, free, erect or curved. FR cylindric to spheric, explosively dehiscent. SEEDS flat, often ridged; aril translucent. $\pm$ 480 spp.: esp temp. (Greek: sour) [Eiten 1963 Amer Midl Nat 69:257–309; Lourteig 1975 Phytologia 42:57–197] Gen heterostylous; many (esp aliens in CA exc *O. laxa*) fine orn; some noxious weeds; contained oxalates may be toxic to stock.

1. Petals yellow
2. Ann; fr < 5 mm
- 2' Per; fr > 6 mm or 0
3. Bulbs present; lvs in loose, $\pm$ basal rosette
- 3' Bulbs 0; lvs cauline
4. Petals > 12 mm; NCo
- 4' Petals < 12 mm; NCo and elsewhere
5. Petals gen < 8 mm; st rooting at nodes; taproot $\pm$ fleshy; disturbed urban places
- 5' Petals gen 8–12 mm; st not rooting at nodes; taproot $\pm$ woody; native of $\pm$ undisturbed places
6. St hairs 0 or gen curled
- 6' St hairs slightly curved
- 1' Petals white to pink, red, or purple
7. Bulbs 0

O. laxa

O. pes-caprae

O. suksdorfii

O. corniculata

O. albicaulis

ssp. *californica*

ssp. *pilosa*

10.—**TURBINA** Rafinesque.—Trepadoras arbustivas con hojas acorazonadas, mayormente enteras; infl. en corimbos o panojas, axilares, pedunculadas, flores grandes o medianas; sépalos aovados a lanceolados, extendidos y ampliados en el fruto, los interiores mayores, margen escarioso, obovados; corola subentera, largo-acompanada; ovario 2-4-locular; estilos parcialmente libres, estigmas globulosos, filamentos de los estambres nacido sobre escamas incurvas vellosas; fruto seco, leñoso, indehiscente, subgloboso u ovoides, 1-locular, mayormente 1-spermo; semillas lampiñas.—Unas 20 esp., de Amér. tropical.

1.—**T. corymbosa** (L.) Raf. (*Convolvulus corymbosus* L.; *C. dominicensis* Desv.; *C. sidaefolius* HBK.; *Ipomoea sidaefolia* Choisy; *Rivea corymbosa* Hall. f.; *I. antillana* Millsp.).—"Aguinaldo de pascua", "Aguinaldo blanco".—Trepadora o rastroja, lampiña; hojas aovadas, enteras, de 4-10 cm., agudas o acuminaadas en el ápice acorazonadas en la base; pedúnculos axilares, tan largos o más como las hojas, pluri-multifloros, flores en panojas o corimbos; pedicelos delgados; sépalos oblongos, persistentes, los 3 int. de 8-12 mm. de casi doble largo que los ext.; corola blanca, de 2.5-3 cm.; fruto ovoides, agudo, mitad del largo de los sépalos, 1-spermo.—Maniguas: toda Cuba e IP.; Fda., Ant., Amér. trop. continental. (Fig. 110).

Planta melifera. Las semillas tienen propiedades narcóticas y han sido empleadas por los Indios mexicanos para producir una embriaguez parecida a la del opio.

Argyrea nervosa (Burm. f.) Boj. (*Convolvulus nervosus* Burm. f.; *A. spectiosa* Sweet).—"Ipomea".—Trepadora con tallo tomentoso, hojas suborbiculares de 10-30 cm., plateado-tomentosas en el envés, flores en umbelas, rosadas, de 5-6 cm., fruto amarillo, abayado.—Cultivada en jardines, y ornamental. Oriunda de la India.

11.—**CUSCUTA** L.—Parásitas herbáceas (algunas especies con un poco de clorofila, y parcialmente autótrofas); tallos filiformes, trepadores sobre huéspedes herbáceos o leñosos, de los que obtienen alimento por haustorios; hojas reducidas a escamas pequeñas; flores pequeñas, mayormente en cimas compactas, gamosépalas, 5-meras (3-5); estambres insertos en la garganta, alternos con lóbulos de la corola; la corola con escamas fimbriadas en el interior en la base, opuestas a los estambres; ovario 2-locular, cada celda 2-ovulada; estilos libres o unidos; estigmas capitados o lineal-alargados; fruto en cápsula indehiscente o circuncisl en la base; embrión sin cotiledones, filiforme o engrosado en un extremo.—158 esp., según Yunker, de amplia distribución.

Algunos autores hacen con este género una familia, **CUSCUTACEAE**. Las especies de este género reciben el nombre vernáculo de "Bejico de Fideo".

Cápsulas abriéndose (circuncisl) en la base.

Lóbulos del cáliz obtusos; lóbulos de la corola más cortos que el tubo de la

misma.

Flores de 2-3 mm.; cápsula cónico-globosa, mayormente 1-sperma.

1.—*C. americana*.

Lóbulos del cáliz agudos; lóbulos de la corola tan largos o más que el tubo. 3.—*C. umbellata*.

Cápsula permaneciendo cerrada.

Lóbulos de la corola obtusos, erguidos a extendidos. 4.—*C. obtusiflora*.
Lóbulos de la corola agudos, comúnmente extendidos o reflejos, con punta inflexa.
Flores de 1.5 mm., pedicelos $\pm$ del largo de las flores; cápsula no engrosada en el ápice. 5.—*C. campestris*.
Flores de 2-2.5 mm., carnosas, pedicelos más largos que las flores; cápsula con estilopodio engrosado en el ápice. 6.—*C. indecora*.

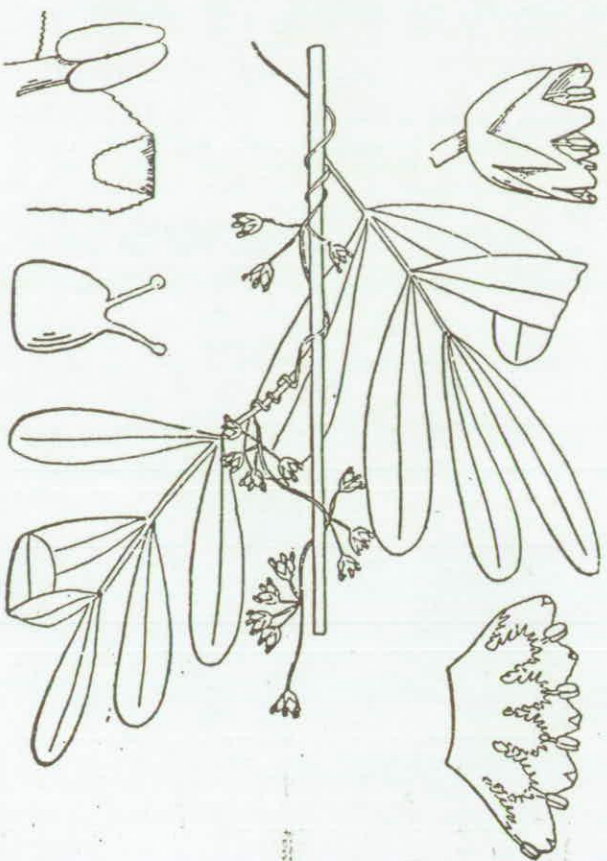
1.—*C. americana* L.—"Fideillo".—Tallos de grueso mediano. Flores de 2-3 mm., subsentadas y agrupadas en glomérulos; cáliz tubular, tan largo o algo más corto que el tubo de la corola, lóbulos aovados, obtusos; corola cilíndrica, lóbulos aovados, obtusos, cortos; escamas triangulares o algo oblongas, más cortas que el tubo, anteras subsentadas; estigmas capitados; cápsula globoso-ovoides u ovoides, semillas de 1.5 mm.—Sobre trepadoras y arbustos: Or., LV., Hab., IP.; Ant., Amér. trop. continental.

2.—*C. globulosa* Benth.—Tallos medianos a gruesos. Flores de 3-4 mm., subsentadas en glomérulos cimosos o racemosos, compactos o algo laxos; cáliz acompañado-cilíndrico, tan largo o más corto que el tubo de la corola, lóbulos aovado-orbiculares, obtusos; corola cilíndrica, lóbulos cortos, aovados, obtusos; escamas oblongas, más cortas que el tubo; anteras subsentadas; estilos largos, exsertos; cápsula deprimido-globosa, semillas ovoides.—Sobre arbustos costeros: Or., LV.; Ant., México.

3.—*C. umbellata* HBK.—Tallos delgados. Flores a veces algo puberúlas, de 2-3 mm., pedicelos más largos que las flores, en cimas compuestas más bien densas; cáliz turbinado, tan largo o más que la corola, lóbulos triangular-aovados, agudos a acuminaados; corola acompañada, lóbulos tan largos o más que el tubo, reflejos, lanceolados, agudos a acuminaados; escamas algo obovadas o espatuladas; estambres más cortos que los lóbulos; cápsula globoso-deprimida, semillas de 1 mm., angulosas.—Cuba (*Wr. 3107*); Ant., S. de N. Amér. a N. de S. América.

4.—*C. obtusiflora* HBK. var. *glandulosa* Engelm. (*C. glandulosa* Small).—Tallos delgados. Flores de 2 mm., sentadas o casi, en glomérulos densos; lóbulos del cáliz aovados, obtusos, margen algo aserrado, no imbricados; lóbulos de la corola aovados, agudos u obtusos, extendidos o reflejos, más cortos que el tubo; escamas aovadas, casi tan largas como el tubo de la corola, exsertas; filamentos más largos que las anteras; cápsula globoso-deprimida, estilos cortos, divergentes; semillas aovadas, de 1.5 mm.—Sobre hierbas en lagunas y pantanos: Or., LV., Hab., PR.; Ant., S. de EE. UU., México.

5.—*C. campestris* Yunker (*C. arvensis* Hook., como sin., *C. pentagona calycina* Engelm.).—Tallos medianos. Flores de 2-3 mm., pedicelos mayormente más cortos que las flores, glomérulos compactos; lóbulos del cáliz ovales a orbiculares, imbricados; lóbulos de la corola triangulares, agudos, del largo del tubo; estambres más cortos que los lóbulos, filamentos más largos que las anteras; escamas aovadas, exsertas; estilos

Fig. 111.—Fidecillo, *Cuscuta indecora*.

6.—*C. indecora* Choisy.—Tallos medianos a gruesos. Flores de 2-5 mm., carnosas, papiloso-hispidas, pedicelos más largos que las flores; lóbulos del cáliz triangular-ovados, agudos o algo obtusos, más cortos que el tubo de la corola; corola acampanada, lóbulos erguidos o extendidos, triangulares, agudos, punta infleja; escamas aovadas a espatuladas; estambres más cortos que los lóbulos, anteras ovales; estilos largos, divergentes; cápsula globosa, semillas de 1.7 mm., 2-4.—Sobre hierbas y arbustos: Ant. May., México, N. y S. América. (Fig. 111).

6a.—var. *indecora*.—Flores de 2-2.5 mm.—Cam.

6b.—var. *neuropetala* (Engelm.) Hitchc. (*C. neuropetala* Engelm.).—Flores de 2-5 mm.—LV, Hab., PR.

Familia 2.—HYDROPHYLLACEAE.

Mayormente hierbas, anuales o perennes, a menudo escabrido-pelosas, glandulosas o espinosas; hojas alternas u opuestas, a menudo en rosetas basales, enteras o pinnatifidas; infl. cimosa, a menudo helicoidal o circinnada, a veces 2 ó más cimbras en dicasios o infl. umbeladas, o flores solitarias y axilares; flores bisexuales, actinomorfas, comúnmente pentámeras; cáliz 3-lobulado, imbricado, los senos a menudo con apéndices; corola mayormente 5-lobulada, imbricada o a veces contorta, rotácea, acampanada o embudada; estambres mayormente 5, epipétalos, adnatos a la base de la corola, alternos con los pétalos, filamentos iguales o no, anteras 2-loculares, de dehiscencia longitudinal, versátiles, introrsas, a menudo alternas con

o subtendidas por apéndices escamosos o pelosos; estaminodios hipoginos, presentes o ausentes; pistilo 1, ovario súpero (semi-infero en alg. esp. de *Nama*), típicamente 1-locular con 2 placentas ± abuladas (a veces reuniéndose y el ovario pareciendo 2-locular), carpelos 2, óvulos a menudo numerosos, péndulos, anátropos o anfítropos, micropilo hacia arriba y afuera, estilo 1 y algo dividido, ó 2, estigma capitado; fruto mayormente una cápsula loculicida dehisciente por 2 ó 4 valvas, a veces indehisciente; semillas numerosas, a veces carunculadas, reticuladas, foveoladas, tuberculadas, o muricadas, endospermo abundante o delgado, embrión pequeño y recto.—Unos 20 géneros y 265 esp., de amplia distribución.

Plantas espinosas 1.—*Hydrolea*.
Plantas inermes.

Plantas prostradas; flores 1-2 en las axilas de las hojas 2.—*Nama*.
Plantas erguidas; inflorescencias terminales, en panojas 3.—*Wiganida*.

Fig. 112.—Tabaco cimarrón, *Hydrolea spinosa*.

1.—*HYDROLEA* L.—Hierbas anuales o perennes, de lugares acuáticos; hojas alternas, enteras; infl. corimbosas, raras veces las flores dispersas o en cincinos; cáliz dividido casi hasta la base; corola acampanada, rotácea, profundamente partida, casi siempre azul; estambres insertos en la base de la corola, filamentos a menudo ensanchados en la base, lampiños; escamas ausentes; estilos 2, raras veces 3-5, estigmas capitados, óvulos ∞ (-400); cápsula ovoides o globosa, loculicida o loculicida y septicida, o de dehiscencia irregular; semillas pequeñas, rugoso-estriadas longitudinalmente; embrión pequeño.—Unas 20 esp. o más, de reg. tropicales.

Sez. I. KOPSIS (DUM., 1822).

2 Fusto normalm. ramoso (ma anche semplice nelle piante meno sviluppate). 3

— Fusto normalm. semplice. 5

3 Fusto munito di squame piccole, ovali, ottuse. Pianta brevem. glanduloso-pelosa (3-40 cm.). Brattee e bratteole uguaglianti il calice, rr. più brevi. Corolla curvata, ristretta nel mezzo, bilabiata, a labbro super. a 2 lobi per lo più rotondato-acuti, cigliati. Stami 4, un po' pelosi alla base o glabri; antere glabre o brevem. cigliate alla base. Cassula 1-loculare, a 2 valve che rimangono aderenti alla base ed all'apice. ☉. *Parasita su diverse piante colt. e spont.*; 2-4. *Prim.-Est.* [*Eur. As. occ. sino Himal. Afr. bor. Abiss., nat. India Kashmir Afr. mer. Am. bor.*]. — *Kopsia* Dum. (1822) — *Phelipaea* C. A. Mey. (1831). — *Volg. Succiamelle ramoso.*

1 *O. ramosa* L. (1753) 2996

A Corolla lunga 7-17 mm., a lobi del labbro infer. interi od ondulati, rr. denticolati.

Spiga lassa e multiflora, alla fine allungata. Denti del calice triangolari-acuminati, più brevi del tubo. Corolla azzurra (rr. bianca). Fusto generalm. ramoso. — *Istria, Pen ed isole.* — *Phelipaea proboscistyla* Bianca ex Carnel (1885) = *O. probosc.* Beck (1890) = *Kopsia ramosa* f. *probosc.* Bég. (1902) (f. *cleistogama*).

α TYPICA

Spiga generalm. abbreviata. Denti del calice lesiniformi, lunghi come il tubo. Corolla intensam. violaceo-azzurra, a lobi più acuti. Fusto semplice, gracile (1-3 dm.). — *Istria, Firenze, Roma, Amalfi, Sic., Sard. e Cors.* [*Eur. mer. ed or. As. occ. Mad.*]. — *Phelipaea* ram. v. *simplex* Vis. (1847) — *Ph. nana* Rehb. f. (1862) — *Kopsia nana* Freyn (1888).

β NANA (NOE, 1847)

B Corolla lunga 15-22 mm., a lobi ± crenulato-dentati od increspati, a fauce più ampia ed a pieghe più sporgenti che nel tipo. — Denti del calice c. s. Spiga e fusto come nel tipo. Corolla azzurra, carnicina o violacea (rr. bianco-paglierina). — *Specialm. sulle rd. delle Composte: Istria, Pen., Sic., Malta, Lamped., Pantell., Sard., Cors., Montecristo e Pianosa.* [*Eur. medit. As. occ. Himal. Afr. bor. Abiss., nat. Capo.*]. — *Phelipaea* Reut. (1847) — *Ph. rufescens* Gris. (1844) = *Phel. Reuteri* Moris (1858-59) = *Orob. ruf.* Nym. (1854-55) (f. *robustior pilosior flor. violaceis*) — *Kopsia* Bég. (1902).

γ MUTELI (F. SCHULTZ., 1835) 2996'

☉ Fusto munito di squame lanceolato-acuminate. 4

Corolla lunga 20-37 mm., poco curvata o quasi diritta. Antere abbondantem. peloso-lanose. Fusto ± ramoso o rr. semplice (1-5 dm.). Spiga multiflora, alla fine lassa. Calice a denti lanceolato-lesiniformi, subeguali al tubo. Corolla azzurra, a lobi largam. rotondati. Il resto c. s. ☉. *Sic. pr. Ilermo sulle pendici sett. del M. Gallo; 2. Magg.* [*Eur. or.-mer. As. occ. Egit.*]. — *Phelip.* elongata Lojac. (1833), non Koch = *O. aegypt.* v. *trinacria* Beck (1890) = *O. trinacr.* Beck (1890) (f. *corolla minor circ. 20 mm. longa*) — *Phelipaea* Walp. (1844-45) — *Kopsia* Carnel (1885).

2 *O. aegyptiaca* Pers. (1807) 2997

- Corolla lunga 17-22 mm., molto curvata. Antere cigliato-glandolose. Fusto gracile, peloso-glandoloso, semplice o con brevi rami (2-6 dm.). Spiga coi fi. alla fine quasi orizzontali. Calice c. s. Corolla intensam. azzurra (tranne la base ch'è bianchiccia), a lobi rotondati ed a pieghe prominenti, con villosità bianca o gialla. ☉. *Parass. su diverse piante e specialm. Psoralea*: Nizz., Lig., M. Argentaro, Giglio, Basil. a Muro, Sic., Malta, Linosa, Cors. e probabilm. Sard.; 2. Apr.-Magg. [Reg. medit. Can.]. — Philip. F. Schultz (1847), Reut. (1847) — Kopsia Caruel (1885).

3 O. lavandulacea Rchb. (1829) 2998

- 5 (2) Tubo del calice bianco-membranaceo fra i denti e parcam. nervoso. Fusto gracile, abbondantem. squamoso, peloso-glandoloso (1-6 dm.). Brattee lanceolate, uguaglianti i denti del calice; bratteole un po' più strette e più brevi. Calice fortem. glanduloso-peloso, a denti lineari-lanceolati, sempre più lunghi del tubo. Corolla un po' curvata in basso, azzurra. Antere spesso lanose. ☉. *Parass. su diverse piante*; 2. Apr.-Giu. [Eur. mer. As. occ. Afr. bor. Abiss.]. — Kopsia Bég. (1902).

4 O. Schultzii Mutel (1835) 2999

- A Lobi della corolla acuti. Spiga per lo più piramidata. — Non ancora segnalata per l'It. α TYPICA
 B Lobi della corolla per lo più acuminati. Spiga per lo più lungam. cilindrica, più stretta e più lassa. — *Su Ferula nodiflora, Rubia peregrina ecc.*: Sic., is. Salina, Sard. e vicine isole della Maddalena, Caprera e Tavolara. [Alger. India?]. — O. caerulea Moris (1827), non Vill. — Philipaea Reut. (1847) — Kopsia Caruel (1885). β STRICTA (MORIS, 1844)
 C Lobi della corolla ottusi o rotondati. Spiga cilindrica, breve. — *Su Rumex ed Artemisia?*: Sic. [Spa. Grec. Cipro As. occ. Afr. bor. Abiss.]. — O. caesia Guss. (1832), non Rchb. — Philip. rufescens Lojac. (1878), non Gris. — Ph. Gussoneana Lojac. (1883) — Kopsia Gusson. Lojac. (1887). γ GUSSONEANA n. comb.

- Tubo del calice non bianco-membranoso fra i denti, percorso da molti nervi. Fusto robusto. 6

- 6 Lobi del labbro infer. della corolla ellittici, acuti od acuminati. Antere per lo più glabre. Pianta glanduloso-lanosa, a fusto con poche squame (eccett. la base), spesso porporino (15-60 cm.). Spiga cilindrica. Brattee lanceolate, più brevi del calice; bratteole più strette. Calice talora con un quinto dente rudimentale. Corolla curvata, lunga 18-30 mm. ☉. *Parass. su Composte (specialm. Achillea ed Artemisia) e su piante di altre fam.*; 2-4? Magg.-Lugl. [Eur. As. occ. sino India Sib.]. — O. caerulea Vill. (1787) — Kopsia caer. Dum. (1822) — Philip. caer. C. A. Mey. (1831) — Kopsia purp. Bég. (1902). 5 O. purpurea Jacq. (1762) 3000

- A Lobi del labbro infer. della corolla acuminati.
 α Denti del calice spesso quasi triangolari, più brevi del tubo. Corolla violacea colla base bianco-giallastra (rr. tutta bianco-giallastra). — *Qua e là nell'It. super., Tosc., Piceno sul M. Vettore, Camp., Capri, Puglie, Basil., Cal., is. Salina, Cors. e Capraia.* α TYPICA
 b Denti del calice lesiniformi (quasi filiformi verso l'apice), lunghi come il tubo. Corolla spesso più intensam. colorata. — *Ischia. [Endem.].* — ? O. caer.

v. Millefolii Rchb. (1830) — Phelip. caer. v. Millefol. Guss. (1854) — Kopsia purp. v. Spitzelii Bég. (1902). β SPITZELII BECK (1890) (BECK, 1890)

B Lobi del labbro infer. della corolla acuti. — Denti del calice acuti, più brevi del tubo. Corolla porporina verso la fauce. — *Alpi Cozie*. [Boemia]. — Phelip. Celak. (1874) — Kopsia purp. v. bohém. Bég. (1902).

γ BOHEMICA (CELAK., 1874)

— Lobi del labbro infer. della corolla rotondati, ottusi. Antere villosa-lanate. Fusto abbondantem. squamoso (2-5 dm.). Brattee lunghe circa come il calice. Calice a denti lanceolato-acuti, uguaglianti o più rr. superanti il tubo. Corolla azzurra (rr. intensam. violacea). Il resto c. s. $\odot$. *Parass. sulle Artemisie*, più rr. su altre piante: *Riva di Trento, Alto Adige, Pavese, Piem., Alpi Mar. e Firenze alle Cascine; 3-5. Magg.-Lugl.* [Eur. centr. e mer. *As. min. Afr.*]. — O. levis L. p. p. (1753) — Kopsia aren. Dum. (1822) — O. comosa Wallr. (1822) — O. Borkhausenii Andr. (1832) — Phelip. aren. Walp. (1844) — Kopsia Borkhauseni Carnel (1885).

6 O. arenaria Borkh. (1797) 3001

Sez. II. EUOROBANCHE FIORI (1926).

7 (1) Corolla molto allargata sotto l'inserzione degli stami, nel mezzo ristretta e fortem. curvata, in alto un po' rigonfia. Stami inseriti circa alla metà del tubo corollino (fig. 1 e 2). A) *Inflatae* 8

— Corolla ristretta sotto l'inserzione degli stami, spesso cilindrica, sopra molto allargata oppure rigonfia-ventricosa. Stami inseriti al disotto della metà del tubo corollino (fig. 3 a 28). B) *Angustatae* 9

A) *Inflatae* Beck (1890).

8 Brattee ovali. Corolla lunga 12-15 mm., all'esterno poco glandolosa o glabra. Pianta generalm. robusta, $\pm$ glandoloso-lanosa (4 dm.). Spiga densa, cilindrica. Pezzi del calice liberi o rr. brevem. connati, ovali-lanceolati, interi o con 2 denti acuminati, assai più brevi del tubo corollino. Corolla azzurro-ametista. Stami glabri o poco pelosi in basso e presso le antere, che sono glabre o presso le suture peloso-lanose. Stigma biancastro. Cassula eguale al calice o più lunga. $\odot$. *Parass. sulle Composte e Solanacee*, rr. su spec. di altre fam.: *Alto Adige a Merano, Basil. a Muro, Sic., Eolie (is. Panaria, Vulcano e Salina), Malta e Cors.; 2. Apr.-Giu.* [Reg. medit. sino India Austral.]. — O. cumana Guss. (1834) — O. gallica Gren. (1838) — O. hispanica Boiss. (1839-45) — O. bicolor Bert. (1844), non C. A. Mey. — O. Grenieri F. Schultz (1845).

7 O. cernua Loeffl. (1758) 3002

— Brattee lanceolate. Corolla lunga 10-23 mm., all'esterno fortem. pelosa o lanosa. Scapo robusto, giallastro, fortem. ragnateloso-lanoso in alto (1-4 dm.). Pezzi del calice liberi, ovali od oblungo-lanceolati, nell'apice o più di rado fino alla metà 2-dentati, a denti lanceolati o lesiniformi, uguali al tubo corollino o più brevi. Corolla di un azzurro slavato o quasi ametistino. Stami un po' pelosi in basso soltanto. Stigma

bianco-giallastro. Cassula cilindrica, 2- o rr. 3-4-valve. $\odot$. Parass. su *Artemisia campestris* nel Friuli (Brumati ex Pir.), ma sec. Beck loc. assai dubbia e sec. Gortani da escludersi, Cal. ad Anzia (F. Pasquale). Magg.-Giu. [Austr. Germ. Russ. mer.-or. Sib. mer. Turkest. Cina Giapp.].

8 *O. caerulescens* Steph. (1801) 3003

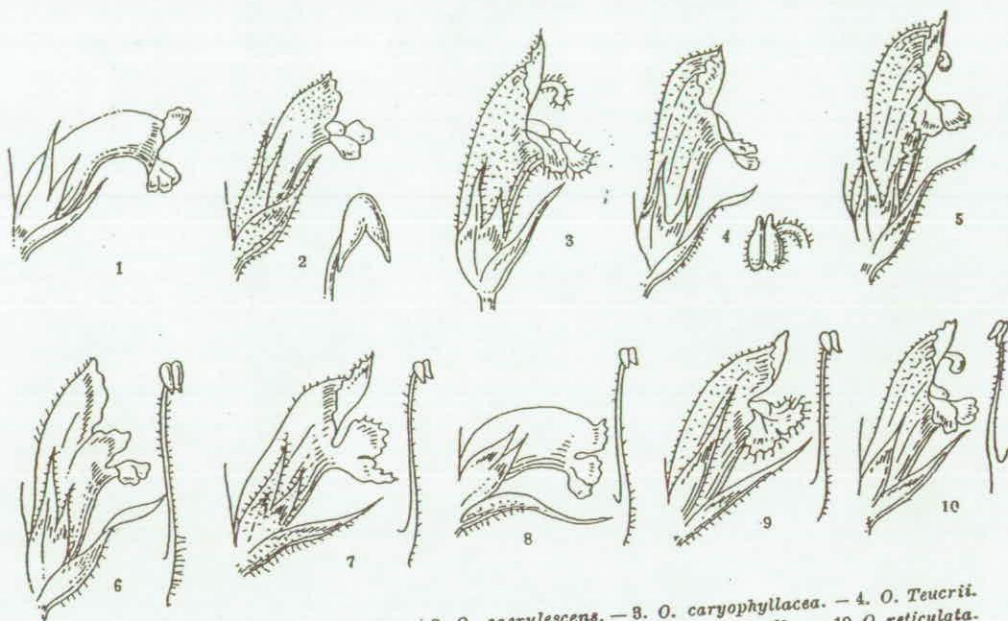


Fig. 18. — 1. *Orobanche cernua*. — 2. *O. caerulescens*. — 3. *O. caryophyllacea*. — 4. *O. Teucrii*. — 5. *O. lutea*. — 6. *O. gracilis*. — 7. *O. variegata*. — 8. *O. sanguinea*. — 9. *O. alba*. — 10. *O. reticulata*.

B) *Angustatae* Beck (1890).

- 9 (7) Fi. piccoli, lunghi 10-20 mm. Corolla angustam. tubulosa, tipicam. biancastra, bianco-giallastra o giallastra, nel labbro super. o lungo i nervi spesso rosso-violacea o porporina, a lobi sempre glabri nel margine. Stigma rosso, violaceo-porporino od anche giallo. g) *Minores* 28
- Fi. grandi, di solito più lunghi. Corolla per lo più ampiam. campanulata, diversam. colorata. 10
- 10 Linea dorsale della corolla curvata alla base, nel mezzo diritta o quasi, oppure (sez. *Galeatae*) concava (rr. un po' curvata), nel labbro super. fortem. curvata od appianata. 11
- Linea dorsale della corolla $\pm$ fortem. curvata (rr. quasi diritta nella sez. *Cruentae*) dalla base al labbro super. o talvolta qui un po' spianata. 13
- 11 Corolla glabrescente o peloso-glandolosa, ma a peli non colorati nè inseriti sopra un piccolo tubercolo. 12
- Corolla peloso-glandolosa, a peli colorati e per lo più inseriti sopra un piccolo tubercolo. Stigma rosso-porporino. Pezzi del calice per lo più liberi fino alla base, interi o rr. 2-dentati. c) *Glandulosae* 20
- 12 Corolla tipicam. fosco-lillacina, concava nel dorso e generalm. prov-

1. Infl glabrous; bracts widely ovate to obovate (width $\pm$ length), densely overlapping; corolla with ring of hairs at base of stamens **BOSCHNIAKIA**
 1' Infl hairy; bracts $\pm$ lanceolate (width $\ll$ length), little or not overlapping; corolla gen lacking ring of hairs at base of stamens **OROBANCHE**

BOSCHNIAKIA GROUND-CONE

Per, glabrous. STS gen simple, ann, 1-many from corm-like thickening surrounding host root. INFL spike-like; bracts densely overlapping, $\pm$ ovate; pedicels gen < 2 mm; bractlets on pedicel 0-3, narrow. FL: calyx cup-shaped, teeth 0-5 (variable on a pl), tip acute or tapered; corolla with ring of hairs in upper tube at base of stamens, upper lip entire or indented, lower lip 3-lobed; upper filament and anther hairy. FR 2-4-valved; placenta 1 per valve. 3 spp.: nw NA, ne Asia. (Boschniakia, Russian botanist) [Gilkey 1945 OR State Monogr Bot 9]

1. Infl < 3 cm diam; largest bracts gen acute, $\ll 10$ mm at widest point; corolla 10-15 mm **B. hookeri**
 1' Infl > 3 cm diam; largest bracts gen obtuse to rounded, > 10 mm at widest point; corolla 15-20 mm **B. strobilacea**

B. hookeri Walp. (p. 807) SMALL GROUND-CONE Pl 7-12 cm. INFL 3-6 cm, < 3 cm diam, purplish to pale yellow; lower bracts 10-12 mm, ovate to narrowly obovate, tip obtuse to acute. FL: calyx cup 2-3 mm, teeth 2-4 mm, deltate; corolla 10-15 mm, gen pale, lips erect, 3-4 mm (upper $>$ lower). SEED ± 1.5 mm. RARE in CA. Open woods, shrubby places, gen on *Gaultheria shallon*; < 300 m. NCoRO (1 site, Humboldt Co.), SnFrB (Mount Tamalpais, Marin Co.); to B.C. CA pls are among the most distinct from *B. strobilacea* in their small size and pale color.

B. strobilacea A. Gray (p. 807) CALIFORNIA GROUND-CONE Pl 10-30 cm. INFL gen 7-18 cm, 3-6 cm diam, gen reddish brown to dark purplish; lower bracts 15-20 mm, ovate to widely obovate, margin gen pale, tip obtuse to rounded. FL: calyx cup 2-4 mm, teeth 3-7 mm, narrowly deltate; corolla 15-20 mm, gen purplish (lobe margins pale), lips 5-6 mm, $\pm$ equal, lower lip gen spreading. SEED ± 2 mm. Open woods, chaparral, on *Arctostaphylos* or *Arbutus*; < 3000 m. CA-FP (exc s SW); s OR; widely scattered, most common NW, TR.

OROBANCHE BROOM-RAPE

Ann, per, gen glandular-puberulent above; root attachment sometimes tuber-like. ST simple or branched. INFL gen $\pm$ spike-like (lower fls often short-pedicelled or on short branches), gen dense; fls gen > 20 ; bracts gen lanceolate to deltate (wider on peduncle); bractlets 0 or 2. FL: calyx lobes gen 4-5; corolla glandular-puberulent (hairs short and tack-shaped or long-stalked), gen lacking ring of hairs at stamen bases, upper lip erect to reflexed, gen 2-lobed, lower lip 3-lobed, spreading, yellow-lined; anthers glabrous to hairy; stigma lobes 2, spreading or peltate. FR 2-valved; placentas gen 2 or 4, often lobed. SEED < 0.7 mm. 140 spp.: worldwide, esp Medit. (Greek: vetch strangler, from parasitic habit) [Heckard 1973 Madrono 22:41-70]

1. Fls 1-20; pedicels long, scapose; bractlets on pedicel 0 (sect. *Gymnocaulis*)
 2. Fls gen 5-20; st (peduncle + infl axis) > 5 cm; bracts > 6 ; upper pedicels $<$ st; corolla lobes glabrous to soft-hairy, hairs colorless **O. fasciculata**
 2' Fls gen 1-3; st (peduncle + infl axis) gen < 5 cm; bracts gen < 6 ; upper pedicels $>$ st; corolla lobes minutely ciliate, hairs violet **O. uniflora**
 1' Fls gen > 20 ; pedicels 0 or short, not scapose; bractlets on pedicel 2
 3. Branches at st base many, slender, yellow; infl open, fls becoming well separated; calyx gen 4-lobed, cut deepest on upper side; agricultural weed (sect. *Trionychon*) **O. ramosa**
 3' Branches at st base few, stout; infl dense, gen remaining so; calyx 5-lobed, cut $\pm$ equally or deepest on lower side; native (sect. *Nothaphyllon*)
 4. Infl and fls $\pm$ dark purple (lighter in *O. pinorum*); calyx gen 5-11 mm (~ 12 mm in *O. cooperi*)
 5. Calyx divided to base on lower side; hairs of infl and corolla papillate, not glandular; root attachment rounded, coral-like; gen on *Adenostoma fasciculatum* **O. bulbosa**
 5' Calyx divided $\pm$ equally; most hairs of infl and corolla glandular, not papillate; root attachment not rounded and coral-like (exc *O. pinorum*, sometimes *O. cooperi*); on various shrubs and herbs
 6. Infl and corolla pale purple-tinged; corolla with a ring of hairs at base of filaments; root attachment rounded, coral-like **O. pinorum**
 6' Infl and corolla dark purple; corolla lacking ring of hairs; root attachment branched (rarely rounded, coral-like in *O. cooperi*)
 7. Infl 4-5 cm wide; corolla 18-32 mm, lips 5-10 mm; on herbs of Asteraceae; D **O. cooperi**
 7' Infl 2-3 cm wide; corolla 12-18 mm, lips 3-5 mm; on shrubs, gen in chaparral **O. valida**
 8. Corolla 14-18 mm, hairy outside, densely so at sinuses, hairs 0.4-0.7 mm; filament base and anther hairy ssp. **howellii**
 8' Corolla 12-14 mm, puberulent outside, weakly so to glabrous at sinus, hairs ± 0.1 mm; filament base and anther glabrous ssp. **valida**
 4' Infl and fls gen buff to pinkish, corolla lips white to pink or lavender with darker veins (purple in *O. californica* ssp. c.); calyx gen 10-20 mm
 9. Corolla 15-30 mm, lips 4-10 mm, upper erect, lower spreading
 10. Infl 3-4 cm, branched, forming a convex or $\pm$ flat-topped cluster; anthers densely hairy throughout; GB, adjacent CaR, SNH, n DMtns **O. corymbosa**
 10' Infl > 4 cm, of long, gen unbranched, $\pm$ raceme-like units; anthers glabrous or hairy along dehiscent margin
 11. Upper corolla lobes acute, tips mostly pointed; bracts lanceolate, veins 3-5, inconspicuous; fls short-pedicelled throughout; CA-FP (exc c&s SW) **O. vallicola**

Open, gen sandy, gen urban, disturbed places; gen < 500 m. CW, SW, DMoj; native to e US, widely naturalized, but occurrences scattered. Self-pollinated. PTH.

O. longissima Rydb. Bien, rosetted, minutely strigose; hairs also gen long, spreading, with red, bristle-like bases, sometimes some glandular. ST erect, 6–30 dm. LVS: cauline 5–22 cm, narrowly oblanceolate to ± elliptic, subentire to dentate. INFL: spike. FL: hypanthium 60–135 mm; sepals 23–47 mm, free tips in bud 2–6 mm; petals 28–65 mm, yellow fading reddish orange. FR 25–55 mm, 4–9 mm wide, narrowly lanceolate, ± straight. SEEDS 1–2 mm, angled, irregularly pitted. $2n=14$. Seasonally moist places in creosote-bush scrub, pinyon/juniper woodland; 1000–1700 m. e DMtns (New York Mtns); to Colorado, AZ. [ssp. *clutei* (Nelson) Munz] Gen cross-pollinated. ⚡TRY.

O. primiveris A. Gray Ann, rosetted, minutely strigose, in infl gen glandular; hairs also coarse, with red, blister-like bases or not. ST gen 0 (sometimes erect or ascending, < 3.5 dm). LF 4–28 cm, oblanceolate, wavy-dentate to 1–2-pinnately lobed. INFL: fls in axils. FL: hypanthium 20–72 mm; sepals 7–30 mm, free tips in bud 0; petals 6–40 mm, yellow fading reddish orange to purple. FR 10–60 mm, 4–8 mm wide, lanceolate to ovate, straight, curved, or S-shaped. SEED 3–3.5 mm, irregularly obovate to oblanceolate, papillate, 1 side coarsely wrinkled in distal 1/2, other side with thick, U-shaped area forming groove and small cavity at tip. $2n=14$. Sandy flats, low hills, dune margins, arroyos; 30–1400 m. D; ± sw US, n Mex. Self- or cross-pollinated. 2 intergrading ssp.

ssp. *bufonis* (M.E. Jones) Munz (p. 807) LF grayish green. FL: petals (22)29–40 mm. Habitats of sp. D; to UT, w AZ, nw Mex. Gen cross-pollinated. ⚡TRY.

ssp. *primiveris* LF gen green. FL: petals 6–25(28) mm. Uncommon. Habitats of sp. D; to TX, nw Mex. [ssp. *caulescens* (Munz) Munz] Self-pollinated. ⚡TRY.

O. pubescens Sprengel (p. 807) Ann, bien, rosetted, minutely strigose; hairs also long, spreading, and gen some glandular. ST decumbent to erect, 0.5–8 dm. LVS: cauline 2–8 cm, narrow-oblanceolate to lanceolate or elliptic, pinnately lobed to subentire. INFL: fls in upper axils; buds nodding. FL: hypanthium 15–50 mm; sepals 5–25 mm, free tips in bud 0.1–1 mm; petals 5–35 mm, yellow fading orange. FR 20–45 mm, 2–4 mm wide, cylindric. SEED 1–1.5 mm, subspheric, pitted. $2n=14$. Open places; ± 600 m. c DMoj (Newberry Springs, San Bernardino Co.); to NM, S.Am. [*O. laciniosa* Hill ssp. *p.* (Sprengel) Munz] PTH. CA pls possibly introduced from AZ.

O. rosea L'Hér. (p. 807) Per, rosetted when young, minutely and sometimes densely strigose (lower st sometimes also long-hairy). ST decumbent to ascending, 1–5(10) dm. LVS: cauline 1.5–4 cm, oblanceolate to elliptic, gen subentire to wavy-dentate. INFL: fls in upper axils. FL: hypanthium 4–8 mm; sepals 5–8 mm, free tips in bud 1 mm; petals 5–10 mm, rose to rose-purple. FR much wider toward tip; body 8–10 mm, 3–4 mm wide; valves each with median rib; stalk-like base 5–20 mm, ribbed, tapered. SEEDS clustered in each chamber, 0.5–0.8 mm, obliquely oblanceolate, finely granular-papillate. $2n=14$. Disturbed places; gen < 500 m. WTR; native to TX, Mex, S.Am. Self-pollinated. PTH.

O. speciosa Nutt. (p. 807) Per, rosetted when young, forming large patches from woody caudices and rhizomes, minutely strigose (some hairs also longer). ST weakly ascending to erect, 1–5 dm.

LVS: cauline 2.5–8 cm, oblanceolate to ± elliptic, wavy-lobed. INFL: fls in upper axils; st tip nodding. FL: hypanthium 10–23 mm; sepals 15–30 mm, free tips in bud 1–1.5 mm, white fading pink or rose-purple. FR widening upward (to 3–5 mm), 8-ribbed; stalk-like base 1–2 mm wide, cylindric. SEEDS clustered in each chamber, 1–1.5 mm, obliquely oblanceolate, finely granular-papillate. 14,28,42. Disturbed places; gen < 500 m. WTR; native to c US, c Mex. [var. *childsii* (L. Bailey) Munz] Gen cross-pollinated.

O. stricta Link ssp. *stricta* Ann, bien, rosetted, minutely strigose; hairs also long, spreading, some glandular. ST gen 0 (decumbent), 2.5–10 dm. LVS: cauline 6–10 cm, very narrow-lanceolate, gen slightly wavy, serrate. INFL: fls in upper axils; buds erect. FL: hypanthium 20–45 mm; sepals 14–20 mm, 15–25 mm, yellow fading reddish orange, bases gen spotted. FR 30–40 mm, 3–4 mm wide, ± cylindric (straight toward tip). SEED 1.4–1.8 mm, widely elliptic, pitted. Uncommon. Gen moist, disturbed places; gen < 500 m. native to Chile. PTH.

O. villosa Thunb. ssp. *strigosa* (Rydb.) W. Dietr. (p. 807) Bien, rosetted, minutely strigose, esp in infl also hairs also long, spreading, gen with red, blister-like bases. ST erect, 5–20 dm. LVS: cauline 10–30 cm, lanceolate or elliptic, minutely dentate. INFL: spike, open, few-fl'd; internodes > fr. FL: hypanthium 25–40 mm; sepals 9–18 mm, yellow fading reddish, free tips in bud 0.5–2.5 mm; petals 7–20 mm, yellow fading duller to pale orange. FR 20–35 mm, 4–7 mm wide, lanceolate, ± straight. SEED 1–2 mm, angled, irregularly pitted. $2n=14$. Moist openings in forests; esp 500–2000 m. (Tehama Co.), CaRH (Plumas Co.), MP; to sw Can. (Rydb.) Mackenzie & Bush; *O. biennis* L. and *O. hookeri* A. Gray misapplied] PTH. ⚡TRY.

O. wolfii (Munz) Raven, W. Dietr. & W. Stubbe (p. 807) EVENING PRIMROSE Bien, rosetted, densely minutely strigose; many hairs also with red, blister-like bases, some glandular. ST erect, 5–10 dm. LVS: cauline 5–18 cm, narrowly lanceolate to elliptic, wavy-dentate, upper dentate. INFL: spike. FL: hypanthium 30–46 mm; sepals 17–28 mm, free tips in bud erect, 1–3 mm; petals 13–23 mm, yellow fading reddish orange. FR 30–48 mm, 3–4 mm wide, narrowly lanceolate, ± straight. SEED 1–2 mm, angled, irregularly pitted. $2n=14$. RARE. Coastal sand, incl dunes, roadsides, gen moist places (perhaps also inland); < 100 m. w KR (Del Norte, Humboldt cos.), e KR (Carrville, ± 800 m. w Co.); OR. [*O. hookeri* Torrey & A. Gray ssp. *w.* Munz] PTH. cult.

O. xylocarpa Cov. (p. 807) Per, rosetted, grayish green, short (on fl long, coarse), erect; taproot fleshy. ST 0. LF: main stem ± round to oblanceolate, 26–62 mm; lobes few, gen 3; INFL: fls in axils. FL: hypanthium 27–45(55) mm; sepals 22 mm, tips not free in bud; petals 25–38 mm, yellow fading salmon-red. FR 35–90 mm, 7–11 mm wide, narrowly lanceolate, curved, twisted, wrinkled. SEEDS in 1 row (or near base 2 rows per chamber, 2.4–3.2 mm, obovate; tip gen truncate, coarsely wrinkled, papillate; 1 side with 2 small ridges. $2n=14$. Gravelly pumice meadows, Jeffrey-pine or lodgepole-pine/fir forests; 2200–3100 m. c&s SNH; w NV. Gen cross-pollinated. Locally common. ⚡TRY;DFCLT.

OROBANCHACEAE BROOM-RAPE FAMILY

Lawrence R. Heckard

Ann, per, non-green root parasites; roots modified into absorptive structures; pl an erect, fleshy, mostly underground st (per duncle) with terminal infl. LF: true lvs 0. INFL: spike, raceme, or panicle; bracts alternate, scale-like. FL bisexual; caly cylindric or cup-shaped, lobes 0–5, persistent; corolla ± 2-lipped, lobes gen 5; stamens 4, epipetalous in 2 pairs (sometimes 5th vestigial); ovary superior, chamber 1, placentas gen 2–4, parietal, simple or lobed, stigma gen 2–4-lobed, gen bowl- to funnel-shaped. FR: capsule, loculicidal; valves 2–4. SEEDS many, small, angled; surface netted. 14 gen, 200 spp.; esp temp. Sometimes placed in Scrophulariaceae. [Thieret 1971 J Arnold Arbor 52:404–432]

- 11' Upper corolla lobes obtuse, tips rounded to blunt; bracts $\pm$ ovate, veins > 5 , conspicuous; only lower fls pedicelled; SW, D
12. Corolla 15–24 mm, lips 4–6 mm; calyx lobes gen 7–10 mm; CCo, SCo, Chl
- 12' Corolla 20–25 mm, lips 6–8 mm; calyx lobes 10–16 mm; TR, PR, DMoj
- 9' Corolla 20–50 mm, lips 10–14 mm, widely flaring (see also *O. corymbosa* for pls of SNH, GB)
13. Corolla lips gen purple; calyx lobes, pedicels, and bracts purplish, drying dark purple; coastal dunes and hills, NCo, n&c CCo
- 13' Corolla lips buff to yellowish to pinkish or purple-tinged; calyx lobes, pedicels, and bracts pale to pink-tinged, drying brown; CA-FP, inland (exc ssp. *grandis*)
14. Corolla tube $\pm$ stout, > 4 mm wide at constriction, abruptly expanded to form hump-back throat; lips moderately recurved — s SNH, Teh, TR, PR, s SNE
- 14' Corolla tube slender below, < 4 mm at constriction, gradually expanded; lips widely recurved
15. Corolla 35–50 mm, lower lobes narrowly ovate, > 5 mm wide
- 15' Corolla 20–35 mm, lower lobes narrowly triangular to oblong, < 5 mm wide
16. Pl 4–10 cm; st below infl < 5 cm; infl $\pm$ flat- or convex-topped cluster < 5 cm; moist or vernal places
- 16' Pl 10–35 cm; st below infl gen > 6 cm; infl elongate, 5–20 cm; dry places

O. bulbosa G. Beck (p. 807) Pl 8–30 cm, dark purplish aboveground, white-papillate, not glandular. ST arising from round, coral-like root attachment, stout, thickened at base, bulb-like, with overlapping scales. INFL sometimes pyramid-shaped. FL: calyx 6–10 mm, tube cut nearly to base on lower side, lobes narrowly triangular, gen $<$ or $=$ tube; corolla 10–18 mm, yellowish to purplish, lobes 2–4 mm, obtuse to acute; anthers glabrous to sparsely hairy; stigma 2-lobed, margins recurved. $2n=48$. Openings in chaparral, gen on *Adenostoma fasciculatum*; < 1700 m. s NCoRO, NCoRI, SNF (Eldorado Co. s), SCoRO, SW; Baja CA.

O. californica Cham. & Schldl. Pl 4–35 cm, pale to dark purple aboveground, glandular-puberulent. STS 1 or clustered, slender to stout, branched below or throughout. INFL long or branched and $\pm$ flat- to convex-topped; pedicels 0–4 cm, shorter upward. FL: calyx 12–20 mm, gen pale to pinkish, lobes linear-triangular, $>>$ tube; corolla 20–50 mm, purplish or white to rose with darker veins, moderately glandular-puberulent, lips 10–14 mm, gen widely flaring; upper lip obtuse to rounded; anthers woolly; placentas 4, stigma lobes 2, triangular, margins recurved. Gen dry, $\pm$ rocky soils, on herbs, gen Asteraceae; < 2500 m. CA-FP; to B.C., Baja CA. [*O. grayana* G. Beck misapplied] Ssp. highly variable, intergrading.

ssp. *californica* Pl 5–27 cm, gen (dark) purple aboveground. ST gen branched. INFL < 8 cm, $\pm$ head-like or round-topped. FL: corolla 22–45 mm, throat abruptly wider than tube, 8–10 mm wide, lips purplish, paler. $2n=48$. Uncommon. Sandy or heavy soils of coastal bluffs, gen on *Grindelia*; < 150 m. NCo, n&c CCo. [*O. grayana* G. Beck vars. *nelsonii* Munz & *violacea* (Eastw.) Munz] Intergrades with ssp. *grandis* in Monterey and San Luis Obispo cos.

ssp. *feudgei* (Munz) Heckard (p. 807) Pl 10–30 cm. ST gen branched above, stout. INFL $\pm$ flat- or round-topped; branches gen < 9 cm. FL: corolla 25–35 mm, tube $\pm$ stout, abruptly expanded above sinus, > 4 mm wide at constriction, forming $\pm$ hump-back throat 8–10 mm wide, lips moderately recurved, whitish to yellowish, purple-tinged and veined. $2n=48$. Dry washes, mtn slopes, flats, on *Artemisia tridentata*; 700–2500 m. s SNH, Teh, TR, PR, s SNE; Baja CA. [*O. grayana* G. Beck var. *f.* Munz]

ssp. *grandis* Heckard Pl 8–30 cm. ST gen branched above, stout. INFL gen < 5 cm, round-topped or not. FL: corolla 35–50 mm, pinkish or pale brownish red, veins dark, tube < 4 mm wide at constriction, throat 9–10 mm wide, lips widely recurved, lower lobes narrowly ovate. Uncommon. s CCo, s SCoRO (Santa Barbara Co.), c SCo (Los Angeles Co.), n Chl (Santa Rosa Island).

ssp. *grayana* (G. Beck) Heckard Pl 4–10 cm. ST branched or not, 1–5 cm. INFL < 5 cm, convex to $\pm$ flat-topped, few-fl. FL: corolla 20–30 mm, tube gradually widening to 5–8 mm, lips whitish to yellowish to pale purplish with lavender veins. $2n=48$. Uncommon. Moderately moist meadows, stream margins, gen on *Eriogonum*, Aster; gen 1200–1800 m. NCoRH, n&c SNH, SnFrB (s Sonoma Co., $\pm$ 60 m), MP; to WA. [*O. grayana* G. Beck var. *g.*]

ssp. *jepsonii* (Munz) Heckard Pl 10–35 cm. ST gen branched, > 6 cm. INFL 5–20 cm. FL: corolla 25–40 cm, whitish or pinkish to pale yellowish brown, tube gradually widened to 5–8 mm, veins gen purplish. $2n=48$. Uncommon. Gen dry flats, slopes, gen on herbs and shrubs of Asteraceae; < 2200 m. KR, NCoR, CaRH, SNF, GV, SnFrB, SCoR. [*O. grayana* var. *j.* Munz]

Pls < 12 cm with flat- to round-topped infl on *Heterotheca*. SCoRO have been called ssp. *condensa* Heckard. SCoRO s CCo, s SCoRO, c SCo, n Chl that key here are an under

O. cooperi (A. Gray) A.A. Heller (p. 813) Pl 10–30 cm, dark purplish aboveground, glandular-puberulent; root sometimes a coral-like thickening. STS simple or branched, forming large clumps, stout, little enlarged at base. INFL: calyx 8–12 mm, tube, triangular, acuminate; corolla 18–32 mm, purple, long-stalked, gen glandular, tube lacking ring of hairs; upper lobes 6–10 mm, $>$ lower, obtuse; anthers gen 2, thin, recurved. $2n=24, 48, 72$. Sandy flats, Asteraceae (gen *Ambrosia*, *Hymenoclea*, *Encelia*) (weeds), toes, DSon, in 1960's; < 500 m. D; to UT, AZ, Baja. *ludoviciana* vars. c. (A. Gray) G. Beck & *latiloba* Munz described form (probably best a ssp.), $2n=96$, with smaller lobed corolla and peltate, & bowl-shaped stigma occurs hosts, over range of sp.

O. corymbosa (Rydb.) Ferris (p. 813) Pl 3–17 cm, pale pink-tinged aboveground, glandular-puberulent. ST: branched, stout, gen thickened at base. INFL 3–4 cm, branched, round-topped, few-fl; lower pedicels 5–30 mm below; upper FL: calyx 12–18 mm, lobes $>$ tube, linear-triangular; corolla 15–20 mm, sparsely short-glandular, lips 5–8 mm, purplish to pink, darker, upper lobes rounded; anthers woolly; stigma 2-lobed, peltate. $2n=48, 96$. Openings in sagebrush scrub, gen on *Artemisia tridentata*; 1200–2800 m. n CaR, SNH, GB, n DMtns (Pana Mtms); to B.C., MT, UT. [*O. californica* var. *co.* (Rydb.) Munz] Closely related to *O. californica*, esp ssp. *feudgei*.

O. fasciculata Nutt. (p. 813) CLUSTERED BROOM-RAPE, STS or clustered, 5–20 cm, branched or not. INFL: raceme, round-topped, gen 5–20-fl; bracts > 6 , glandular-puberulent; pedicels 15 cm, shorter upwards; bractlets 0. FL: calyx lobes 3–7 mm, gen tube, deltate, gen $\pm$ acuminate; corolla 15–30 mm, curved, becoming erect, yellow to purple-tinged, lobes rounded to narrowly acute; anthers gen hairy; stigma 2-lobed, recurved. $2n=48$. Dry, gen bare places, gen on shrubs (esp *Artemisia*, *Eriodictyon*, *Eriogonum*); < 3300 m. CA-FP, GB, DMtns; to Yukon, c N.Am, n Mex [var. *franciscana* D.B. Achey; var. *lutea* (C. Parry) D.B. Achey] Intermediate to *O. uniflora*, gen on *Galium*, are scattered in CA (esp w WTR, SNF, NCoR), s OR.

O. parishii (Jepson) Heckard Pl 5–26 cm, $\pm$ yellowish white. ST gen simple, stout, glandular-puberulent. INFL: bracts narrowly ovate, with > 5 conspicuous, parallel veins. FL: calyx 10–20 mm, $\pm$ narrowly triangular, pale; corolla 15–25 mm, buff to pinkish, lips 4–8 mm, lobes rounded, veins reddish; anthers glabrous to hairy. Bare, sandy to rocky soils, gen on shrubs; < 2800 m. SNH, Teh, CCo, SW, W&I, DMtns; Baja CA. [*O. californica* Cham. & Schldl var. *p.* Jepson]

ssp. *brachyloba* Heckard (p. 813) SHORT-LOBED BROOM-RAPE Pl 5–18 cm. INFL 3–8 cm. FL: calyx lobes 7–10 mm; corolla 15–24 mm, lips 4–6 mm, erect or slightly spreading; anthers gen glabrous; stigma lobes gen narrow, recurved. $2n=96$. RARE. Sandy soil near ocean, on shrubs such as *Isocoma Menziesii*; < 300 m. CCo, SCo, Chl; Baja CA.

- 3' Mature fr and ovary oblong or ovate, gen not tapered to a beak, not striped green, prickles $\pm$ dense, stiff; seeds gen > 6 , ovate or oblong, sometimes flat at 1 end; SNF, SW, D *M. horridus*
 4. Corolla deeply cup-shaped; seeds very flat at 1 end; c&s SNF, Teh *M. macrocarpus*
 4' Corolla shallowly cup-shaped; seeds not very flat at either end; SW, Dson var. *macrocarpus*
 5. Staminate fls 8–13 mm wide; seeds 15–20 mm; mainland var. *major*
 5' Staminate fls 14–30 mm wide; seeds 20–33 mm; Chl

M. fabaceus (Naudin) E. Greene (p. 543) CALIFORNIA MAN-ROOT
 Herbage gen not glaucous. FL: corolla rotate, yellowish green, cream-colored or (esp inland) white. FR 4–5 cm, $\pm$ round; prickles sparse to dense, < 12 mm, $\pm$ stiff, unhooked. SEEDS 2–4, 18–24 mm, ovate to oblong, $\pm$ flat on sides or not. $2n=32$. Streamsides, washes, shrubby and open areas; < 1600 m. CA-FP (exc n NW, n CaR). Highly variable; pls outside SnFrB and CCo are assignable to var. *agrestis* (E. Greene) K.M. Stocking (fr prickles flexible, < 5 mm; seeds gen 2–3, not flat on sides), which intergrades $\pm$ completely with the pls considered var. *f.*; more study needed. DRN: 7,8–10,14–24;INV.

M. horridus (Congdon) Dunn (p. 543) Herbage not glaucous. FL: corolla deeply cup-shaped, white. FR 9–20 cm, oblong, rounded at both ends; prickles dense, stiff. SEEDS gen 6–16(24), 26–32 mm, oblong or ovate, very flat at 1 end. Shrubby and open areas; < 1000 m. c&s SNF, Teh.

M. macrocarpus (E. Greene) E. Greene (p. 543) Herbage not glaucous. FL: corolla shallowly cup-shaped, white. FR 5–12 cm, oblong, gen rounded at both ends (sometimes with sharp beak); prickles $\pm$ dense, stiff. SEEDS gen 4–12(24), 13–33 mm, $\pm$ round,

oblong, or ovate, angled at tip or not. $2n=32,64$. Washes, shrubby or open areas; < 900 m, SW, Dson; Baja CA.

var. *macrocarpus* FL: staminate 8–13 mm wide. SEED 13–20 mm. Habitats of sp. SW mainland, Dson; Baja CA.

var. *major* (Dunn) K.M. Stocking FL: staminate 14–30 mm wide. SEED 20–33 mm. Habitats of sp. Chl. Larger, but much like var. *macrocarpus*; more study warranted.

M. oreganus (Torrey & A. Gray) Howell (p. 543) COAST MAN-ROOT Herbage not glaucous. FL: corolla deeply cup-shaped, white. FR 4–8 cm, ovate, tapered to a beak, gen striped dark green; prickles sparse to dense (gen 0 at tip), flexible. SEEDS gen 3–6, 16–22 mm, disc-shaped, $\pm$ flat. $2n=32$. Shrubby or open areas, forest edges; < 1800 m. NW, SnFrB; to B.C.

M. watsonii (Cogn.) E. Greene (p. 543) Herbage glaucous. FL: corolla deeply cup-shaped, white. FR 2–3.5 cm, $\pm$ round, often striped dark green; prickles ± 0 to dense, flexible, often hooked. SEEDS 1–4, 11–14 mm, $\pm$ round. Shrubby areas, forest edges; < 1200 m. NCoRI, CaRF, n SNF, ScV.

CUSCUTACEAE DODDER FAMILY

Tania Beliz

Ann, parasitic vine. ST twining, $\pm$ thread-like, yellow-green to bright orange, gen glabrous. LVS 0 or scale-like, ± 2 mm, gen triangular to lanceolate. INFL: cyme or cluster (rarely fls solitary), gen head- or spike-like, axillary, sometimes bracted. FL bisexual, radial; calyx gen persistent, lobes gen 4–5, gen overlapped; corolla gen deciduous, < 6 mm, mostly white, tube gen appendaged opposite stamens, lobes 4–5; stamens 4–5, alternate corolla lobes; ovary superior, chambers 2(3), 2-ovuled styles gen 2, stigma gen 1 per style, gen $\pm$ head-like. FR: capsule (circumscissile or irregularly dehiscent) or berry-like. 24 genus, ± 150 spp.: esp Am trop; some crop pests. Sometimes incl in Convolvulaceae.

CUSCUTA DODDER

The only genus (Arabic: ancient name)

1. Corolla appendages 0–0.1 mm *C. californica*
 2. Ovary and fr conic, top acute var. *apiculata*
 2' Ovary and fr obovoid, top depressed var. *papillosa*
 3. Perianth papillate var. *breviflora*
 3' Perianth not papillate var. *californica*
 4. Corolla bulged out between stamens *C. approximata*
 4' Corolla not bulged out between stamens *C. denticulata*
 1' Corolla appendages 0.7–2.5 mm *C. pentagona*
 5. Stigma cylindric *C. indecora*
 5' Stigma $\pm$ head-like var. *indecora*
 6. Corolla shallowly bell- to urn-shaped, tube $\pm$ shorter than wide var. *neuropetal*
 7. Corolla appendage divisions gen 0–few, knob-like *C. subinclusa*
 7' Corolla appendage divisions few–many, finger-like *C. cephalanthi*
 8. Ovary and fr top unthickened
 8' Ovary and fr top thickened
 9. Pedicel and calyx not papillate
 9' Pedicel and calyx $\pm$ papillate
 10. Corolla tube longer than wide
 10' Corolla tube shorter than wide
 11. Perianth parts obtuse, gland-dotted, not papillate; corolla appendage divisions few, scattered, finger-like; near streams, rivers, lakes



Pastizales y zonas abiertas sobre suelos preferentemente básicos, entre 200-1000 m. Poco frecuente. Sierra Norte cordobesa, Subbética cordobesa, Grazalema.
Distribución general. W de la Región Mediterránea.

3. *Tragopogon crocifolius* L., *Syst. Nat.*, ed. 10, 2: 1191 (1759)

T. castellanus Levier in Leresche & Levier, *Deux Excurs. Bot.* 26 (1881)

T. stenophyllum Jordan, *Obs. Pl. Crit.* 7: 42 (1849)

Anuales o bienales, con raíz gruesa fusiforme. Tallos de 30-60 cm, simples o ramificados. Hojas lineares, ligeramente ensanchadas en la base, glabras; las caulinares de 6-10 mm de anchura en la base. Pedúnculos ligeramente engrosados en la zona apical. Involucro con 5-7 brácteas. Brácteas involucrales 1,5-2 veces más largas que las lígulas. Lígulas purpúreas. Brazos estilares amarillos. Aquenios de 36-40 mm, muricados longitudinalmente, con pico de 17-26 mm, tetragono y marcadamente ensanchado en la parte superior. Vilano de 23-30 mm, plumoso. $2n = 12$. Florece en Mayo.



68. *Chondrilla* L., *Sp. Pl.* 796 (1753) [*Gen. Pl.*, ed. 5: 348, 1754] (*)

Hierbas bienales o perennes, caulescentes. Hojas alternas, de enteras a pinnatífidas. Capítulos generalmente sentados, formando una panícula espiciforme. Involucro cilíndrico, con 2 filas de brácteas. Brácteas involucrales externas mucho más cortas que las internas. Receptáculo plano, glabro, sin brácteas interseminales. Lígulas amarillas. Aquenios con numerosas costillas y con pico muricado en la parte superior y con una corona de 5 escamas entre el cuerpo del aquenio y el pico. Vilano formado por pelos simples.



Bordes de caminos, campos incultos, generalmente sobre suelos básicos. Muy común. Todo el territorio.
Distribución general. C y S de Europa, NW de África, W y SW de Asia.

1. *Chondrilla juncea* L., *Sp. Pl.* 796 (1753)

Tallos de 40-80 cm, generalmente ramificados desde la base, glabros o con pelos rígidos en la parte inferior. Hojas basales oblanceoladas, pinnatífidas; las caulinares lineares, enteras o dentadas, semejantes a las brácteas. Involucro generalmente con indumento farinoso. Brácteas externas ovadas, de 6-8 veces más cortas que las internas; las internas linear-lanceoladas. Lígulas con tubo de 3-5 mm y limbo de 5,5-8 mm. Brazos estilares amarillos. Anteras de 3,5-4,2 mm, amarillas. Aquenios de 6-9,5 mm, con pico de 2,5-5 mm. Vilano de 5-6 mm. $2n = 15, 30$. Florece y fructifica de Junio a Agosto (Septiembre-Noviembre).



(*) Por S. Talavera

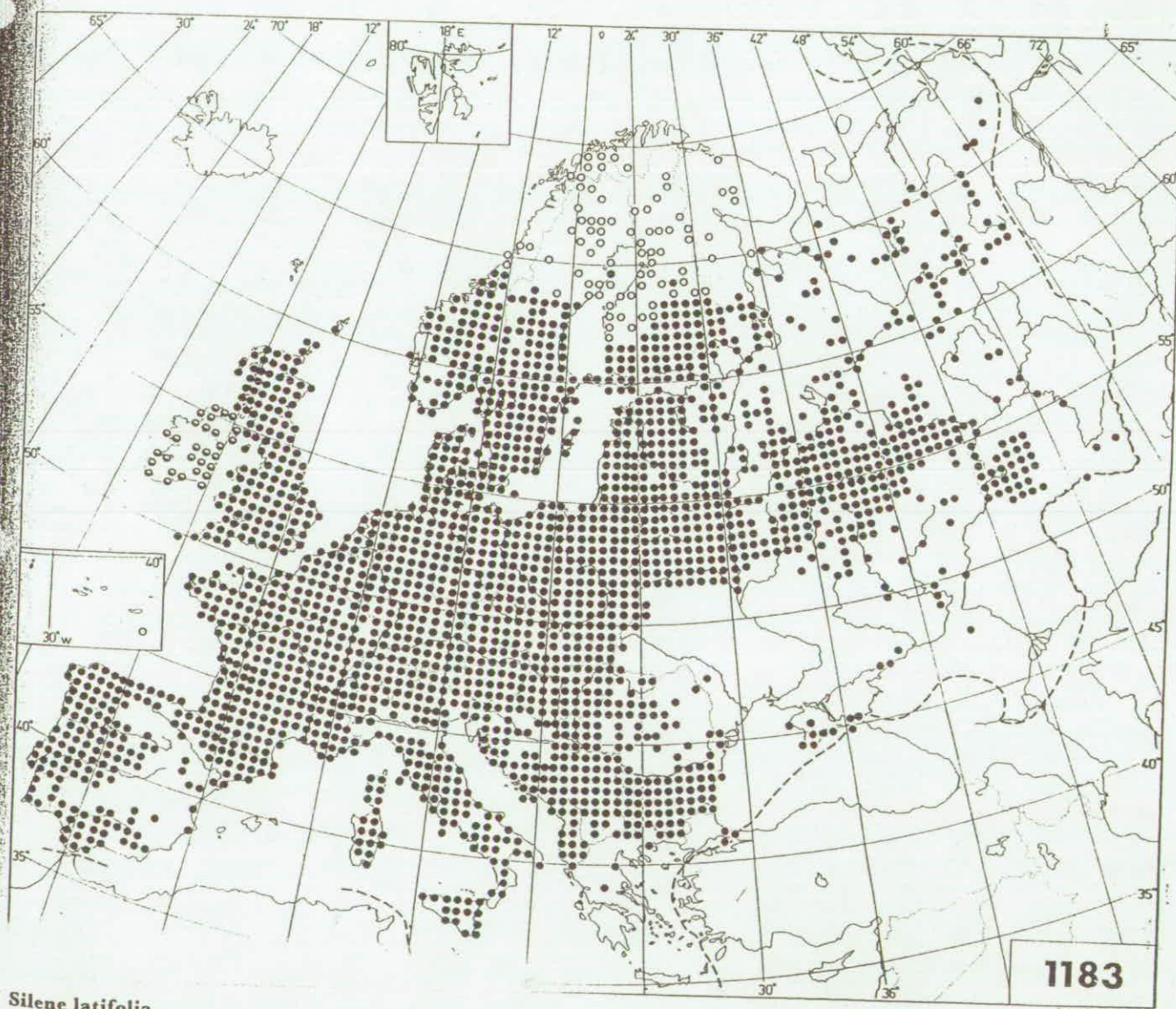
***S. latifolia* subsp. *alba* (Miller) Greuter & Burdet**

Lychnis alba Miller; *L. arvensis* P. Gaertner, B. Meyer & Scherb.; *L. pratensis* Rafn; *L. vespertina* Sm.; *Melandrium album* (Miller) Garcke; *M. dioicum* (L.) Cosson & Germ. subsp. *album* (Miller) D. Löve; *M. pratense* (Rafn) Röhling; *M. vespertinum* (Sm.) Fries; *Silene alba* (Miller) E.H.L. Krause, non Muhl. ex Britton; *S. pratensis* (Rafn) Godron & Gren.

Nomenclature. W. Greuter & T. Raus (eds.), *Willdenowia* 12 (Optima Leaflet 127): 189 (1982).

Diploid with $2n=24$ (Br, Bu, Cz, Fe, Ga, Ge, Gr, Ho, It, Ju, Po): *Fl. Eur.*; V. Sorsa, *Ann. Acad. Scient. Fenn. A IV* 58: 9 (1962); M. Skalińska et al., *Acta Biol. Cracov., ser. Biol.* 9: 37 (1966); Májovský et al. 1970 a: 17 (all three as *Melandrium album*); J.N. Findlay & J. McNeill, *Taxon* 22: 286 (1973) (as *Silene alba*); T.W.J. Gadella, *Proc. K. Nederl. Akad. Wetensch., ser. C* 76: 304 (1973); S.I. Kožuharov & A.V. Petrova, *Taxon* 23: 377 (1974) (as *S. alba*); B. Kieft & J.C. van Loon, *Taxon* 27: 524 (1978); J.C. van Loon & B. Kieft, *Taxon* 29: 538 (1980) (both as *S. alba* subsp. *alba*); G. Natarajan, *Taxon* 30: 698 (1981); A. Strid & R. Franzén, *Taxon* 30: 833 (1981) (both as *S. alba*); Uotila & Pellinen 1985: 10.

Notes. Al, Au, [Az], Be, Br, Bu, Co, Cz, Da, Fe, Ga, Ge, Gr, *Hb, He, Ho, Hs, Hu, It, Ju, Lu, No, Po, Rm, Rs(N, B, C, W, K, E), ?Sa, Si, Su. "Widespread" (*Fl. Eur.*). Presence in Sa doubtful, according to Pignatti *Fl.* 1982: 252, and W. Greuter & T. Raus (eds.), *Willdenowia* 14 (Optima Leaflet 140): 47 (1984). Not mapped separately.



Silene latifolia

Silene noctiflora L. — Map 1182.

Elisanthe noctiflora (L.) Rupr.; *Melandrium noctiflorum* (L.) Fries

Diploid with $2n=24$ (Cz, Su): Fl. Eur.; Májovský et al. 1970 a: 17; L. Frey, *Fragm. Flor. Geobot.* 17: 252 (1971) (both as *Melandrium noctiflorum*).

Notes. Cr and Hs omitted (given in Fl. Eur.): W. Greuter, *Mem. Soc. Brot.* 24: 155 (1974). Gr added (not given in Fl. Eur.). Only as a casual in Is ([Is] in Fl. Eur.). Not native in Rs(N) (given as native in Fl. Eur.).

Total range. MJW 1965: 140c; Hultén Alaska 1968: 444; A. Zajac, *Origin Archaeoph. Poland*, p. 32 (Kraków 1980).

Silene latifolia Poiret — Map 1183.

Lychnis alba Miller; *L. arvensis* P. Gaertner, B. Meyer & Scherb.; *L. divaricata* Reichenb.; *L. macrocarpa* Boiss. & Reuter; *L. pratensis* Rafn; *L. vespertina* Sm.; *Melandrium album* (Miller) Garcke; *M. balansae* Boiss.; *M. boissieri* Schischkin; *M. dioicum* auct. pro parte, non *Lychnis dioica* L.; *M. divaricatum* (Reichenb.) Fenzl; *M. eriocalycinum* Boiss.; *M. latifolium* (Poiret) Maire; *M. macrocarpum* (Boiss.) Willk.; *M. marizianum* Gand.; *M. pratense* (Rafn) Röhling; *M. vespertinum* (Sm.) Fries; *Silene alba* (Miller) E.H.L. Krause, non Muhl. ex Britton; *S. pratensis* (Rafn) Godron & Gren. — Excl. *Melandrium astrachanicum* Pacz. and *M. glutinosum* Rouy

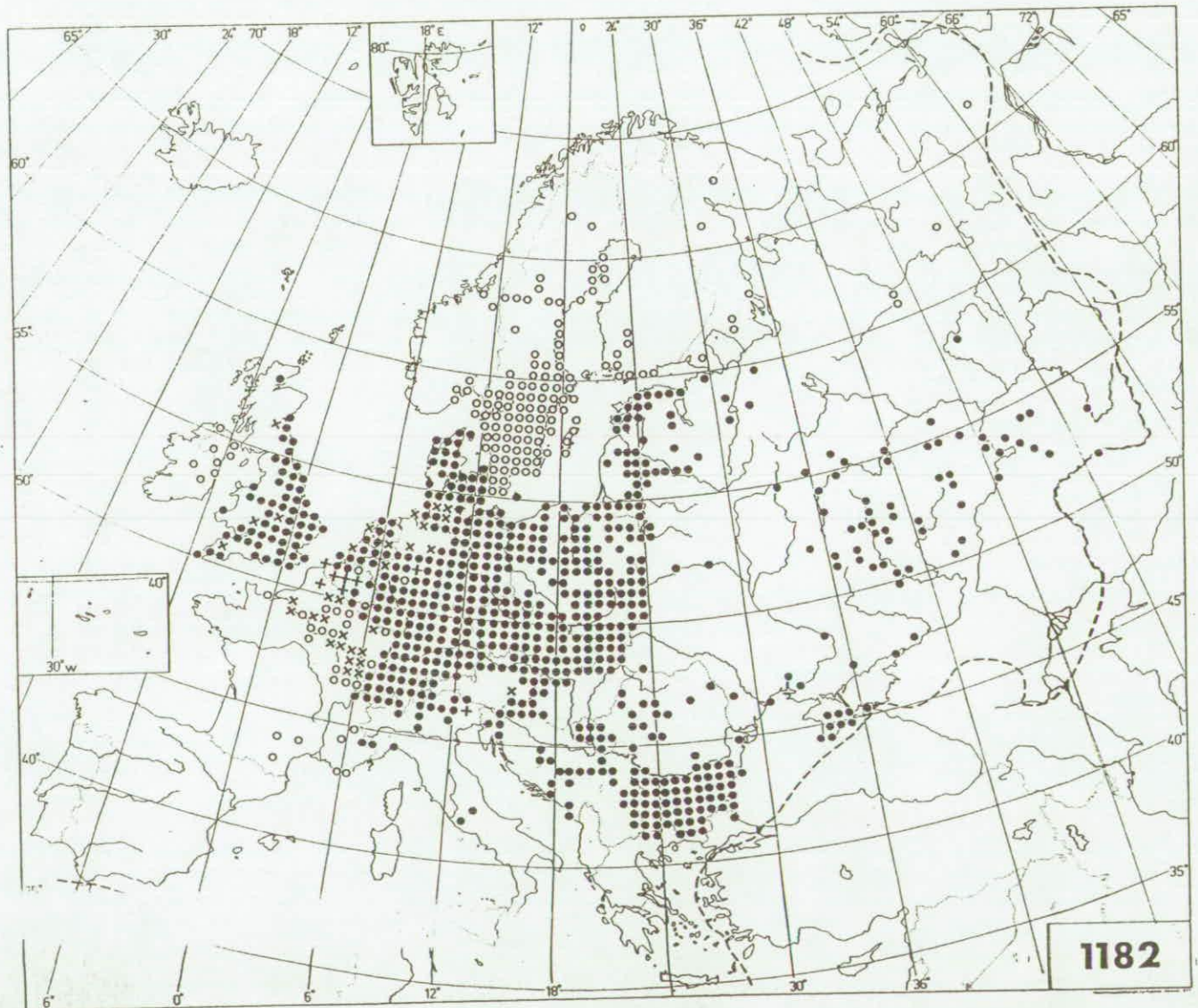
Generic delimitation. J. McNeill, *Canad. Jour. Bot.* 56: 297—308 (1978).

Nomenclature. J. McNeill & H.C. Prentice, *Taxon* 30: 27—32 (1981).

Taxonomy. Concerning infraspecific differentiation (pollen morphology), see H. C. Prentice et al., *Canad. Jour. Bot.* 62: 1259—1267 (1984).

Notes. [Az] added (not given in Fl. Eur.): A. Hansen, *Anuário Soc. Brot.* 41: 46 (1975). Cr omitted (indirectly given in Fl. Eur.): W. Greuter, *Mem. Soc. Brot.* 24: 139 (1974).

Total range. Hegi 1979: 1134.



Silene noctiflora

- (1887) = *P. Kernerii* $\times$ *tuberosa* Ohenev. (1910). — *C. Tic.* (*A. Ribbia*, *V. Tremola*, *M. Generoso*) e *V. d'Ossola* in *V. Formazza*.
- P. cenisia* $\times$ *tuberosa* = *P. Rouyana* F. O. Wolf (1902). — *V. d'Aosta al Bronillot di Cogne*.
- P. cenisia* $\times$ *rhaetica* = *P. Mantzii Bonati* (1912). — *V. d'Aosta in V. di Cogne*.
- P. cenisia* $\times$ *rostrata* = *P. Vaccarii Wilcz.* (1903). — *V. d'Aosta a Valnontey*.
- P. cenisia* $\times$ *verticillata* = *P. Mailleferii L. Vacc. et Wilcz.* (1903). — *V. d'Aosta a Valnontey*.
- P. rhaetica* $\times$ *cenisia* = *P. Martellii Bonati* (1911). — *Alpi piem. al M. Cenisio e fra Candore e la Colombara*.
- P. tuberosa* $\times$ *gyroflexa* Bég. (1902) = *P. Verloti et P. gyrofl. x tuber.* Arv.-T. (1873). — *Trento a M. Gazzo, C. Tic. al M. Generoso*.
- P. gyroflexa* $\times$ *tuberosa* Penzig (1883) = *P. tuberosa* $\times$ *fasciculata* Bell. (1857) = *P. incarnata* $\times$ *tuber.* Caruel (1885) = *P. Penzigi Stein.* (1887). — *C. Tic. al M. Generoso e S. Gottardo, Aosta a Gressoney, Alpi Mar. al Pizzo d'Ormea*.
- P. gyroflexa* $\times$ *leptostachya* Bég. (1902) = *P. Kernerii et P. gyroflexa* $\times$ *elongata* Huter (1873). — *Bellun. sui M. Serva e Pavione, Trent. in V. di Non sul M. Roen.*
- P. leptostachya* $\times$ *gyroflexa* n. comb. = *P. veneta et P. elongata* $\times$ *gyroflexa* Huter (1873). — *Bellun. sul M. Serva*.
- P. gyroflexa* $\times$ *cenisia* = *P. pedemontana* F. O. Wolf (1903). — *V. d'Aosta in V. di Cogne sul M. Brunillat a 2200 m.*
- P. recutita* $\times$ *tuberosa* = *P. Huteri Kern.* (1870) = *P. murithiana et P. tuber.* $\times$ *recutita* Arv.-T. (1880). — *Trent. a Campagnazza di S. Pellegrino, Gr. S. Bernardo*.
- P. rosea* $\times$ *rostrato-capitata* Bonati (1918) = *P. Hausmanni et P. rosea* $\times$ *rostrata* Huter (1883). — *Friuli occ. sul M. Boscada (m. Garofala) fra Cimolais ed Erto*.

FAM. CXIII. OROBANCHACEAE.

(Gen. 11, spec. 150 circa, per la massima parte dell'Eur., Afr. bor., As. extra-trop. ed Am. bor. e mer., poche fra i Trop.)

Proprietà ed usi. — Hanno proprietà astringenti ed amare, ma ora non si usano più. Alcune spec. sono assai dannose alle piante colt. sulle cui rd. vivono parassite.

Chiave dei generi.

- 1 Rz. nullo. Corolla a labbro super. 2-loba o 2-fida. 778 *Orobanche*
— Rz. ramoso. Corolla a labbro super. intero o smarginato. 779 *Lathraea*

Gen. 778. *Orobanche* L. (1735) (1).

(Spec. 120, delle Reg. temp. e calde bor., 1 del Chile ed Austral. occ., 3 nat. al Capo di B. Sp.).

1 bratteole laterali. Calice 4- più rr. 5-dentato. Sez. I. KOPSIA 2
1 bratteole. Calice di 2 pezzi distinti o brevem. saldati, bifidi,
1 bratteole o rr. interi. Sez. II. EUOROBANCHE 7

La specie già accuratam. elaborato, nella Flora Anal., dal Béguinot sulla guida del Beck: *Monographie d. Gatt. Orobanche*, in « Bibl. Bot. » n. 19, Cassel 1890 e che qui non subisce modificazioni sostanziali, all'infuori della riunione del *Lathraea* con *Orobanche*.

femeninas de 2,5-3,5
línea ovados y obtuso;
línea bipartida, elíptica
nales vilosos en la b.
Cápsula 10-14 x 8-12
1,2-1,5 mm, densame-
convexos. $2n=24^*$; n

Sotobosques, orlas de
europeoiberiana, rara en la m
Península Ibérica. Esp.: (B

72. *S. marizii* Samp.
Porto 4: 126 (190

Melandrium viscosum
M. glutinosum Rouy
S. dioica subsp. *glutin*
Ind. loc.: "Terrenos
do Castello, arred. de
Monte (Hennig)." [sc
lc.: Mariz in Bot. Soc

Planta perenne, d
sa, fétida. Tallos erect
herbácea; las basales
gamente pecioladas;
mente pecioladas; la-
diciosos paucifloros.
flores femeninas de
ción; flores masculin
verdoso -a veces los
gular-subulados. Lim-
lígula corolína bipart
tos estaminales vilos
dientes rectos. Semill
sos, de caras convexas
dorso convexo. $2n=24$.

Subrúpica, en roqueños graníticos; 600-1500 m. IV-VIII (IX). ● C de la Península Ibi-
de Portugal. Esp.: Av. Port.: BA (BB) BL DL MI (TM).

73. *S. latifolia* Poirer, Voy. Barbarie 2: 165 (1789)

Melandrium pratense (Rafn) Röhling, Deutschl. Fl. ed. 2: 274 (1812)
M. divaricanum (Reichenb.) Fenzl in Ledeb., Fl. Ross. 1: 328 (1842)
S. alba subsp. *divaricata* (Reichenb.) Walters in Feddes Rept. Spec. Nov.
(1964)
M. macrocarpum (Boiss. & Reuter) Willk., Icon. Descr. Pl. Nov. 1: 28 (1833)
M. album (Miller) Garcke, Fl. N. Mitt.-Deutschland ed. 4: 55 (1858)
S. alba (Miller) E. H. L. Krause in Sturm, Deutschl. Fl. ed. 2: 5: 98 (1901)
ton (1893)
S. latifolia subsp. *alba* (Miller) Greuter & Burdet in Willdenowia 12: 165 (1981)
S. alba subsp. *mariziana* (Gand.) Franco, Nova Fl. Portugal 1: 550 (1971)

judos -a veces los de las flores mascu-
s 7-14 mm, bífido, rosado; lígula coro-
la parte superior. Filamentos estami-
noco desarrollado y soldado al cáliz.
dientes recurvados. Semillas 1-1,5 x
tubérculos obtusos, de caras y dorso

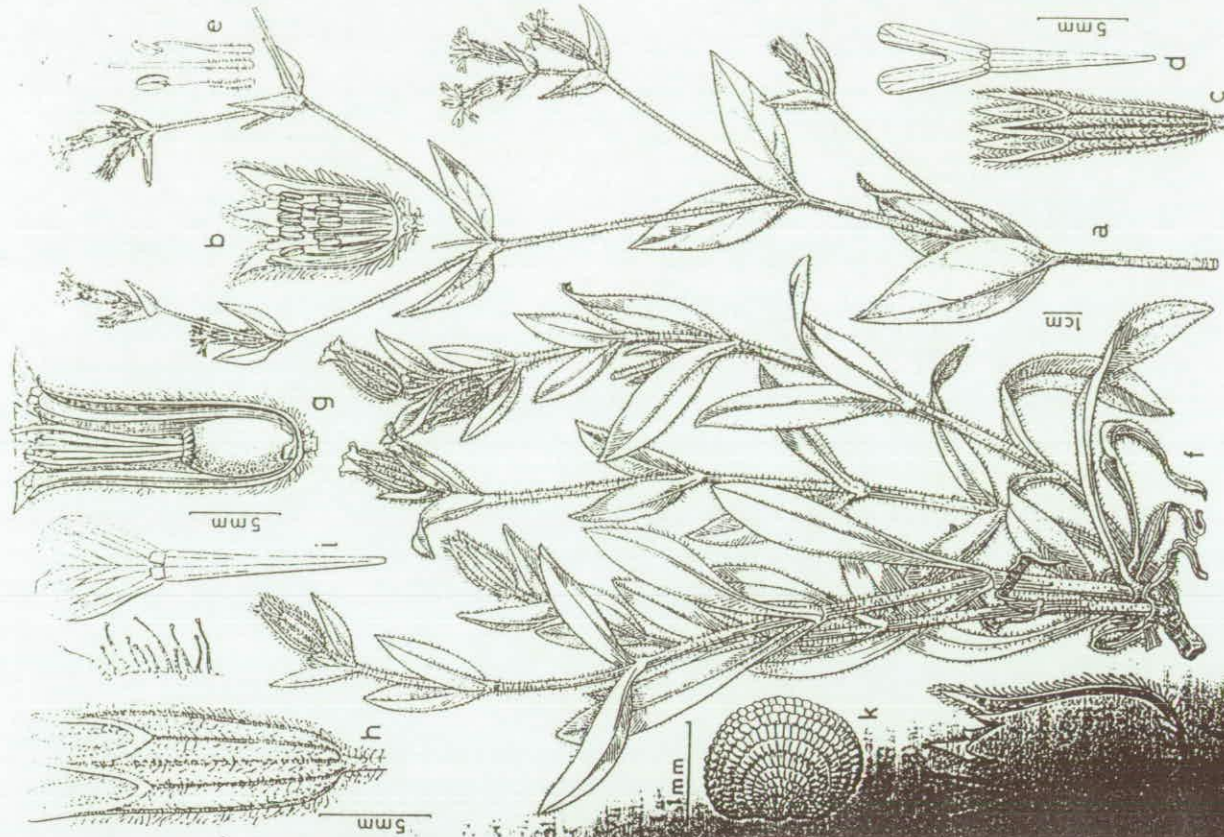
0-2100 m. IV-VIII. Muy frecuente en la región
; como introducida, en el N de América. N de la
O Or P (Po) S (Sa) So SS Vi Za. Port.: BA Mi.

Polytechn. [Marizii]

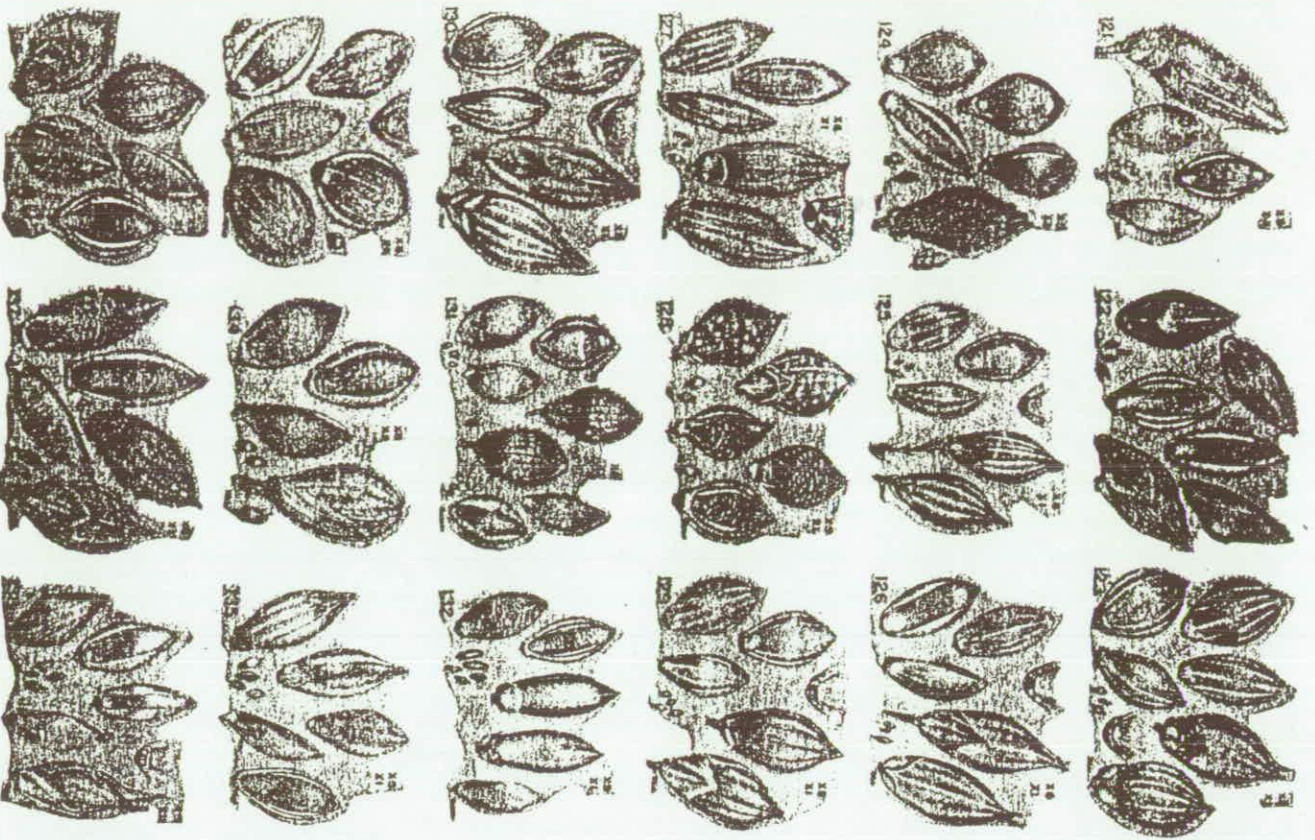
5: 98 (1887), nom. illeg. [syn. subst.]
1: 327 (1894)
Fl. Portugal 1: 550 (1971)
Pantíficas da região submontan. Mangualdes: Senhora
Marreiro (M. Ferreira), serra do Caramulo: S. João do
So. Brot. 5: 98 (1887)
pag. 104 (1887) [sub *M. viscosum*]; lám. 113

rizomata. pluricaule, densamente glandu-
lentes, poco ramificados. Hojas de consisten-
x 3,5 cm, de espatuladas a oblanceoladas; la-
de oblanceoladas a oval-lanceoladas; cor-
semejantes a las hojas superiores. Pedicelos
arqueados, patentes o reflejos, en la fructi-
esies. Cáliz 10-16(20) mm, ovoideo, glandu-
Flores masculinas rojizas; dientes (3)4-7 mm
los pétalos 5-10 mm, bífido, blanco o blanco-
lígula; una auriculada en la parte superior. Sp-
Cápsula 12-15 x 10-13 mm, subcóni-
dientes rectos. Semillas 1,3 x 1,4-1,7 mm, tuberculadas, con tubérculo
sos, de caras convexas y dorso convexo. $2n=24$.

Subrúpica, en roqueños graníticos; 600-1500 m. IV-VIII (IX). ● C de la Península Ibi-
de Portugal. Esp.: Av. Port.: BA (BB) BL DL MI (TM).

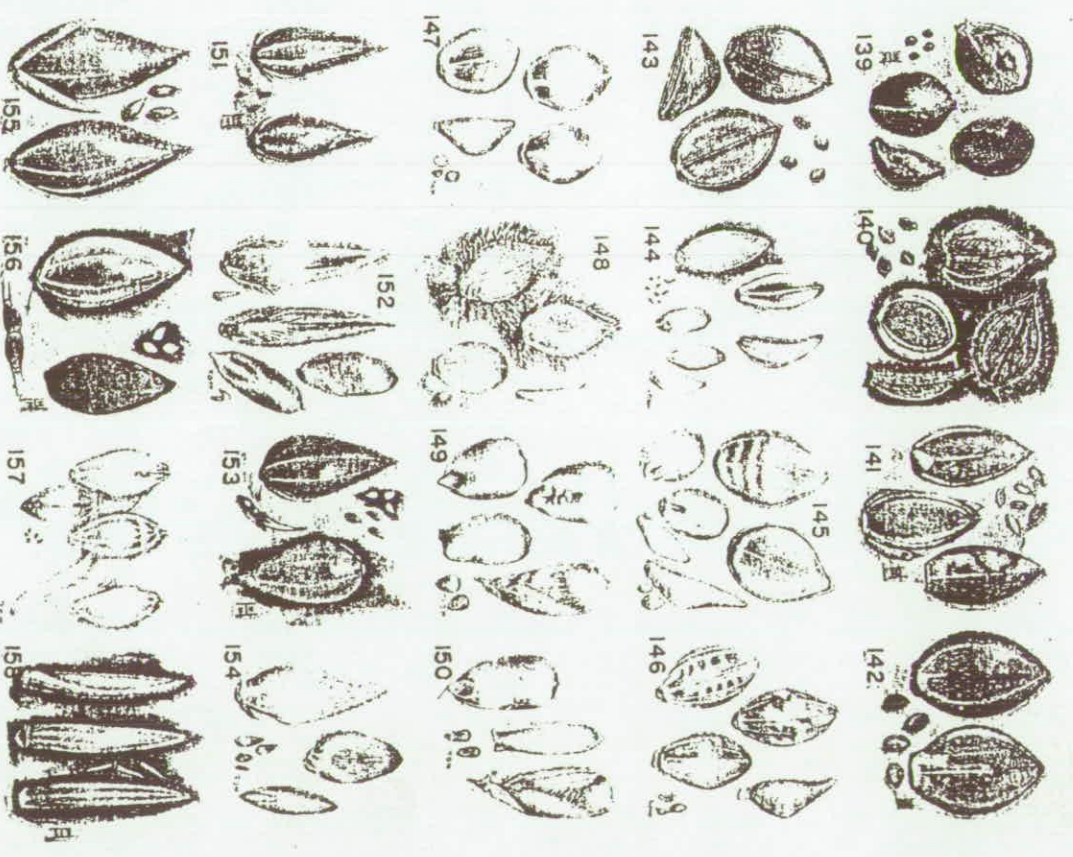


Marizii, a-c) Serra Amarela, Minho (MA 271135); f-i) Valle de Ambles, Ávila (MA 256635); a) hábito de un pie masculino; b) sección longitudi-
nal en la antesis; d) pétalo; e) estambres; f) hábito de un pie femenino; g) sección
longitudinal del cáliz en la antesis y detalle del indumento; h) cápsula; i) cápsula; k) semilla.



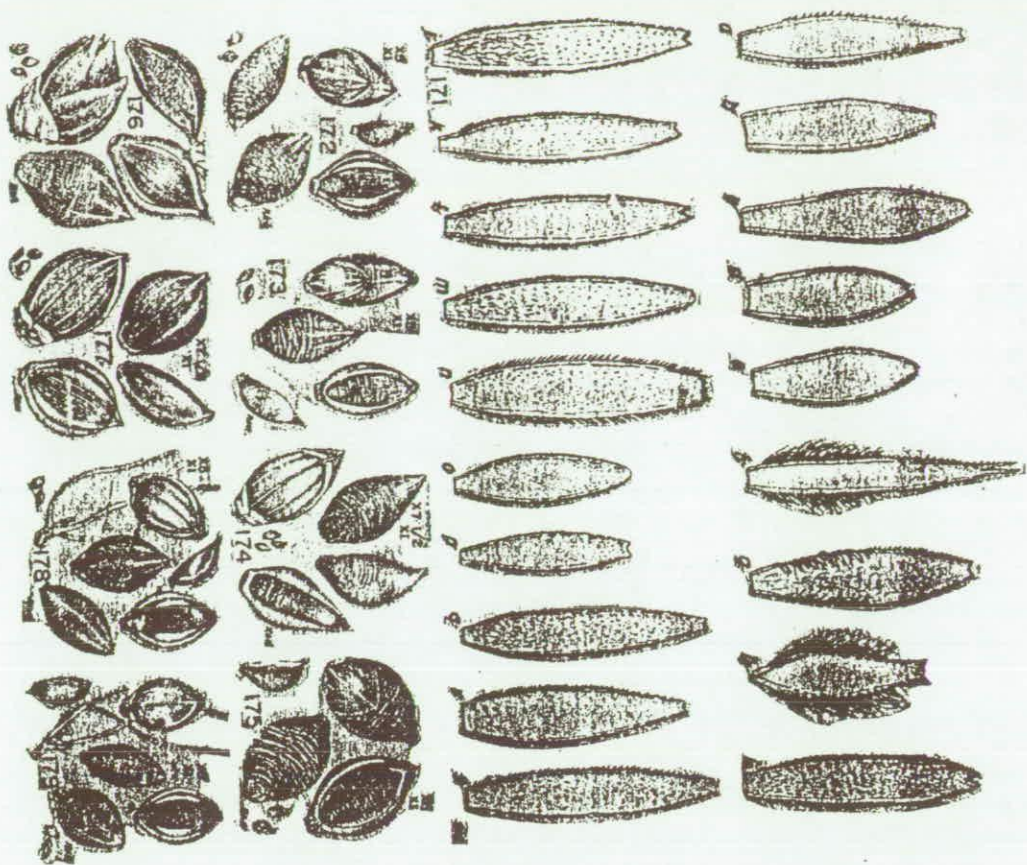
(Gramineae (121-138))

121. *Panicum anceps*
 122. *Panicum antidotale*
 123. *Panicum beryll*
 124. *Panicum brevigranatum*
 125. *Panicum guttifer*
 126. *Panicum capillare* var. *occidentale*
 127. *Panicum dielsianum*
 128. *Panicum fastigiatum*
 129. *Panicum guttifer*
 130. *Panicum himalaicum*
 131. *Panicum huachucae*
 132. *Panicum maximum*
 133. *Panicum miliaceum*
 134. *Panicum obtusum*
 135. *Panicum purpurascens*
 136. *Panicum ramosum*
 137. *Panicum teranum*
 138. *Panicum tygatum*



(Gramineae (139-158))

139. *Phalaris boeotica*
 140. *Phalaris distachya*
 141. *Phalaris distachya*
 142. *Phalaris distachya*
 143. *Phalaris distachya*
 144. *Phalaris distachya*
 145. *Phalaris distachya*
 146. *Phalaris distachya*
 147. *Phalaris distachya*
 148. *Phalaris distachya*
 149. *Phalaris distachya*
 150. *Phalaris distachya*
 151. *Phalaris distachya*
 152. *Phalaris distachya*
 153. *Phalaris distachya*
 154. *Phalaris distachya*
 155. *Phalaris distachya*
 156. *Phalaris distachya*
 157. *Phalaris distachya*
 158. *Phalaris distachya*

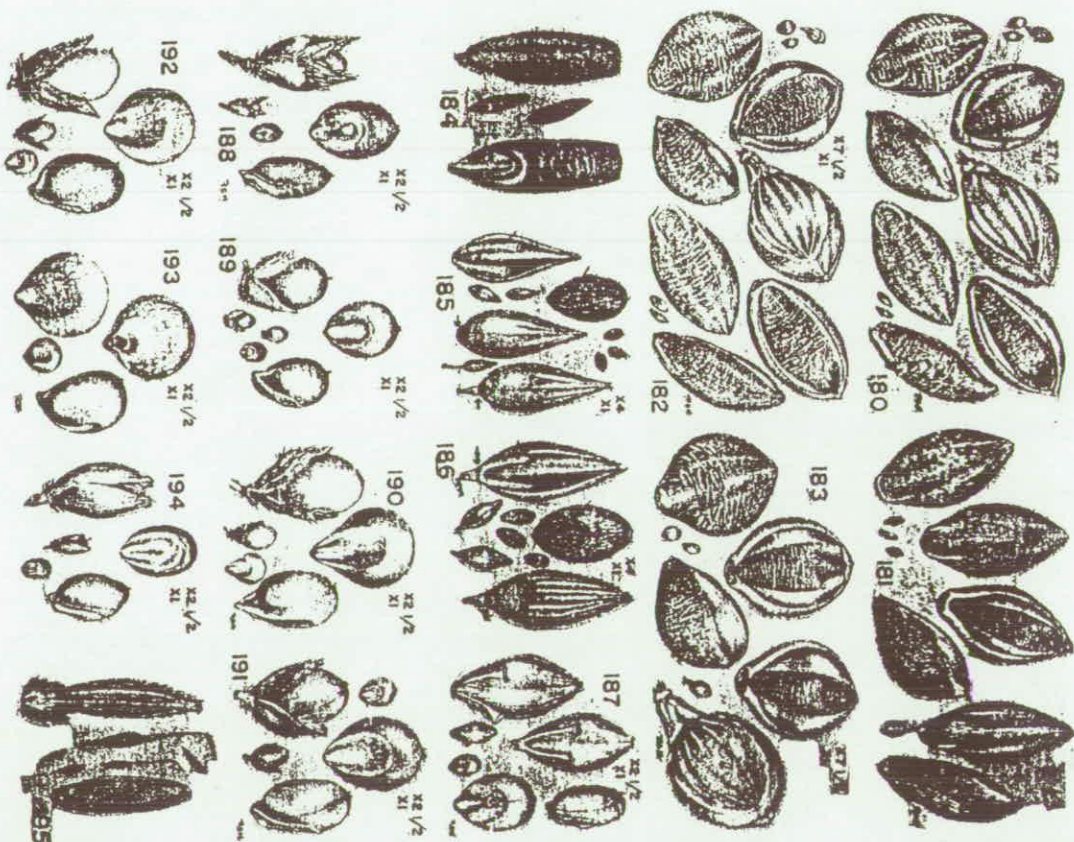


Gramineae (171-179)

171. *Poa* spp. Shape and pubescence of paleas.
 a. *P. pratensis*
 b. *P. trivialis*
 c. *P. nemoralis*
 d. *P. compressa*
 e. *P. palustris*
 f. *P. annua*
 g. *P. arvensis*
 h. *P. juncea*

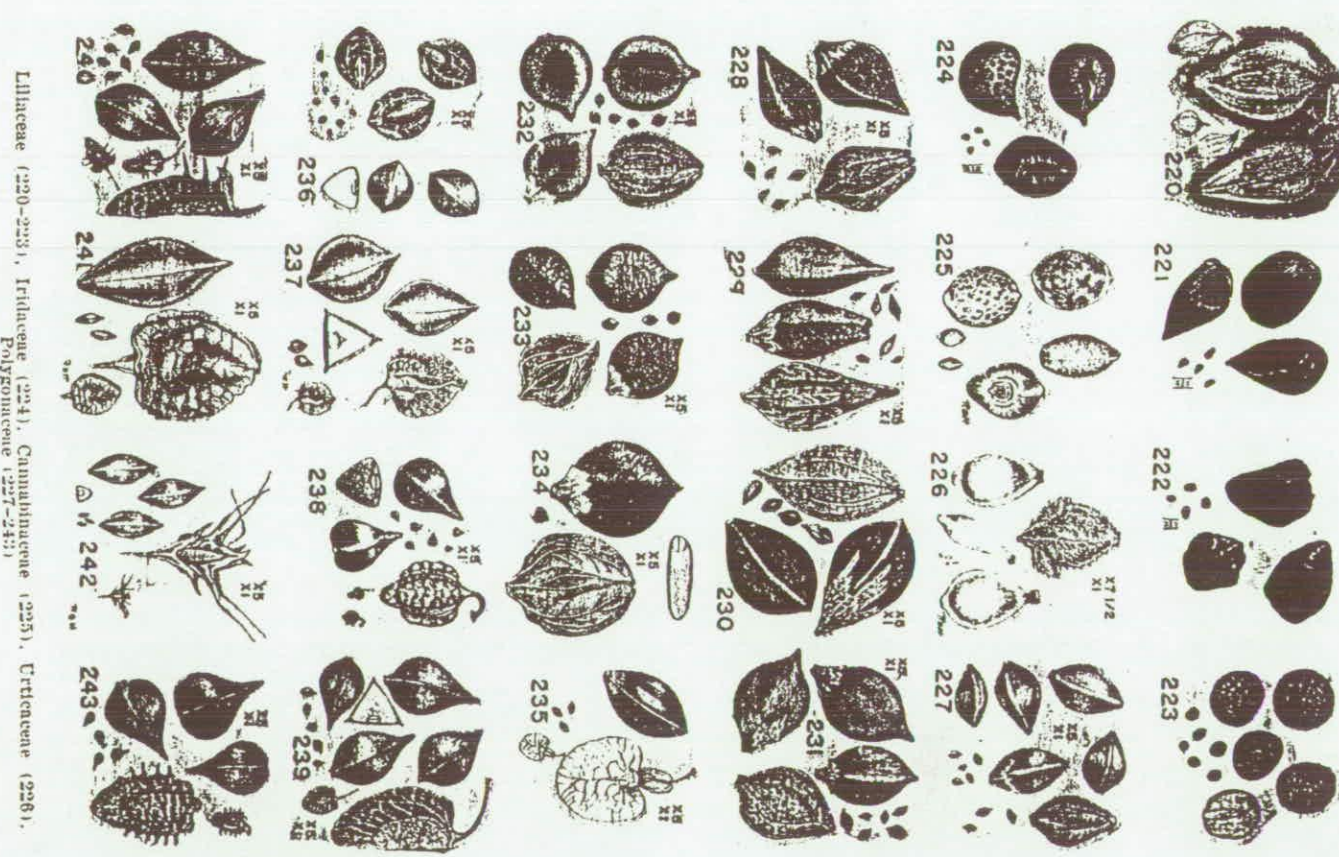
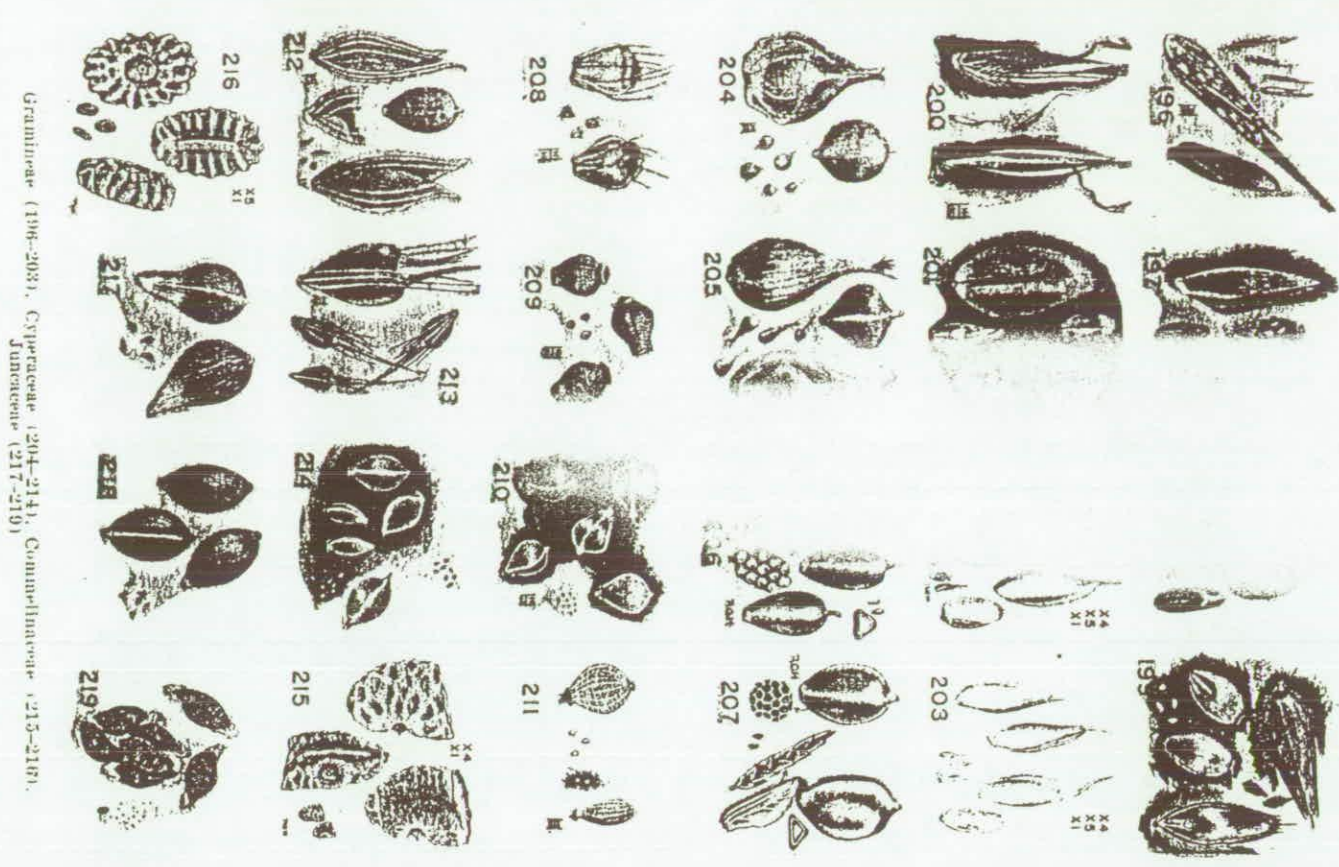
i. *P. secunda*
 k. *P. nutans*
 l. *P. annua*
 m. *P. canina*
 n. *P. canina*
 o. *P. glauca*
 p. *P. interior*
 q. *P. longiligula*
 r. *P. pendulana*
 s. *P. pendulana*
 t. *P. pendulana*

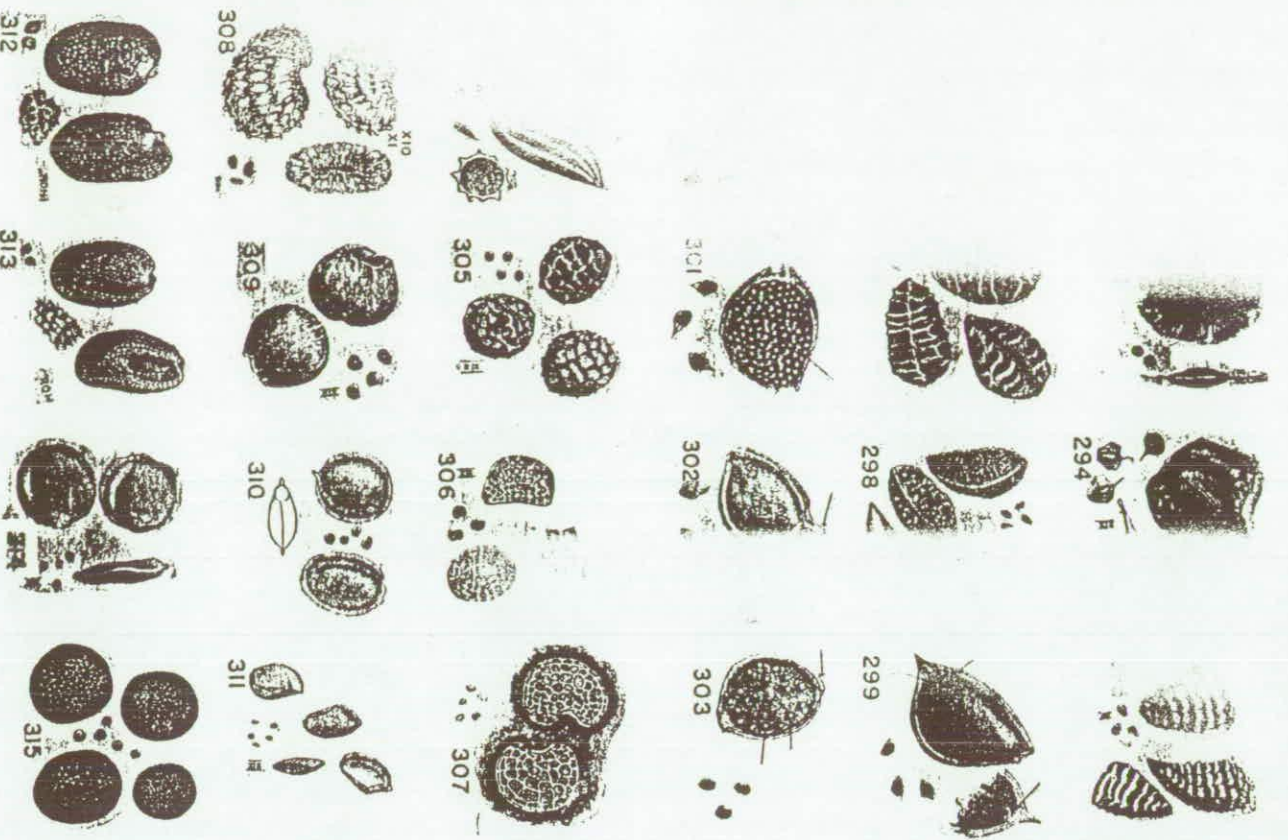
172. *Setaria faberii*
 173. *Setaria geniculata*
 174. *Setaria grisebachii*
 175. *Setaria lutescens*
 176. *Setaria macrostachya*
 177. *Setaria magna*
 178. *Setaria reticulata*
 179. *Setaria viridis*



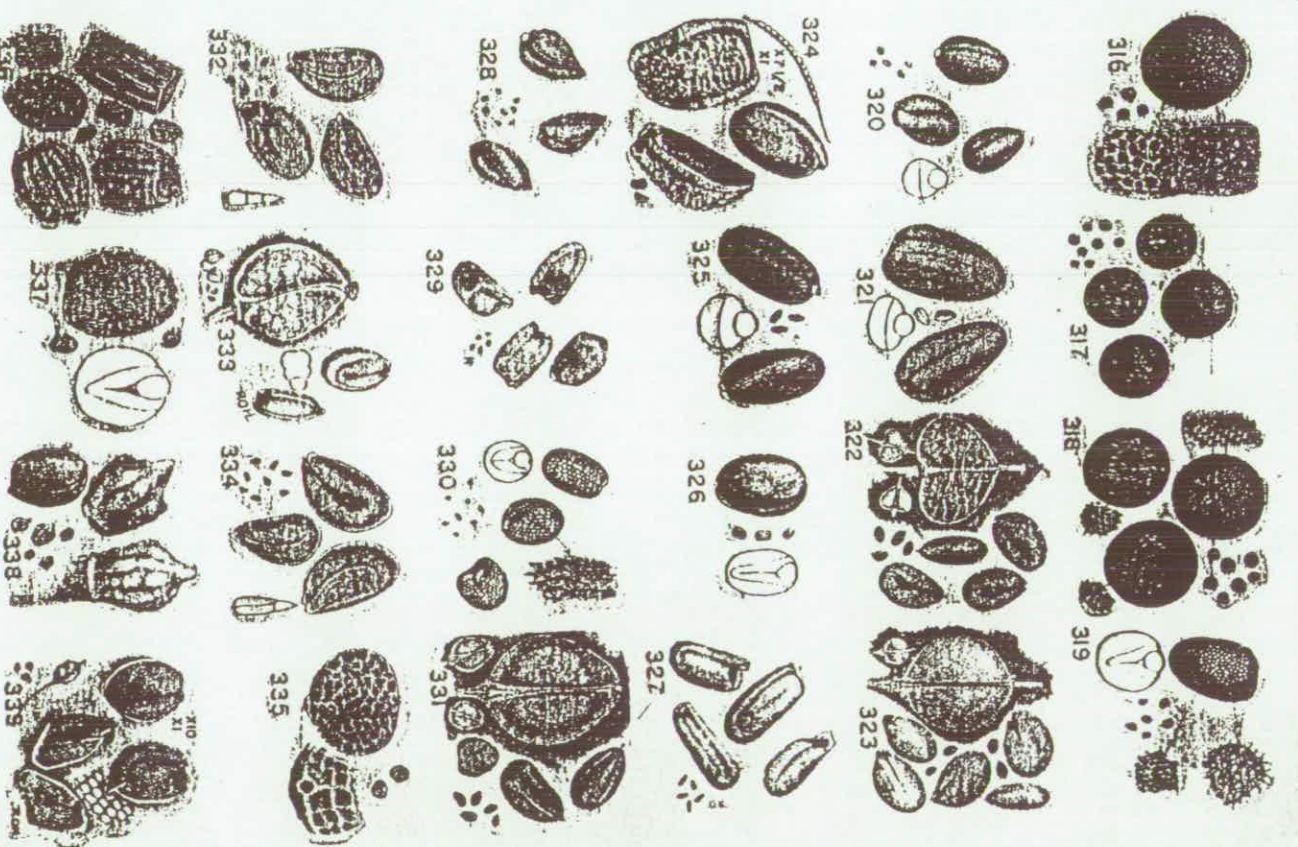
Gramineae (180-195)

180. *Sorghum italica* (Com.)
 181. *Sorghum italica* (Hun.)
 182. *Sorghum italica* (Hun.)
 183. *Sorghum italica* (Hun.)
 184. *Sorghum italica* (Hun.)
 185. *Sorghum italica* (Hun.)
 186. *Sorghum sudanense*
 187. *Sorghum sudanense*
 188. *Sorghum sudanense*
 189. *Sorghum sudanense*
 190. *Sorghum sudanense*
 191. *Sorghum sudanense*
 192. *Sorghum sudanense*
 193. *Sorghum sudanense*
 194. *Sorghum sudanense*
 195. *Sorghum sudanense*





Curculionidae (292-293), Ranunculaceae (294-304), Papaveraceae (305-308),
Fumariaceae (309), Cruciferae (310-315)

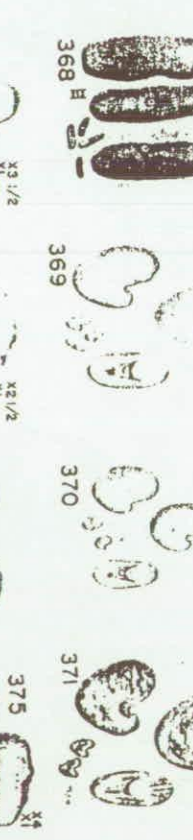


Cruciferae (316-339)

292. *Spergula arvensis*
293. *Spergula pentandra*
294. *Anemone canadensis*
295. *Delphinium consolida*
296. *Delphinium consolida*
297. *Nigella damascena*
298. *Nigella arvensis*
299. *Ranunculus acris*
300. *Ranunculus bulbosus*

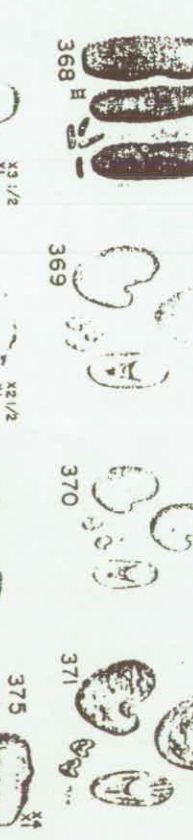
301. *Ranunculus parviflorus*
302. *Ranunculus repens*
303. *Ranunculus scordalis* (R.
parviflorus)
304. *Thalictrum* sp.
305. *Facelis tomentosa*
306. *Glacium consolida*
307. *Papaver somniferum*
308. *Rumex crispus*
309. *Rumex crispus*
310. *Alisma albidum*
311. *Arabis glabra*
312. *Barbarea vulgaris*
313. *Barbarea vulgaris*
314. *Barbarea vulgaris*
315. *Brassica campestris*

316. *Brassica juncea*
317. *Brassica kaber* (B. ar-
vensis)
318. *Brassica napus* var.
bursa
319. *Brassica nigra*
320. *Camelina microcarpa*
321. *Camelina sativa*
322. *Camelina sativa*
323. *Camelina sativa*
324. *Chorizanthe tenella*
325. *Coronilla varia*
326. *Erysimum asperum*
327. *Erysimum asperum*
328. *Erysimum asperum*
329. *Erysimum asperum*
330. *Erysimum asperum*
331. *Erysimum asperum*
332. *Erysimum asperum*
333. *Erysimum asperum*
334. *Erysimum asperum*
335. *Erysimum asperum*
336. *Erysimum asperum*
337. *Erysimum asperum*
338. *Erysimum asperum*
339. *Erysimum asperum*



Cruciferae (340-344), Rosellaceae (345), Rosaceae (346-352), Leguminosae (353-363)

340. *Rorippa sylvestris*
341. *Sisymbrium officinale*
342. *Sisymbrium officinale*
343. *Thlaspi arvense*
344. *Rorippa sylvestris*
345. *Rosella*
346. *Potentilla monspeliensis*
347. *Rosa* sp.
348. *Rosa* sp.
349. *Rosa* sp.
350. *Rosa* sp.
351. *Rosa* sp.
352. *Rosa* sp.
353. *Acacia* sp.
354. *Acacia* sp.
355. *Acacia* sp.
356. *Acacia* sp.
357. *Acacia* sp.
358. *Acacia* sp.
359. *Acacia* sp.
360. *Acacia* sp.
361. *Acacia* sp.
362. *Acacia* sp.
363. *Acacia* sp.

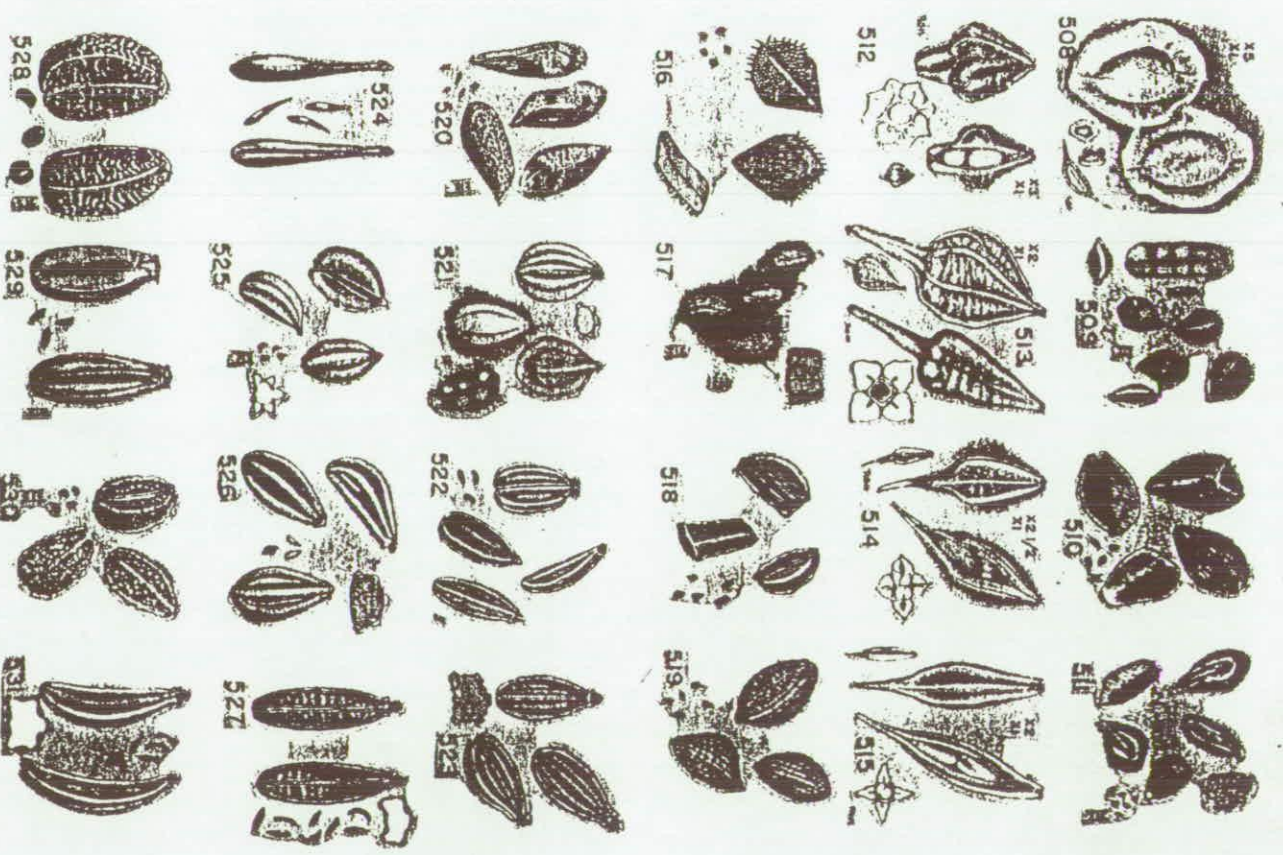


Leguminosae (364-387)

364. *Cassia* sp.
365. *Cassia* sp.
366. *Cassia* sp.
367. *Cassia* sp.
368. *Cassia* sp.
369. *Cassia* sp.
370. *Cassia* sp.
371. *Cassia* sp.
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386. *Cassia* sp.
387. *Cassia* sp.

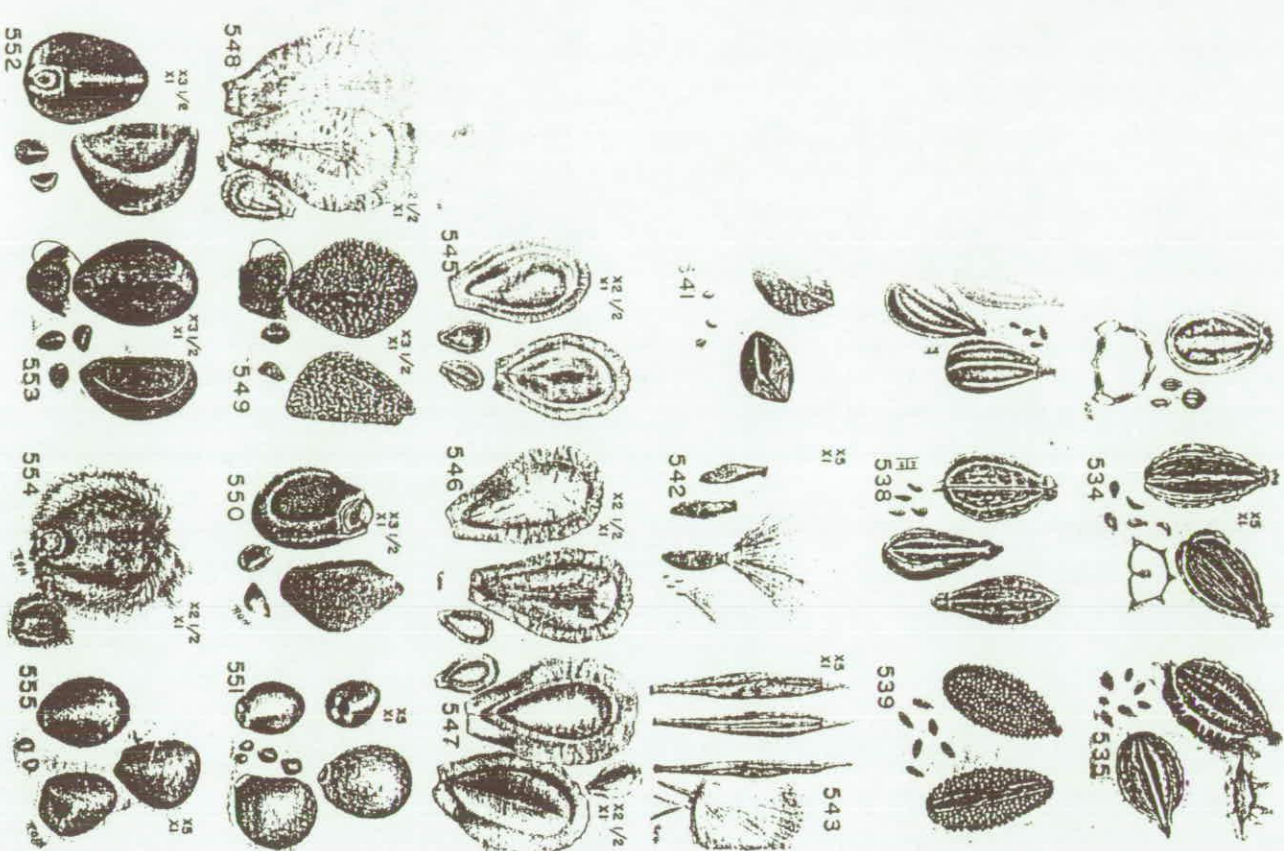


Euphorbiaceae (484-488), Malvaceae (489-502), Sterculiaceae (503), Hypericaceae (504),
 Violaceae (505), Lamiaceae (506-507)



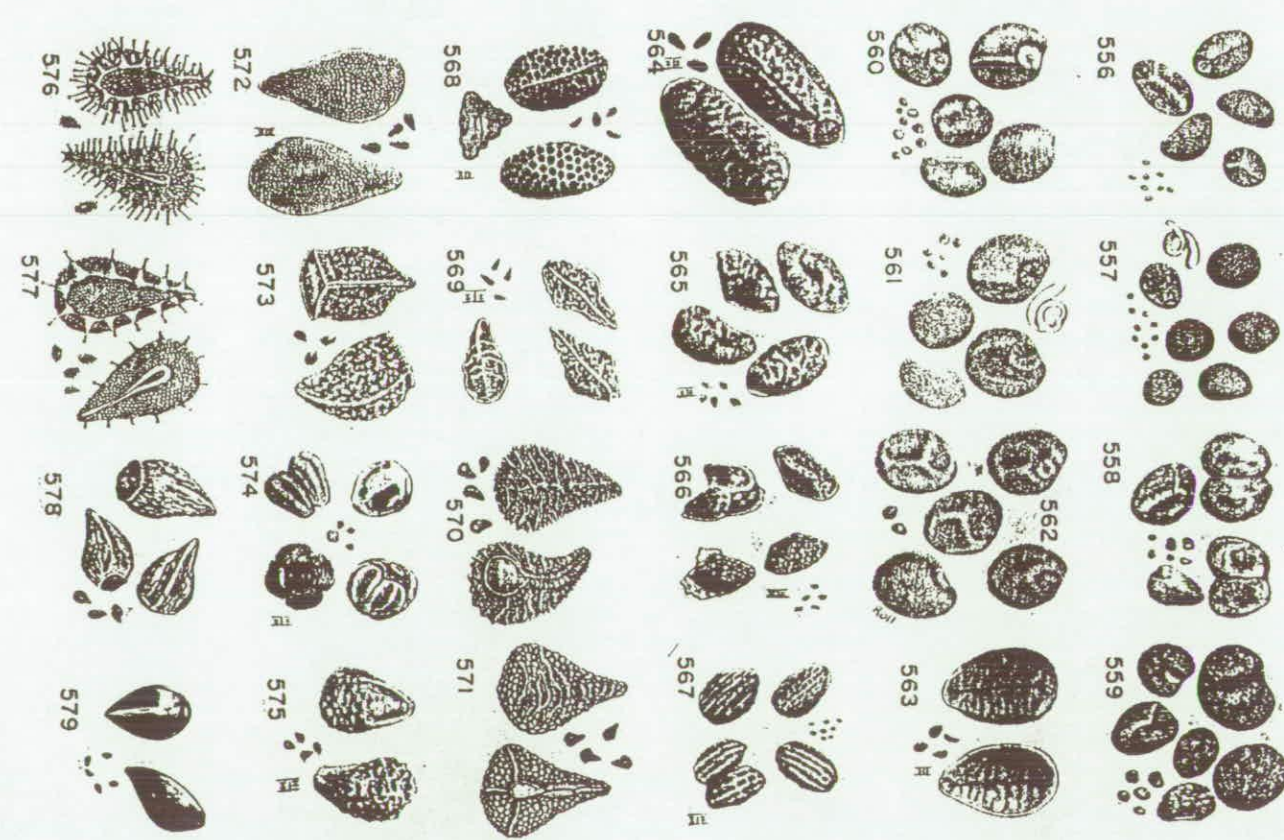
Lamiaceae (508), Lythraceae (509), Onagraceae (510-520), Umbelliferae (521-531)

508. *Mentzelia nuda*
 509. *Lithrum hyssopifolia*
 510. *Boraginella densiflora*
 511. *Boraginella stricta*
 512. *Gaura coccinea*
 513. *Gaura odorata*
 514. *Gaura sinuata*
 515. *Gaura villosa*
 516. *Mentzelia texensis*
 517. *Mentzelia texensis*
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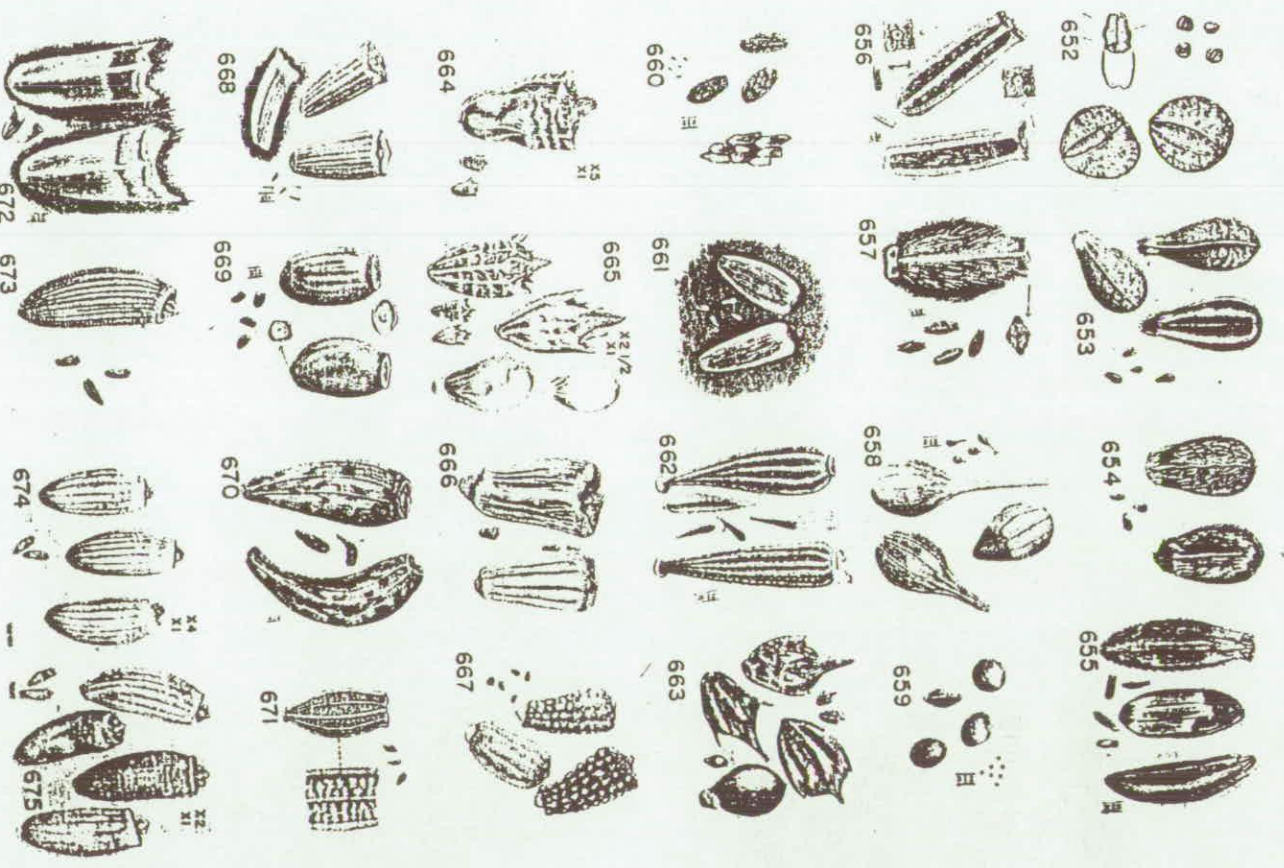
Umbelliferae (532-540), Primulaceae (541), Apocynaceae (542-543), Asclepiadaceae (544-548), Convolvulaceae (549-555).

Convolvulaceae (556-562), Polygonaceae (563-567), Hydrophyllaceae (568).





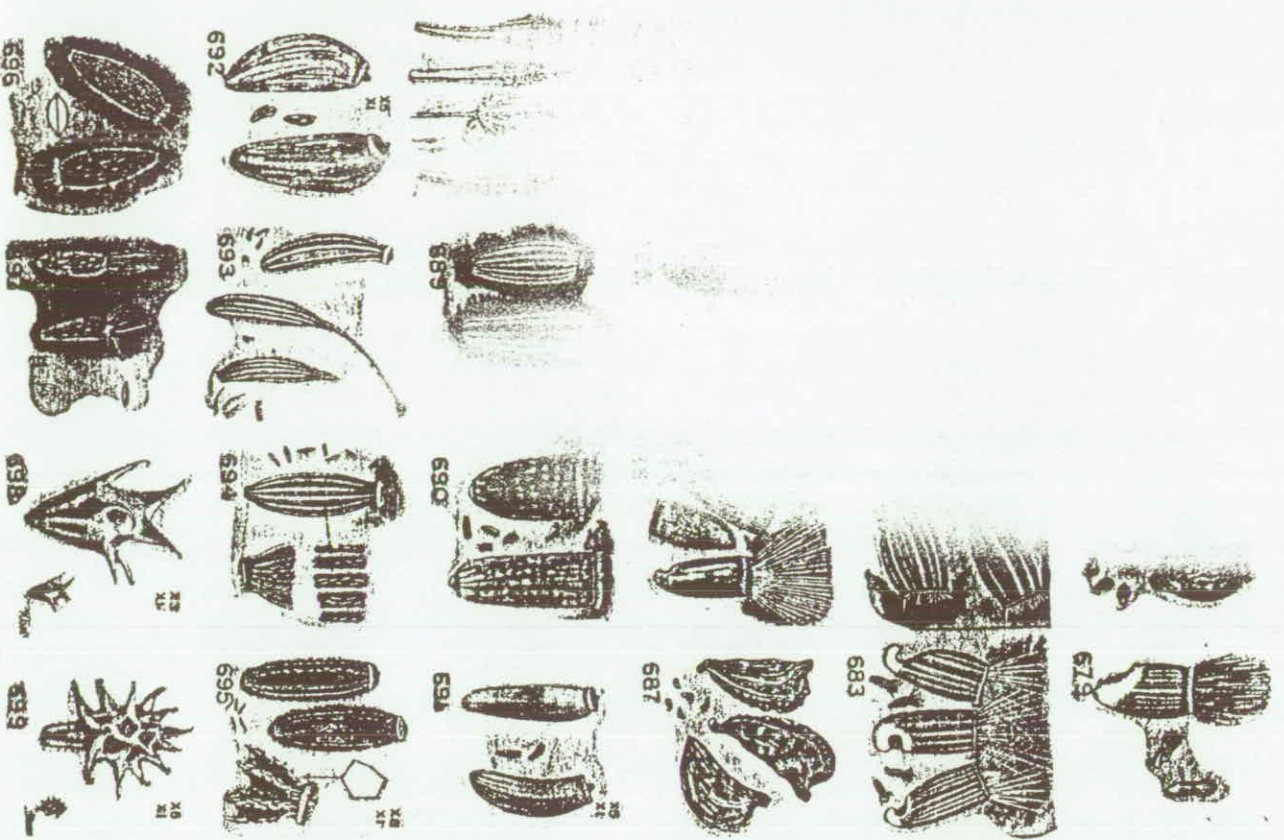
Rubiaceae (628-631), Pedaliaceae (632), Plantaginaceae (633-644),
Rubiaceae (645-650), Caprifoliaceae (651)



Valerianaceae (652-654), Dipsacaceae (655-658), Campanulaceae (659), Lobeliaceae (660),
Compositae (661-675)

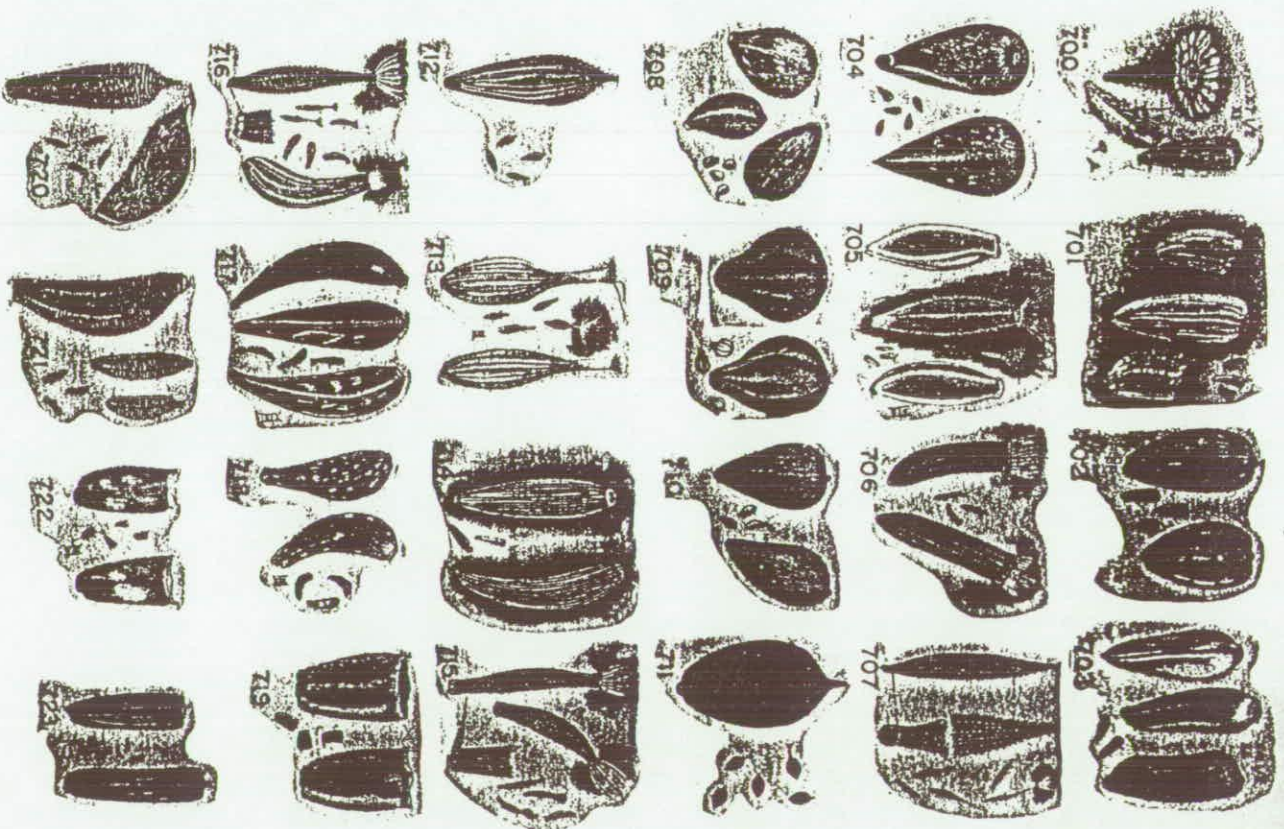
628. *Verbascum thapsus*
629. *Veronica asperula*
630. *Veronica asperula*
631. *Veronica asperula*
632. *Veronica asperula*
633. *Plantago major*
634. *Plantago rugelii*
635. *Plantago rugelii*
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637. *Plantago rugelii*
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651. *Plantago rugelii*

645. *Dioscorea*
646. *Dioscorea*
647. *Dioscorea*
648. *Dioscorea*
649. *Dioscorea*
650. *Dioscorea*
651. *Dioscorea*
652. *Valeriana*
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674. *Valeriana*
675. *Valeriana*



Compositae (676-699)

676. *Carduus arvensis*
 677. *Carduus marianus*
 678. *Carduus edentatus*
 679. *Carduus arvensis*
 680. *Carduus marianus*
 681. *Carduus marianus*
 682. *Carduus marianus*
 683. *Carduus marianus*
 684. *Carduus marianus*
 685. *Carduus marianus*
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 696. *Carduus marianus*
 697. *Carduus marianus*
 698. *Carduus marianus*
 699. *Carduus marianus*



Compositae (700-723)

700. *Carduus marianus*
 701. *Carduus marianus*
 702. *Carduus marianus*
 703. *Carduus marianus*
 704. *Carduus marianus*
 705. *Carduus marianus*
 706. *Carduus marianus*
 707. *Carduus marianus*
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 720. *Carduus marianus*
 721. *Carduus marianus*
 722. *Carduus marianus*
 723. *Carduus marianus*

B Fg. larghe 5-15 mm., quasi lineari, spesso falcate. Bacca giallognola (rr. bianca) a maturità, ovoida. Seme come nella v. *Abietis*. — *Parassita sui Pinus silvestris, Laricio e Pinaster*, più rr. su *Picea excelsa* e *Juniperus Oxycedrus*: Friuli, Veron., Trent., Bresc., V. d'Aosta, Nizz., Cal., Etna e Cors. [Eur.]. — V. austriacum Wiesb. (1883) — V. album v. hyposphaerosperm. f. angustifolium R. Kell. (1905). γ LAXUM (Boiss. et Reut., 1842)

Gen. 284. **Arcenthobium M. B.** (1819).

(Spec. 10 circa dell'Emisf. bor. e specialm. Am. bor. e Messico).

Arbusto ramosissimo, articolato, dall'aspetto di una *Salicornia*, di 1 dm. al più. Fg. ridotte a squame triangolari, saldate in breve guaina. Fi. dioici: i masch. 1-3, giallognoli, sessili nelle ultime articolazioni, a perigonio 2-5-partito, con un'antera sessile sopra ogni lacinia, deiscente per una fessura; i femm. terminali, pedicellati, a perigonio minimo. 2-partito e stimma quasi sessile. Bacca ovoida (2 per 1 mm.), maturante nella primavera successiva, azzurra, alla fine deiscente elasticam. e lanciante a distanza il seme avvolto da uno strato vischioso che lo fa aderire ai rami vicini. ♂. *Parassita sui Juniperus*: Istria e Cors. ?; 2. Genn.-Lugl., Sett. [Eur. mer. Cauc. As. occ. e centr. Afr. bor. Am. bor.]. — Viscum DC. (1805).

A. *Oxycedri* M. B. (1819) 940

FAM. XXXVIII. **BALANOPHORACEAE.**

(Gen. 14, spec. 35 circa, la maggior parte delle Foreste trop., poche dell'Afr. mer., 1 della N. Zelanda e la nostrale).

Proprietà ed usi. — Il *Cynomorium coccineum* era anticom. usato come astringente nelle diarree.

Gen. 285. **Cynomorium L.** (1735).

(Spec. unica).

Rz. ramoso e squamoso, da cui nascono dei grossi fusti carnosì (1-2 dm.), fosco-rossastri o porporino-nerastri, pur coperti di squame ovate ed appressate. Fi. poligami, in spiga simile ad uno spadice, densa, oblungo-clavata, lunga 6-12 cm., formata da piccole cime contratte, accompagnate da brattee e bratteole; perigonio a 4-6 (rr. 1-8) pezzi, lineari-clavati. Stame unico, con rudimento d'ovario nei fi. masch. Ovario infero o semiinfero, 1-ovulato; stilo allungato, scanalato, con stimma troncato-ottuso. Achenio a pericarpio coriaceo, con perigonio e stilo persistenti. γ. *Spiaggie arenose, parassita sulle rd. di varie piante*: Basil. or., Sic., Malta, Lamped., Sard. ed alcune piccole isole; 2. Apr.-Magg. [Spa. Creta Palest. Arab. Pers. Songaria Afr. bor.]. — Volg. Fungo di Malta.

C. *coccineum* L. (1753) 941

FAM. XXXIX. **CYTINACEAE.**

(Gen. 7, spec. 22 circa dell'Eur. mer., Afr., Am. temp. e trop. ed As. trop.).

Proprietà ed usi. — Il succo spremuto dal *Cytinus Hypocistis* è stato in passato usato come tonico ed astringente.

Var. *pinnatifida* Coss. *Cat. Tun.* 50.

Hab. : Oran, Saïda, prairie rocheuse, alt. ca. 900 m. 10 mai (n. 153).

DILOTAXIS DC.

D. virgata DC. *Syst.* II, 631.

Formæ inter f. *brachycarpa*, *saharensis* et *longisiliqua* Coss. *Comp.* II, 165. *intermediæ*.

Hab. : Oran, Djebel Aïssa, dans l'alfa, au-delà du télégraphe optique, alt. ca. 1650 m. 2 juin (n. 555) : id. steppe d'alfa au pied du Djebel Morghad alt. ca. 1200 m. 24 mai (n. 426).

Obs. — Notre plante ne ressemble guère à aucune des formes que nous avons vues dans les herbiers, sauf aux spécimens récoltés au Maroc par Balansa. Elle réunit les caractères de plusieurs des formes admises par Cosson, et pour qu'on puisse s'en convaincre, nous indiquerons quelques caractères pris sur un seul et même exemplaire.

Plante haute, rameuse, pourvue de feuilles radicales et caulinaires: siliques de longueur très variable égalant le pédicelle ou quatre fois plus longues que lui; valves parfois très convexes, parfois $\pm$ applanées, style linéaire ou ové, dans ce dernier cas souvent séminifère et caréné.

Par contre, notre plante a des feuilles plus velues qu'aucun des autres exemplaires vus par nous.

Var. *Aissæ* Hochr., var. nov. — Planta annua, humilis vel paulo elata, ramosa vel simplex. Caulis 5-17 cm. longus, parce hirsutus vel hirsutissimus, inferne vel usque ad medium, et ultra, foliatus. Folia dense villosa basi exauriculata, lyrato-pinnatisecta, segmentis pinnatis-partitis vel-dentatis. Flores lutei apice ramorum congesti; pedunculi 3-5 mm. longi; pedunculi fructiferi ad 7 mm. longi. Siliquæ maturæ lineares, crassæ, 11 mm. longæ et 2 mm. latæ usque ad 9 mm. longæ et 1.5 mm. latæ, rostro $\pm$ conico, seminifero, 1-2 mm. longo.

Hab. : Oran, Djebel Aïssa, rocaïlles près du télégraphe optique, alt. ca. 1600 m. 2 juin (n. 575); Oran, Col de Merbah, Djebel Morghad, rocaïlles, alt. ca. 700 m. 24 mai (n. 475).

Obs. — Cette plante nous semble très caractéristique et se distingue au premier coup d'œil de toutes les autres formes du *D. virgata*; en particulier, les feuilles très découpées, les siliques

CRUCIFERAE

Diplotaxis kohlaanensis A. Miller & J. Nyberg, sp. nov. (sect. *Catocarpum* DC.).

D. harra (Forssk.) Boiss. similis sed herba perennis glabra caespites magnos formans, fructu etiam plerumque rostro stipiteque longiore petalisque generaliter longioribus recedit.

Perennial herb or shrublet, glabrous throughout excepting the sepals; stems many, arising from a woody rootstock, ascending or hanging, 25–50 (–200) cm long, much branched. *Leaves* petiolate, slightly fleshy, yellowish or bluish green, sometimes pinkish tinged on the midrib and beneath with age, ovate to oblong-ovate, 8–80 × 5–30 mm, obtuse at the tip, the margin unevenly serrate with 4–6 pairs of teeth or sinuate to entire, the base attenuate into the petiole; upper leaves smaller and narrower. *Inflorescence* ebracteate, ascending or hanging, ± corymbose with the flowers overtopping the buds, in fruit lax and elongating to 30 cm; pedicels 10–18 mm long. *Sepals* erect spreading, oblong, c. 6 mm long, externally hairy particularly at the base and on the midrib; inner sepals 2–2.5 mm broad, somewhat saccate at the base, slightly hooded at the tip; outer sepals 1.5–2 mm broad, the base not saccate, distinctly hooded at the tip. *Petals* clear yellow, broadly obovate and narrowing below into a linear claw, 9.5–13.5 × 4.5–6 mm, the tips rounded. Nectarial glands prominent at the base of the median stamens. *Ovary* cylindric, glabrous, shortly stipitate; stigma bilobed. *Median stamens* 7.5–11 mm long; lateral stamens 5.5–7 mm; anthers 2.25–3 mm long. *Fruit* erect or hanging, linear to linear-oblong, flattened, 15–40 × 2.25–3.5 mm, with the seeds in two rows, valves thin, glabrous, becoming yellowish; beak seedless, 1.5–2 mm long; stigma bilobed; style 1.25–1.5 mm long. *Seeds* numerous, pale reddish brown, ± oblong, flattened, 1–1.5 × 0.5–1 mm, without prominent surface sculpturing, microlaginous on wetting. (Fig. 2).

Type: Republic of Yemen, Amran to Kuhlān [Kohlaan] road, on limestone cliffs, 15 km E of Kuhlān, 2800 m, 26 iii 1981, A. G. Miller & D. G. Long 3213 (holo. E; iso. K).

Habitats: limestone and sandstone cliffs; 2300–3000 m.



FIG. 2. *Diplotaxis kohlaanensis*. A, fruiting and flowering branch (× 0.6), B, fruit (× 2.5).

de Genève, nous avons pu la comparer avec des spécimens du var. *crassifolia* O. F. Schultz déterminés par cet auteur, récoltés par J. Bouquet dans les Alpes Lémaniques.

2190. *Alyssum kranatense* Boiss. var. *Wetherli* Emh. et Maire in Maire, (cont. n° 1179. Sud oranais: Djebel Aissa, vers 1700 m. au dessus de l'Aïn-Aïssa.

Variété nouvelle pour l'Algérie.

2191. *Malcolmia parviflora* L. C. var. *brachypoda* Emh. et Maire, n. var. (3-4 mm, nec 4-9 mm) siliques acquiescentes l. crassiflorus (nec siliques lenitioribus) ; siliques paulo crassioribus. Moyen Atlas : Ifrane, dans les sables parmi les pierres calcaires, 1500-1600 m.

2192. *Sisymbrium maureum* Maire, (cont. n° 236. Abonde dans le Grand Atlas oriental autour d'Imtichil, sur calcaire, vers 2300 m. Plante nouvelle pour le Grand Atlas.

2193. X *Trachycnemum mirabile* Maire et Samuelson. Hybride de *Trachystoma Battii* O.F. Schultz et de *Cerodantherum rupestroides* Gross. qui sera décrit par les auteurs dans une publication ultérieure. (Cf. Bull. Soc. Hist. Nat. Afr. Nord, 28, p. 10, 1937, Planche 29.

2194. *Otocarpus virgatus* Dur. — Cette plante se présente sous deux variétés :
var. *erlocarpus* Maire, n. nom. — Siliques unilique pilosae ... C'est le type de l'espèce, figuré par Duruy dans l'Atlas de l'Exploration scientifique de l'Algérie.
var. *lelocarpus* Maire, n. var. — Siliques glabres. Avec le type aux environs de Saïda, mais plus rare.

2195. *Diplotaxis Olivieri* Maire, n. sp. (sect. *Anocarpum* D.C.). — *Italeres*, vridi-glaucescens. Herba tota *glabra* plus minuscule *glaucescens*. *Folia* inferiora plus minuscule rosulata, in petiolum longum adnata, imo *indistincta* lacinia 3-4-jugis, alternis l. suboppositis, interdum bifidis lacinia inaequalibus, lacinia omnibus *anguste linearibus integris* apice *rotundatis*, interdum plus minuscule *spatulatis* ; *folia* caulina similia, *corymbiformi elongatis*, laxis, *chraceolus*, 7-18-florus. Petioli *graciles* *erecto-patula*, c. 3,5 mm longa, oblonga, apice *rotundata*, *glabra*, *intervi-*

rentia. Petala aurea, c. 6 - 3 mm; lobus latero-obovatus apice *rotundatus*, basi in unguem vix 2 mm longum adnatus. Stamina *lateralia* c. 1,5 mm longa, *Nectarium* 2 mm longum, filamenta *albida*, *antherae* *oblongae* usque ad 160-ovulum. Stylus brevissimus *stigmati* *capitato* *valde* *crasse* *complanatae* *subrotundae*, sessile, *rostrum* *brevissimum* (0,2-0,5 mm compresso, *asperum*, apice paulo *lobato* l. *acquilato*, *stigmati* *laterale* *extremo* *medio* *longi* et *arctis* *lateralibus* *bravissimis* *anatomosantibus* *praefatis*, flavo-virentes. Semina *ovoides*, *modica* *atro-virentia*, *bravia* *600-650* *µ* 300-350 *µ*.

Maroc *austro-occidental* : vallée de l'oued Soum près du post. *oued* *laire* (Y. Chavert).

l'espèce affine au *D. virgata* D.C., et au *D. aurea* D.C., dont elle diffère nettement par ses liges et ses feuilles glabres et par les antères des lobes très étroites. Nous sommes heureux de la devoir à son inventeur.

2196. *Erucastrum latirostre* Br. & B. Bull. Soc. Hist. Nat. Afr. Nord, 14, p. 181, 1922. Nous n'avons jamais pu retrouver cette plante, qui avait été récoltée par l'auteur au cours d'une excursion qu'il avait faite seul dans les dunes de Mogador pendant que nous explorions le Djebel Ane silet. Le type ayant été égaré, nous n'avons pu l'identifier. Or, en avril 1936, en recherchant cette plante dans les dunes de Mogador nous avons récolté une forme du *Diplocaris strobila* Kunze qui correspond bien à la description de *Erucastrum latirostre*. Le *D. strobila* a des siliques qui sont souvent plus semblables à celles d'un *Erucastrum* qu'à celles qui *Diplocaris* typique, ce qui explique la création de l'*E. latirostre* par Buayx-Bauxguet, cet auteur n'étant pas à cette époque familiarisé avec les nombreuses variations du *D. strobila*.

2197. *Eruca yescientia* (L.) Cav. La plante se présente sous trois variétés :
var. *trichocarpa* Maire, n. nom. Siliques pilis *conformibus* *hirsutae*. Espagne : Huescar 1 (Bourcier, 1851, n° 1023) : Algérie : Oran; Mossagamen, Maroc : Saïda.

Cette variété constitue le type de l'espèce.
var. *ditrichocarpa* Maire, n. var. Siliques pilis *brevibus* et *longis* *imixtis* *vestitae*. Espagne : Valencioche 1 (dreyer nov. 1893, n° 825). 1851, n° 99).

2198. *Pseudocytisus Maurei* (Humbert) Maire, comb. nov. *Vella Maurei* Humbert. L'emploi de la méthode des types oblige à réserver le nom

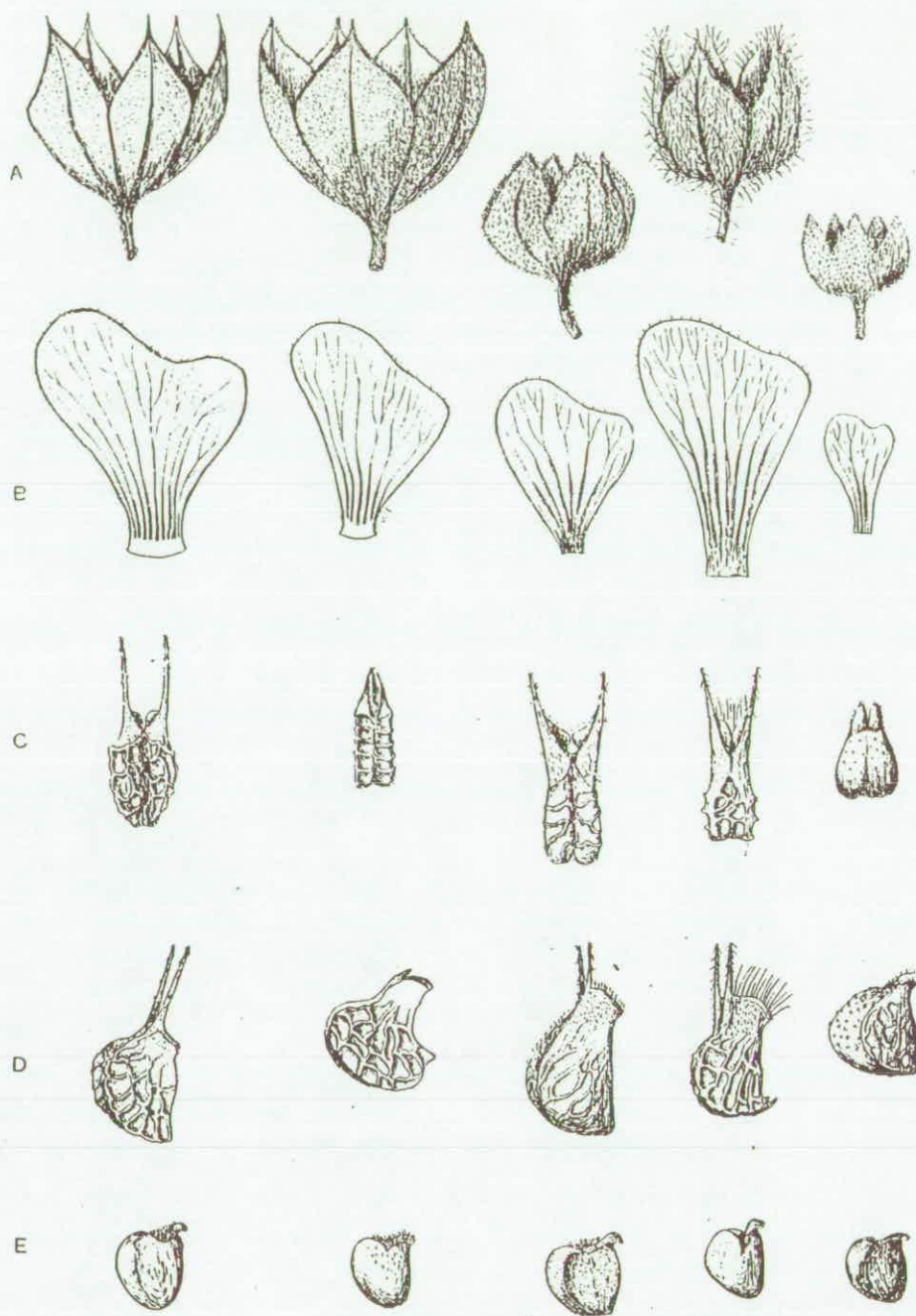


Fig. 37. — *Malvinda*: 1, *S. rhombifolia* var. *canariensis*; 2, *S. Glaziovii*; 3, *S. cordifolia*; 4, *S. montana*; 5, *S. acuminata*: A, cálices, $\times 2$; B, pétalos, $\times 3$; C, carpelos dorsalmente, $\times 5$; D, carpelos lateralmente, $\times 5$; E, semillas $\times 5$.

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Observaciones. — Los dos tubérculos que presenta esta especie debajo de las estipulas, son muy semejantes a los de *S. spinosa*, pero se diferencian de ésta por ser obtusos, redondeados, mientras que en *S. spinosa* son agudos y en forma de gancho dirigidos hacia abajo.

27. *Sida rhombifolia* L.

Figura 38

Linneo, C., *Hort. Cliff.* (1837), p. 346, en la presente obra describe la especie, pero en esa época aún no se había implantado la nomenclatura binaria. El material estudiado coincide con el fototipo. — *id.*, *op. cit.* (1853), p. 684 : « *Sida foliis lanceolato-rhomboidibus ferratis* ». — Burmann, N. L., *Flora Indica* (1768), p. 146. — De Candolle, A. P., *op. cit.* (1824), p. 462. — Saint Hilaire, A. de, *op. cit.* (1827), p. 177. — Presl, C. B., *Iteliq. Haenk.*, II (1831), p. 108. — Grisebach, A. R. H., *op. cit.* (1864), p. 74. — *Plant. Lorent.* (1874), p. 43 ; *op. cit.* (1879), p. 44. — Schumann, C., in Martius, *op. cit.*, XII^a (1892), pág. 338, lám. 63. — Arechavaleta, J., *op. cit.* (1901), p. 126. — Spegazzini, C., *Fl. Prov. Bs. As.* (1905), p. 112. — Rodrigo, A. P., *Especies de Sida* (1943), p. 373. *Rev. Arg. Agr.* 10, n° 4.

Nombres vulgares : Afata, mata-alfalfa, escoba dura, tipichá-guazú (Matoso), malvavisco falso (*Hieronymus*).

Planta perenne, caméfito, erguida, subarborescente, de 50-80 cm de altura, con raíces muy profundas, leñosas y resistentes. Tallos subleñosos, fuertes, ramificados, cilíndricos en la parte inferior y angulosos o poliédricos, a veces algo aplanados, en las ramas superiores; cubiertos por un fino indumento formado por pelitos estrellados. En las ramas inferiores los tallos son glabros y estriados. Estípulas aleznadas, angostas, casi filiformes, de igual o mayor largo que los pecíolos, de 5-8 mm de longitud. Debajo de las estipulas a veces hay dos pequeños tubérculos en forma de gancho. Hojas cortamente pecioladas, con pecíolos triangulares, planos en la parte superior; articulados y geniculados en la mitad; miden 3-6 mm de largo. Lámina oval-romboide, rómbica o rombanceolada, más o menos ancha o alargada según las variedades, con la base cuneada y el ápice obtuso o agudo. Las dimensiones caracterizan a las variedades, fluctuando entre 3 y 7 cm de largo por 0.3-2 cm de ancho. Las hojas tienen 3-5 nervaduras basales prominentes en la superficie inferior. Ambas superficies pueden ser discolores o no, según las variedades. El borde foliar es dentado en la mitad o en los 2/3 superiores. Inflorescencias solitarias con pedúnculos largos, que alcanzan la longitud de las hojas y con frecuencia la superan; las inflorescencias son axilares y a veces van acompañadas de ramitas accesorias que llevan numerosas hojas cada una de las cuales con su correspondiente inflorescencia, formando corimbos. Pedúnculos cilíndricos, articulados entre la mitad y el tercio superior; desde la articulación hasta el cáliz, los pedúnculos son canaliculados, expandiéndose cada cresta y continuán-



Fig. 38. — *Sida rhombifolia* var. *typica* (ejemplar dibujado :
Punta Lara, A. P. Rodrigo 2001), $\times 2/3$

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plegado a
exterior y
Lóbulos de
el borde pr
la base de
resto super
diámetro.
amarillas y
anchos, ob
rodeado de
por un anc
corto, de 3
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lateralment
con dos car
2 mm de l
alto (sin la
dorso. Sam
brillante.

Especi
cuales
a) var.
boidea
teras

dose con las nervaduras centrales y los límites de los sépalos. La longitud de cada pedúnculo varía entre 1 y 4 cm. Cáliz piramidal-campanulado, plegado antes de la antesis, con un fino indumento ceniciento en la parte exterior y glabro en el interior, lo mismo que en el borde, el cual es liso. Lóbulos de los sépalos rombo-trianguulares, acuminados, muy agudos, con el borde prominente y la nervadura central pronunciada; con frecuencia la base del cáliz es color anaranjado, destacándose del verde-ceniciento del resto superior de los sépalos. Durante la antesis el cáliz mide de 7-8 mm de diámetro por 6-7 mm de altura. Corola color crema con las nervaduras amarillas y el centro rojo-oscuro; pétalos asimétricos, con dos lóbulos anchos, obtusos, uno mucho más grande, y con el borde superior de ambos rodeado de finos pelos papilosos; los sépalos miden de 10-12 mm de altura por un ancho máximo de 10 mm en la parte superior. Tubo estaminal corto, de 3-4 mm de altura. Gineceo globoso-cónico aplanado, con 10-14 carpelos cuyas aristas forman una pequeña prominencia en la cúspide del cono. Carpelos maduros reticulados, membranáceos, trigono-aplanados lateralmente, color castaño claro, o amarillentos, unas veces indehiscentes con dos aristas rudimentarias unidas o bien dehiscentes con dos aristas de 2 mm de largo que llevan pelitos estrellados; los carpelos miden 3 mm de alto (sin las aristas) por 2.8 mm de profundidad y 1.8 mm de ancho en el dorso. Semillas castaño-oscuro, negruzcas, glabras, con pelitos blancos y brillantes rodeando el hilio; miden 1.8 mm de diámetro.

Especie sumamente polimorfa, que presenta diversas variedades de las cuales tres de ellas están representadas en el país, siendo las siguientes: a) var. *typica* K. Schum., b) var. *canariensis* K. Schum., y c) var. *rhomboidea* (Roxb.) Mast., las que pueden diferenciarse entre sí por estos caracteres:

- A. Plantas con dos pequeños tubérculos en la base de las hojas. Lámina foliar rombo-lanceolada con el ápice subagudo u obtuso y la base obtusa, ancha, y el diámetro longitudinal dos veces el transversal; de 17-30 mm de largo por 5-15 mm de ancho. var. *rhomboidea*.
- B. Plantas sin tubérculos en la base de las hojas. Lámina foliar netamente rómbica o rombo-lanceolada.
 - 1. Hojas rómbicas, con el ápice acuminado o agudo y la base cuneada. Superficies rara vez discolores. Hojas grandes, de 3.5-6 cm de largo, con el diámetro longitudinal 2.1-2.8 veces el transversal. Pedúnculos florales de 3-4 cm de largo. Carpelos indehiscentes con aristas oblicuas, unidas de 0.5-1 cm de largo. En toda la planta predomina el follaje. var. *typica*.
 - 2. Hojas rómbicas, con el ápice obtuso y la base cuneada. Superficies rara vez discolores. Hojas grandes, de 3.5-6 cm de largo, diámetro longitudinal 3.3-4 veces el transversal. Pedúnculos florales de 1-2 cm de largo. Carpelos maduros, con dos aristas verticales libres de 2 mm de largo. En toda la planta predominan las flores. var. *canariensis*.

var. *typica* K. Schum.

Schumann, G., in Martius, *op. cit.*, XII (1892), p. 339. — Arechavaleta, J., *op. cit.* (1901), p. 126. — Ekman, E. L., *op. cit.* (1910), p. 18. — Hassler, E., *op. cit.* *Ostenia* (1933), p. 338.

Hojas netamente rómbicas, o rombo-ovaladas, con el ápice acuminado o agudo y la base cuneada, grandes, de 3.5-6 cm de largo, anchas con el diámetro longitudinal 2-2.8 veces el transversal. Pedúnculos florales largos, de 3-4 cm. Carpelos maduros con las aristas casi siempre unidas, cortas (de 0.5-1 mm de largo) con frecuencia indehiscentes.

Material estudiado:

ARGENTINA. — Jujuy: Jujuy, E. L. Holmberg, XII-1903 (BAB.). — Río Grande, Schreiter 2828, II-1924 (LIL.). — Volcán, Castillón 178, I-1927 (LIL.).

Salta: El Manzano, Rosario de Lerma, Zabala 40, II-1941 (LIL.). — Rosario de la Frontera, E. Holmberg, (h.), XI-1900 (BAB.). — Embarcación, Río Bermejo, Schreiter 5394, III-1927 (LIL.).

Catamarca: Gracián, A. Castellanos, I-1940 (BA.).

La Rioja: Cerco, A. Giacomelli, I-1901 (BAB.).

Tucumán: Río Chico, La Calera, L. Monetti 1505, XI-1913 (LIL.). — La Cocha, E. Bailetti 244, III-1919 (LIL.). — Santa Ana, E. Bailetti 489, IV-1919 (LIL.). — Escava, E. Bailetti 1699, XII-1913 (LIL.). — Siambón, A. Castellanos, I-1935 (BA.); id., Schreiter 6788, XI-1931 (LIL.). — Tafi del Valle, Venturi 264, II-1919 (LIL., SI.). — Valle de Tafi, S. Roth, sin fecha, (LP.). — Burruyacu, E. Bailetti 1250, I-1918 (LIL.); id., Peirano 9079, IX-1932 (LIL.). — Leales, Florida, L. Monetti 234, VI-1913 (LIL.). — Cruz Alta, Ranchillos, E. Bailetti, n° 30, V-1917 (LIL.). — Sarmientos, Lillo 9896, IX-1909 (LIL.). — Muñecas, Schreiter 230, XI-1917 (LIL.). — Quebrada de Caspinchango, Lillo 770, II-1908 (LIL.). — Salada del Timbó, Holmberg, (h.), XII-1900 (BAB.).

Formosa: Riacho Formosa, Hepper, II/IV-1941 (BA.). — Las Lomitas, M. von Bübow, n° 9, II-1943 (LP.).

Chaco: Colonia Río de Oro, n° 29, IV-1930 (SI.). — Colonia Benítez, A. G. Schultz, n° 21, I-1928 (BAB.). — Resistencia, C. y G., V-1883 (LPS. 13370).

Misiones: Posadas, Gallardo, XII-1900 (BA.); id., C. Spegazzini, I-1917 (BAB.); id., C. Rius, XII-1928 (BAB.); id., P. Issouribehere, verano 1907 (BAB.). — San Javier, E. C. Clos, I-1926 (BAB.). — San Ignacio, M. Birabén 5317, XII-1941 (LP.). — Loreto, P. Grüner 80, III-1930 (LP.). — Puerto Bemberg, A. P. Rodrigo 1033, VII-

Mercedes, Bosques del Pay-ubre Grande, A. P. Rodri-

go 736, XI-1936 (LP.). — Esquina, A. P. Rodrigo 1025, 3325, XII-1936, X-1943 (LP.).

Santa Fé: Reconquista, Covas y Ragonese 4446, XI-1939 (LP.).
Córdoba: San Javier, A. Castellanos, II-1939 (BA.); id., J. C. Castellano, XII-1927 (BA.). — Yacanto, J. C. Castellano, sin fecha, (BA.). — Los Reartes, A. Castellanos 262, IV-1917 (SI.). — Sierra de San Ignacio, T. Stuckert 15770, II-1908 (LIL.). — Ascochinga, G. Lorentz, sin fecha, (SI.); id., M. L. Giardelli 331, I-1936 (SI.). — Ongamira, A. P. Rodrigo 350, II-1936 (LP.). — Los Cocos, A. L. Cabrera 6398, III-1940 (LP.). — Cosquín, A. P. Rodrigo 294, II-1936 (LP.). — Argüello, A. P. Rodrigo 3297, IV-1943 (LP.).

San Luis: Entre Merlo y Rincón, Yepes, III-1929 (BA.). — Dep. Santa Rosa, Rincón, A. S. de Yepes 884, II-1929 (LP.).

Buenos Aires: Palermo, Hicken, XII-1897 (SI.). — Buenos Aires, C. Spegazzini, XI-1884 (LPS. 13371). — Anchorena, J. C. Vattuone 105, V-1911 (BAF.). — Adrogué, J. F. Mollino 407, II-1918 (BAF.). — Ituzaingó, E. L. Holmberg, XII-1913 (SI.). — San Isidro, Bettfreund, XII-1900 (BA.). — Tigre, sin colector, XII-1900 (SI.). — Delta del Paraná, Cruz Colorada, A. Burkart 4902, XI-1932 (LP.); id., Largo del Mini, A. C. Scala 250, año 1914 (LP.); id., Carabelas, A. Burkart 4448, II-1932 (LP.). — Pergamino, F. A. Urquiza, IV-1917 (BAB.). — Estancia Santa Catalina, E. C. Clos, XII-1926 (BAB.). — Punta Lara, Mollino y Clos, II-1925 (BAB.); id., A. P. Rodrigo 2001, IV-1938 (LP.); id., A. L. Cabrera 619, I-1929, 1360, III-1938, 4899, I-1939, 6342, IV-1940 (LP.). — La Plata, C. Spegazzini, X-1896 (LPS. 1280); id., Camino de cintura, A. P. Rodrigo 1087, III-1938 (LP.). — Atalaya, Mollino y Clos, II-1936 (BAB.). — Los Talas, P. Boffa 975, V-1935 (LP.). — Melchor Romero, J. Zalba, 93, V-1937 (LP.). — Rincón de Viedma, E. J. Ringuelet 360, I-1934 (LP.). — Mar del Plata, T. Joan, II-1911 (SI.). — Bahía Blanca, Reniede, X-1899 (LIL.). — Junín, E. C. Clos 4104, XII-1928 BAB.).

URUGUAY. — Montevideo, Arroyo Carrasco, D. Legrand 3152, 451, II-1942/1935 (LP.); id., Parque Tonkinson, F. Rosa Mato 1514, I-1937 (LP.); id., Campos de los alrededores, J. Arechavaleta, IV-1900 (LP.); id., Malvín, F. Rosa Mato 1524, I-1937 (LP.). — Sin localidad, Doe-
llo Jurado, IV-1925 (BA.).

BOLIVIA. — Dep. La Paz, B. A. Krukoff, 10278, VII-1939 (LP.).

Distribución geográfica. — Esta variedad crece en el norte y centro del país, llegando por el oeste hasta un límite en línea recta que comprende desde La Rioja hasta Bahía Blanca en el sur de Buenos Aires, cerca del paralelo 30, que es la localidad más austral de dispersión de la variedad.



var. *canariensis* K. Schum.

Figura 37¹

Schuman, G., in Martius, *op. cit.*, XII^o (1892), p. 339. — Arechavaleta, J., *op. cit.* (1901), p. 127. — Fries, R. E., *op. cit.* (1906), p. 9. — Ekman, E. L., *op. cit.* (1910), p. 18.

Hojas lanceoladas, con el ápice obtuso y la base cuneada; ambas superficies netamente discolores; miden 1.5-2 cm de largo, siendo el diámetro longitudinal de 3.3-4 veces el transversal. Pedúnculos cortos, de 1-2 cm de largo. Carpelos maduros dehiscentes, con las dos aristas verticales de 2 cm de altura.

Material estudiado:

ARGENTINA. — Jujuy: Ledesma, C. Spegazzini, I-1906 (LPS. 1282). — Abra Pampa, Venturi 9367, II-1919 (LP.). — Santa Laura, Dres. Birabén 1339, III-1939 (LP.).

Salta: Orán, A. Calcagnini 56, VII-1902 (BAB.); id., Tartagal, Schreiter 3727, I-1925 (LIL.). — Anta, Los Puestos, Ragonese 158 b, VI-1934 (BA.). — Quijano, M. M. Job 1532, I-1937 (LP.). — Pampa Grande, C. Spegazzini I-1897 (LPS. 1278).

Catamarca: Ambato, Castellón 1381, III-1909 (LIL.). — Dep. El Alto, Balcozna, Venturi 7095, I-1928 (SI.). — Alto, F. E. Santillán, II-1915 (LP.). — Andalgalá, P. Jorgensen 1015, V-1915 (SI.).

Tucumán: Capital, quintas, Lillo 152 (a), III-1886 (LIL.); id., Lillo 2173, XII-1898 (LIL.). — Tafi, Yerba Buena, Venturi 236, II-1920 (LIL., SI.). — Villa Luján, Venturi 33, XII-1918 (LIL., SI.). — Sierra de San Javier, A. P. Rodrigo 2015, VII-1938 (LP.). — Río Chico, La Calera, L. Monetti 1554, XI-1913 (LIL.). — Elcano, L. Monetti 1685, XII-1913 (LIL.). — Burruyacu, L. Monetti 2003, 3106, II/III-1914 (LIL.). — Leales, La Florida, L. Monetti, VI-1913 (LIL.). — Tafi, Raco, H. Descole, II-1938 (LIL.). — Chigligasta, Cochuna, O'Donnell 63, III-1941 (LIL.). — Río Trancas, Venturi 4304, IV-1926 (LP., SI., LIL.). — Prov. Tucumán, Alzogaray 48, XII-1900 (BAB.).

Santiago del Estero: Dep. Pellegrini, Cerro del Remate, Venturi 5988, IV-1928 (LIL.).

Formosa: Formosa, Jørgensen 3164, II-1919 (LIL., SI.). — Valle Grande, sin colector, VII-1908 (SI.). — Fortín Nuevo Pilcomayo (Dep. Patiño), Codini n° 29, VII-2941 (SI.). — Puerto Bermejo, Dennler, XI-1929 (BA.).

Chaco: Fontana, T. Meyer 261, VIII-1932 (LP.). — Villa Angela, P. Bolla 1004, II-1940 (LP.). — Sáenz Peña, Lillo 64942, sin fecha (LIL.). — Sin Localidad, R. Bazzi, 73, 243, 434, año 1919 (SI.). — Id., L. Rothkugel 120, año 1921 (SI.).

Misiones: Posadas, Vattuone y Bianchi Lischetti 49, II-1914 (BAF.);

Arechavaleta, J.,
9. — Ekman, E.

; ambas super-
do el "ámetro
tos, de 1-2 cm
s verticales de

PS. 1282). —
aura, Dres. Bi-

id., Tartagal,
ragonese 158 b,
P.). — Pampa

). — Dep. El
F. Santillán,
15 (SI.).

(LIL.); id.,
Venturi 236, II-
8 (LIL., SI.).

(LP.). — Río
cano, L.
2003, 3106,

-1913 (LIL.).
sta, Cochuna,
304, IV-1926

-1900 (BAB.).
mate, Venturi

SI.). — Valle
o Pilcomayo
rto Bermejo,

Villa Angela,
42, sin fecha
919 (SI.). —

-1914 (BAF.);

id., M. Birabén 5342, XII-1941 (LP.). — Santa Ana, sin colector, 191, X-1912 (LIL.). — Entre Santa Ana y Candelaria, N. Alboff XI-1896 (LP.). — Cataratas del Iguazú, A. P. Rodrigo, 1037, VII-1937 (LP.). — Caá Guazú, H. R. Mangieri n° 28, XI-1940 (LP.).

Corrientes: Apipé Chico, sin colector, ni fecha, n° 35 (SI.). — La Cruz, A. Burkart 8045, XI-1936 « Escoba dura; la atan y barren pisos de tierra (nota del colector) » (SI.). — Mercedes, A. P. Rodrigo 630, XI-1936 (LP.). — Goya, J. J. Nájera, III-1913 (SI.).

Entre Ríos: Concordia, Raffaelli 67, IV-1926 (LPS. 1276); id., A. Castellanos, I-1931 (BA.). — Colón, Parque Quirós, Alugasti, V-1927 (BA.). — Concepción del Uruguay, Raffaelli 32, IV-1926 (LPS. 1273). — Lucas González, Raffaelli, n° 4, IV-1926 (LPS. 1274). — Escuela Las Delicias, Raffaelli 136, IV-1926 (LPS. 1275). — Holt, R. Martínez Crovetto 2268, V-1943 (RMC.).

Santa Fe: Reconquista, Covas y Ragonese 3552, II-1939 (LP.). — Entre Sastre y Glucellas, Ragonese 2296, IV-1936 (LP., BA.). — Mocoví, Venturi 140, III-1904 (SI.). — De Reconquista a Dr. Barros Pazos, M. M. Job 823, II-1936 (LP.). — Ocampo, Venturi, III-1904 (SI.). — Alrededores de Santo Tomé, M. M. Job 1043, 1056, II-1936 (LP.).

Córdoba: Valle de los Reartes, A. Castellanos 155, II-1920 (LIL., SI.). — Ascochinga, M. L. Giardelli 333, III-1936 (SI.). — Villa Allende, R. Lahitte, V-1939 (BAB.).

San Juan: Sin localidad, C. Arnáez, I-1913 (LP.).

La Pampa: General Pico, Williamsson, III-1932 (BAB.).

Buenos Aires: Capital, Parque 3 de Febrero, J. F. Molfino 149, XI-1917 (BAF.). — Barracas al Sur, Venturi, IV-1898 (LP.). — Belgrano, L. R. Parodi 9880, III-1931 (PAR.). — Núñez, J. F. Molfino 148, III-1917 (BAF.). — Palermo, R. Martínez Crovetto 2048, XII-1941 (RMC.). — Olivos, G. Dawson 717, II-1939 (LP.). — Isla Martín García, Molfino y Clos, VI-1926 (BAB.). — Pergamino, C. D. Girola, IV-1917 (BAB.); id., L. R. Parodi III-1926 (PAR). 7142 La Plata, Bosque, A. L. Cabrera 755, III-1929 (LP.). — id., A. P. Rodrigo 77, III-1929 (LP.); id., Camino de Cintura, A. P. Rodrigo 1087, III-1938 (LP.); id., Los Talas, C. Marelli 46, año 1905 (SI.); id. A. P. Rodrigo, 47, III-1930 (LP.). — 25 de Mayo, Vivero Nacional, R. Castro, IV-1934 (BAB.). — 9 de Julio, Dres. Birabén 803, III-1938 (LP.). — Chascomús, R. Martínez Crovetto 1098, IV-1942 (RMC.). — Martín Coronado, R. Martínez Crovetto 383, IV-1942 (RMC.).

URUGUAY. — Montevideo, Parque Tonkinson, F. Rosa Mato 394, IV-1934 (LP.). — Riachuelo, A. L. Cabrera 3299, 3306, IV-1935 (LP.). — Paysandú, Rosengurt 3346, III-1940 (LP.). — Salto, C. Osten 5404, III-1910 (SI.). — Tacuarembó, Paso Quirino, D. Legrand 1860, I-1940 (LP.).

BRASIL. — Uruguayana, sin colector, n° 5, III-1909 (LP.). — Brasil austral, Mocareti, V-1882 (LPS. 1279).

Distribución geográfica. — Posce casi la misma distribución que la var. *typica*, corriéndose un poco más al oeste al llegar a San Juan y La Pampa. Su límite austral es el paralelo 36.

var. *rhomboidea* (Roxb.) Mast.

Figura 39

Masters, M. T., in Hooker, J. D., *Flora of British India*, I (1874), p. 323. — Watt, M. B., George, A., *Dictionary of The economic Prod. of India*, VI* (1893), p. 681.

S. rhomboidea Roxburgh, W., *Hortus Beng.* (1813), p. 501; *id.*, *Fl. Ind.*, III (1832), p. 176. — De Candolle, A. P., *Prodromus*, I (1824), p. 462.

Hojas angostas, rombo-lanceoladas, con el ápice subagudo u obtuso y la base cuneada, de 17-30 mm de largo por 5-15 mm de ancho; el diámetro longitudinal es dos veces el transversal. En la base de las hojas se encuentran dos pequeños tubérculos o mamelones más o menos desarrollados en forma de gancho. Los carpelos maduros tienen dos aristas cortas de 1 mm de largo.

Material estudiado:

ARGENTINA. — Chaco: Colonia Benítez, A. G. Schultz 549, I-1935 (LP.).

Enrique Urien, A. P. Rodrigo 2387, XI-1940 (LP.).

Misiones: Puerto Aguirre, J. Frenguelli 280, VII-1938 (LP.). —

San José de Pindapoy, A. Bridarolli 2597, I-1942 (LP.). — San José, Lomas secas, J. F. Mollino, II-1922 (BAF., LP.).

Corrientes: Capital, Isla Meza, A. P. Rodrigo 871, XI-1936 (LP.).

— Alrededores de la ciudad, N. Alboff, XI-1896 (LP.). — Corrientes, J. A. Laffont n° 9, VII-1917 (LP.).

Santa Fe: Río Paraná, Canal Viejo, M. M. Job 708, I-III-1936 (LP.).

Buenos Aires: Isla Martín García, A. Pastore 247, IV-1935 (LP.).

— La Plata, Isla Santiago, A. L. Cabrera 1402, III-1930 (LP.).

URUGUAY. — Treinta y Tres, D. Legrand 731, IV-1936 (LP.).

BRASIL. — Río Grande do Sul, Porto Alegre, n° 160, año 1898 (BA., LP.)

y C. Spegazzini, XII-1898 (LPS. 13372). — Santa Catalina, C. Spegazzini 306, sin fecha (LPS. 1271).

Distribución geográfica. — Esta variedad crece en el litoral, especialmente a lo largo de la costa del Paraná hasta la isla Martín García.

Utilidades. — Es la especie más cosmopolita del género, por lo cual ha sido la más conocida y estudiada, habiéndosele encontrado múltiples apli-

caciones especialmente en la India y Australia, donde crece en abundancia. En nuestro país se la utiliza como emoliente por el mucilago que contienen sus hojas y raíces, además de las semillas que son diuréticas (Matoso y Hieronymus).

Las fibras son posiblemente el elemento que mayor importancia puede darle, habiendo sido estudiada su aplicación con óptimos resultados para cordelería y fabricación de papel. Esta tiene un alto porcentaje de celulosa.

En el Brasil y campo de la Argentina se utiliza para hacer escobas.

Según Maiden el ganado vacuno come las ramas y hojas y los nativos de la India la utilizan para combatir la consunción y el reumatismo, tomándola en infusión para favorecer la transpiración. Las hojas las usan como cataplasma para las mordeduras de serpientes y en los casos de picaduras de avispas y otros insectos.

Burkill dice que los malayos le atribuyen poderes mágicos utilizándola para curar la tuberculosis pulmonar y el reumatismo. Además está incluida en la terapéutica de los elefantes.

Esta planta, a pesar de comerla el ganado, no puede considerarse como forrajera.



Fig. 39. — *Sida rhombifolia* var. *rhomboides* (ejemplar dibujado: Misiones, San José, J. F. Mollido, 11-1922), X 1.

28. *Sida montana* K. Schum.

Figuras 40 y 37*

Schumann, G., in Martius, *op. cit.*, XII^o (1892), p. 335. Especie bien definida, fácilmente reconocible y que he determinado con toda seguridad por coincidir exactamente la descripción con la foto del tipo y de los tres cotipos, de los cuales poseo además varios trozos que me fueron gentilmente obsequiados por el Museo de Berlín-Dahlem. Estos fragmentos y las fotografías pertenecen a los ejemplares que cita Schumann en su descripción. Además me fueron enviados la fotografía y trozos del n° 597 coleccionado por Hieronymus en 1876; los cuatro traen el sello *Typus*. — Fries, R. E., *op. cit.* (1906), p. 9.

Sida cordifolia L. var. *variegata* Griseb., Grisebach, B. P. G., *Symbolae* (1879), p. 44.

Nombre vulgar. — Malva del campo, en Corrientes, según Matoso.

Planta perenne, hemicriptófita, erguida, ramificada, con tallos leñosos, cilíndricos y rugosos en la parte inferior y poliédrico-aplanados, canalicu-

PAPERS 02

Quantitative aspects of *Orobanche crenata* infestation in faba beans as affected by abiotic factors and parasite soil seedbank

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Summary

The interactions between the root parasitic weed *Orobanche crenata* Forsk. and its host plant faba bean (*Vicia faba* L.) were quantified under controlled and field conditions at ICARDA's Tel Hadya research station. In the field experiments conducted in 1993–94 and 1994–95 faba beans were sown on two dates, in plots with 0, 50, 200 and 600 *O. crenata* seeds kg⁻¹ soil, under both limited and sufficient moisture supply. The effects of temperature on the duration of the early developmental stages of *O. crenata* were investigated in a growth chamber. The extent of *O. crenata* infestation was closely related to the number of parasite seeds in the soil. The seed-density treatment with 600 seeds kg⁻¹ soil resulted in complete crop failure. Furthermore, *O. crenata* infestation was higher under sufficient than under limiting water supply conditions, irrespective of sowing date. Only in the moderately infested plots, did shifting of the planting time of faba bean result in a significant decrease in parasite dry weight and an increase in crop seed yield. The timing of germination, attachment and further developmental stages of *O. crenata* was not related to faba bean growth stage and was affected primarily by soil temperature. The duration of *O. crenata* developmental stages was estimated using the thermal time concept. The relationship between total number of parasite attachments at the harvest of the faba bean crop and *O. crenata* seed density was dependent on maximum faba bean root-length density measured by the start of pod-filling in each treatment combination of sowing date and moisture supply. The results are discussed with reference to implications for the development of a dynamic simulation model for the prediction of faba bean yield losses caused by *O. crenata*.

Keywords: *Vicia faba*, *Orobanche crenata*, irrigation, sowing date, root-length density, thermal time.

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Introduction

The root parasitic weed *Orobanche crenata* Forsk. is one of the economically most important *Orobanche* species (Orobanchaceae). Its distribution is restricted mainly to the Mediterranean region, but it extends eastwards through the Middle East into Iran. *Orobanche crenata* causes most damage in the cool-season food legumes faba bean (*Vicia faba* L.), lentil (*Lens culinaris* Medic.), chickpea (*Cicer arietinum* L.) and pea (*Pisum sativum* L.). Other host crops are groundnut, carrot, celery, lettuce, sunflower, safflower, melon and tomato (Riches & Parker, 1995). Reported faba bean yield losses caused by *O. crenata* infestation range from 5% to complete crop failure (Sauerborn, 1991a).

In general, owing to the complex relationship that exists between the parasite and its host plant, the development of effective control strategies for parasitic weeds is very difficult. Possible methods for *O. crenata* control include hand-weeding, soil solarization, spraying of herbicides, shifting the planting time of the crop, use of tolerant faba bean cultivars and biological control by insects (Mesa-García & García-Torres, 1986; Sauerborn *et al.*, 1989; Linke *et al.*, 1990; García-Torres *et al.*, 1991; Sauerborn, 1991b). However, at present, none of the economically feasible control measures is by itself able to reduce the parasite infestation satisfactorily. An integration of several control methods (tolerant cultivars, delayed planting date, application of herbicides) appears to be more effective (Linke & Saxena, 1991a; Pieterse *et al.*, 1994; Saxena *et al.*, 1994). More quantitative insight into the mechanisms of the host:parasite system would help to: (i) predict more realistically the expected faba bean yields and yield losses under various environmental conditions, management options and parasite control measures; and (ii) develop and evaluate integrated *O. crenata* control strategies.

It is well known that the level of *O. crenata* infestation depends mainly on the parasite seedbank in the soil and on climatic conditions, i.e. temperature and soil moisture during the growing season (ter Borg, 1986; ter Borg & van Ast, 1991; Linke *et al.*, 1991a; Sauerborn, 1991b). According to the few available quantitative studies, the yield of infected faba beans is negatively correlated with the *O. crenata* soil seedbank or with the number of emerged parasite shoots (Linke *et al.*, 1991a; Zaitoun *et al.*, 1991). About 200 parasite seeds kg^{-1} soil lead to 50% yield loss in several crops (Linke *et al.*, 1991a; Bernhard *et al.*, 1998) and at parasite seed densities of more than 400 seeds kg^{-1} soil the faba bean yields drop to zero (Linke *et al.*, 1991a). Depending on the climatic conditions during the growing season, an infestation level of 2.1 (Linke *et al.*, 1991a) to 4.0 (Mesa-García & García-Torres, 1984) emerged *O. crenata* shoots per faba bean at harvest caused, approximately, a 50% reduction in crop yield.

At a given *O. crenata* seed density, the root-length density (RLD, cm roots cm^{-3} soil) of faba bean in the upper soil layers has been found to determine the probability of *O. crenata* infestation (Aalders & Pieters, 1986; ter Borg & van Ast, 1991; Manschadi *et al.*, 1997). Under Mediterranean conditions, soil moisture is the major factor affecting the RLD and rooting depth of faba beans (Manschadi *et al.*, 1998b). However, the interactions among *O. crenata* soil seedbank, faba bean RLD and number of parasite attachments under different climatic conditions have not yet been studied quantitatively.

The objectives of this study were to quantify the effects of *O. crenata* seed density in the soil, soil temperature and soil moisture regimes on: (1) the occurrence and duration of various developmental stages of *O. crenata*; (2) the number and dry weight of *O. crenata* plants; (3) the relationship between faba bean RLD and number of *O. crenata* attachments; and (4) faba bean seed yield.

Materials and methods

Field experiments

Two field experiments were carried out in 1993–94 and 1994–95 at the principal research station of the International Centre for Agricultural Research in the Dry Areas (ICARDA) at Tel Hadya (36°N, 37°E, 284 m above sea-level) in north-west Syria. The trials were designed as split-split-plots with moisture supply as main plot, sowing date as subplot and *O. crenata* seed load as subsubplot, and replicated four times (Table 1).

Irrigation treatments, plant sampling procedures and standard measurements have previously been described in detail (Manschadi *et al.*, 1998a). Briefly, in both seasons a large-seeded faba bean genotype (ILB 1814; Syrian Land Race, *Orobanche*-susceptible) was sown by hand on two dates at 22 seeds m⁻². The crops in the moisture supply treatment MS1 were grown mainly under rainfed conditions. Only one supplemental irrigation was applied at the beginning of the growing period in each season. In MS2, plots were irrigated with 180 and 265 mm water in 1993–94 and 1994–95 respectively. The total water input (rainfall plus irrigation) in this treatment amounted to 538 mm in 1993–94 and 585 mm in 1994–95.

The experimental field was naturally infested with *O. crenata* seeds. Therefore, in order to create control plots (without parasite seeds) as well as plots with controlled differentiation in *O. crenata* seed densities, the experimental area was first solarized during the hot weather period in July and August by covering soil pre-irrigated with 50 mm of water with clear polyethylene sheets (0.18 mm thick) for 40 d. This duration of solarization is reported to give more than 90% control of *Orobanche* (Sauerborn *et al.*, 1989). One week before sowing faba bean, different *O. crenata* seed densities were created artificially by spreading *O. crenata* seeds mixed with 50 g sand uniformly over each plot. The seeds were then mixed with the top 15 cm soil using a rake in the 1993–94 and a rotavator in the 1994–95 season. *Orobanche crenata* seeds had been collected in 1991 from a faba bean field at ICARDA. The amount of parasite seeds needed for each plot was calculated according to the viability of the seeds, the 1000-seed weight of *O. crenata* (4 mg) and the weight of the top 15 cm soil layer using a bulk density of 1.1 g cm⁻³. The viability of *O. crenata* seeds was determined by the 2,3,5-triphenyl tetrazolium chloride (TTC) test (Linke & Saxena, 1991b).

Sequential samples were taken during faba bean growth, beginning 4 weeks after emergence and ending at physiological maturity. Plants from five adjacent positions were collected at each sampling date and separated into stems, leaves, inflorescences, pod walls and seeds. Numbers and dry weights of these organs were measured. Leaf areas were determined with a calibrated Licor Leaf Area Meter (model LI-3100, LI-COR, USA).

Table 1 Summary of the experimental factors in the growing seasons 1993–94 and 1994–95

Factor	Level	Description
Moisture supply	MS1	Limited moisture supply
	MS2	Sufficient moisture supply
Sowing date	SD1	Nov. 10 (1993–94); Nov. 7 (1994–95)
	SD2	Dec. 20 (1993–94); Dec. 12 (1994–95)
<i>O. crenata</i> seed load	OS0	Without <i>O. crenata</i> seeds
	OS1	50 viable <i>O. crenata</i> seeds kg ⁻¹ soil (0–15 cm)
	OS2	200 viable <i>O. crenata</i> seeds kg ⁻¹ soil (0–15 cm)
	OS3	600 viable <i>O. crenata</i> seeds kg ⁻¹ soil (0–15 cm)

The root-length density (RLD) and root dry weight of two adjacent plants – out of the five collected for dissection – were measured in two plots of each factor combination. Three soil samples were taken around each plant with an auger (diameter 11 cm). The first sample was taken as a core centring around the plant (C_M) and the two others as adjacent left/right cores ($C_{L/R}$). The soil samples were collected from the soil depths 0–15, 15–30, 30–45, and 45–60 cm. The methods of root sampling and root-length measurement have previously been described in detail (Manschadi *et al.*, 1998b). For each soil sample, the number of *O. crenata* plants that were attached to faba bean roots was determined and the parasites were classified into the following developmental stages: (a) visible tubercles > 1 mm with or without crown roots; (b) buds; (c) underground shoots; and (d) emerged plants, according to the key described by Linke *et al.* (1989). Thereafter, the parasites were separated from the faba bean roots and their dry weight was determined.

At physiological maturity, an area of 1 m² from the centre of each plot was harvested. From the harvested sample, the numbers and dry weights of faba bean stems, pods, and seeds were determined. Afterwards, the emerged *O. crenata* shoots and the underground attachments (down to 15 cm soil depth) were collected and counted. The dry weights of above- and below-ground parasites were determined separately.

The soil temperature was recorded continuously in 5, 15 and 25 cm soil depths using temperature sensors connected to a data logger (Delta-T Devices, UK).

Growth chamber experiments

The effects of temperature on the duration of the early developmental stages of *O. crenata* were investigated under optimal water supply conditions and with high *O. crenata* seed density in the soil. Three experiments were conducted successively in a growth chamber (Model E7 Conviron, Canada) in 1995.

A 1:1 mixture of steam-sterilized soil and sand was used for each experiment. The sterilized soil was artificially infested with 20 mg of *O. crenata* seeds (approximately 5000 seeds) kg⁻¹ soil. Plastic pots (9 cm diameter, 0.8 L volume) were filled with the infested soil, irrigated and stored for 7 d at room temperature to pre-condition the parasite seeds. *Orobanche crenata* seeds had been collected in 1993 from a faba bean field at ICARDA and stored in plastic containers at room temperature. The viability of *O. crenata* seeds was about 80% at the beginning of 1995, as determined by the 2,3,5-triphenyl tetrazolium chloride (TTC) test (Linke & Saxena, 1991b). After the conditioning period, one pre-germinated seed of faba bean genotype ILB 1814 was planted in each pot. Thereafter, in each experiment, 27 pots were put in the growth chamber at 12/12 h dark/light and alternating (12 h) temperature. In the first experiment (GC1) the night/day temperatures were set to 3/7 °C, for the second to 6/18 °C (GC2) and for the last to 12/26 °C (GC3). The selected temperatures for the experiments GC3, GC2 and GC1 corresponded to the long-term maximum and minimum temperatures at Tel Hadya in October, November and December–January respectively.

Pots were irrigated as required to avoid drought stress. At weekly intervals, beginning one week after faba bean emergence, three randomly chosen pots were taken from the growth chamber. The roots of faba beans were carefully washed free of soil and the underground developmental stages of *O. crenata* on faba bean roots (appressoria, tubercles, and buds) were observed under the dissecting microscope. At the final sampling, about 2 months after faba bean emergence, six pots were taken.

Calculations

The thermal time approach (Ritchie & NeSmith, 1991) was used to estimate the dates of occurrence of various developmental stages of *O. crenata*. Thermal time (d °C, day-degrees) was calculated as the summation of daily mean soil temperature at 10 cm depth above a base temperature, TBASES, below which the developmental rate equals zero.

Statistical analysis

Analysis of variance was carried out using the GLM (General Linear Model) procedure of the SAS statistical package (SAS Institute, 1991). Prior to analysis of variance, a test was carried out to check whether the data followed the normal distribution using the UNIVARIATE procedure of SAS (Dufner *et al.*, 1992). Significant differences in the mean values were determined using the TUKEY-Test (Tukey's honest significant difference) at a significance level of 0.05. Regression analysis and curve fitting were obtained with SigmaPlot (version 2.01, Jandel Scientific Software).

Results

In the field experiments, the faba bean crop in control plots (OS0) were almost totally free from *O. crenata* infection. Only two parasite shoots were observed in a control plot of earlier sown crops in 1994–95. This indicates that soil solarization had provided a very good control of *O. crenata* because the experimental field was naturally infested with parasite seeds. The experimental data obtained from the control plots describing the effects of temperature and soil moisture on faba bean root and shoot growth have been reported elsewhere (Manschadi *et al.*, 1998a,b). In this paper, we present the results of *O. crenata* infested plots.

In the 1993–94 season, the *O. crenata* infection in artificially infested plots (OS1, OS2, OS3) was very low and much delayed. The few observed parasite attachments had a bulb-shaped underground shoot directly below the soil surface, indicating that the *O. crenata* seeds were situated in the upper 6–7 cm soil layer. This was most probably caused by the use of a rake, which failed in mixing the parasite seeds with the top 15 cm soil. Therefore, this study shows only the results of the field experiment in 1994–95 when the parasite seeds were thoroughly mixed with the top 15 cm of soil using a rotavator.

Phasic development of *O. crenata*

Few *O. crenata* appressoria were formed in the first growth chamber experiment (GC1) with 3/7 °C night/day temperatures. No *O. crenata* tubercles or buds were observed at the final sampling (about 60 d after faba bean emergence, DAE). In GC2 and GC3 as well as under field conditions, *O. crenata* development rate was positively correlated with the soil temperature. The thermal duration of various *O. crenata* developmental stages is shown in Fig. 1. A base temperature (TBASES) of 4 °C was assumed for the phase from faba bean emergence to formation of *O. crenata* appressorium because some appressoria were formed at 5 °C in GC1. A TBASES of 6 °C was used to calculate the thermal time from appressorium to formation of tubercle, as no tubercles were observed in the first growth chamber experiment conducted at 5 °C. For the further development stages of *O. crenata*, a TBASES of 8 °C gave the best fit to the data.

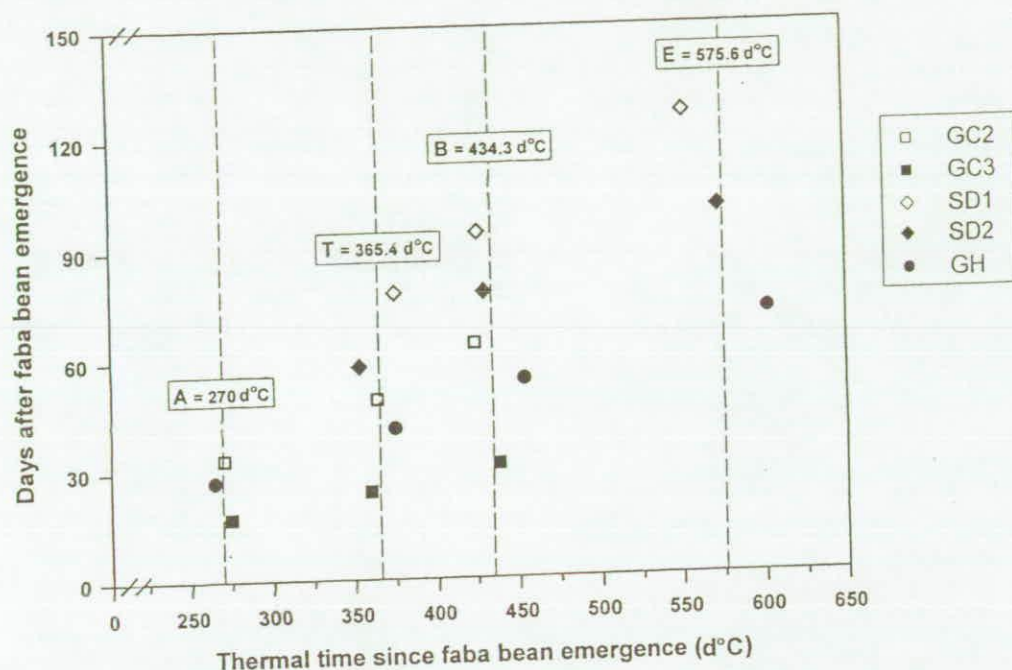


Fig. 1 Thermal duration of different developmental stages of *O. crenata* on faba bean; A, T, B and E indicate appressorium, tubercle, bud and emergence of *O. crenata* respectively; GC2 and GC3 are for growth chamber experiments and SD1 and SD2 represent first and second sowing date in the field experiment; GH is for a greenhouse experiment (Manschadi *et al.*, 1996).

The occurrence of *O. crenata* developmental stages was not related to faba bean phenology. In the heavily infested plots (OS3), the formation of parasite buds coincided with the onset of flowering in faba beans.

Orobancha crenata infestation

The total number of *O. crenata* attachments, i.e. tubercles, buds, underground and emerged shoots, counted at faba bean harvest was closely related to the parasite seed density in the soil. Averaged over all water and sowing date treatments, the highest attachment number (482.7 parasites m^{-2}) was observed in plots with 600 (OS3) *O. crenata* seeds kg^{-1} soil (Table 2). In comparison to OS3, the total numbers of parasites in plots with 200 (OS2) and 50 (OS1) seeds kg^{-1} soil were reduced by 46 and 86% respectively. When faba bean crops were grown with sufficient moisture supply (MS2), delaying of sowing did not significantly affect the number of *O. crenata* attachments. However, with limited moisture, the number of parasites in OS2 and OS3 treatments of later sown crops were reduced by about 50%. The lowest *O. crenata* attachment was observed in the later sown crops (SD2), grown under limited moisture supply.

The number of emerged parasite shoots increased with increased parasite seed density in the soil (Fig. 2). Only the difference between OS2 and OS3 of earlier sown crops in MS1 was statistically not significant. The number of emerged parasites was not affected by sowing date. With the exception of OS1, the number of emerged *O. crenata* in MS2 plots was greater than

Table 2 Total number of *O. crenata* attachments m^{-2} on faba bean in the 1994–95 season

Moisture supply	Sowing date	<i>O. crenata</i> seed density kg^{-1} soil		
		50 (OS1)	200 (OS2)	600 (OS3)
Limited (MS1)	Nov. 7 (SD1)	51.9 (5.0)	300.2 (21.1)	528.6 (72.5)
	Dec. 12 (SD2)	35.3 (9.2)	152.2 (20.8)	277.0 (22.0)
Sufficient (MS2)	Nov. 7 (SD1)	91.3 (8.0)	290.3 (32.8)	538.9 (31.7)
	Dec. 12 (SD2)	81.4 (6.3)	292.0 (13.1)	586.1 (62.2)
Mean		65.0	258.7	482.7

The values in parentheses represent standard errors; the LSD_{05} values for comparing two means are: 105.5 for OS means in a row; 104.6 for SD means at the same combination of MS and OS; 86.1 for MS means at the same combination of SD and OS.

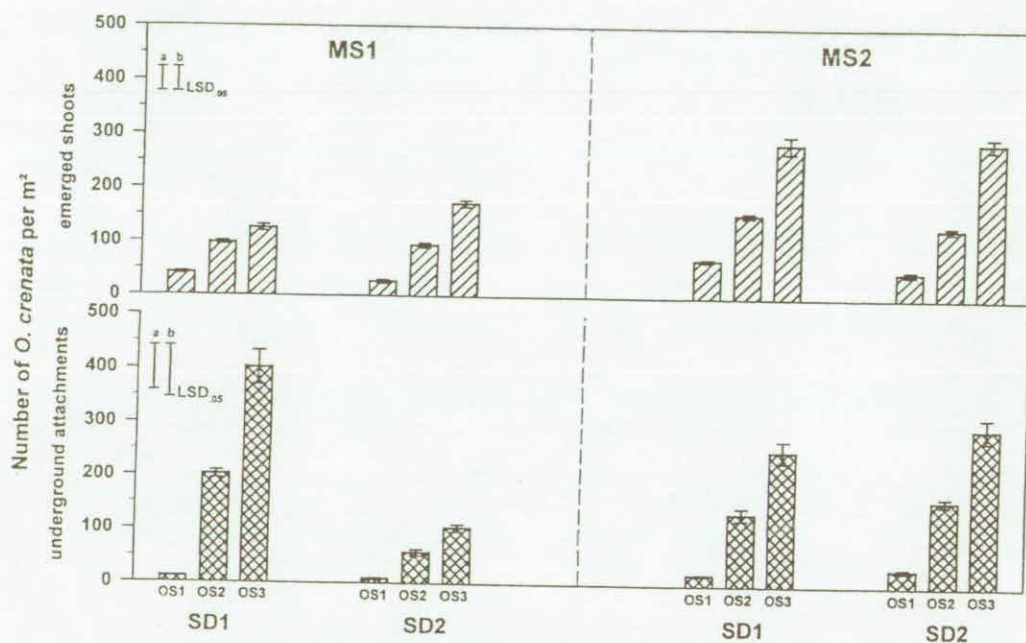


Fig. 2 Number of emerged shoots and underground attachments of *O. crenata* on faba bean genotype ILB 1814 grown under limited (MS1) and sufficient (MS2) moisture supply. OS1, OS2 and OS3 indicate 50, 200 and 600 *O. crenata* seeds kg^{-1} soil respectively. SD1 and SD2 are for the first and second sowing date respectively. Vertical bars marked with letters represent LSD for comparing OS means within the same SD as well as SD means at the same combination of MS and OS (a); and MS means at the same combination of MS and OS (b). Vertical bars indicate $\pm$ SE.

those in MS1 plots. On average, the lowest numbers of underground attachments (i.e. tubercles, buds, underground shoots) were found in OS1. In OS2 and OS3 of earlier sown crops grown under limited moisture supply, around 67% and 76% of the parasites were found below the soil surface (Fig. 2). When crops were fully irrigated, only about 50% of parasites were counted as underground attachments.

Dry weight of faba bean and *O. crenata*

Compared with uninfected plants, *O. crenata* infestation reduced the total dry weight of faba bean crops on average by 24%, 48% and 62.5% in OS1, OS2 and OS3 respectively (Fig. 3). Delayed sowing resulted in a significant reduction of dry weights in uninfected and highly infected (OS3) crops only. With the exceptions of OS3 and earlier-sown crops of OS2, crops grown under full irrigation produced significantly more dry matter.

The greatest dry weights of *O. crenata* were observed in earlier-sown crops under full irrigation in OS2 and OS3. Although the total number of *O. crenata* attachments in OS2 was significantly lower than that in OS3, the dry weights of the parasites were similar in both seed-density treatments (Fig. 3). Delay of sowing date only caused a significant reduction in *O. crenata* dry weights in OS2 and OS3.

In general, *O. crenata* infestation reduced the grain yield of faba bean (Fig. 4). Under severe *O. crenata* infestation (OS3) in both moisture supply treatments, no pods were observed in the earlier-sown crops and grain yields of later-sown faba beans were negligible. In OS2, the seed yields of earlier-sown crops were very low and did not differ significantly from those in OS3. However, in contrast to OS3, delay of sowing increased the faba bean yield substantially. In both OS2 and OS3 treatments, full irrigation did not improve the seed yield of infected faba beans. Under relatively low *O. crenata* infestation (OS1), delaying of sowing did not affect faba bean seed yield. The highest faba bean seed yield (284 g m^{-2}) in OS1 was obtained in later-sown crops grown under sufficient moisture supply.

In the earlier-sown crops of both moisture supply treatments, there were no differences between the uninfected and infected faba beans for total dry matter partitioned into both faba bean fruits (pod husk + seed) and *O. crenata* (Fig. 4). When crops were sown later, a similar pattern of dry matter partitioning was observed between OS0, OS1 and OS2 treatments. However, in OS3, the combined dry weight of faba bean fruits and *O. crenata* was significantly lower than those in other treatments, irrespective of moisture supply.

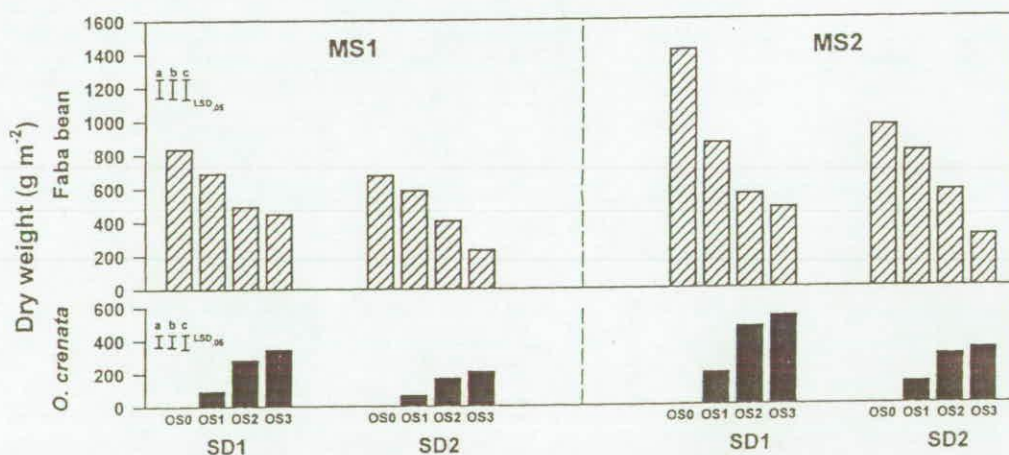


Fig. 3 Dry weight of faba bean genotype ILB 1814 and *O. crenata* under limited (MS1) and sufficient (MS2) moisture supply in 1994–95; OS0, OS1, OS2 and OS3 indicate 0, 50, 200 and 600 *O. crenata* seeds kg^{-1} respectively. SD1 and SD2 are for the first and second sowing date respectively. Vertical bars marked with letters indicate LSD for comparing OS means within the same SD (a); SD means at the same combination of MS and OS (b); and MS means at the same combination of SD and OS (c).

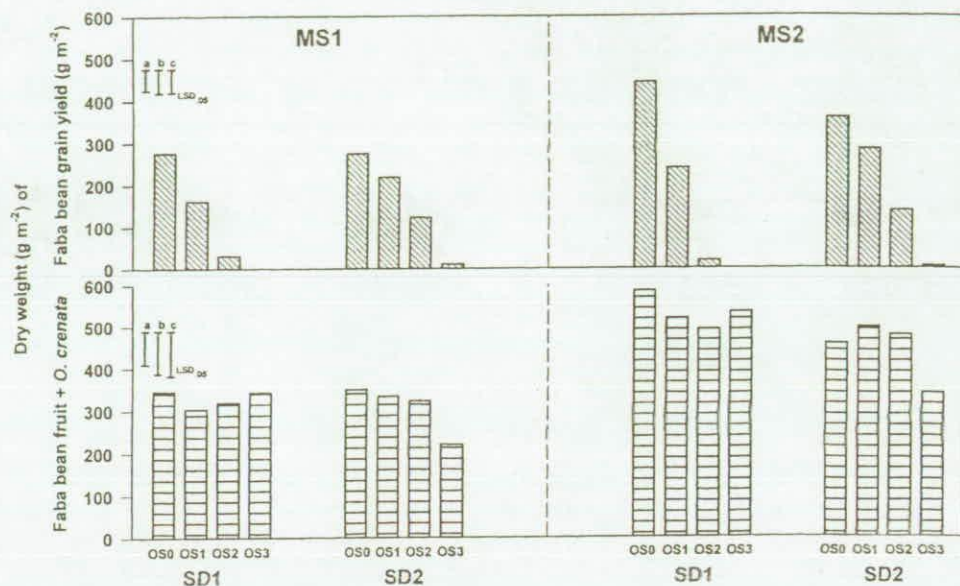


Fig. 4 Grain yield and dry weight of fruit (pod, husk and seed) plus *O. crenata* in faba bean genotype ILB 1814 grown under limited (MS1) and sufficient (MS2) moisture supply in 1994–95. Vertical bars indicate LSD for comparing OS means within the same SD (a); SD means at the same combination of MS and OS (b); and MS means at the same combination of SD and OS (c) (Legends see Fig. 3).

Orobanche crenata dry weight measured in fully irrigated plots with 50 parasite seeds kg^{-1} soil (OS1) were used to calculate the potential growth rate of an *O. crenata* plant (PGORO) as a function of temperature sum (DTTSUM) (Fig. 5). We assume that in this treatment no intraspecific competition between *O. crenata* attachments occurred because more than 80% of the parasites emerged and completed their life cycles successfully. DTTSUM was determined using air temperature sum ($^{\circ}\text{C}$) accumulated from faba bean emergence using a base temperature of 0°C .

Faba bean root-length density and number of *O. crenata* attachments

The relationship between the total number of parasite attachments at faba bean harvest (TORNO) and *O. crenata* seed density (ORSD) was dependent on maximum faba bean RLD in the top 15 cm soil measured by the start of pod-filling in each treatment combination of sowing date and moisture supply (Fig. 6).

When the RLDs were greater than 2 cm cm^{-3} , the differences between TORNOs in each ORSD treatment were not significant, and TORNO seemed to be dependent on ORSD only. In this case, the relationship between TORNO and ORSD was best described by a monomolecular equation (Thornley & Johnson, 1990):

$$\text{TORNO} = 685.4 \times [1 - \text{EXP}(-0.0027 \times \text{ORSD})] \quad (1)$$

For $\text{RLD} \leq 2 \text{ cm cm}^{-3}$, the relationship between TORNO and RLD was assumed to follow a linear model. The dependency of TORNO on ORSD in this domain seemed to be the same as for higher values of RLD described by eqn 1 (see Fig. 6, dashed line). Therefore, for $1.039 \leq \text{RLDs} \leq 2 \text{ cm cm}^{-3}$, the overall function was:

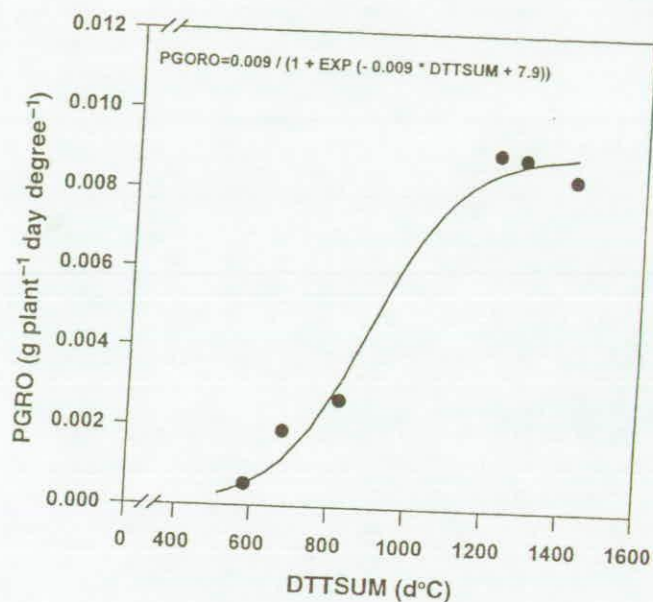


Fig. 5 Relationship between potential growth rate of an *O. crenata* plant (PGRO) and accumulated air temperature (DTTSUM) in fully irrigated faba bean plots (MS2) with 50 parasite seeds kg⁻¹ soil (OS2).

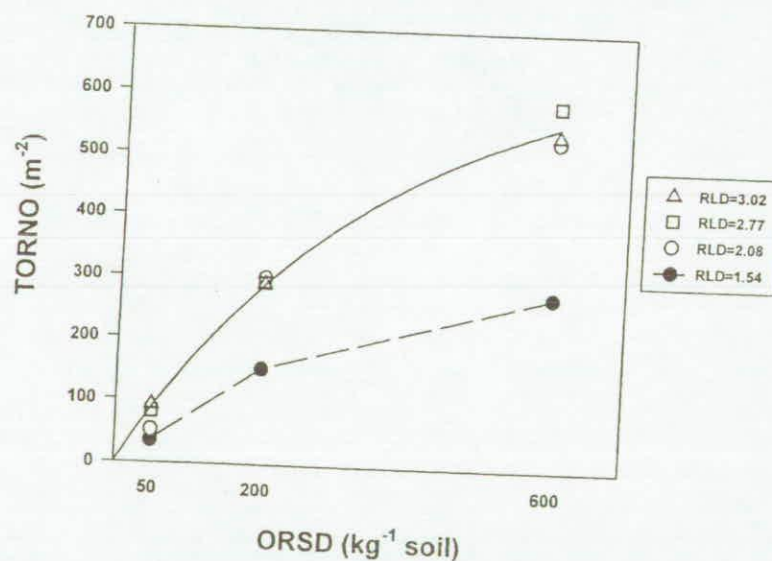


Fig. 6 Relationship between number of *O. crenata* at faba bean harvest (TORNO) and *O. crenata* seed density (ORSD) at different root-length densities (RLD; cm cm⁻³ in the top 15 cm soil) of faba beans planted at two different dates and grown under limited and sufficient moisture supply; Regression equations: eqns (1) and (2).

$$\text{TORNO} = 685.4 \times [1 - \text{EXP}(-0.0027 \times \text{ORSD})] \times (-1.083 + 1.042 \times \text{RLD}) \quad (2)$$

The parameters a (-1.083) and b (1.042) were estimated from the linear regression between $\{\text{TORNO}/685.4 \times [1 - \text{EXP}(-0.0027 \times \text{ORSD})]\}$ and RLD ($r^2 = 0.91$), so that for $\text{RLD} = 2$ the equation could be joined continuously, i.e. $a + b \times 2 = 1$.

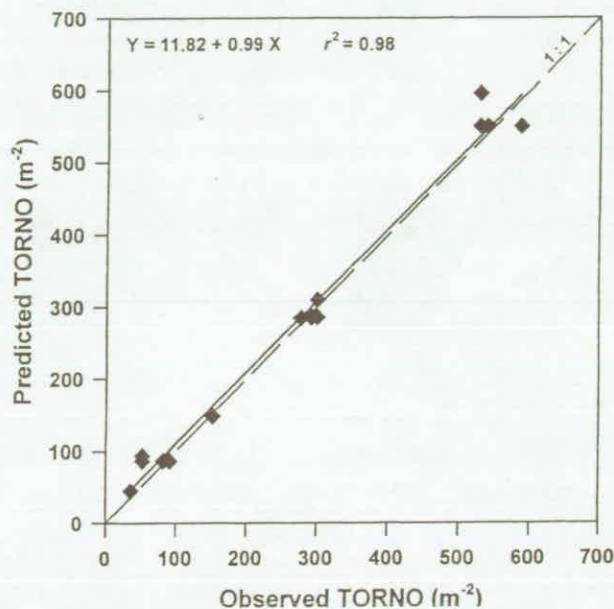


Fig. 7 Predicted and observed number of *O. crenata* attachments (TORNO) on faba bean genotype ILB 1814 at crop harvest in 1994–95.

In all treatments, TORNO at the harvest of faba bean crops was predicted realistically using equations 1 and 2 (Fig. 7).

Discussion

The effects of *O. crenata* soil seedbank, temperature and soil moisture on the parasite infestation level in faba beans were quantified in this study. The phasic development of *O. crenata* was closely related to soil temperature and not to faba bean phenology. A similar finding from field experiments with other faba bean cultivars was reported by ter Borg (1987). Prediction of occurrence and duration of *O. crenata* developmental stages based on the thermal time concept has been reported by Kropff & Schippers (1986) and ter Borg (1987). However, these authors assumed a base temperature of 0 °C for the calculation of thermal duration of *O. crenata* developmental stages from germination to maturity. Our results and those of Sauerborn (1989) show that *O. crenata* attachments do not reach the tubercle stage at temperatures lower than 5 °C. Therefore, use of different TBASES more accurately predicts *O. crenata* development.

In agreement with previous reports (Mesa-García & García-Torres, 1986; Linke *et al.*, 1991a), the extent of *O. crenata* infestation in our study was closely related to the number of parasite seeds in the soil. The seed-density treatment with 600 seeds kg⁻¹ soil (OS3) resulted in complete crop failure. A similar finding was reported by Linke *et al.* (1991a).

Although a delay in crop sowing consistently decreases crop yield compared with early sowing, it has been reported to be an effective method to reduce the parasite infestation and increase faba bean seed yield (Mesa-García & García-Torres, 1986; Arjona-Berral *et al.*, 1987; van Hezewijk *et al.*, 1987; Sauerborn, 1991b). However, our results revealed that the effect of delayed sowing on *O. crenata* infestation was dependent on the parasite seedbank in the soil. Shifting the planting time of faba bean only resulted in a decrease in parasite dry weight and an increase in crop seed yield in the moderately infested plots (OS2). In the treatments with lower

(OS1) and higher (OS3) infestation levels, crop yields were not improved, although delayed sowing did reduce the dry weight of parasites.

In our study, *O. crenata* infestation was higher under sufficient (MS2) than under limiting (MS1) water supply conditions, irrespective of sowing date. The positive effect of supplemental irrigation on the numbers and dry weights of parasites can be attributed to a better development of the faba bean root system and a better crop vigour, which are both known to increase the chance of infection and to enhance the development of parasites (Aalders & Pieters, 1986; ter Borg & van Ast, 1991; Manschadi *et al.*, 1997). Sufficient water supply only increased the seed yield of infected faba beans in plots with the lowest parasite seed density (OS1). However, in the long term, supplemental irrigation should not be recommended as a measure to improve the seed yield of infected faba bean plants because it increases both dry weight and numbers of emerged parasites. This leads to a higher seed production and, consequently, an increase in the *O. crenata* seedbank in the soil (Linke *et al.*, 1991b).

The combined dry weights of *O. crenata* and faba bean fruits (Fig. 4) confirm previous observations (ter Borg, 1986; Manschadi *et al.*, 1996; Manschadi *et al.*, 1997) that *O. crenata* acts as an additional sink in the host:parasite system without influencing host metabolism. The combined dry weights of parasite and faba bean fruits were only reduced in the later-sown crops of the heavily infested plots (OS3). This was mainly because of an *O. crenata*-induced acceleration of faba bean senescence, as in these treatments the host plants died about 2 weeks earlier than the control plants.

When the bud stage of *O. crenata* coincided with the onset of flowering in faba beans (OS3), no seed-containing pods were observed on host plants. This is in agreement with the results of a greenhouse experiment reported by Manschadi *et al.* (1996), indicating that the sink strength of *O. crenata* in the bud stage is comparable with that of faba bean seeds in the rapid seed-filling phase. As soon as *O. crenata* starts growing an underground shoot, all assimilates are partitioned into the parasite, unless the faba bean is in the stage of rapid seed-filling of a pod. The pods, at this stage, will continue to develop and produce seeds but subsequent pods will not receive any assimilates. Therefore, the dry matter partitioning between *O. crenata*, as an additional sink, and faba bean organs is closely related to the developmental stages of both parasite and host plant.

There have been no quantitative studies on the effects of *O. crenata* soil seedbank and faba bean root-length density on the number of parasite attachments. The relationships presented in this study (eqns 1 and 2) should be considered as a preliminary attempt to address this issue and need to be evaluated and improved with data sets from other faba bean cultivars and locations. Of particular importance is the fact that these equations are only valid for *Orobanche*-susceptible faba bean cultivars, as it has been reported that in *Orobanche*-tolerant faba beans the number of *O. crenata* attachments is not related to faba bean root-length density (Manschadi *et al.*, 1997).

In conclusion, the above findings provide useful quantitative information for modelling the interactions between the parasitic weed *O. crenata* and its host plant *Vicia faba*. The occurrence and duration of *O. crenata* developmental stages can be easily estimated on the basis of thermal time. As *O. crenata* acts only as an additional sink for photosynthates, dry matter partitioning into parasites may be modelled based on the potential growth rate of an individual *O. crenata* plant and the total number of parasite attachments that can be calculated from the faba bean root-length density and parasite soil seedbank. More knowledge about the faba bean senescence rate in relation to *O. crenata* infestation level appears to be necessary.

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A SURVEY OF SURFACE CHARACTERISTICS OF SEEDS OF SCROPHULARIACEAE AND OROBANCHACEAE USING SCANNING ELECTRON MICROSCOPY¹

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Abstract

Seed surface characteristics of 23 species in 11 genera of the Scrophulariaceae and two species in two genera of the Orobanchaceae from the southeastern United States were examined using scanning electron microscopy. All species exhibit a form of reticulation, and three general types are recognized: deeply reticulate, shallowly reticulate, and obscurely reticulate. The internal surface and the ridges of a reticulum may be ornamented or unornamented by either wax deposits or cell outgrowths. In those genera with several species, seed surface characteristics have systematic value.

This study is part of a research effort on the biology of root parasites of the southeastern United States to determine their potential danger as pathogens of commercial forest trees. It sought to characterize the morphology of seeds of 25 species of Scrophulariaceae and Orobanchaceae by scanning electron microscopy. The seeds are small, ranging from 440 to 309,000 per gram, which makes them ideal for SEM study. Such information is useful in the identification of the parasites and has systematic value.

Twenty-three of the 25 species of Scrophulariaceae investigated are hemiparasites. The Orobanchaceae, closely related to the Scrophulariaceae, are represented by two genera of holoparasites.

The value of SEM studies in pollen is well known, but little work has been done on seed surfaces (Tomb, 1974).

Chuang & Heckard (1972) published the first paper on the structure of seeds of a parasitic angiosperm using SEM. They worked on *Cordylanthus*, a root parasite of the Scrophulariaceae closely allied with some of the genera included in this study. Other work on the seeds of parasitic Scrophulariaceae is well summarized by Kuijt (1969) who also presents detailed drawings of seeds of this alliance.

Unfortunately, the terminology needed to adequately describe seed surface characters has not yet been evolved. Therefore, the general terminology used by Chuang & Heckard (1972) is employed here.

Material and Methods

Seeds were collected from various populations throughout the southeastern

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TABLE 1 — COLLECTION DATA FOR SPECIES USED FOR SEM STUDY

NAME	LOCALITY	COLLECTOR
SCROPHULARIACEAE		
<i>Agalinis aphylla</i> (Nutt.) Raf.	Savana, near junction of U.S. 31 and Ala. 47, Baldwin County, Alabama	Rich, 226
<i>A. fasciculata</i> (Ell.) Raf.	Dry oak site, Phillips County, Arkansas	No voucher
<i>A. linifolia</i> (Nutt.) Britt.	Roadside ditch, ca. 4 miles north of Calhoun County line, Jackson County, Florida	Rich, 230
<i>A. obtusifolia</i> Raf.	Pine forest at Pine Belt Airport, Jones County, Mississippi	Rich, 206
<i>A. purpurea</i> (L.) Penn.	Pine Plantation ca. 4 miles west of Raleigh, Mississippi	Rich, 203
<i>A. selacea</i> (J. W. Gmelin.) Raf.	Intersection I-20 and U.S. 1, Aiken County, South Carolina	Rich, 312
<i>A. tenella</i> Penn.	Pine plantation near intersection I-20 and U.S. 1, Aiken County, South Carolina	Rich, 313
<i>A. tenuifolia</i> (Vahl.) Raf.	Pine plantation 5 miles north of Sampson County line, Rankin County, Mississippi	Rich, 202
<i>A. virgata</i> Raf.	Sandhill north of Aiken, Aiken County, South Carolina	Rich, 311
<i>Aureolaria flava</i> (L.) Farw.	Stream bank, 2 miles north of Torreya State Park, Liberty County, Florida	Rich, 256
<i>A. lasvigata</i> Raf.	Forest opening, Mountain Lake Biological Station, Giles County, Virginia	No voucher
<i>A. pedicularia</i> (L.) Raf.	Sandhill, ca 5 miles west of Darlington County line, Chesterfield County, South Carolina	Musselman and Rich, 4869
<i>A. virginica</i> (L.) Penn.	Oak forest, Crumps Bottom, Summers County, West Virginia	Musselman, 4892
<i>Buchnera americana</i> L.	Roadside, Fla. Hwy. 9 at Oklawaha Canal, Putnam County, Florida	Musselman, 4692
<i>Castilleja coccinea</i> (L.) Spreng.	Meadow, 3 miles west of junction U.S. 211 and Va. 8, Floyd County, Virginia	Musselman, 4864
<i>Dasistoma macrophylla</i> (Nutt.) Raf.	Stream bottom, junction of Tenn. Hwy. 96 and I-40, Dickson County, Tennessee	Rich, 199
<i>Macranthera flammea</i> Bartr.	Margin of swamp, just south of Angie on Hwy. 21 Washington Parish, Louisiana	Rich, 209
<i>Melampyrum lineare</i> Desr.	Rock outcropping, Wind Rock Overlook, Blue Ridge Parkway, Avery County, North Carolina. (By permit)	No voucher
<i>Pedicularis canadensis</i> L.	Deciduous forest; fire tower near Mountain Lake Geological Station, Giles County, Virginia	Musselman, 4865

TABLE 1 (Contd)

NAME	LOCALITY	COLLECTOR
SCROPHULARIACEAE		
<i>Schwalbea americana</i> L.	Savanna, junction of S.C. Hwys. 41 and 99, Berkeley County, South Carolina	Musselman and Rich, 4686
<i>Seymeria cassioides</i> (Walter) Blake	Sandy flatwoods soil, stand of young pines with no overstory, Gulf County, Florida	No voucher
<i>S. pectinata</i> Pursh	Sandy scrub, Mill Dam Recreation area, Ocala National Forest, Marion County, Florida	No voucher
<i>Striga asiatica</i> (L.) Kuntz (= <i>S. lutea</i> Lour.)	Devitalized seeds provided by U.S.D.A. Witchweed Laboratory, Whiteville, North Carolina	No voucher
OROBANCHACEAE		
<i>Conopholis americana</i> (L.) Waltr.	Deciduous forest, Crumps Bottom, Summers County, West Virginia	Musselman, 4866
<i>Epifagus virginiana</i> (L.) Bart.	Roadside, Great Dismal Swamp, City of Suffolk, Virginia	Musselman, 4904

United States and immediately sent to the laboratory where they were stored at 5°C in sealed containers until ready for examination. Representative populations and voucher specimens are noted in Table 1. Voucher specimens are deposited in the Old Dominion University (ODU) herbarium. Nomenclature of Radford et al. (1968) has been followed. Seeds were selected for uniformity from populations using a binocular microscope.

Seeds were mounted on pin-type stubs using double-stick tape or conductive silver paint, coated with 200 angstroms palladium gold (40%-60%) in a Denton vacuum evaporator, model DV 502 and recoated to eliminate charging of the specimens. An Advanced Metals Re-

search Corporation 900 scanning electron microscope was used to examine the seeds. A working distance of 12 mm was used. Photographs were taken with an Oscilloscope camera, series 125, f 1.4, 1:1 magnification.

Observations

AGALINIS—It is the largest genus included in this study. Nine species were examined. Relative to seed surface characteristics, these fall into two groups illustrated by *A. tenella* (Fig. 1E, F) and *A. aphylla* (Fig. 1G, J). In the former, the surface of the reticulum is not ornamented (Fig. 1F) although shallow papillae are present, perhaps a result of underlying cells. In *A. aphylla* and

Fig. 1A-K—A. *Aureolaria pedicularia*, seed in surface view. $\times 103$. B. *Aureolaria pedicularia*, detail of reticula showing ornamentation of surface. $\times 520$. C. *Aureolaria flava*, note deep honeycombing. Each reticulum is asymmetrical. $\times 45$. D. *A. virginica*, crest on margin of seed; reticula have a faint ornamentation. $\times 52$. E. *Agalinis tenella*, seed. $\times 255$. F. *Agalinis tenella*, individual reticula lack ornamentation (cf., Fig. G and J), although outlines of underlying cells are evident. $\times 1275$. G. *Agalinis aphylla*, reticula are shallow with distinct ornamentation. $\times 98$. H. *Buchnera americana*, entire seed. $\times 171$. I. *Castilleja coccinea*, surface of reticula are broken. $\times 110$. J. *Agalinis fasciculata* showing fine network in each reticulum. $\times 525$. K. *Buchnera americana*, reticulum consists of cellular outgrowths. $\times 1070$.

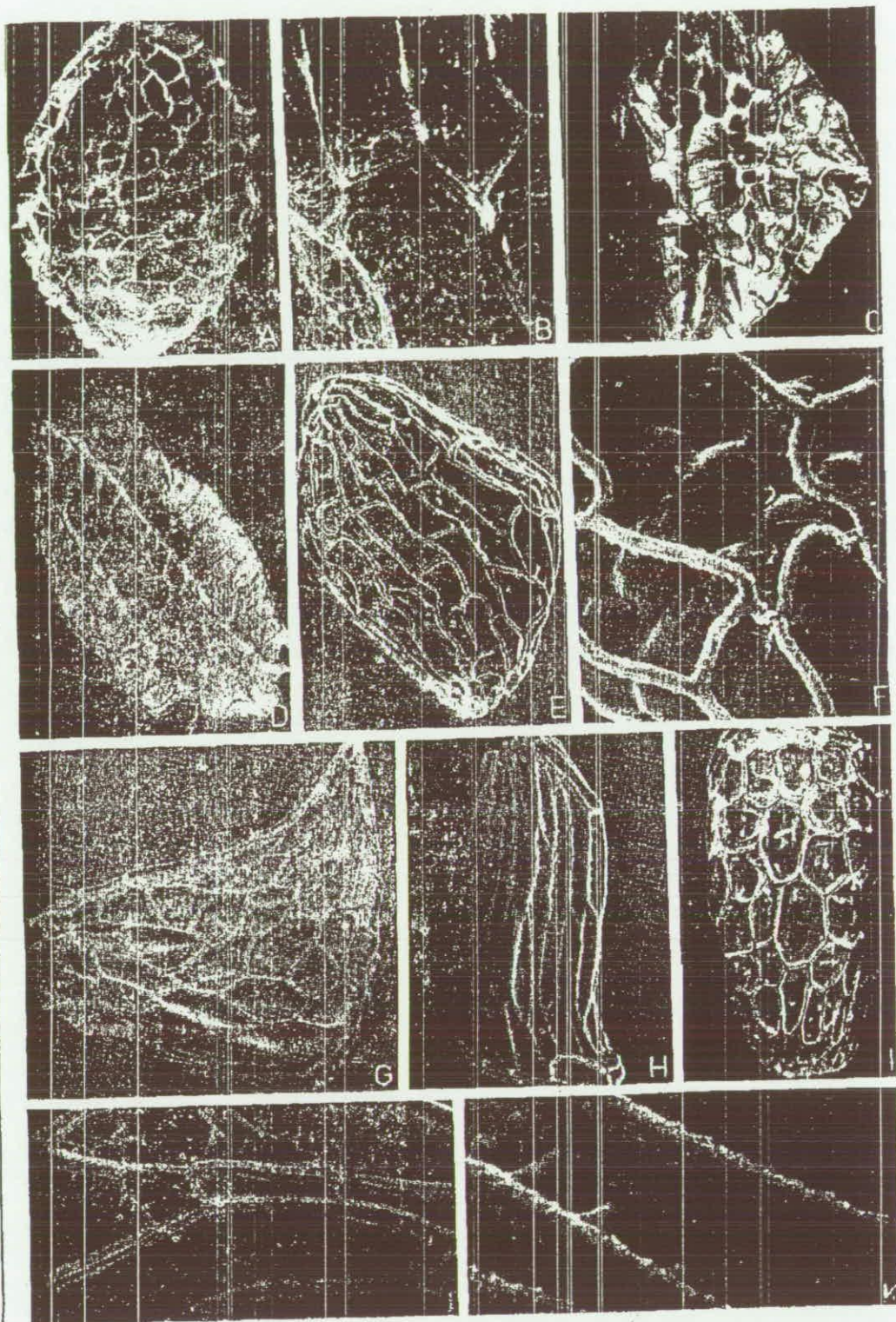


Fig. 1A-K

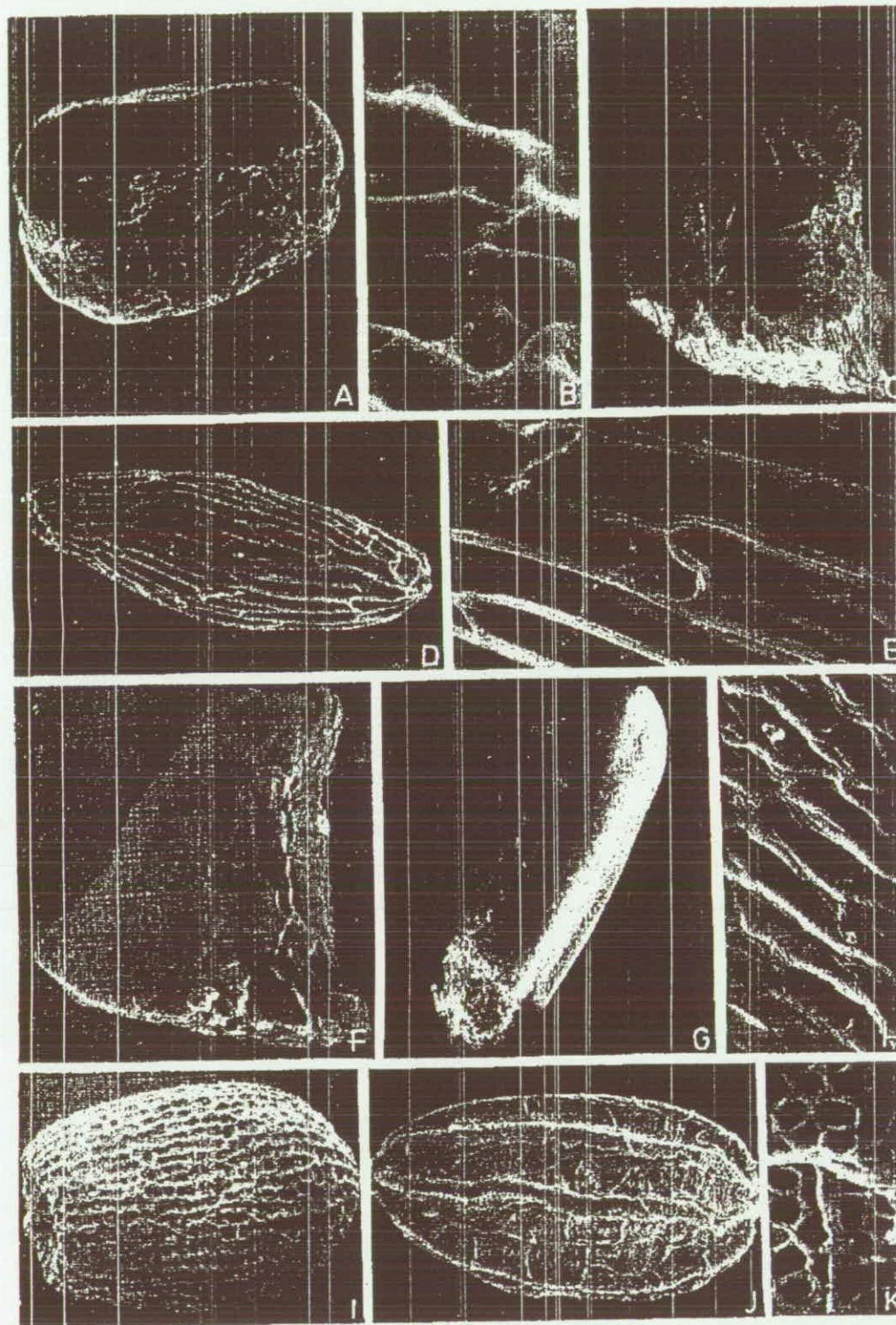


Fig. 2A-K

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A. fasciculata a prominent network of thickenings is evident on the surface of the reticulum (Fig. 1G, J). This was noted previously by Kuijt (1969). These thickenings are similar to those illustrated by Chuang & Heckard (1972) for *Cordylanthus laxiflorus*. The first group, lacking thickenings within the reticula, includes *A. linifolia*, *A. obtusifolia*, *A. sectacea*, *A. tenuifolia*, *A. virgata* and *A. tenella*. The second group includes only *A. aphylla*, *A. fasciculata*, and *A. purpurea*.

AUREOLARIA — The four species in this small genus showed considerable variation in the surface structure of seeds. All four species possess what appears to be papillate wax (Fig. 1B) as described by Chuang & Heckard (1972). *Aureolaria pedicularia* (Fig. 1A), *A. laevigata*, and *A. flava* (Fig. 1C) have deep reticula. The deeply reticulate seed coat of *A. pedicularia* (= *Gerardia pedicularia*) apparently arises by the collapse of the integument (Arekal, 1964). The reticula of *A. virginica* are shallower (Fig. 1D).

BUCHNERA AMERICANA — Seeds of this species have shallow, elongate reticula (Fig. 1H). The surface of the ridges and, to a lesser extent, the surface of the reticula, are covered by knob-like projections (Fig. 1K).

CASTILLEJA COCCINEA — The surface of the reticulum ruptures, perhaps as a result of differential growth rates, giving the appearance of shattered glass (Fig. 1I). At first it was thought this was an artifact but careful examination of fresh material with the light microscope confirmed the presence of ruptures. This phenomenon was also observed in some

reticula of *Macranthera flammea*, and *Aureolaria virginica*, but never to the extent of *C. coccinea*.

CONOPHOLIS AMERICANA — The surface of the seed is almost psilate, except where it comes into contact with another seed in the developing fruit (Fig. 2A). The ridges and surface of the reticula are smooth (Fig. 2B). Tiagi (1965) has shown that the testa of *C. americana*² is the sclerified epidermis of the thick, single integument.

DASISTOMA MACROPHYLLA — The seed is irregularly crested (Fig. 2C) with shallow reticula. The surface of the reticula appears to possess wax deposits similar to those of *Aureolaria*.

EPIFAGUS VIRGINIANA — Very regular, rectangular reticula characterize the surface of the seeds (Fig. 2D). Reticula have angled walls and prominent, narrow ridges on the tops (Fig. 2E).

MACRANTHERA FLAMMEA — The seeds are among the largest included in this study and have a prominent, deeply reticular crest (Fig. 2F) resembling the crests of *Aureolaria* and *Dasistoma*. Unlike the latter, however, no wax is evident on the surface of the reticula.

MELAMPYRUM LINEARE — This is the smoothest of all seeds examined (Fig. 2G). The surface and ridges of the reticula lack any ornamentation (Fig. 2H). According to Arekal (1963)

2. Remarkably, Tiagi records *Conopholis americana* as growing on *Quercus petraea*, one of the white oaks, in the University Botanical Garden in Copenhagen. In nature, it has been noted repeatedly as being entirely restricted to members of the red oak group of the genus *Quercus*.

Fig. 2A-K — A, B. *Conopholis americana*. A. Roughened portion of seed indicates point of contact with another seed in developing fruit. × 93. B. Wrinkled surface represents sclerified epidermis of integument. × 1010. C. *Dasistoma macrophylla*, seed has a curved, winged testa with shallow reticula and fine network of wax depositions within each reticulum. × 48. D, E. *Epifagus virginiana*. D. Seed in surface view. × 210. E. Outer cells of integument become thickened in the middle, leaving a narrow ridge on top of cells. × 1050. F. *Macranthera flammea*, note prominent, honeycombed crest, remaining part of testa is irregularly striate. × 41. G, H. *Melampyrum lineare*. G. Entire seed. × 32. H. Individual reticula represent sclerified outer layer of integument. × 682. I. *Pedicularis canadensis*, seed in surface view. × 52. J. *Seymeria cassioides*, distinguished by uniform reticula and a well-developed pattern of thickenings within them. × 175. K. *Seymeria cassioides*, detail of reticulum thickenings. × 1140.

the surface layer of the testa develops by the thickening of the radial and longitudinal walls of the cells of the epidermis of the integument followed by a collapse of these same cells.

PEDICULARIS CANADENSIS — The seeds are round in cross section and uniformly reticulate (Fig. 2I). The reticula are relatively small and quite shallow. Under higher magnification (not illustrated) the surface of the reticula is finely rugose.

SCHWALBEA AMERICANA — The testa is an elongate and loose-fitting structure with a very simple, uniformly reticulate surface (Fig. 3C, D).

SEYMERIA — *S. pectinata* (Fig. 3B) and *S. cassioides* (Fig. 2J) are very different in shape and ornamentation. *S. pectinata* has a prominent crest on its margin and large, deep, reticula with only weak surface thickenings (Fig. 3B), whereas *S. cassioides* lacks a conspicuous crest, has shallow reticula (Fig. 2J) and a prominent network of thickenings on the reticula (Fig. 2K).

STRIGA ASIATICA — The surface of the seed is covered with uniform, elongate reticula which slightly spiral around the body of the seed (Fig. 3A). Superficially, the details of the reticula in this species resemble those of *Buchnera americana* (cf., Figs. 3E and 1K). However, the papillae of the reticula ridges and surfaces are different. Those of *Striga* are more angular whereas those of *Buchnera* are rounded.

Discussion

All the species studied have reticulate seed coats. The characteristics of the reticula may be classed into three somewhat artificial categories following, in part, the suggestions of Chuang & Heckard (1972). These are: deeply reticulate, shallowly reticulate, and obscurely reticulate. The boundary between each category is not well defined and applies only to the surface (not the crest) of the seed. Deeply reticulate seeds would include only *Aureolaria pedicularia* (Fig. 1A), *A. flava* (Fig. 1C), *A. laevigata*, and *Seymeria pectinata* (Fig. 3B). Obscurely reticulate seeds include *Conopholis ameri-*

cana (Fig. 2A) and *Melampyrum lineare* (Fig. 2G) in which the walls of the outer layer of the integument become exceptionally thick and *Dasistoma macrophylla* (Fig. 2C) with very shallow reticula and narrow, wavy ridges. The surfaces of the reticula may lack ornamentation (e.g., *Schwalbea americana*, Fig. 3C; and *Epifagus virginiana*, Fig. 2D) or have a network composed of either wax deposits (*Aureolaria pedicularia*, Fig. 1B) or actual wall outgrowths (*Buchnera americana*, Fig. 1K; and *Striga asiatica*, Fig. 3E). Species with well-developed crests may have deep (e.g., *Aureolaria flava*, Fig. 1C; and *Macranthera flammea*, Fig. 2F) or shallow (e.g., *Dasistoma macrophylla*; Fig. 2C, and *Seymeria pectinata*, Fig. 3B) reticulations on the crest.

In their studies of the species of *Cordylanthus*, Chuang & Heckard (1972) showed that the surface pattern is due to enlarged epidermal cells of the integument. No doubt many of the species included in this study exhibit a similar pattern of reticulum development, but this must be substantiated by anatomical work. Likewise, the surface feature of the reticula cannot be correctly interpreted without developmental studies. In some species, these thickenings appear to be wax depositions (species of *Aureolaria*; see also Chuang & Heckard, 1972). In *Buchnera americana* and *Striga asiatica*, the thickenings are actual cell outgrowths as revealed by anatomical studies (Rich & Musselman, unpublished).

Chuang & Heckard (1972) found seed surface characteristics to be of systematic value in the genus *Cordylanthus*. While the present study did not include in-depth survey of any one genus, some features of systematic value were found. The species of *Agalinis* with thickenings on the surface of the reticula (Fig. 1G, J) are restricted to the section *Purpureae* (Pennell, 1935). Likewise, this study indicates morphological dissimilarity between the seeds of *Seymeria pectinata* (Fig. 3B) and *S. cassioides* (Fig. 2J). The former has a prominent crest on the seed and is deeply reticulate unlike *S. cassioides*. Pennell (1935) places these two species in different sections. Lastly, *Aureolaria pedicularia* (section *Panctenis*;

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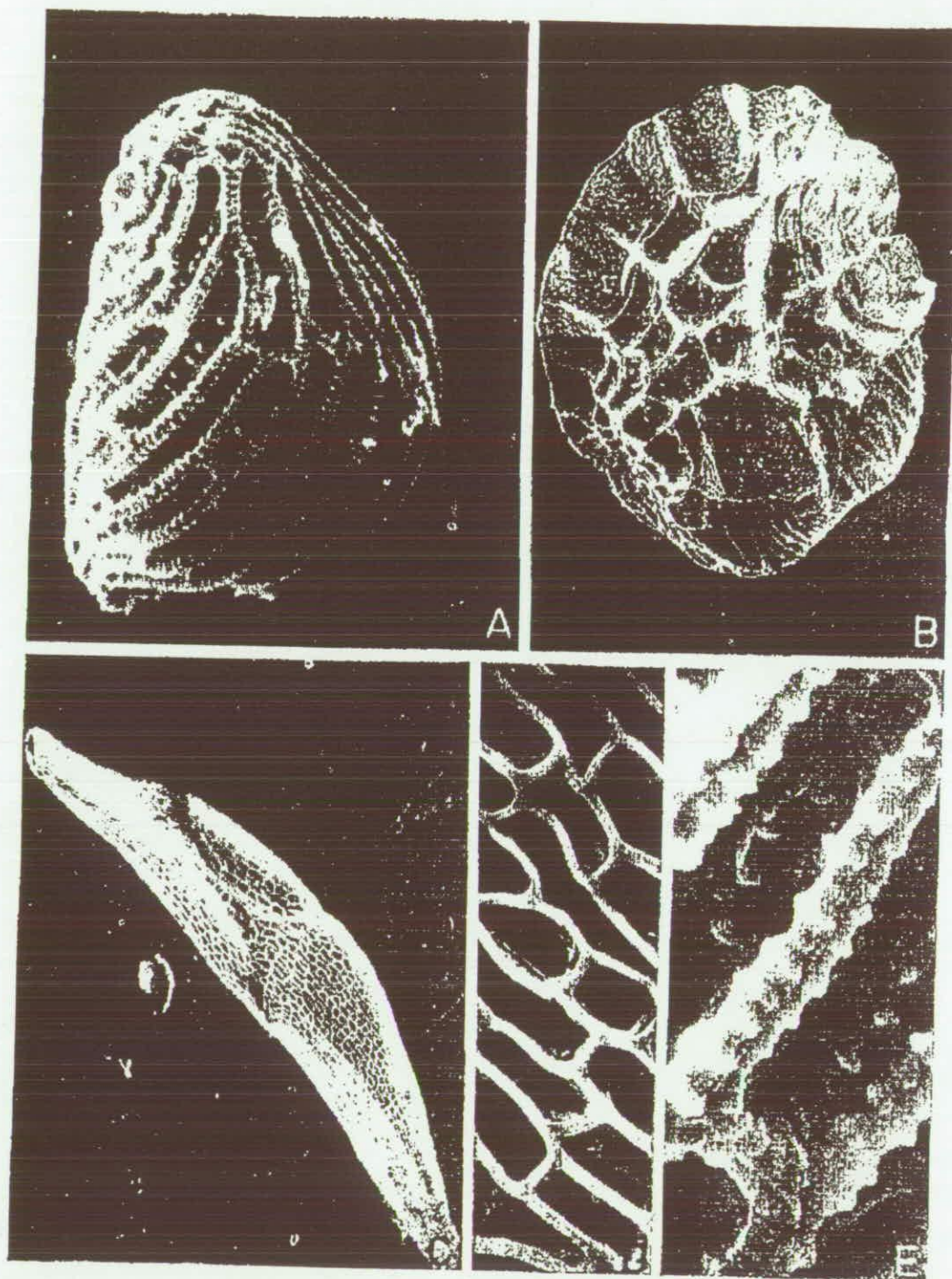


Fig. 3A-E. A. *Striga asiatica*, entire seed. $\times 468$. B. *Senecio jacobina* showing prominent wing and irregular reticula. $\times 120$. C. D. *Senecio jacobina*. C. Seed in surface view. $\times 48$. D. Simple unornamented reticula. $\times 490$. E. *Striga asiatica* with characteristic crested projections on walls and scattered projections in the center of reticula. $\times 1860$.

Pennell, 1935) and the three species in the section *Aureolaria* differ in both the amount and the morphology of wax deposition (Fig. 1A, B, C).

While the surface features of seeds may provide information of systematic value, it is very difficult, at present, to interpret the adaptive value for the various patterns revealed in this and other studies. In general, Pennell (1935) has suggested that the smaller seeds with their honeycombed testae are adapted for wind dispersal and the larger, heavier seeds (*Melampyrum lineare* and *Pedicularis canadensis*) are transported by animal vectors. It will be noted that the latter two species as well as *Conopholis americana* (Fig. 3A) have relatively smooth surfaces. In *Conopholis*, however, the unit of diaspore is almost certainly the fleshy fruit. As to the reticulate seeds, Kuijt (1969) has suggested that the reticula are adaptations for water dispersal, by trapping air and aiding in buoyancy. The almost total lack of information on how these seeds behave in nature limits any mean-

ingful interpretation of the adaptive value of seed ornamentation in this group. Almost all of the species of parasitic Scrophulariaceae have stiff, erect fruiting stalks which shake seeds from the capsule. Likewise, the habitat of many of these root parasites (*Aureolaria pedicularia*, *Seymeria cassioides*) on dry, coarse sand would seem to preclude any movement by water over a long distance. The situation in *Conopholis* of the Orobanchaceae has already been referred to; the seeds of *Epifagus* alone are dispersed by water. The fruit forms a sort of "splash cup" where a drop of water will spill the extremely small, light seeds (309,000 per gram; Mann & Musselman, unpublished).

A true understanding of the role of the seed coat in seedling biology must take into account that all of these species are, as far as is known, obligate root parasites. Perhaps the small seed size is an adaptation to filtering through vegetation and litter so as to be positioned as close as possible to a host.

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Le système endophytique d'*Arceuthobium oxycedri*. II. Aspects ultrastructuraux des zones de contact entre les tissus de l'hôte et du parasite

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SADIK, A., L. REY ET S. RENAUDIN. 1986. Le système endophytique d'*Arceuthobium oxycedri*. II. Aspects ultrastructuraux des zones de contact entre les tissus de l'hôte et du parasite. Can. J. Bot. 64 : 2778-2784.

L'étude ultrastructurale des zones de contact entre le système endophytique d'*Arceuthobium oxycedri* et les tissus de son hôte, le genévrier oxycèdre, montre qu'autour des plus gros cordons et sur les flancs des suçoirs primaires existe souvent, au niveau du phloème secondaire de l'hôte, une zone d'écrasement qui paraît peu favorable aux transferts de substances. En revanche, la présence, au niveau du xylème secondaire, de demi-punctuations aréolées au contact direct des cellules des suçoirs primaires et surtout secondaires est certainement de nature à faciliter les échanges. À la pointe des suçoirs, les cellules du parasite, au cours de leur progression, endommagent les cellules de l'hôte et font parfois irruption dans la lumière de ses trachéides. Une forte activité phosphatase acide et ATP-ase est mise en évidence en microscopie électronique au niveau des plasmalemmes, des plasmodesmes ainsi que de certaines petites vésicules d'endocytose ou d'exocytose dans les suçoirs primaires et secondaires. Elle témoigne de l'intensité des phénomènes de transport actif dans ces parties du système endophytique. Dans la région des zones de contact, une convergence d'aspect apparaît entre les cellules de type cellulósique du parasite et de l'hôte.

SADIK, A., L. REY, and S. RENAUDIN. 1986. Le système endophytique d'*Arceuthobium oxycedri*. II. Aspects ultrastructuraux des zones de contact entre les tissus de l'hôte et du parasite. Can. J. Bot. 64 : 2778-2784.

Ultrastructural study of the contact areas between the endophytic system of *Arceuthobium oxycedri* and the tissues of its host, *Juniperus oxycedrus*, shows that a crushed zone often occurs around the large cortical strands and along the primary sinkers in the secondary phloem of the host; such a structure seems rather unfavourable to the transfer of substances. On the other hand, the presence in the secondary xylem of half-bordered pits in direct contact with the cells of the primary and especially secondary sinkers certainly makes it easier for exchanges to take place. At the tip of the sinkers, the cells of the parasite, in the course of their growth, damage the cells of the host and sometimes penetrate into the lumen of its tracheids. Electron microscopy shows important acid phosphatase and ATPase activities at the level of the plasmalemma, plasmodesmata, and also some small endo- or exo-cytotic vesicles in the primary and secondary sinkers. Such activities are a sign of intense active transfer processes in these parts of the endophytic system. Around the contact zones, the parenchymatous cells of the host become very similar in aspect to those of the parasite.

Introduction

L'*Arceuthobium*, communément appelé «gui nain» est une Viscacée hémiparasite qui pousse sur les rameaux des conifères.

Au cours d'un travail précédent (Sadik *et al.* 1986), nous avons étudié les caractères cytologiques et cytochimiques des différents cordons et suçoirs qui forment le système endophytique.

Le but du présent article est de compléter les résultats obtenus par une étude plus précise, au niveau ultrastructural, des zones de contact entre les tissus de l'hôte et ceux du parasite, zones particulièrement importantes puisqu'elles sont le lieu des transferts de substance entre les deux partenaires.

Matériel

Les échantillons d'*Arceuthobium oxycedri* (DC.) M. Bieb. que nous avons utilisés proviennent de la région de Manosque (Alpes de Haute-Provence, France) où ils ont été récoltés sur le genévrier oxycèdre (*Juniperus oxycedrus* L.). Pour notre étude cytologique et cytoenzymologique, plusieurs dizaines de blocs sont découpés à des emplacements divers dans les rameaux parasités.

Méthodes

Préparation des échantillons pour l'étude en microscopie électronique

Le matériel a été fixé au glutaraldéhyde à 2% dans un tampon phosphate ou cacodylate 0,1 M (pH 7,3) pendant 2 h à température ambiante, puis au tétroxyde d'osmium à 1% dans le même tampon

pendant 1 h à température ambiante et inclus dans l'Epon selon la technique de Luft (1961). Les coupes ultra-fines ont été contraincées par l'acétate d'uranyl et le citrate de plomb selon Reynolds (1963).

Localisation ultrastructurale d'activités enzymatiques

La mise en évidence de l'activité ATP-ase a été effectuée selon la technique de Wachstein et Meisel (1957) selon le protocole de Marx *et al.* (1982); la localisation des phosphatases acides a été étudiée par la technique de Gomori (1956) selon le protocole de Coulomb (1971).

Résultats

Étude de la zone de contact

Les zones de contact entre l'hôte et le parasite n'ont pas le même aspect selon les différentes parties du système endophytique et les différents tissus du rameau de genévrier qu'elles traversent.

Les cordons de l'*A. oxycedri*, qu'ils soient longitudinaux ou circulaires, sont toujours disposés à l'intérieur du phloème secondaire du rameau parasité (Sadik *et al.* 1986). Les cordons n'entraînent aucun bouleversement notable de l'organisation de ce tissu et leurs cellules aux parois épaissies sont au contact direct des cellules phloémiennes. En revanche, les gros cordons sont entourés, en raison même de leur développement, d'une zone d'écrasement confuse et de lumière qui les sépare plus ou moins du tissu environnant.

Les suçoirs primaires qui s'enfoncent profondément dans le cylindre central de l'hôte et se prolongent vers l'extérieur d'une tige aérienne, traversent de ce fait plusieurs tissus.

La pointe d'un suçoir primaire est toujours constituée de cellules de type cellulósique caractérisées par une paroi

épaisse, de nombreux pectates, des microfibrilles celluliques; on y observe des profils de réticulum endoplasmique et des trachéides du xylème. La épaisseur de leur paroi est endommagée (fig. 2). À la pointe du suçoir, dans la lumière d'une trachéide. Sur les flancs du suçoir, le genévrier, les cellules sont étroitement en contact direct ne dépendant, des coupes montrent qu'autour d'elles se forment une sorte de paroi perpendiculairement. Plus vers l'extérieur du phloème secondaire, le suçoir primaire lisse, plus ou moins lisse, parmi lesquels on remarque (fig. 4). Au delà de la zone, le tissu est fortement modifié. Le phloème secondaire est irrégulièrement aligné en fusions (fig. 6), les cellules sont plus grandes, il y a tout des inclusions nombreuses (fig. 4). On observe également une zone de moindre automatisme où se trouve le phloème formé. De même, les cellules cambiales sont présentes. Au niveau du phloème de jonction, les cellules sont plus grandes et plus nombreuses. Les cellules de la paroi primaire à l'extérieur sont de tanins et de tanins et nous n'avons pas vu de cellule saine. Les suçoirs secondaires, dans le xylème, sont primaires, et de trachéides (Sadik 1986). Cet aspect paraît jamais secondaires, ni au niveau du phloème. Les cellules cellulósiques des tissus de la pointe du suçoir ont une paroi très épaisse, même que les cellules de la paroi de la tige aérienne du genévrier. En effet, les suçoirs secondaires se distinguent de ceux primaires par une ponctuation et une cellule aux cellules aya

¹Auteur à qui faire parvenir toute correspondance.

paisses, de nombreux chloroplastes, d'abondantes inclusions lipidiques; on y observe aussi souvent des accumulations de filaments de réticulum endoplasmique. À leur contact immédiat, les trachéides du xylème secondaire du genévrier, malgré l'épaisseur de leur paroi lignifiée, apparaissent fréquemment endommagées (fig. 2). À la faveur d'une déchirure, une cellule de la pointe du suçoir peut parfois faire directement irruption dans la lumière d'une de ces trachéides.

Sur les flancs du suçoir, au niveau du xylème secondaire du genévrier, les cellules cellulósiques ou les trachéides du parasite sont étroitement accolées aux trachéides de l'hôte mais ce contact direct ne donne lieu à aucune particularité notable. Cependant, des coupes semi-fines tangentielles à un suçoir montrent qu'autour de celui-ci les trachéides du genévrier peuvent former une sorte d'enveloppe concentrique en s'orientant perpendiculairement à leur direction habituelle (fig. 3).

Plus vers l'extérieur, au niveau du cambium et surtout du phloème secondaire du genévrier, on observe souvent autour du suçoir primaire la présence d'une zone d'écrasement confuse, plus ou moins épaisse, formée de divers débris cellulaires parmi lesquels on reconnaît çà et là quelques fibres libériennes (fig. 4). Au delà de cette zone, le tissu phloémien apparaît nettement modifié: alors que dans les rameaux sains, le phloème secondaire se présente sous forme de petites cellules régulièrement alignées, fortement vacuolisées et pauvres en inclusions (fig. 6), dans les rameaux parasités, ces cellules sont plus grandes, possèdent un cytoplasme plus abondant et surtout des inclusions amyloféres et lipidiques beaucoup plus nombreuses (fig. 5). Il est à noter que ces modifications s'observent également autour des suçoirs secondaires et à un degré moindre autour des cordons, si bien que dans une partie du rameau où suçoirs et cordons sont nombreux, c'est l'ensemble du phloème secondaire de l'hôte qui apparaît ainsi transformé. De même que les cellules phloémiennes, les cellules cambiales s'enrichissent en cytoplasme au contact des suçoirs.

Au niveau du parenchyme cortical de l'hôte, autour de la zone de jonction riche en vaisseaux lignifiés qui relie un suçoir primaire à une tige aérienne, les cellules se chargent souvent de tanins et contiennent des chromoplastes (fig. 7) que nous n'avons pas retrouvés dans les cellules correspondantes du rameau sain.

Les suçoirs secondaires s'enfoncent également profondément dans le xylème secondaire de l'hôte. Plus minces que les suçoirs primaires, ils sont constitués de cellules de type cellulósique et de trachéides disposées sans ordre apparent (Sadik *et al.* 1986). Cette organisation a deux conséquences: il n'apparaît jamais de zone d'écrasement autour des suçoirs secondaires, ni au niveau du xylème secondaire de l'hôte, ni au niveau du phloème secondaire; par ailleurs, ce sont soit des cellules cellulósiques, soit des trachéides qui se trouvent au contact des tissus de l'hôte.

À la pointe du suçoir, l'aspect des cellules cellulósiques avec leur paroi très épaisse et leurs abondantes inclusions lipidiques est le même que dans le cas d'un suçoir primaire et l'on peut observer de nombreuses figures de progression de ces cellules à l'intérieur du rayon médullaire envahi (fig. 8).

C'est en effet clairement au niveau des rayons médullaires que les suçoirs secondaires s'enfoncent dans les tissus de l'hôte. Bien que sur leurs flancs on observe des trachéides à ponctuations aréolées, ponctuations qui à l'origine assurent une communication avec les cellules du rayon ligneux, ces cellules ayant été remplacées par des cellules de suçoir

secondaire d'*Arceuthobium*, il existe donc de nombreux endroits où la paroi des éléments de xylème de l'hôte est amincie au contact du parasite (fig. 9).

Lorsqu'un rayon médullaire est envahi par un suçoir secondaire et que, sur une coupe, on peut observer côte à côte les cellules du parasite et les cellules du rayon médullaire qui subsistent (fig. 10), on constate que les deux catégories de cellules se ressemblent beaucoup par la densité de leur cytoplasme et leur richesse en inclusions lipidiques. Cependant, les plastides, de type chloroplaste dans les cellules du parasite, de type amyloplaste dans les cellules des rayons médullaires sont nettement différents.

Il est à noter que dans les rayons médullaires non envahis mais situés à proximité de l'appareil haustorial du parasite, les cellules sont également transformées: alors que dans le rameau sain, ces cellules sont pauvres en cytoplasme, elles deviennent ici plus grandes avec un cytoplasme plus abondant, un vacuome plus morcelé et des inclusions amyloféres et lipidiques plus nombreuses.

Étude cytoenzymologique en microscopie électronique

Localisation de l'activité phosphatase acide

Par comparaison avec les coupes témoins (fig. 14), les dépôts de phosphate de plomb dans les coupes essais indiquent une activité des phosphatases acides dans les cellules du système endophytique, au niveau du plasmalemme souligné sur toute sa surface, au niveau des noyaux, au niveau des plasmodesmes et au niveau des petites vacuoles (Fig. 11 à 13). Tous ces dépôts sont plus abondants dans les suçoirs primaires et secondaires que dans les cordons. Les cellules de l'hôte voisines de système endophytique, surtout dans le phloème secondaire et les rayons médullaires, présentent également un certain marquage, en particulier au niveau du plasmalemme et du noyau.

Localisation de l'activité ATP-asiqne

La réaction qui se traduit par le même dépôt de phosphate de plomb (comparer la fig. 15 essai à la fig. 16 témoin) révèle une activité ATP-asiqne dans les cellules du système endophytique, en particulier au niveau du plasmalemme des cellules des suçoirs primaires. Les petites invaginations du plasmalemme et les vésicules sous-jacentes que nous avons déjà signalées dans ces cellules (Sadik *et al.* 1986) sont marquées aussi.

Discussion et conclusion

L'examen des zones de contact entre le système endophytique d'*A. oxycedri* et les tissus de genévrier amène à se demander comment se fait le passage des substances de l'hôte au parasite. L'existence de zones d'écrasement autour des gros cordons et des suçoirs primaires, surtout au niveau du phloème, ne paraît pas être favorable aux échanges. Cette zone d'écrasement a été également observée par Sallé (1977) autour du suçoir primaire du gui, au niveau du parenchyme cortical et du phloème primaire et secondaire; l'écrasement et l'orientation perturbée des cellules environnantes sont causés par la largeur du cône de pénétration du suçoir primaire qui ne rencontre pas beaucoup de résistance de la part de ces tissus. Mais au niveau du xylème secondaire de l'hôte où les parois cellulaires lignifiées sont plus résistantes, les perturbations sont minimales; selon Sallé (1977), cela est dû également à la présence d'une zone méristématique intercalaire au niveau du cambium qui permet une croissance du suçoir primaire en har-

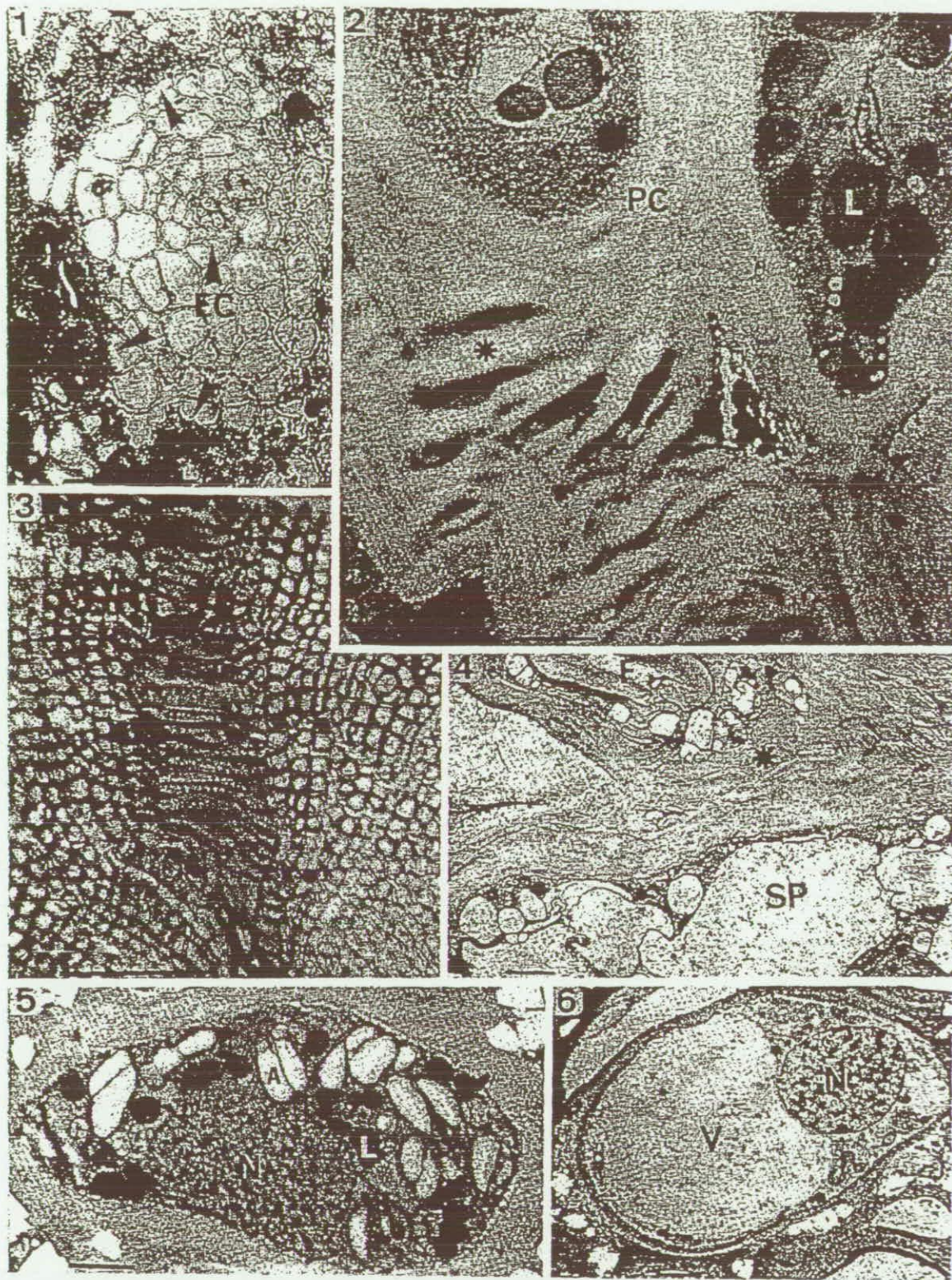


FIG. 1. Gros cordon longitudinal, en section transversale. Il est formé d'un grand nombre de cellules et comporte en son centre des éléments conducteurs (EC), trachéides ou vaisseaux. À sa périphérie, des zones comprimées ou écrasées sont visibles dans le phloème secondaire qui l'entoure (flèches). $\times 220$ (échelle, $100\ \mu\text{m}$). FIG. 2. Extrémité d'un suçoir primaire. Au-dessous des cellules de la pointe caractérisées par leur richesse en inclusions lipidiques (L) et leur paroi cellulaire épaisse (PC) on observe une zone d'écrasement (*) résultant de la compression des trachéides du xylème secondaire de l'hôte. $\times 7000$ (échelle, $2\ \mu\text{m}$). FIG. 3. Coupe tangentielle d'un suçoir primaire : les trachéides du génévrier forment autour de lui une enveloppe concentrique en s'orientant perpendiculairement à leur direction habituelle. $\times 220$ (échelle, $100\ \mu\text{m}$). FIG. 4. Contact entre un suçoir primaire (SP) et le phloème secondaire de l'hôte. Le long des cellules du suçoir, on observe une zone irrégulière d'écrasement plus ou moins épaisse (*). Dans cette zone confuse, on reconnaît ici une fibre libérienne lignifiée (F). $\times 3800$ (échelle, $2\ \mu\text{m}$). FIG. 5. Cellule libérienne de rameau parasité de génévrier riche en cytoplasme et en inclusions lipidiques (L) et amylofères (A). N, noyau. $\times 3800$ (échelle, $2\ \mu\text{m}$). FIG. 6. Cellule libérienne témoin de rameau sain de génévrier. V, vacuole. $\times 3900$ (échelle, $2\ \mu\text{m}$).

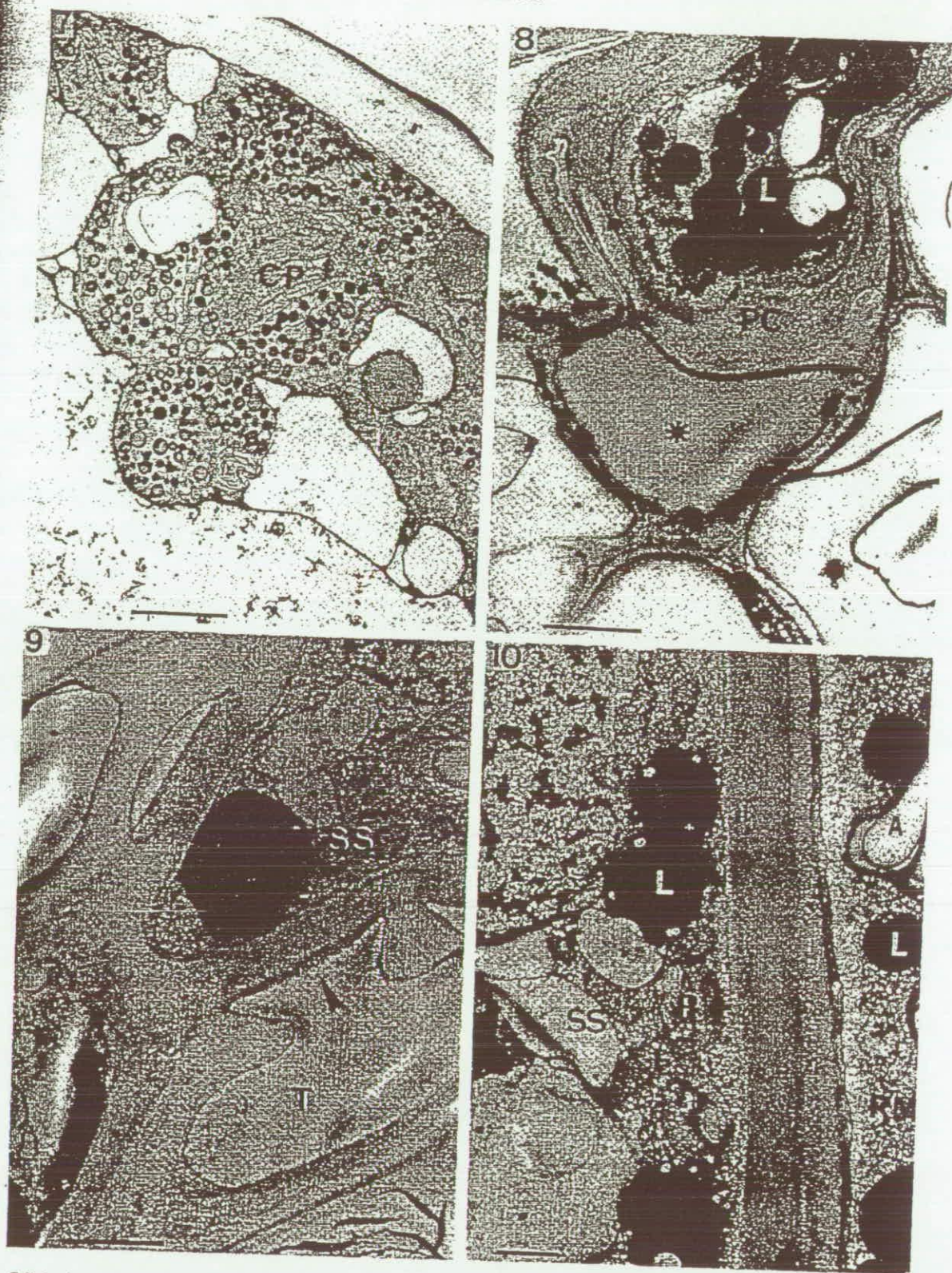


Fig. 7. Cellule du parenchyme cortical dans un rameau de genévrier parasité présentant des chromoplastes (CP). $\times 8000$ (échelles, $2\ \mu\text{m}$).
 Fig. 8. Cellule de l'extrémité d'un sucoir secondaire avec ses inclusions lipidiques (L) et sa paroi épaisse (PC) caractéristiques, en cours de progression dans un rayon médullaire : la cellule comprime (ou envahit) presque complètement une cellule de ce rayon ligneux dont on ne distingue qu'une petite partie de la lumière (*). $\times 8250$ (échelle, $2\ \mu\text{m}$).
 Fig. 9. Contact entre une cellule cellulosique de sucoir secondaire (SS) et une trachéide (T) du xylème de l'hôte. Ayant pris la place d'une cellule de rayon ligneux, la cellule de sucoir se trouve au contact d'une demi-ponticelle aréolée (flèche). $\times 9000$ (échelle, $2\ \mu\text{m}$).
 Fig. 10. Contact entre une cellule de sucoir secondaire (SS) et une cellule intacte du rayon médullaire envahi (RM). Les deux sortes de cellules présentent une grande ressemblance par leur richesse en cytoplasme et en inclusions lipidiques (L). Cependant, les plastes sont des chloroplastes (P) dans la cellule de sucoir alors qu'il s'agit plutôt d'amyloplast à larges inclusions d'amidon (A) dans la cellule de genévrier. $\times 11\ 400$ (échelle, $1\ \mu\text{m}$).

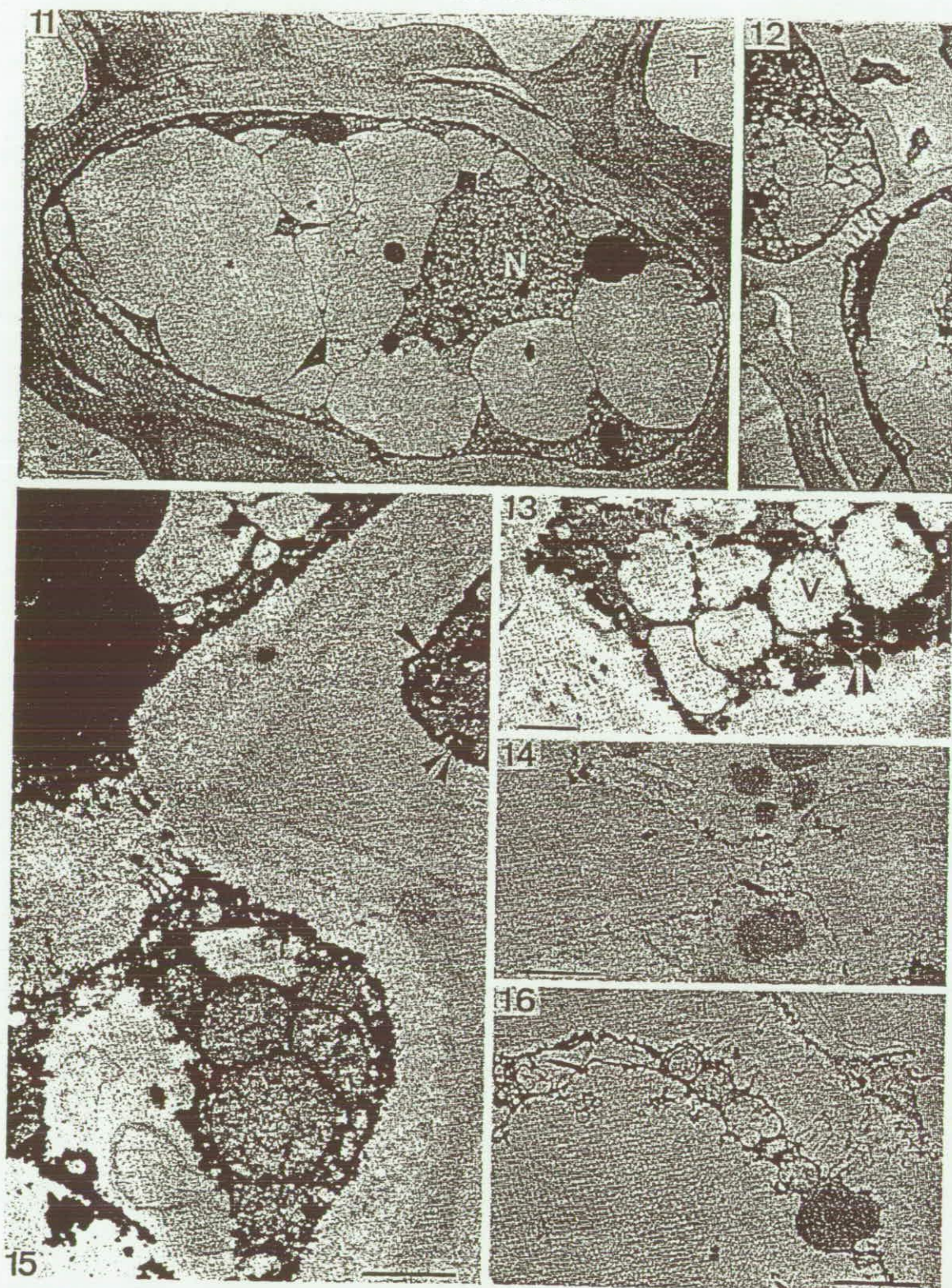


FIG. 11 à 14. Mise en évidence de l'activité phosphatase acide dans les cellules d'un suçoir secondaire. Fig. 11 à 13. Essai. Fig. 14. Contrôle. Fig. 11. Coupe essai. Le précipité de phosphate de plomb indiquant une activité enzymatique est présent surtout au niveau du plasmalemme. Le noyau (N) est également un peu marqué. On ne note en revanche aucune réaction dans les trachéides (T). $\times 4800$ (échelle, 2 μm). Fig. 12. Marquage des plasmodesmes indiquant une forte activité phosphatase à leur niveau. $\times 4200$ (échelle, 2 μm). Fig. 13. Marquage des petites vacuoles (V) ainsi que de vésicules dont certaines sont situées dans le cytoplasme (flèche) et d'autres ouvertes sur l'espace périplasmique (double flèche). $\times 9600$ (échelle, 1 μm). Fig. 14. Sur le témoin n'apparaissent que de légers dépôts qui correspondent peut-être à la présence de phosphates libres. $\times 6600$ (échelle, 2 μm). FIG. 15 et 16. Mise en évidence de l'activité ATP-ase dans les cellules d'un suçoir primaire. Fig. 15. Coupe essai. Le marquage indiquant une activité enzymatique est surtout important au niveau du plasmalemme et des plasmodesmes. Certaines petites vésicules, les unes situées dans le cytoplasme périphérique (flèche), les autres ouvertes sur l'espace périplasmique (double flèche), sont marquées. $\times 15\,300$ (échelle, 1 μm). Fig. 16. Coupe témoin. $\times 14\,950$ (échelle, 1 μm).

niée avec celle de l'hôte. En ce qui concerne l'*A. oxycedri*, nous n'avons pas observé l'existence d'une telle zone méristématique.

Quoi qu'il en soit, c'est au niveau du xylème de l'hôte que nous observons les contacts les plus étroits entre les tissus de l'hôte et du parasite. Ici, nous trouvons des trachéides aréolées et les cellules cellulodiques des trachéides des suçoirs. Dans cette zone, les semi-ponts cellulaires aréolés qui sont en contact direct avec les cellules des suçoirs secondaires contribuent certainement à favoriser le passage des substances. Un dispositif particulier qui a parfois été observé est la pénétration d'une cellule à paroi cellulodique de l'extrémité d'un suçoir à l'intérieur d'une trachéide du xylème secondaire de l'hôte. Ce phénomène rappelle ce que Renaudin (1974) a observé chez *Lathraea clandestina* L. et ce que Renaudin et Capdepon (1979) ont observé chez *Tozzia alpina* L. au niveau des cellules absorbantes. Mais nous n'avons pas constaté ici de résorption des parois permettant un passage direct entre la cellule du parasite et la trachéide de l'hôte. Existe-t-il d'autres voies pour le passage des substances? Le phénomène de pénétration étant rare, les substances ont certainement à traverser en général la paroi des éléments conducteurs puis celle des cellules du système endophytique souvent très épaisses. Nous n'avons en effet jamais observé de plasmodesmes entre les cellules de l'hôte et celles du parasite, contrairement à ce que Tainter (1971) a avancé au sujet de l'*Arceuthobium pusillum* Peck. Les échanges sont en tous cas certainement très importants au niveau du plasmalemme des cellules des suçoirs comme en témoignent les fortes activités phosphatase et ATP-ase que nous y avons enregistrées. On sait en effet que les phosphatases acides sont impliquées dans les mécanismes de transports actifs trans-membranaires (Ziegler 1965; Sauter 1966) et notamment que ces enzymes sont toujours présentes dans les cellules où transitent les glucides (Sauter et Braun 1968; Sauter 1972; Figier 1972; Sauter et Braun 1972; Caussin *et al.* 1979; Cronshaw 1980). Il a été également montré qu'elles interviennent dans les processus de différenciation des éléments conducteurs (Mia et Pathak 1968; Hebant 1973). Chez les plantes parasites, Rodriguez et Pannier (1967) avaient déjà émis l'hypothèse que les phosphatases y jouaient un rôle important dans le transport actif de l'eau et des substances dissoutes en particulier des glucides. Les travaux de Renaudin (1977) sur le suçoir de *L. clandestina* vont dans le même sens en montrant la présence d'une forte activité phosphatase acide tout le long du pont-transfert reliant les éléments conducteurs de l'hôte à ceux du parasite. En outre, Tripodi (1970) et Onofeghara (1972) ont avancé que les phosphatases acides intervenaient dans la cytolise des cellules de l'hôte, la différenciation et la maturation des cellules du parasite et dans le transfert d'énergie. Dans le même ordre d'idée, Toth et Kuijt (1977) pensent que chez *Comandra* les phosphatases, en association avec d'autres enzymes, agissent en ramollissant les parois des cellules de l'hôte favorisant ainsi l'action mécanique du parasite. Chez *Striga hermonthica* (Del.) Benth. et *Striga gesnerioides* (Willd.) Watke., Ba (1983) estime également que ces enzymes, très actives dans la zone de contact hôte-parasite, sont impliquées dans les mécanismes de pénétration dans l'hôte ainsi que dans le transport des substances de l'hôte vers le parasite.

En ce qui concerne les ATP-ases, leur localisation au niveau des plasmalemmes leur confère un rôle central dans le transport des ions (Leigh *et al.* 1975; Leonard et van der Woude 1976) et dans les processus de cotransport des ions et des

glucides (Caussin *et al.* 1979; Komor et Tanner 1980; Georgieva 1980). Plus précisément, Korenbrot (1977) a montré que la molécule d'ATPase (phosphatase neutre) comprend deux sites fonctionnels, l'un étant engagé dans la synthèse de l'ATP, l'autre dans le transport d'ions à travers l'apoplaste.

Chez *Arceuthobium oxycedri*, nos observations ont montré que les activités phosphatasiques acides et ATP-ases étaient importantes dans les cellules des suçoirs, au niveau de leur plasmalemme, sans être particulièrement intenses à la pointe de ces suçoirs, c'est-à-dire dans la zone de pénétration. Par conséquent, ces enzymes semblent impliquées ici surtout dans les phénomènes de transfert. En outre, il faut souligner que nous avons également mis en évidence une forte activité phosphatase acide dans les cellules de l'hôte entourant le système endophytique, toujours au niveau des plasmalemmes; c'est le cas principalement des cellules du phloème secondaire. On peut donc se demander si le transfert des substances se fait uniquement au niveau du xylème de l'hôte ou également au niveau du phloème et si dans ce cas un passage est possible au niveau des cordons. Par ailleurs, les trachéides de l'hôte étant parfois au contact immédiat des trachéides du parasite dans les suçoirs secondaires et la partie profonde des suçoirs primaires, des échanges de substances organiques ont-ils lieu directement entre ces trachéides ou bien y a-t-il obligatoirement transport actif par l'intermédiaire de cellules de type cellulodique? Une étude autoradiographique, en utilisant en particulier des substances migrant spécifiquement par le phloème ou le xylème de l'hôte permettra sans doute d'éclairer au moins une partie de ces problèmes.

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E. Sobrino Vesperinas & J. P. del Monte Díaz de Guereñu

Two alien *Solanum* species new to the Spanish flora, and their characterization within the *Solanum nigrum* complex (*Solanaceae*)

Abstract

Sobrino Vesperinas, E. & del Monte Díaz de Guereñu, J. P.: Two alien *Solanum* species new to the Spanish flora, and their characterization within the *Solanum nigrum* complex (*Solanaceae*). — Fl. Medit. 4: 101-109, 1994. — ISSN 1120-4052.

The distribution of *Solanum physalifolium* var. *nitidibaccatum* and *Solanum sarrachoides* in Spain is described. These alien species are not included in any Spanish Flora and are not mentioned in any European or Mediterranean Flora as occurring in Spain. Both species show marked similarities and were long considered to belong to a single species, *S. sarrachoides*; however there are clear and precise differences between them.

Useful differential characters, here studied, are found among morphological (size and form of cotyledons, size and form of calyx, pubescence, etc.), micromorphological (microstructure of the berry, of the epispem, of the types of hairs, etc), physiological (band patterns obtained by electrophoresis) and ecological features.

Introduction

Solanum sect. *Solanum*, also known as *S. sect. Maurella* Nees or sect. *Morella* (Dunal) Bitter, mainly consists of weedy and cosmopolitan species.

The great morphological, ecological and genetic variability found in the genus as a whole is well expressed in this section, which has led to numerous problems of identification and denomination. All species belonging here are usually grouped together in the "*Solanum nigrum* complex". Within this complex, the specific limits are blurred due to the great vegetative plasticity resulting from the interaction of the environment with a variable genome, evidenced i. a. by a wide range of chromosome numbers ($2n = 24, 48, 72, 96$). Dunal (1852) recognized 53 species within the group, Bitter (1912, 1913) an even larger number, while other authors reduced the complex to a single species, *S. nigrum* L. According to Edmonds (1972) 300 "variants" have been recognized at specific and subspecific levels. Currently it is accepted that the "*Solanum nigrum* complex" comprises some 30 species (Schilling 1981).

In this paper two alien species of the "*Solanum nigrum* complex" new to the Spanish flora, both native of South America, are studied. Their nomenclature is confused, as for other taxa of the complex. *S. sarrachoides* has been misnamed "*S. nigrum* var. *villosum*" or "*S. villosum*" (Stebbins & Paddock 1949), and *S. physalifolium* has been misidentified as "*S. villosum*", "*S. luteum*" and "*S. nigrum* var. *villosum*" (Edmonds 1986). The confusion may be due to the fact that both, as also the true *S. villosum* Mill. (= *S. luteum* Mill.), have hairy stems and leaves.

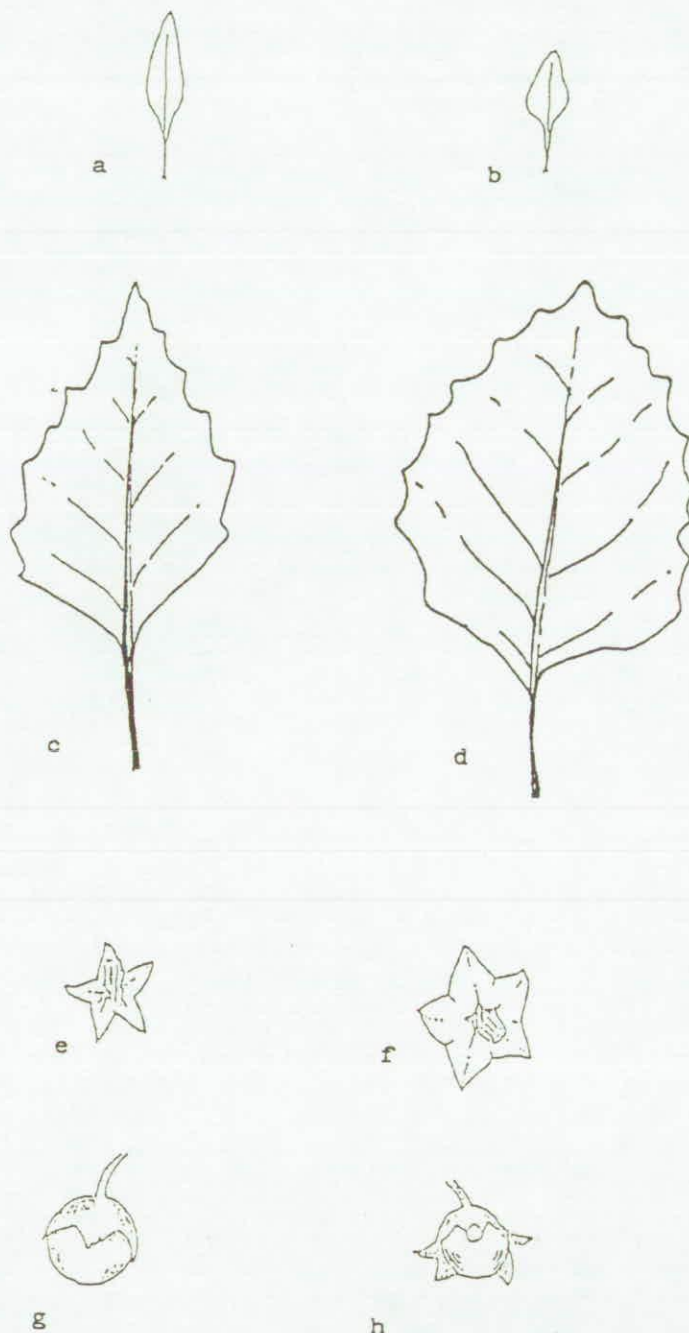


Fig. 1. Cotyledon, leaf, flower and berry shape of: *Solanum physalifolium* var. *nitidibaccatum* (a, c, e, g) and *S. sarrachoides* (b, d, f, h).

Table 1. Average (of 30 mea
Solanum sarrachoides and *S. p*

<i>S. sarrachoides</i>	
<i>S. physalifolium</i>	

Table 2. Ranges of dimensions
berry of *Solanum sarrachoides*
largest width; c = smallest width

	Berry dim.
<i>S. sarrachoides</i>	a = 6 b = 6 c = 5
<i>S. physalifolium</i>	a = 4 b = 4 c = 4

Table 3. Seed dimensions (avera
colour of *Solanum sarrachoides*

	Length mm
<i>S. sarrachoides</i>	1.4
<i>S. physalifolium</i>	1.8

Solanum sarrachoides Sc
nitidibaccatum from it, which
Rusby, var. *nitidibaccatum* (Bi
number of flowers per inflores
and size of sclerotic granules.
In this paper some morphologic
two taxa found in Spain are con
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different phenological states.

Up to now only a few scattere
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In fact, *S. physalifolium* is w
known Spanish collection date
think that it must have been intr
sarrachoides in Spain was made t

At present both taxa are wide
from Belgium, Czechoslovakia,
Sweden, and Switzerland; and
Hungary and Norway.

Table 1. Average (of 30 measures) and range of length-width ratio of cotyledons of *Solanum sarrachoides* and *S. physalifolium* var. *nitidibaccatum*.

	Origin	L/W
<i>S. sarrachoides</i>	Toledo	2.14 (1.75 - 2.34)
<i>S. physalifolium</i>	Navarra	3.42 (3.25 - 3.75)
	Palencia	3.86 (3.33 - 4.70)
	Soria	3.50 (3.30 - 3.82)

Table 2. Ranges of dimensions (of 30 measures) of berries, seed and granule numbers per berry of *Solanum sarrachoides* and *S. physalifolium* var. *nitidibaccatum*. (a = length; b = largest width; c = smallest width)

	Berry dimensions mm	Seeds per berry	Granules per berry
<i>S. sarrachoides</i>	a = 6.4 - 7.2 b = 6.3 - 7.2 c = 5.9 - 6.9	30 - 53	six
<i>S. physalifolium</i>	a = 4.3 - 6.7 b = 4.9 - 6.7 c = 4.6 - 6.3	15 - 26	two or none

Table 3. Seed dimensions (average of 80 measures), weight (average of 15 measures) and colour of *Solanum sarrachoides* and *S. physalifolium* var. *nitidibaccatum*.

	Length mm	Width mm	Index L/W	mg/100 seeds	Colour
<i>S. sarrachoides</i>	1.4	1.1	0.79	21.4	white
<i>S. physalifolium</i>	1.8	1.4	0.78	70.4	beige

Solanum sarrachoides Sendt. was described in 1846. Bitter (1912) split off *S. nitidibaccatum* from it, which Edmonds (1986) treated as a variety of *S. physalifolium* Rusby, var. *nitidibaccatum* (Bitter) Edmonds, said to differ from var. *physalifolium* in the number of flowers per inflorescence, pedicel length, sepal shape, berry size, and number and size of sclerotic granules.

In this paper some morphological, micro-morphological and physiological features of the two taxa found in Spain are compared, and data on their ecology and chorology in Spain are given. Their detailed characterization will permit their correct identification in their different phenological states.

Up to now only a few scattered Spanish records of these taxa have been published, and neither is mentioned in any of the current works devoted to the Spanish flora, probably due to their being mistaken for *Solanum nigrum* L.

In fact, *S. physalifolium* is widely distributed in the northern half of Spain. The first known Spanish collection dates from 1976, but its present wide distribution makes us think that it must have been introduced into Spain much earlier. The first collection of *S. sarrachoides* in Spain was made by Laorga (1983).

At present both taxa are widely distributed throughout Europe. Both have been recorded from Belgium, Czechoslovakia, England, France, Finland, Germany, Netherlands, Spain, Sweden, and Switzerland; and *Solanum physalifolium* var. *nitidibaccatum* alone, from Hungary and Norway.

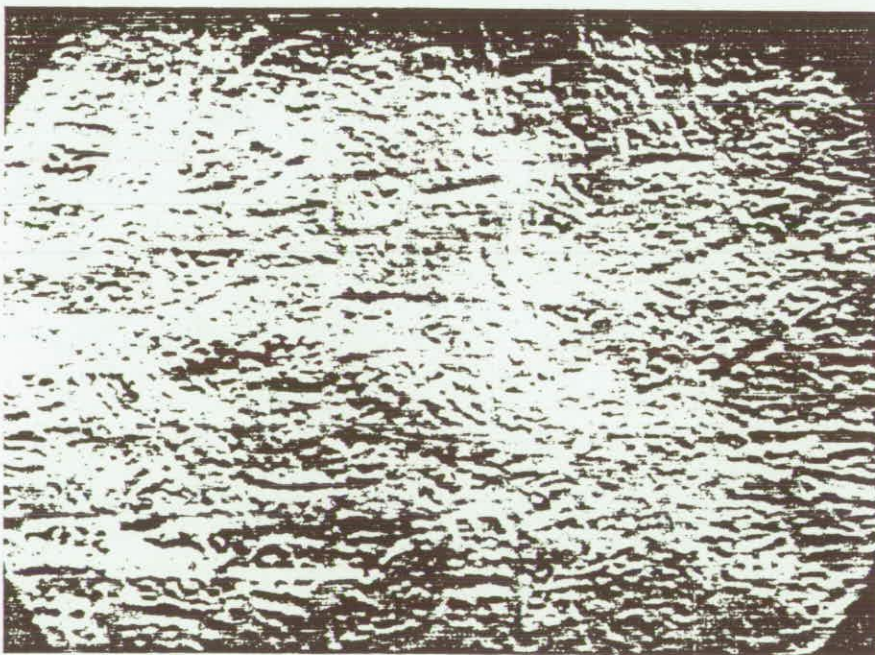
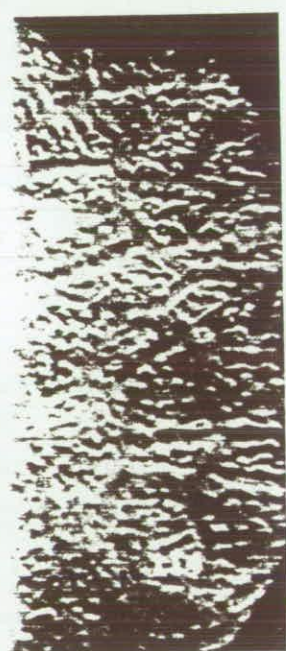
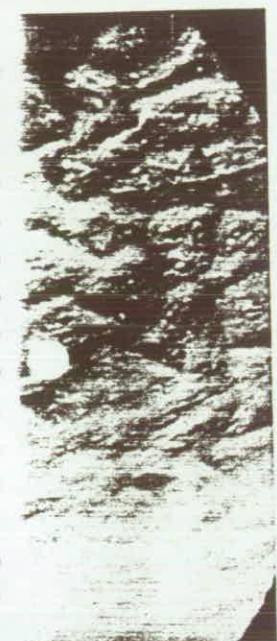


Fig. 2. Surface of the berries of *Solanum physalifolium* var. *nitidibaccatum* (above) and *S. sarrachoides* (below). Scale bar = 5.6 μ m.

Fig. 3. Ornamentation of the berries of *S. physalifolium* var. *nitidibaccatum* (above) and *S. sarrachoides* (below). Scale bar = 5.6 μ m.



nitidibaccatum (above) and *S.*

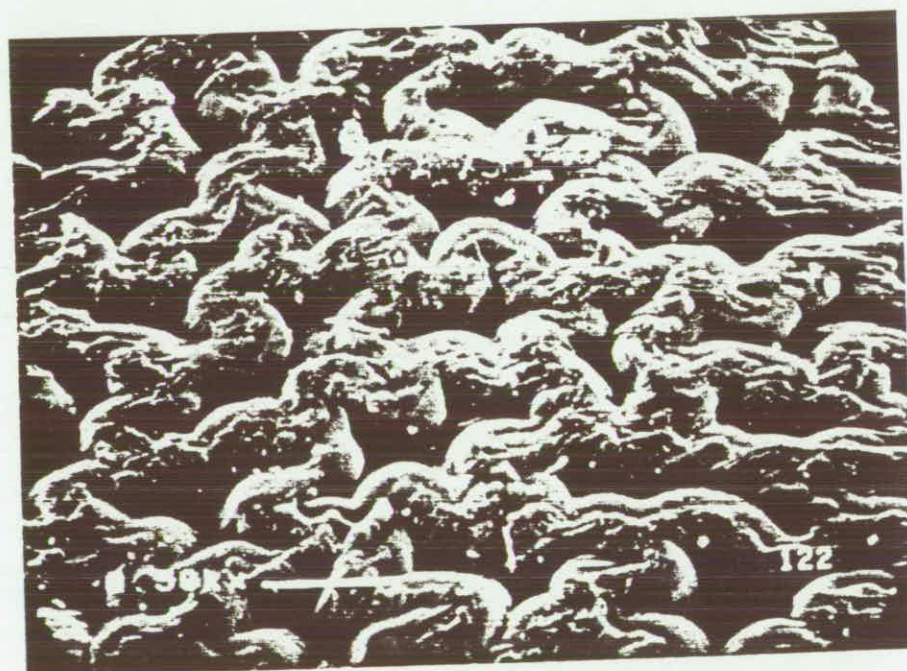
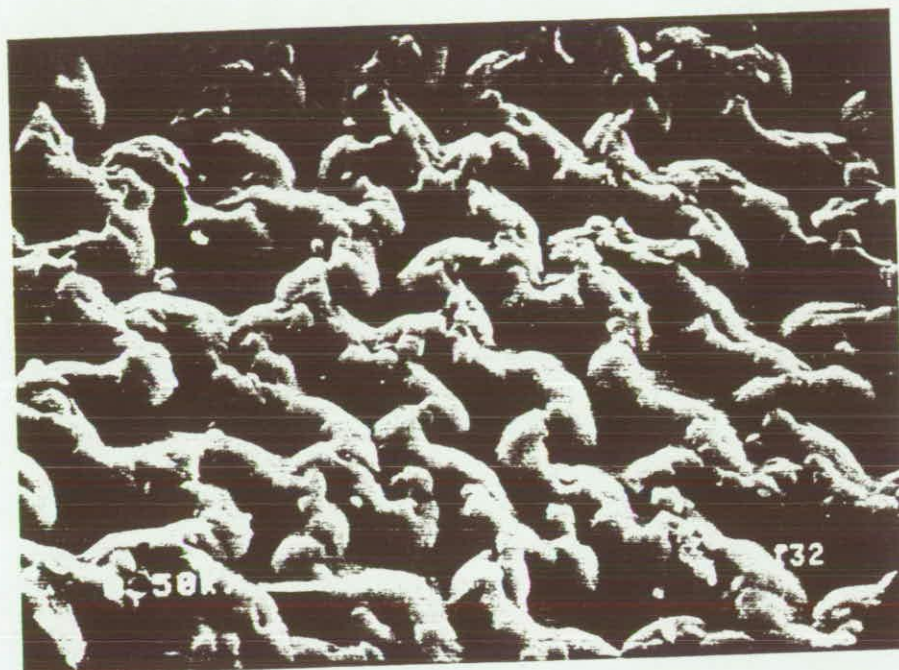


Fig. 3. Ornamentation of the seed testa in *Solanum physalifolium* var. *nitidibaccatum* (above) and *S. sarrachoides* (below). Scale bar = 2.8 μ m.

Material and methods

Specimens collected in the wild in 1987, 1988, 1989 were used. In addition, the herbaria of the Royal Botanical Garden of Madrid (MA) and of the Faculty of Pharmacy of the Universidad Complutense of Madrid (MAF) were consulted.

In order to eliminate modification by the environment, some plants grown from seeds of *Solanum sarrachoides* collected in Malpica de Tajo (Toledo), and from *S. physalifolium* seeds collected in Mendavia (Navarra), San Esteban de Gormaz (Soria) and Palencia, were, in addition, cultivated in a glasshouse under identical conditions. Seed germination was enhanced by a treatment with 1000 ppm. of gibberellic acid. Seeds of each provenance were sown three times in succession into pots of 24 cm diameter.

Cotyledons were sampled at maximum development while being still green. Adult leaves were taken randomly from the middle stem portion (5th to 8th node). Sugar content was determined six times for each sample of completely mature fruits, using a high-contrast hand refractometer (0-32 %). Micromorphological observations were made by scanning electron microscopy, on gold-palladium coated preparations. Seed size was determined under a binocular stereo-microscope by means of an ocular micrometer, and seed weight with a precision scale. Polyacrylamide gel electrophoresis of the denaturated total seed proteins was effected in accordance with the methods of Laemmli (1970) and Payne & al. (1980).

Results and discussion

General habit.- Both taxa are herbaceous annuals, under a Mediterranean climate. In *Solanum sarrachoides* the stem is erect, or slightly prostrate as a result of abundant branching. In *S. physalifolium* var. *nitidibaccatum* the stem is mostly prostrate or decumbent, but can also be erect. Both species are up to 40-60 cm tall, villous and covered with glandular hairs.

Cotyledons.- In *Solanum sarrachoides* they are ovate-lanceolate (Fig. 1b), with a length/width index (il) of 1.75-2.34. In *S. physalifolium* var. *nitidibaccatum* they are lanceolate (Fig. 1a), with an il value always >3 (Table 1). Cotyledon shape is thus diagnostic for these two weedy species, at an early stage of their life cycle.

Leaves.- The leaf blades of *Solanum sarrachoides* are light green, elliptic-rhombic with a maximum width in the middle, and with sinuate-dentate margins (Fig. 1d). In *S. physalifolium* var. *nitidibaccatum* they are dark green, ovate-rhombic with a maximum width in the proximal third, and with sinuate-lobulate margins (Fig. 1c). Differences in leaf shape are slight, and unsuited for separating the two taxa.

The three trichome types defined by Edmonds (1982) in *Solanum* sect. *Solanum* - stalked glands, multicellular hairs and uniseriate hairs, glandular or eglandular - all occur in the two studied taxa, although the indumentum is denser in *S. sarrachoides* than in *S. physalifolium* var. *nitidibaccatum*. The former also shows a lower density of stomata than the latter. Probably both characters are influenced by the habitat, with *S. physalifolium* var. *nitidibaccatum* growing under cooler and moister conditions.

Flower.- The corollas in *Solanum sarrachoides* are white with a central light yellow star, small and rotate, with petals coalescent for half their length (Fig. 1f). The flowers are grouped in umbel-like inflorescences. In *S. physalifolium* var. *nitidibaccatum* the corollas are white with a purple central zone, stellate (Fig. 1e). The flowers are arranged in raceme-



Fig. 4. Protein bands pattern d); *S. sarrachoides* (e, f); and

like inflorescences. These may be due to geographical

Calix.- The calyx is strongly distinguishing them from the lower half of the berry, by acuminate tips, whereas in the lower half of berry, and the

Micromorphological differences in *Solanum sarrachoides* do not occur in *S. physalifolium* segments bear the same mucous occupy extends over more one fifth in *S. physalifolium*

Fruit.- The berry in both taxa is whitish with a whitish cross at the apex, larger. The size range of both taxa also show significant differences (Table 2). The sugar content in *nitidibaccatum* (6.5 %) is

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e margins (Fig. 1d). In *S.*
e-rhombic with a maximum
ns (Fig. 1c). Differences in

Solanum sect. *Solanum* -
lar or eglandular - all occur
n *S. sarrachoides* than in *S.*
lower density of stomata than
pitat, with *S. physalifolium*
s.

a central light yellow star.
(Fig. 1f). The flowers are
nitidibaccatum the corollas
ers are arranged in raceme-

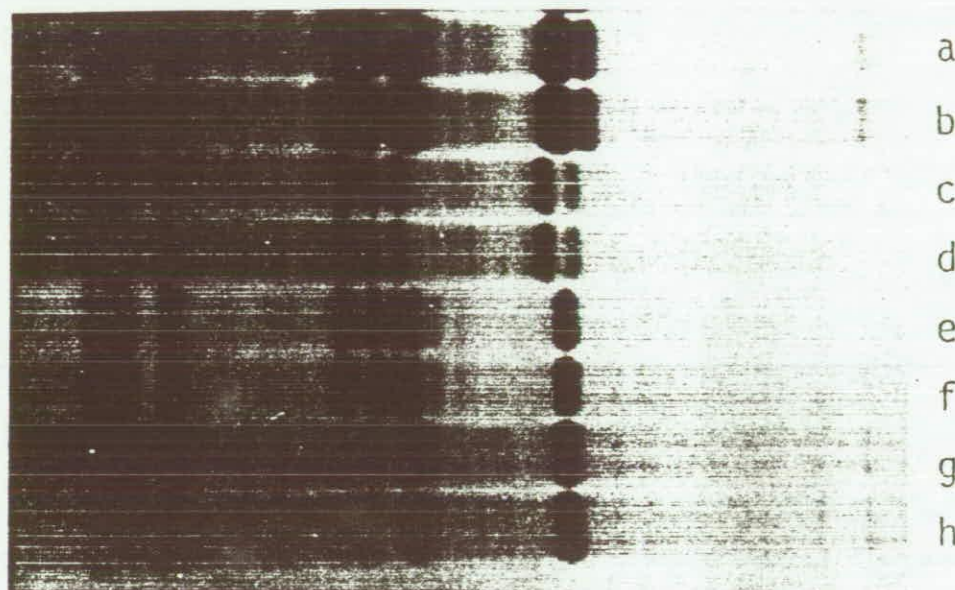


Fig. 4. Protein bands pattern of *Solanum nigrum* (a, b); *S. physalifolium* var. *nitidibaccatum* (c, d); *S. sarrachoides* (e, f); and *S. villosum* (g, h).

like inflorescences. These descriptions do not agree with those of Edmonds (1986), which may be due to geographical variation of corolla features.

Calix. The calyx is strongly accrescent in both taxa, which is a good character for distinguishing them from their relatives. In *Solanum sarrachoides* it encloses at least the lower half of the berry, being the sepals united in their inferior half or third, and with acuminate tips, whereas in *S. physalifolium* var. *nitidibaccatum* it encloses at most the lower half of berry, and the sepals are fused more than halfway to their blunt tips (Fig. 1h, g).

Micromorphological differences between the two taxa include the following: (1) In *Solanum sarrachoides* no stomata occur on the inner face of the sepals, whereas they do occur in *S. physalifolium* var. *nitidibaccatum*. (2) Whereas in both taxa the calix segments bear the same multicellular glandular and uniseriate hairs inside, the surface they occupy extends over more than half the total sepal length in *S. sarrachoides* but over only one fifth in *S. physalifolium* var. *nitidibaccatum*.

Fruit. The berry in both taxa is almost exactly spherical, usually green when ripe, with a whitish cross at the apex and an irregular whitish net. That of *Solanum sarrachoides* is larger. The size range of the berries of both species is shown in Table 2. The fruits of both taxa also show significant differences in numbers of seeds and sclerotic granules (Table 2). The sugar content of the mature berry is lower in *S. physalifolium* var. *nitidibaccatum* (6.5 %) than in *S. sarrachoides* (11.2 %).

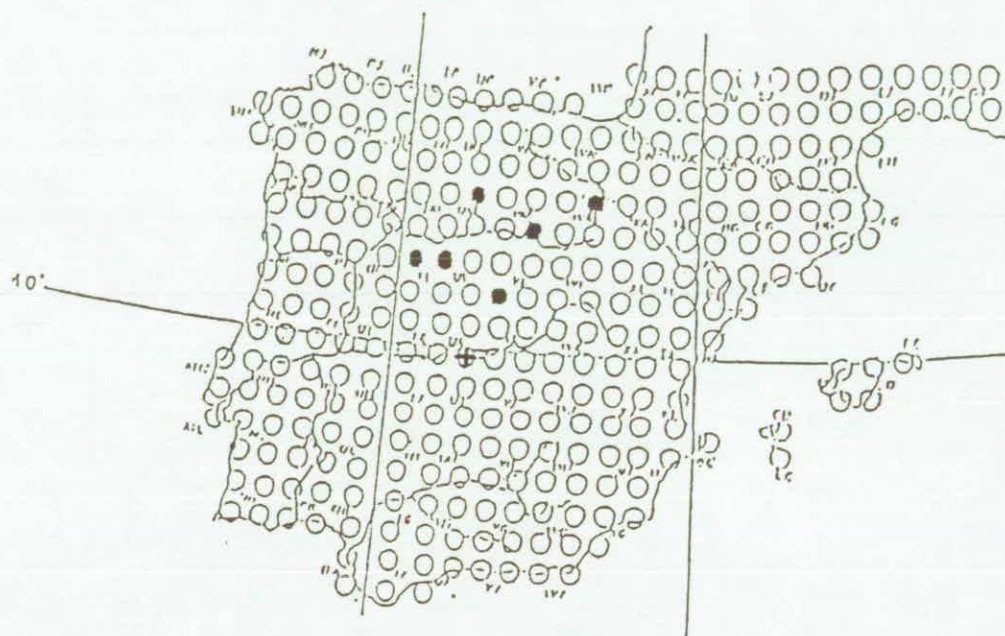


Fig. 5. Distribution in Spain of *Solanum physalifolium* var. *nitidibaccatum* (dots) and *S. sarrachoides* (cross).

The microstructure of the epicarp is shown in Fig. 2. In *Solanum physalifolium* var. *nitidibaccatum* the ornamentation of the berry consists of a network of grooves which delimit slightly granular raised areas, while in *S. sarrachoides* the netted grooves are shallower and areas in between are much rougher. Perhaps due to these morphological differences, the berry of *S. physalifolium* var. *nitidibaccatum* shows greater resistance to rupture of its epidermis.

Seed.—The seeds of *Solanum sarrachoides* are smaller than those of *S. physalifolium* var. *nitidibaccatum*, and have a different colour (Table 3). The micro-ornamentation of the testa is of the same type in both taxa but the raised bands are wider and denser in *S. sarrachoides* (Fig. 3).

The gel electrophoretic analysis of the total seed proteins shows a clear qualitative difference between the two species, and also between them, *S. nigrum* and *S. villosum* (Fig. 4).

Ecology and distribution in Spain.—The distribution in Spain of the two taxa does not overlap. *Solanum physalifolium* var. *nitidibaccatum* is found in the northern half of Spain, most frequently along the Duero river valley where it is a locally successful summer weed of irrigated areas (Fig. 5), whereas *S. sarrachoides* is confined to a very restricted area in the central part of the Tajo river valley and is also a summer weed on irrigated ground.

Average yearly summer region, a meseta at an altitude separates the Spanish area.

Solanum sarrachoides de Tajo (Toledo), on the summer. This was not the season (with maximum cold despite of irrigation. The corroborates these observations var. *nitidibaccatum*, such adapted to mild summer temperatures.

Dispersal strategy is the ground together with the long period of time, particularly to their harder epicarp. This appears to be the main adaptation species in important river valleys.

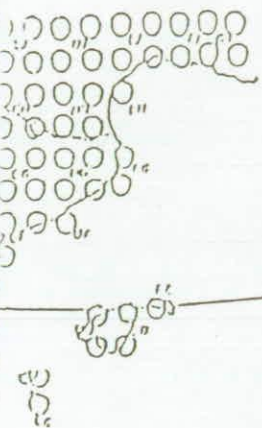
Acknowledgements

We are most grateful to Rodríguez de Quijano for his

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Average yearly summer temperatures are lower in northern Spain than in the central region, a meseta at an altitude of c. 700-800 m. The Central System mountain range also separates the Spanish areas of the two taxa.

Solanum sarrachoides grew without problems under experimental cultivation at Malpica de Tajo (Toledo), on the central meseta, and produced flowers and fruits throughout summer. This was not the case of *S. physalifolium* var. *nitidibaccatum* which in the hot season (with maximum day temperatures of 35-40°C) did not produce flowers or fruits despite of irrigation. The climate of the areas of Spain in which the two taxa are found corroborates these observations. Certain morphological characteristics of *S. physalifolium* var. *nitidibaccatum*, such as its less dense indumentum, possibly explain its being better adapted to mild summer temperatures.

Dispersal strategy is the same in both taxa: at the slightest shock, ripe berries fall to the ground together with the calyx and peduncle, and remain there without drying out for a long period of time, particularly those of *Solanum physalifolium* var. *nitidibaccatum* due to their harder epicarp. Thus, dispersal is very limited, except for carriage by birds. Water appears to be the main agent of dispersal, which accounts for the occurrence of both species in important river valleys and in irrigated areas, in Spain.

Acknowledgements

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INDEX SEMINUM 03



Bancos de Germoplasma Vegetal.

Margarita Clemente Muñoz

La conservación *ex situ* de recursos fitogenéticos se realiza a través de un conjunto de técnicas, que tienen por finalidad el mantenimiento de colecciones vegetales fuera de su hábitat natural, ya sea en forma de ejemplares completos o partes de ellos tales como semillas, polen, propágulos vegetativos o leñosos, tejidos y células. En general, el tipo de instalaciones que aplicando diferentes métodos, consiguen esta forma de conservación, se denominan bancos de germoplasma vegetal.

Los bancos de germoplasma actuales están, en su gran mayoría, dedicados a la conservación de especies cultivadas y más en particular, a las que resultan básicas para la alimentación humana. No obstante, en la última década se están realizando importantes esfuerzos para la instalación y desarrollo de bancos de germoplasma cuyo objetivo es la conservación de especies silvestres, ocupándose especialmente de aquellas sobre las que se cierne un eminente riesgo de extinción.

Según la forma del material vegetal a conservar se pueden considerar varios modelos de bancos de germoplasma:

1. Colecciones en campo
2. Colecciones *in vitro*
3. Bancos de polen
4. Bancos de semillas

El modelo actualmente más plenamente desarrollado y extendido, dentro de estos tipos de bancos de germoplasma, es el banco de semillas. Pero este sistema sólo es óptimo para mantener especies con semillas de tipo ortodoxo, es decir, aquellas que pueden desecarse hasta un contenido de humedad de aproximadamente del 5% y conservarse sin problemas durante largos períodos de tiempo en condiciones frías. Para las especies con semillas que no pueden secarse por debajo de un contenido de humedad relativamente alto sin pérdida de la viabilidad, ni ser mantenidas a baja temperatura sin sufrir daño, hay que aplicar métodos alternativos.

1. Colecciones en campo

Muchas especies, especialmente en los trópicos, poseen semillas recalcitrantes o bien no producen semilla fácilmente. Otras, como muchos frutales de pepita y hueso, tienen dificultad para ser conservadas a

causa de la latencia que presentan sus semillas o bien, porque no es suficiente con el mantenimiento de éstas si se persigue conservar la calidad de la variedad, como en el caso de los clones de patata o de caña de azúcar. Para todas estas especies es necesario mantener por vía asexual plantas completas, o propágulos tales como tubérculos, rizomas, bulbos o estacas y establecer con estos materiales colecciones en campo.

Las instalaciones requeridas, para esta modalidad de banco de germoplasma, son entre otras: áreas de propagación especiales; parcelas de tamaño adecuado; invernaderos con sistemas de control de temperaturas; umbráculos; sistemas de riego y habitaciones a baja temperatura para el almacenamiento temporal de propágulos.

La propagación asexual conlleva dificultades y complicaciones. Por ejemplo, para las plantas que producen tubérculos es preciso utilizar contenedores para evitar que los clones se mezclen en el suelo. A veces, es necesaria la limpieza periódica en el caso de especies rizomatosas, o incluso levantar toda la colección y obtener nuevos especímenes, a partir de las plantas madres originales. Las colecciones de propágulos tales como tubérculos, rizomas y bulbos pueden mantenerse sin plantar, en habitaciones a baja temperatura, tan sólo uno o dos años por término medio, dependiendo de las especies. En el caso de especies arbóreas el problema se complica porque requieren más espacio, un considerable trabajo de cuidado y tomar una serie de precauciones. Por ejemplo, es preciso aislar las diferentes accesiones, de la misma o diferente especie, para evitar su hibridación, y en el caso de las especies frutales será necesario conservar los patrones además de las variedades.

Las colecciones en campo ocupan mucho espacio y en general, raramente abarcan todo el rango de variabilidad genética. Además, difícilmente se mantienen las condiciones ecológicas que las plantas tenían en la naturaleza y son susceptibles a enfermedades y daños fortuitos producidos por incendios, depredadores y tormentas.

Sin embargo y a pesar de todos sus inconvenientes, las colecciones en campo son una forma muy efectiva para la conservación de especies con semillas recalcitrantes, o de las que presenten otros problemas, que impidan la aplicación de otras técnicas. En la actualidad, algunas instituciones y jardines botánicos

de la India, Honduras, Cuba, Malasia, Estados Unidos de América, etc., poseen excelentes bancos de germoplasma de este tipo.

2. Colecciones *in vitro*

Es éste un método alternativo de banco de germoplasma, a veces único, para conservar especies con semillas recalcitrantes o con baja o nula producción de semillas fértiles o de polen. También resulta adecuado para mantener especies perennes, que presentan ciclos de vida muy largos, con producción de semillas al cabo de muchos años. O bien, para conservar líneas clonales con elevado grado de heterocigosis o especies silvestres, con poblaciones muy reducidas, donde la mera recolección de semilla puede afectar su supervivencia en la naturaleza.

Con este tipo de colecciones *in vitro* se evitan las posibles pérdidas por ataques de patógenos, incidentes climatológicos o desastres naturales que se producen en las colecciones en campo. Permite la obtención de un elevado número de unidades en un corto tiempo y en un espacio reducido. También se facilita el intercambio y distribución de las colecciones entre instituciones de diferentes países por ser materiales libres de patógenos. Pero hay que señalar que este sistema también presenta inconvenientes, porque resultan costosas las instalaciones necesarias para su aplicación, origina una serie de problemas técnicos, para los que es preciso contar con personal especializado, que conozca los métodos que van a ser desarrollados y finalmente porque es necesario cuidar, de forma especial, que la estabilidad genética y el potencial regenerativo se mantengan.

El término cultivo *in vitro* se aplica a un conjunto de técnicas que se han desarrollado en los últimos años y que han resuelto numerosos problemas prácticos en el campo de la agricultura. En síntesis se trata de una forma de cultivar el material vegetal en condiciones asépticas, en medio sintético definido y bajo condiciones ambientales controladas.

El cultivo puede iniciarse a partir de cualquier parte de la planta madre: yemas, raíces, hojas, tejidos, células aisladas, protoplastos, semillas, embriones, etc. Es muy importante que las plantas madre sean preparadas adecuadamente, para que su estado sanitario y fisiológico sea óptimo, antes de extraer el explanto o fragmento a cultivar.

Mediante un adecuado manejo del material vegetal, de los medios de cultivo donde crecerá y de las condiciones ambientales controladas en cámara, es posible provocar en el explanto:

- dediferenciación de tejidos y proliferación de una masa de callo.

- organogénesis o formación de yemas y/o raíces adventicias.
- desarrollo de meristemos ya existentes.
- embriogénesis asexual o formación de embriones a partir de células que no son producto de fusión gamética.

Las técnicas de cultivo *in vitro* han sido aplicadas de forma extensiva en la conservación de recursos fitogenéticos de plantas cultivadas y recientemente han comenzado a ser utilizadas para especies en peligro de extinción. Existen tres formas de mantener las colecciones *in vitro*: 1) mediante crecimiento continuo en condiciones normales; 2) por crecimiento limitado, retardando el cultivo y 3) a través de crioconservación, suprimiendo todo crecimiento y metabolismo mediante temperaturas ultrabajas.

Para las colecciones *in vitro* mediante crecimiento continuo, se utilizan los métodos habituales de cultivo, es decir: iniciación en condiciones de asepsia; estimulación de la multiplicación y mantenimiento del crecimiento, mediante condiciones ambientales óptimas y cambios periódicos a medio de cultivo nuevo. Tiene la ventaja de suministrar constantemente material apto para ser aclimatado a las condiciones de exterior, pero presenta la desventaja de aumentar los riesgos de contaminación, o de pérdida de la estabilidad genética, al depender de pasajes o repiques frecuentes a medio nuevo.

En las colecciones *in vitro* por crecimiento limitado, se trata de modificar las condiciones de cultivo de forma tal, que se reduzca el desarrollo y así se alargue el periodo de tiempo entre cambios sucesivos a medio nuevo. Esto puede conseguirse por: reducción de la temperatura y/o iluminación; alteración del potencial osmótico; desecación; modificación del medio nutritivo mediante la reducción de componentes esenciales para el crecimiento normal; o por incorporación de niveles subletales de retardantes del crecimiento.

La mayoría de los trabajos de conservación mediante crecimiento limitado publicados han utilizado la reducción de temperatura como factor esencial. Sin embargo, la elección de temperaturas bajas como medio de reducir el crecimiento, está sujeta a ciertas condiciones que dependen de la naturaleza de cada especie. Así, para especies de zonas templadas la inhibición del crecimiento *in vitro* puede darse entre 0 y 10°C; en tanto que en las especies tropicales, muy sensibles al frío, las temperaturas de menos de 15°C pueden ser suficientes para provocar una inhibición total e irreversible en los tejidos.

Mediante la crioconservación se mantienen materiales vegetales a la temperatura del nitrógeno líquido (-196°C) o temperaturas próximas a ésta. Los pasos generales de este método son: elección del

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explanto y establecimiento de un cultivo estéril; tratamiento con un agente crioprotector; congelación y almacenamiento en nitrógeno líquido; descongelación y eliminación del agente crioprotector; determinación de la supervivencia de los cultivos después del proceso.

Este método difiere del de crecimiento limitado en que los procesos metabólicos quedan totalmente paralizados en lugar de producirse a velocidad reducida. El problema radica en mantener viables los especímenes, que han sido transferidos a tan bajas temperaturas y después devueltos a temperaturas normales.

La preservación de germoplasma *in vitro* con los métodos de la criobiología, es un área relativamente nueva en la que se están realizando notables avances en los últimos años, pero en la que aún queda mucho camino por recorrer. Esta técnica puede ser una poderosa herramienta para conservar numerosas especies tropicales de gran valor, posibilitando el almacenamiento de cultivos por períodos indefinidos, con total garantía sobre su estabilidad genética.

3. Bancos de polen.

Estas instalaciones pueden resultar de gran utilidad cuando es necesario realizar cruzamientos, después el material obtenido se puede mantener por multiplicación vegetativa. El polen presenta además la ventaja de tener un volumen muy pequeño frente al amplio rango de diversidad genética que se puede conservar en él.

En principio, su conservación requiere las mismas condiciones que las semillas ortodoxas es decir, baja humedad y baja temperatura, pero será necesario poner a punto las técnicas oportunas antes de que su utilización sea rutinaria. Las bajas temperaturas pueden provocar pérdidas de viabilidad en los pólenes de ciertos grupos de plantas y lo mismo ocurre con respecto a la humedad, si bien se recomiendan niveles comprendidos entre el 10 y el 30%. El proceso subsiguiente de rehidratación hasta conseguir el 80% necesario para su utilización, es también delicado, pues unos niveles hídricos inadecuados producen irregularidades en la germinación del polen. Hay familias como las Fabáceas, Rosáceas y Pináceas que tienen pólenes cuya viabilidad dura bastante tiempo. Sin embargo los de Poáceas y Ciperáceas son de vida corta y los de Salicáceas y Escrofulariáceas tienen una longevidad intermedia.

4. Bancos de semillas.

Desde sus orígenes, la agricultura ha dependido de las semillas por lo que el mantenimiento de su viabilidad, durante el período de su almacenaje, ha sido una cuestión de vital importancia para el hombre. Quizás por esta razón, la tecnología de semillas es un área en la que se ha trabajado intensamente desde hace mucho tiempo y los bancos de semillas son uno de los métodos de conservación *ex situ* más extendidos.

La viabilidad de las semillas -es decir su capacidad para germinar si se dieran las condiciones adecuadas- puede oscilar según las especies, entre unos pocos días a unos pocos cientos de años, habiéndose citado incluso, que algunas semillas permanecen viables hasta 3.000 años. Esta característica, intrínseca de algunos grupos de plantas, puede modificarse si las semillas se desecan y almacenan, en recipientes herméticos, a bajas temperaturas. De esta manera permanecerán viables durante períodos más largos, que los manifestados de forma natural.

En 1973, ROBERTS propuso los términos «ortodoxas» y «recalcitrantes» para describir el comportamiento de las semillas cuando se baja su contenido de humedad y son almacenadas en condiciones frías. Las ortodoxas toleran la desecación y las temperaturas de congelación, mientras que las recalcitrantes mueren si su contenido en humedad es reducido por debajo de un valor crítico (12-31%). Este último tipo de semillas, es el que presentan muchas de las especies arbóreas frutales o maderables así como herbáceas originarias de los trópicos, todas ellas de gran interés económico actual o potencial. Desafortunadamente, no se ha prestado mucha atención a este problema hasta hace pocos años y tan sólo unos cuantos grupos de investigación están actualmente intentando encontrar soluciones.

La mayor diferencia entre un tipo y otro de semillas se establece según sea su respuesta a la desecación. Por ello HANSON propuso en 1984 términos más precisos: semillas sensibles a la desecación y semillas tolerantes. Pero también hay que tener en cuenta que la mayoría de las recalcitrantes, son sensibles a las bajas temperaturas o no toleran la congelación.

Los pesos medios y volúmenes de las semillas recalcitrantes son usualmente mayores que las de las ortodoxas, debido a sus altos contenidos en humedad (30-70%) y a sus grandes tamaños. La mayoría tienen forma esférica u oval, son dicotiledóneas y algunas de ellas están cubiertas por gruesos endocarpos. Es importantísimo conocer las estructuras básicas de las semillas si se quiere interpretar correctamente su fisiología.

Las características propias de las semillas recalcitrantes

tes tales como gran tamaño, corta vida y sensibilidad a bajas temperaturas son típicas pero no diagnósticas. Por ejemplo, el limonero y la palmera de aceite fueron dadas durante mucho tiempo por recalcitrantes y ahora se clasifican como ortodoxas.

El agua en las semillas se encuentra en dos formas: agua libre, necesaria para el movimiento de las moléculas de un centro a otro del metabolismo y agua subcelular, estrechamente asociada a la estabilidad de las macromoléculas y superficies subcelulares. CLEGG en 1979, sugirió que para asegurar el correcto funcionamiento de los sistemas multienzimáticos de la semilla es necesaria la presencia del agua subcelular y su pérdida da lugar a la disrupción del metabolismo. En el caso de las ortodoxas esto no ocurre a causa de su tolerancia a la desecación, pero en las recalcitrantes sí parece tener una importancia vital (BERJAK *et al.*, 1984).

El grado de sensibilidad de las semillas recalcitrantes a la desecación varía según las especies. Por ejemplo *Dryobalanops aromatica* resulta dañada por debajo del 35% de humedad, *Theobroma cacao* al 27% y *Nephelium lappaceum* al 20%. La humedad crítica varía de una especie a otra y oscila entre el 12% y el 31%. Estas diferencias en susceptibilidad a la desecación se observan no sólo interespecificamente, sino también dentro de la misma especie o lote de semillas.

La razón de porqué la deshidratación provoca la muerte de las semillas recalcitrantes no está clara aún. Varios autores han emitido diversas hipótesis que señalan entre otras causas: la pérdida de la integridad de las membranas y desintegraciones nucleares, fenómenos éstos ya observados en las semillas del árbol del caucho cuando son desecadas al sol. Además, en algunas especies, se liberan altas concentraciones de oxidasas y compuestos fenólicos que se oxidan, provocando la pérdida de la actividad enzimática.

Los grados de tolerancia a las bajas temperaturas varían para las semillas recalcitrantes, pero muchas de ellas mueren por debajo de la temperatura ambiental. Las ortodoxas admiten rangos de variación mucho más amplios, si bien es sabido desde hace 50 o 60 años, que mueren por debajo de 0°C si no están bien secas. La causa es similar en este caso a lo que ocurre en las semillas recalcitrantes, ya que el daño se produce por formación de cristales de hielo, cuando el contenido de humedad es del 14-20%. Sin embargo, la razón de porqué mueren las semillas recalcitrantes a temperaturas por debajo de la ambiental no es bien conocida.

4. ¿Cómo conservar las semillas recalcitrantes?

Se han propuesto muchos métodos durante los últimos cincuenta años para su almacenamiento a largo plazo, pero las experiencias no han sido buenas. Como mucho, y con los últimos avances, las semillas realmente recalcitrantes apenas pueden ser almacenadas por un año y por lo tanto su conservación en banco no es práctica.

Para una conservación a corto plazo se propone un mantenimiento con humedad media. Esto se ha experimentado con diversas especies como cacao y caucho, pero tiene graves inconvenientes porque hay que evitar la germinación y controlar la aparición y crecimiento de hongos. No obstante, y a pesar de los cortos periodos de almacenamiento que se consiguen con este método, resulta de utilidad para mantener la supervivencia de las semillas al menos durante su transporte, desde los lugares de colecta y hasta el momento de su siembra, ya que en este lapso de tiempo las semillas recalcitrantes pierden rápidamente la viabilidad. Por ejemplo, de las 70.000 semillas de caucho que WICKHAM colectó en Brasil en 1876 sólo germinó el 4%, al llegar al Jardín Botánico de Kew, en el Reino Unido.

Un método prometedor es el almacenamiento de embriones en nitrógeno líquido, pero no se ha llegado muy lejos con semillas verdaderamente recalcitrantes y los problemas técnicos son enormes. Para especies reproducidas asexualmente con ciclos de vida largos, una alternativa posible sería almacenar embriones somáticos, que son producidos *in vitro* en gran número fácilmente. De hecho, los embriones somáticos de algunas especies vegetales se obtienen hoy día para ser utilizados como semillas artificiales.

Se estima que más del 20% de las especies de la flora vascular mundial, es decir aproximadamente 50.000, presentan este tipo de semillas. La mayoría crecen en zonas tropicales, donde el grado de amenaza por desaparición de su hábitat natural es muy elevado, y tienen un interés económico actual o potencial grande. Por todo ello, es necesario abordar de forma urgente el desarrollo de metodologías dirigidas a la conservación de semillas recalcitrantes.

4.2. Cómo conservar las semillas ortodoxas

El periodo durante el cual las semillas ortodoxas se mantienen viables, es mucho mayor que el de las recalcitrantes y así lo han puesto de manifiesto diferentes experimentos realizados durante más de 40 o 50 años, para corroborar este hecho. A veces se han utilizado semillas conservadas largos periodos en pliegos de herbario a temperatura ambiente, o semillas

encontradas en yacimientos arqueológicos con dataciones conocidas. Algunas Fabáceas destacan por su larga viabilidad, siendo frecuentes duraciones de más de 50 años o incluso de 100. También han sido citados periodos de 40 años para algunas Poáceas y en el tabaco, de 20 para la chufa y de 600 para la mostaza y el diente de león.

Para conservar semillas de tipo ortodoxo en banco, hay que tener en cuenta en primer lugar, que el estado fisiológico y sanitario de las mismas sea adecuado. Deben haber madurado perfectamente de forma natural, estar libres de enfermedades y no presentar daños físicos.

La colecta es un proceso importante en el cual debe participar personal especializado y ha de elegirse cuidadosamente el momento preciso para efectuarla, ya que las semillas además de presentar un grado de madurez adecuado, deben tener el menor contenido de humedad posible. Aunque las de tipo ortodoxo admiten la desecación forzada, no por ello deja de ser recomendable el coleccionar semillas que por medios naturales hayan conseguido niveles bajos de humedad. Así, las procedentes de zonas con clima seco si se recogen en el momento óptimo, pueden contener entre un 8 y un 10% sin necesidad de forzar la eliminación de agua y de esta manera, se facilitará extraordinariamente su ulterior conservación.

La limpieza o separación de las semillas de los frutos y de otros fragmentos inútiles, debe ser atentamente cuidada para evitar daños mecánicos o de otro tipo que provocan pérdidas de viabilidad. Los métodos habitualmente empleados dependen de las características de los frutos. Así para los carnosos, se debe remover la pulpa por inmersión en agua y posterior abrasión o presión. Los coriáceos se secan hasta provocar su apertura y algunos frutos indehiscentes se conservan completos o bien se les retiran algunas partes, como por ejemplo las alas a las sámaras. Para separar finalmente las semillas de otros restos con ellas mezclados, se utilizan diversos sistemas o varios de ellos, tales como: tamizado a través de un sistema de cribas; aventamiento mediante una corriente de aire, que separará las diversas fracciones en función de su peso; flotación en un líquido; fricción por deslizamiento sobre una superficie; separación electrónica, electrostática o magnética, etc.

A veces se recomienda la aplicación de fungicidas o insecticidas a las semillas una vez limpias, para mantenerlas en buen estado sanitario. No obstante, se deben tomar precauciones porque los productos químicos utilizados pueden afectar la viabilidad de muchas especies y además, en las condiciones de conservación de las colecciones, a bajo contenido de humedad y temperatura por debajo de cero, es altamente improbable que se produzcan ataques de agentes

patógenos:

Otro factor importante a considerar es la existencia de latencia en las semillas, es decir la presencia de mecanismos que impiden la germinación de muchas especies, aunque sus semillas sean perfectamente viables y las condiciones favorables para que se desarrolle el proceso. Hay diferentes tipos de latencia y las clasificaciones más simples distinguen entre:

- 1) Exógena, debida a impedimentos que actúan en el pericarpo del fruto o en la cubierta de la semilla tales como: impermeabilidad al agua, presencia de inhibidores y resistencia mecánica.
- 2) Endógena, producida por el desarrollo incompleto del embrión o por mecanismos fisiológicos que impiden la germinación.
- 3) Combinada, provocada por la presencia conjunta de dos o más mecanismos que afectan al embrión y a las cubiertas.

Es necesario detectar estos fenómenos, porque en caso contrario se corre el riesgo de eliminar muestras de semillas, que estando vivas no llegan a germinar por tener latencia. Existen procedimientos para romperla artificialmente tales como: eliminación de las estructuras vegetales -brácteas, glumas- que en ciertos casos inducen este proceso; escarificación mecánica o química; estratificación en frío; tratamientos térmicos o con agua; exposición a la luz; aplicación de ácido giberélico, etc., pero el problema no es simple. A veces, las semillas de ciertas especies adquieren latencias secundarias o impuestas, muy difíciles de eliminar, que son producidas por daños o tratamientos sufridos durante la colecta, o en la manipulación posterior. En teoría, las semillas conservadas en el banco no deberían presentar ningún tipo de latencia, pero en la práctica real es imposible frecuentemente cumplir con este requisito.

Para comprobar la viabilidad de las semillas en los casos de latencia -y en aquellos para los que sea necesaria una prueba rápida- se deben utilizar métodos demostrativos de las buenas condiciones del embrión, en lugar de la germinación como prueba determinante de éstas. La Asociación Internacional de Ensayo de Semillas recomienda tres formas para determinar la viabilidad:

- 1) Ensayo topográfico de tetrazolio, a través del cual las células vivas del embrión se tiñen de rojo por la reducción de una sal de tetrazolio. El método es bueno, pero tiene algunos inconvenientes por las dificultades que algunas especies presentan en su tinción y la interpretación de la diferente gradación de ésta, además el método es destructivo del material.
- 2) Ensayo de excisión, que simplemente consiste en cortar y observar el color y aspecto interior de las semillas, así como el grado de desarrollo del em-

brión. Es una prueba destructiva y requiere de un personal experimentado para conseguir una buena interpretación.

- 3) Ensayo de contraste con rayos X, que permite detectar semillas vacías y si las estructuras seminales presentan daños o desarrollos anormales. El método es útil, si se tienen en cuenta los grandes avances técnicos logrados en los equipos de rayos X, así como su considerable abaratamiento.

La temperatura de conservación debe analizarse junto con el grado de humedad de las semillas. Hace ya más de 25 años que se conoce la llamada «regla de HARRINGTON»: cada reducción de la humedad en un 1% duplica la vida de la semilla; cada reducción en 5°C, la duplica asimismo. No es una regla absoluta, pues hay que considerar otros factores como el contenido en aceite, pero tiene un gran valor orientativo.

En términos generales puede afirmarse que es mucho mejor tratar de bajar el contenido en humedad lo máximo posible, porque así no será necesario bajar mucho la temperatura para obtener los mismos resultados. Desechar es mucho más económico que mantener cámaras a temperaturas por debajo de cero, pero se debe tener cuidado, pues las fuertes desecaciones pueden inducir problemas secundarios como son los daños provocados por una fuerte imbibición de agua, cuando las semillas se ponen a germinar. Así mismo, para ciertas especies es muy difícil conseguir contenidos de humedad por debajo del 5%, por eso resulta más aconsejable mantener unos niveles del 5 al 7% y almacenar las semillas en condiciones herméticas.

La desecación de las semillas puede realizarse de dos maneras: sometiendo a una corriente de aire calentado por encima de 40°C, o colocándolas en un ambiente de baja humedad relativa sin calentar el aire.

El primero de los métodos presenta la ventaja de ser más rápido, pero tiene el inconveniente del riesgo de disminuir la viabilidad, al estar sometido el material a altas temperaturas. Además hay que añadir los peligros inherentes a posibles fallos técnicos del control de temperatura, que provocarían la muerte de la totalidad de las semillas. En ocasiones la operación de secado debe realizarse en dos pasos sucesivos y en climas húmedos, es necesario efectuar un tratamiento químico del aire para la eliminación de agua.

La desecación a baja humedad ambiental puede conseguirse con deshumificadores químicos y el más utilizado es el gel de sílice, por su bajo coste y capacidad de regeneración. Tiene el inconveniente de ser un proceso más lento, pero resulta más económico y de más fácil control.

Una vez conseguida la desecación de las semillas es importante la elección de los envases en los que se incluirán, durante su permanencia en la cámara fría. Pueden ser de diversos materiales como vidrio, latón, aluminio laminado, polietileno o incluso papel, según que la colección tenga por finalidad el ser conservada a largo, medio o corto plazo. Como regla general debe prestarse gran atención a su hermeticismo, si las colecciones van a ser mantenidas durante largos períodos. Pues si bien se recomienda el control de las humedades relativas de las cámaras con deshumificadores químicos, éste puede ser muy difícil de obtener particularmente a muy bajas temperaturas. Por esta razón es de vital importancia mantener estancos los envases que contienen las semillas. Además, si éstos se rellenan al máximo de su capacidad, el oxígeno que resta en el volumen de aire incluido en el recipiente es rápidamente consumido y así se posibilita un incremento de la longevidad, al eliminarse la actividad respiratoria. A veces se introducen gases inertes en los envases para conseguir este efecto, pero realmente no parece que esta operación sea crucial.

Para mantener las colecciones de semillas en frío pueden ser perfectamente adecuados los frigoríficos de tipo doméstico, que alcanzan -20°C o incluso temperaturas más bajas. Tienen la ventaja de su adquisición rápida y económica. Son aptos para colecciones de reducido tamaño y puede ir incrementándose el número de unidades, según aumenta la cantidad de material a conservar. También estos frigoríficos pueden utilizarse como solución temporal mientras se consigue presupuesto y lugar para la instalación de una cámara o habitación frigorífica, que sin duda es una solución más definitiva y recomendable, para albergar colecciones más grandes durante períodos prolongados.

En la instalación de habitaciones o cámaras frigoríficas de gran tamaño hay que tener en cuenta las temperaturas a las que se desea mantener las colecciones. Es conveniente contemplar al menos dos ambientes diferentes, uno dedicado a la conservación a largo plazo y otro para mantener las colecciones con las que habitualmente se trabaja en propagación, o las de intercambio a corto o medio plazo. Para éstas últimas, dado que su previsible permanencia en la cámara será corta o media, no es necesario utilizar temperaturas muy bajas y esto supone un ahorro considerable. Es de vital importancia la instalación de buenos termostatos de control y de un grupo eléctrico en previsión de cortes de luz fortuitos.

Las condiciones generales de conservación a largo plazo, recomendadas por el IBPGR para especies ortodoxas, son de almacenamiento en recipientes herméticos, con un contenido en humedad de las semi-

llas entre el 5 y el 1% y a -18°C o menos. Así, la pérdida de su viabilidad es muy lenta y por lo tanto no es necesario realizar muestreos demasiado frecuentes para controlar el estado de las colecciones.

Los inconvenientes y ventajas de la Conservación *Ex situ*

Una de las principales objeciones que se hacen a los diferentes modelos descritos de banco de germoplasma, es que conservan sólo parte de la variabilidad. Efectivamente, en ocasiones las colecciones están formadas por un pequeño número de individuos por especie. En otros casos, el muestreo inicial de colecta ha sido mal diseñado, lo que produce una baja representación de los genotipos presentes en las poblaciones naturales. Si el material vegetal se reproduce asexualmente y así es mantenido en colecciones en campo o *in vitro*, significará que sólo se está conservando una estrecha base genética, no representativa de la variabilidad total de la especie.

Los sistemas de conservación *in vitro* tienen la dificultad del mantenimiento de la estabilidad genética del material, si bien hay que señalar que los métodos que utilizan el crecimiento limitado o la criopreservación minimizan este problema.

En cuanto a las colecciones en campo son evidentes los riesgos de hibridación, las bajas tasas de supervivencia y los daños que pueden sufrir por agentes externos.

Para los bancos de semillas a largo plazo se han señalado los inconvenientes de ausencia de evolución continua del material en ellos conservado y la vulnerabilidad de las colecciones ante eventuales cortes del suministro eléctrico que impidan mantener de forma adecuada las bajas temperaturas.

Denominadores comunes a todas las técnicas *ex situ* son: la exigencia de contar con personal especializado para su desarrollo y los altos costes de instalaciones y mantenimiento. Sin embargo, en muchas ocasiones representan la única opción para conservar ciertos tipos de taxones vegetales.

La destrucción de hábitats por impactos humanos, es irreversible la mayoría de las veces y avanza de forma alarmante en áreas muy sensibles como las tropicales o la mediterránea. Así pues, la conservación *ex situ* puede ser una solución válida para miles de especies silvestres, que se extinguirán irremisiblemente a principios del siglo XXI, dado el grado de desaparición observado de los lugares donde viven de forma natural. En el caso de cultivares primitivos de especies utilizadas por el hombre, puede ser la única forma de conservar un acervo genético que de otra manera se perdería, al ser desplazados primero y sustituidos finalmente por otros cultivares más avanzados.

Las colecciones en campo y los sistemas *in vitro*, resultan de gran interés para mantener especies de tipo recalcitrante o aquellas que presentan alguna dificultad para ser conservadas por otros métodos.

Los bancos de semillas ortodoxas son altamente eficaces si se utilizan las condiciones adecuadas de desecación y bajas temperaturas. Además, permiten el almacenamiento de numerosas muestras en espacios reducidos, que representan considerables proporciones de la variabilidad genética de las poblaciones naturales.

Todas las colecciones *ex situ* hacen posible el suministro de material vegetal para su utilización en programas de mejora vegetal o para otras finalidades. De ésta manera, se evita también la continua extracción de recursos, fitogenéticos, a veces escasísimos, a partir de sus hábitats naturales.

En conclusión, no sería muy optimista aventurar que, si se comparasen los costes dedicados a las técnicas de conservación *ex situ* con los de las técnicas *in situ*, probablemente los beneficios obtenidos resultarían mayores en muchas de las situaciones. No obstante, conservación *ex situ* y conservación *in situ* nunca deben ser términos contrapuestos. Sólo con la integración y utilización de ambos métodos, será posible garantizar la supervivencia de los recursos fitogenéticos amenazados, de una extinción cierta, en las próximas décadas.

Botanischer Garten

der

Johann Wolfgang Goethe-Universität

Frankfurt am Main



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2002

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1544	1586	1628	1670	1712	1754	1796	1838	1880	1922	1964	2006	2048	2090	2132	2174	2216
1545	1587	1629	1671	1713	1755	1797	1839	1881	1923	1965	2007	2049	2091	2133	2175	2217
1546	1588	1630	1672	1714	1756	1798	1840	1882	1924	1966	2008	2050	2092	2134	2176	2218
1547	1589	1631	1673	1715	1757	1799	1841	1883	1925	1967	2009	2051	2093	2135	2177	2219
1548	1590	1632	1674	1716	1758	1800	1842	1884	1926	1968	2010	2052	2094	2136	2178	2220
1549	1591	1633	1675	1717	1759	1801	1843	1885	1927	1969	2011	2053	2095	2137	2179	2221
1550	1592	1634	1676	1718	1760	1802	1844	1886	1928	1970	2012	2054	2096	2138	2180	2222
1551	1593	1635	1677	1719	1761	1803	1845	1887	1929	1971	2013	2055	2097	2139	2181	2223
1552	1594	1636	1678	1720	1762	1804	1846	1888	1930	1972	2014	2056	2098	2140	2182	2224
1553	1595	1637	1679	1721	1763	1805	1847	1889	1931	1973	2015	2057	2099	2141	2183	2225
1554	1596	1638	1680	1722	1764	1806	1848	1890	1932	1974	2016	2058	2100	2142	2184	2226
1555	1597	1639	1681	1723	1765	1807	1849	1891	1933	1975	2017	2059	2101	2143	2185	2227
1556	1598	1640	1682	1724	1766	1808	1850	1892	1934	1976	2018	2060	2102	2144	2186	2228
1557	1599	1641	1683	1725	1767	1809	1851	1893	1935	1977	2019	2061	2103	2145	2187	2229

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220	221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240	241	242	243	244	245	246	247	248	249	250	251	252	253	254	255	256	257	258	259	260	261	262	263	264	265	266	267	268	269	270	271	272	273	274	275	276	277	278	279	280	281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300	301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320	321	322	323	324	325	326	327	328	329	330	331	332	333	334	335	336	337	338	339	340	341	342	343	344	345	346	347	348	349	350	351	352	353	354	355	356	357	358	359	360	361	362	363	364	365	366	367	368	369	370	371	372	373	374	375	376	377	378	379	380	381	382	383	384	385	386	387	388	389	390	391	392	393	394	395	396	397	398	399	400	401	402	403	404	405	406	407	408	409	410	411	412	413	414	415	416	417	418	419	420	421	422	423	424	425	426	427	428	429	430	431	432	433	434	435	436	437	438	439	440	441	442	443	444	445	446	447	448	449	450	451	452	453	454	455	456	457	458	459	460	461	462	463	464	465	466	467	468	469	470	471	472	473	474	475	476	477	478	479	480	481	482	483	484	485	486	487	488	489	490	491	492	493	494	495	496	497	498	499	500	501	502	503	504	505	506	507	508	509	510	511	512	513	514	515	516	517	518	519	520	521	522	523	524	525	526	527	528	529	530	531	532	533	534	535	536	537	538	539	540	541	542	543	544	545	546	547	548	549	550	551	552	553	554	555	556	557	558	559	560	561	562	563	564	565	566	567	568	569	570	571	572	573	574	575	576	577	578	579	580	581	582	583	584	585	586	587	588	589	590	591	592	593	594	595	596	597	598	599	600	601	602	603	604	605	606	607	608	609	610	611	612	613	614	615	616	617	618	619	620	621	622	623	624	625	626	627	628	629	630	631	632	633	634	635	636	637	638	639	640	641	642	643	644	645	646	647	648	649	650	651	652	653	654	655	656	657	658	659	660	661	662	663	664	665	666	667	668	669	670	671	672	673	674	675	676	677	678	679	680	681	682	683	684	685	686	687	688	689	690	691	692	693	694	695	696	697	698	699	700	701	702	703	704	705	706	707	708	709	710	711	712	713	714	715	716	717	718	719	720	721	722	723	724	725	726	727	728	729	730	731	732	733	734	735	736	737	738	739	740	741	742	743	744	745	746	747	748	749	750	751	752	753	754	755	756	757	758	759	760	761	762	763	764	765	766	767	768	769	770	771	772	773	774	775	776	777	778	779	780	781	782	783	784	785	786	787	788	789	790	791	792	793	794	795	796	797	798	799	800	801	802	803	804	805	806	807	808	809	810	811	812	813	814	815	816	817	818	819	820	821	822	823	824	825	826	827	828	829	830	831	832	833	834	835	836	837	838	839	840	841	842	843	844	845	846	847	848	849	850	851	852	853	854	855	856	857	858	859	860	861	862	863	864	865	866	867	868	869	870	871	872	873	874	875	876	877	878	879	880	881	882	883	884	885	886	887	888	889	890	891	892	893	894	895	896	897	898	899	900	901	902	903	904	905	906	907	908	909	910	911	912	913	914	915	916	917	918	919	920	921	922	923	924	925	926	927	928	929	930	931	932	933	934	935	936	937	938	939	940	941	942	943	944	945	946	947	948	949	950	951	952	953	954	955	956	957	958	959	960	961	962	963	964	965	966	967	968	969	970	971	972	973	974	975	976	977	978	979	980	981	982	983	984	985	986	987	988	989	990	991	992	993	994	995	996	997	998	999	1000	1001	1002	1003	1004	1005	1006	1007	1008	1009	1010	1011	1012	1013	1014	1015	1016	1017	1018	1019	1020	1021	1022	1023	1024	1025	1026	1027	1028	1029	1030	1031	1032	1033	1034	1035	1036	1037	1038	1039	1040	1041	1042	1043	1044	1045	1046	1047	1048	1049	1050	1051	1052	1053	1054	1055	1056	1057	1058	1059	1060	1061	1062	1063	1064	1065	1066	1067	1068	1069	1070	1071	1072	1073	1074	1075	1076	1077	1078	1079	1080	1081	1082	1083	1084	1085	1086	1087	1088	1089	1090	1091	1092	1093	1094	1095	1096	1097	1098	1099	1100	1101	1102	1103	1104	1105	1106	1107	1108	1109	1110	1111	1112	1113	1114	1115	1116	1117	1118	1119	1120	1121	1122	1123	1124	1125	1126	1127	1128	1129	1130	1131	1132	1133	1134	1135	1136	1137	1138	1139	1140	1141	1142	1143	1144	1145	1146	1147	1148	1149	1150	1151	1152	1153	1154	1155	1156	1157	1158	1159	1160	1161	1162	1163	1164	1165	1166	1167	1168	1169	1170	1171	1172	1173	1174	1175	1176	1177	1178	1179	1180	1181	1182	1183	1184	1185	1186	1187	1188	1189	1190	1191	1192	1193	1194	1195	1196	1197	1198	1199	1200	1201	1202	1203	1204	1205	1206	1207	1208	1209	1210	1211	1212	1213	1214	1215	1216	1217	1218	1219	1220	1221	12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1991 Primula	bulleyana	2016 Pulsatilla	virginica alba	KK	2161 Saxifraga	obconata	2246 Sedium	AS
1992 Primula	capitata ssp. mucronata	2017 Pulsatilla	virginica 'Heller Hybrids'	ER	2162 Saxifraga	oxylopetiolata	2247 Sedium	
1993 Primula	chrysantha	2018 Pulsatilla	virginica 'Red'		2163 Saxifraga	oxylobasis	2248 Sedium	
1994 Primula	chrysantha	2019 Primula	myconi	OVN	2164 Saxifraga	oxylobasis 'Probynyi'	2249 Sedium	
1995 Primula	chrysantha	2020 Primula	myconi fl. rosea		2165 Saxifraga	oxylobasis	2250 Sedium	
1996 Primula	chrysantha	2021 Primula	nathaliae		2166 Saxifraga	oxylobasis	2251 Sedium	
1997 Primula	chrysantha	2022 Primula	arvensis		2167 Saxifraga	oxylobasis	2252 Sedium	
1998 Primula	chrysantha	2023 Primula	bulbosus		2168 Saxifraga	oxylobasis	2253 Sedium	
1999 Primula	chrysantha	2024 Primula	garganicus		2169 Saxifraga	oxylobasis	2254 Sedium	
2000 Primula	chrysantha	2025 Primula	angulata		2170 Saxifraga	oxylobasis	2255 Sedium	
2001 Primula	chrysantha	2026 Primula	angulata		2171 Saxifraga	oxylobasis	2256 Sedium	
2002 Primula	chrysantha	2027 Primula	lutea		2172 Saxifraga	oxylobasis	2257 Sedium	
2003 Primula	chrysantha	2028 Primula	franguloides		2173 Saxifraga	oxylobasis	2258 Sedium	
2004 Primula	chrysantha	2029 Primula	franguloides		2174 Saxifraga	oxylobasis	2259 Sedium	
2005 Primula	chrysantha	2030 Primula	franguloides		2175 Saxifraga	oxylobasis	2260 Sedium	
2006 Primula	chrysantha	2031 Primula	franguloides		2176 Saxifraga	oxylobasis	2261 Sedium	
2007 Primula	chrysantha	2032 Primula	franguloides		2177 Saxifraga	oxylobasis	2262 Sedium	
2008 Primula	chrysantha	2033 Primula	franguloides		2178 Saxifraga	oxylobasis	2263 Sedium	
2009 Primula	chrysantha	2034 Primula	franguloides		2179 Saxifraga	oxylobasis	2264 Sedium	
2010 Primula	chrysantha	2035 Primula	franguloides		2180 Saxifraga	oxylobasis	2265 Sedium	
2011 Primula	chrysantha	2036 Primula	franguloides		2181 Saxifraga	oxylobasis	2266 Sedium	
2012 Primula	chrysantha	2037 Primula	franguloides		2182 Saxifraga	oxylobasis	2267 Sedium	
2013 Primula	chrysantha	2038 Primula	franguloides		2183 Saxifraga	oxylobasis	2268 Sedium	
2014 Primula	chrysantha	2039 Primula	franguloides		2184 Saxifraga	oxylobasis	2269 Sedium	
2015 Primula	chrysantha	2040 Primula	franguloides		2185 Saxifraga	oxylobasis	2270 Sedium	
2016 Primula	chrysantha	2041 Primula	franguloides		2186 Saxifraga	oxylobasis	2271 Sedium	
2017 Primula	chrysantha	2042 Primula	franguloides		2187 Saxifraga	oxylobasis	2272 Sedium	
2018 Primula	chrysantha	2043 Primula	franguloides		2188 Saxifraga	oxylobasis	2273 Sedium	
2019 Primula	chrysantha	2044 Primula	franguloides		2189 Saxifraga	oxylobasis	2274 Sedium	
2020 Primula	chrysantha	2045 Primula	franguloides		2190 Saxifraga	oxylobasis	2275 Sedium	
2021 Primula	chrysantha	2046 Primula	franguloides		2191 Saxifraga	oxylobasis	2276 Sedium	
2022 Primula	chrysantha	2047 Primula	franguloides		2192 Saxifraga	oxylobasis	2277 Sedium	
2023 Primula	chrysantha	2048 Primula	franguloides		2193 Saxifraga	oxylobasis	2278 Sedium	
2024 Primula	chrysantha	2049 Primula	franguloides		2194 Saxifraga	oxylobasis	2279 Sedium	
2025 Primula	chrysantha	2050 Primula	franguloides		2195 Saxifraga	oxylobasis	2280 Sedium	
2026 Primula	chrysantha	2051 Primula	franguloides		2196 Saxifraga	oxylobasis	2281 Sedium	
2027 Primula	chrysantha	2052 Primula	franguloides		2197 Saxifraga	oxylobasis	2282 Sedium	
2028 Primula	chrysantha	2053 Primula	franguloides		2198 Saxifraga	oxylobasis	2283 Sedium	
2029 Primula	chrysantha	2054 Primula	franguloides		2199 Saxifraga	oxylobasis	2284 Sedium	
2030 Primula	chrysantha	2055 Primula	franguloides		2200 Saxifraga	oxylobasis	2285 Sedium	
2031 Primula	chrysantha	2056 Primula	franguloides		2201 Saxifraga	oxylobasis	2286 Sedium	
2032 Primula	chrysantha	2057 Primula	franguloides		2202 Saxifraga	oxylobasis	2287 Sedium	
2033 Primula	chrysantha	2058 Primula	franguloides		2203 Saxifraga	oxylobasis	2288 Sedium	
2034 Primula	chrysantha	2059 Primula	franguloides		2204 Saxifraga	oxylobasis	2289 Sedium	
2035 Primula	chrysantha	2060 Primula	franguloides		2205 Saxifraga	oxylobasis	2290 Sedium	
2036 Primula	chrysantha	2061 Primula	franguloides		2206 Saxifraga	oxylobasis	2291 Sedium	
2037 Primula	chrysantha	2062 Primula	franguloides		2207 Saxifraga	oxylobasis	2292 Sedium	
2038 Primula	chrysantha	2063 Primula	franguloides		2208 Saxifraga	oxylobasis	2293 Sedium	
2039 Primula	chrysantha	2064 Primula	franguloides		2209 Saxifraga	oxylobasis	2294 Sedium	
2040 Primula	chrysantha	2065 Primula	franguloides		2210 Saxifraga	oxylobasis	2295 Sedium	
2041 Primula	chrysantha	2066 Primula	franguloides		2211 Saxifraga	oxylobasis	2296 Sedium	
2042 Primula	chrysantha	2067 Primula	franguloides		2212 Saxifraga	oxylobasis	2297 Sedium	
2043 Primula	chrysantha	2068 Primula	franguloides		2213 Saxifraga	oxylobasis	2298 Sedium	
2044 Primula	chrysantha	2069 Primula	franguloides		2214 Saxifraga	oxylobasis	2299 Sedium	
2045 Primula	chrysantha	2070 Primula	franguloides		2215 Saxifraga	oxylobasis	2300 Sedium	
2046 Primula	chrysantha	2071 Primula	franguloides		2216 Saxifraga	oxylobasis	2301 Sedium	
2047 Primula	chrysantha	2072 Primula	franguloides		2217 Saxifraga	oxylobasis	2302 Sedium	
2048 Primula	chrysantha	2073 Primula	franguloides		2218 Saxifraga	oxylobasis	2303 Sedium	
2049 Primula	chrysantha	2074 Primula	franguloides		2219 Saxifraga	oxylobasis	2304 Sedium	
2050 Primula	chrysantha	2075 Primula	franguloides		2220 Saxifraga	oxylobasis	2305 Sedium	
2051 Primula	chrysantha	2076 Primula	franguloides		2221 Saxifraga	oxylobasis	2306 Sedium	
2052 Primula	chrysantha	2077 Primula	franguloides		2222 Saxifraga	oxylobasis	2307 Sedium	
2053 Primula	chrysantha	2078 Primula	franguloides		2223 Saxifraga	oxylobasis	2308 Sedium	
2054 Primula	chrysantha	2079 Primula	franguloides		2224 Saxifraga	oxylobasis	2309 Sedium	
2055 Primula	chrysantha	2080 Primula	franguloides		2225 Saxifraga	oxylobasis	2310 Sedium	
2056 Primula	chrysantha	2081 Primula	franguloides		2226 Saxifraga	oxylobasis	2311 Sedium	
2057 Primula	chrysantha	2082 Primula	franguloides		2227 Saxifraga	oxylobasis	2312 Sedium	
2058 Primula	chrysantha	2083 Primula	franguloides		2228 Saxifraga	oxylobasis	2313 Sedium	
2059 Primula	chrysantha	2084 Primula	franguloides		2229 Saxifraga	oxylobasis	2314 Sedium	
2060 Primula	chrysantha	2085 Primula	franguloides		2230 Saxifraga	oxylobasis	2315 Sedium	
2061 Primula	chrysantha	2086 Primula	franguloides		2231 Saxifraga	oxylobasis	2316 Sedium	
2062 Primula	chrysantha	2087 Primula	franguloides		2232 Saxifraga	oxylobasis	2317 Sedium	
2063 Primula	chrysantha	2088 Primula	franguloides		2233 Saxifraga	oxylobasis	2318 Sedium	
2064 Primula	chrysantha	2089 Primula	franguloides		2234 Saxifraga	oxylobasis	2319 Sedium	
2065 Primula	chrysantha	2090 Primula	franguloides		2235 Saxifraga	oxylobasis	2320 Sedium	
2066 Primula	chrysantha	2091 Primula	franguloides		2236 Saxifraga	oxylobasis	2321 Sedium	
2067 Primula	chrysantha	2092 Primula	franguloides		2237 Saxifraga	oxylobasis	2322 Sedium	
2068 Primula	chrysantha	2093 Primula	franguloides		2238 Saxifraga	oxylobasis	2323 Sedium	
2069 Primula	chrysantha	2094 Primula	franguloides		2239 Saxifraga	oxylobasis	2324 Sedium	
2070 Primula	chrysantha	2095 Primula	franguloides		2240 Saxifraga	oxylobasis	2325 Sedium	
2071 Primula	chrysantha	2096 Primula	franguloides		2241 Saxifraga	oxylobasis	2326 Sedium	
2072 Primula	chrysantha	2097 Primula	franguloides		2242 Saxifraga	oxylobasis	2327 Sedium	
2073 Primula	chrysantha	2098 Primula	franguloides		2243 Saxifraga	oxylobasis	2328 Sedium	
2074 Primula	chrysantha	2099 Primula	franguloides		2244 Saxifraga	oxylobasis	2329 Sedium	
2075 Primula	chrysantha	2100 Primula	franguloides		2245 Saxifraga	oxylobasis	2330 Sedium	

ICONOGRAFIAS 04



988. *Atriplex hortense* L.
It. — 2-4, colt., nat. (As. bor.).



989. *Atriplex hastatum* L.
Italia — 2-5.



989¹. v. *litorale* (L.)
It. bor., centr., ins. — 2-3, lit.



990. *Atriplex laciniatum* L.
It. — 2 e 3 per lo più lit.



990¹. v. *roseum* (L.)
Col tipo.



991. *Atriplex portulacoides* L.
It. — 2-3 lit. e Mantov.



Spinacia L.
It. — 2 lit.



994. *Spinacia oleracea* L.
It. — 2-4, colt., nat. (As. occ.).



1001. Cher
It. pen., Is

1970

ITALIA E ITALICAE / ENACIACI





995. *Beta vulgaris* L.
It. — 2 lit., rr. 3-4, e colt., nat.



996. *Beta trigyna* W. et K.
Genova, Orvieto — 2, nat. (Or.).



997. *Chenopodium capitatum* Asch.
It. bor. — 4-5 e colt., nat.



998. *Chen. Bonus-Henricus* L.
Italia — 4-7.



999. *Chenop. polyspermum* L.
Italia — 2-4.



1000. *Chenop. Vulvaria* L.
Italia — 2-4.



1001. *Chenop. hybridum* L.
It. pen., Istr., Catania — 2-4.



1002. *Chenop. murale* L.
Italia — 2-4.



1003. *Chenop. urbicum* L.
Italia — 2-4.



1004. *Chenopodium rubrum* L.
It. pen., Ischia, Cors. — 24.



1005. *Chenop. glaucum* L.
It. bor., Lig. — 34.



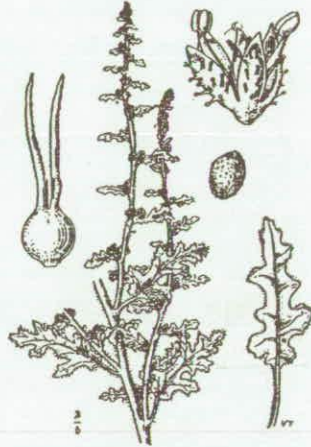
1006. *Chenop. album* L.
Italia — 2-5.



1013. *Kochia*
Napoli



1007. *Chenop. ambrosioides* L.
Italia — 2-6, nat. (Amer.).



1008. *Chenop. Botrys* L.
It. pen., Sic., Cors. — 24.



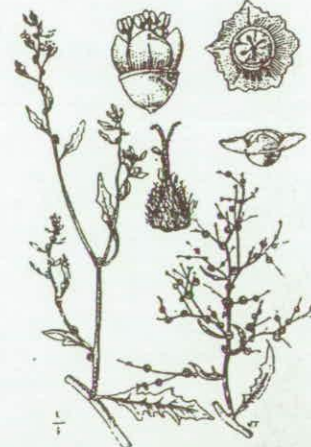
1009. *Chenop. multifidum* L.
Italia — 2-4, nat. (Am. mer.).



1016. *Kochia*
Val



1010. *Chenop. aristatum* L.
Venezia, Chioggia, Bobbio — 3-4, nat.
(As. ed Am. bor.).



1011. *Cycloloma platyphyllum* Moq.
It. bor., Pisa — 2-3, nat. (Am. bor.).



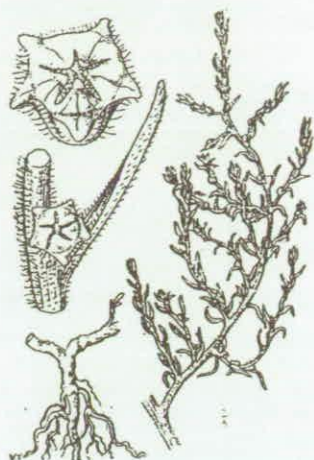
1012. *Kochia scoparia* Schrad.
It. — 2-4, colt., nat. (Or.).



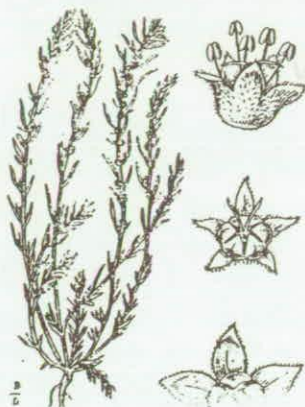
1015
m
It. —



1013. *Kochia hyssopifolia* Roth
Napoli — 2, nat. (Or.).



1014. *Kochia hirsuta*
Veneto, Nap., Cagliari



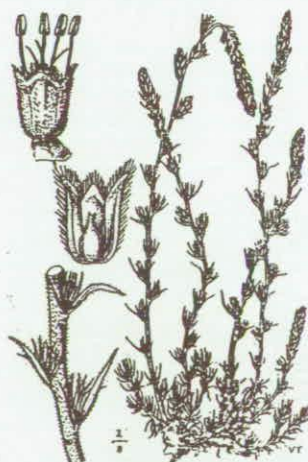
1016. *Kochia prostrata* Schrad.
Val d'Aosta — 4.



1017. *Kochia saxicola* Guss.
Ischia, Capri, Strombolicchio — 2.



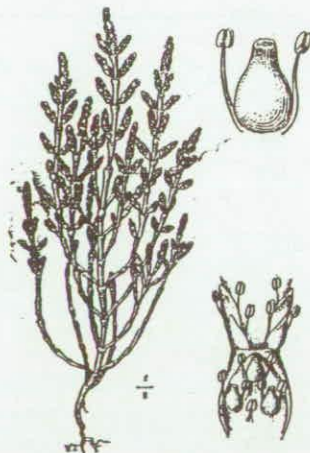
1018. *Corispermum hyssopifol.* L.
It. bor., Sic. — 2-3.



1019. *Camphorosma monspeliacum* L.
It. — 2 e 4, per lo più lit.



1020. *Polycnemum arvense* L.
It. (escl. mer. e Sic.) — 2-4.



1021. *Salicornia herbacea* L.
It. — 2 e 3, per lo più lit.



1022. *Salicornia fruticosa* L.
It. — 2 lit. e Ferrar.



1023. *Arthrocnemum glaucum* Ung.
It. (escl. Lig., Cal.) — 2 lit.



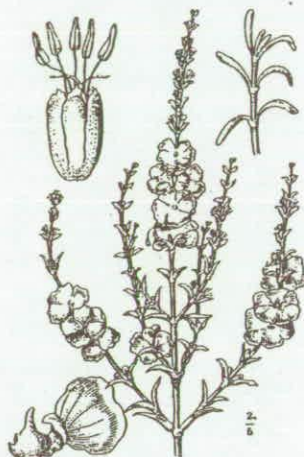
1024. *Halocnemum strobilaceum* M. B.
Sic., Malta, Sard. — 2 lit.



1031. *Suaeda*
It. (escl. bor.)



1025. *Haloepelis amplexicaulis* Ung.
Golfo di Taranto, Sic., Sard. — 2 lit.



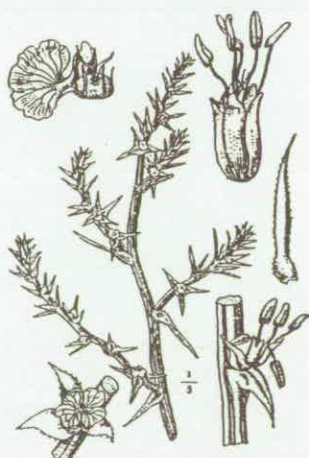
1026. *Salsola longifolia* Forsk.
Sic., Eolie, Lamp. — 2, per lo più lit.



1027. *Salsola vermiculata* L.
Sic., Malta, Sard. — 2 lit.



1034. *Achillea*
Cal.,



1028. *Salsola Kali* L.
It. — 2-3, per lo più lit.



1029. *Salsola Soda* L.
It. — 2 lit. e Mantov., Ferrar.



1030. *Halogeton sativus*
C. A. Mey.
Friuli — 2 lit., colt. (Spa. Afr. bor.-
occ.).



1037. *Amaranthus*
It. — 2



2537. *Malva crispa* L.
Alpi — 4-5, colt., nat. (Russia).



2538. *Malva rotundifolia* L.
It. pen., Trapani — 4-6, rr. 2 e 3.



2540. *Malva parviflora* L.
It. (escl. bor.) — 2.



2541. *Abutilon Theophrasti* Medic.
It. pen., Malta, Cors. — 2 e 3.



2542. *Hibiscus syriacus* L.
Italia — 2-4, colt. (As. occ.).



2543. *Hibiscus Trionum* L.
It. pen., Sic., Malta — 2-4.

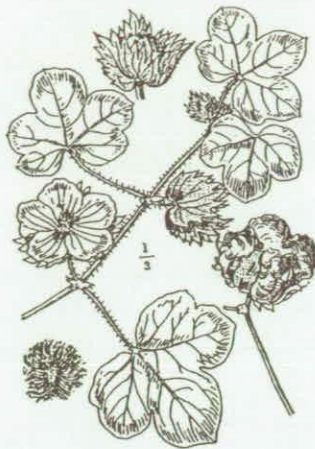


2544. *Hibiscus roseus* Thore
Ven., Mantov., Lucchese — 2 e 3.



2545. *Hibiscus pentacarpos* L.
Ven., Laz., Nap. — 2 e 3.

2550
It. —



2546. *Gossypium herbaceum* L.
It. mer., Sic. — 2, colt. (India?)



2547. *Tilia europaea* L.
α *vulgaris* (Hayne)
It. pen., Messinese — 3-5 e colt.



2547.¹ *T. v. platyphylla* (Scop.)
It. pen. — 4-5 e colt., nat.



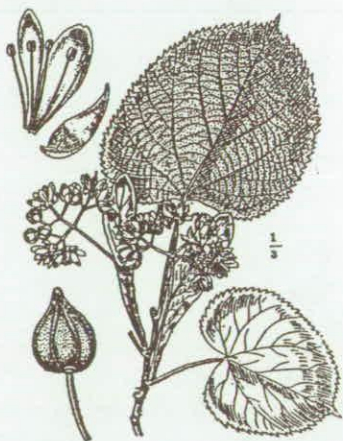
2547.² *T. v. cordata* (Mill.)
It. pen., Cors. — 3-5 e colt., nat.



2548. *Tilia americana* L.
It. — 2-5, colt. (Am. bor.).



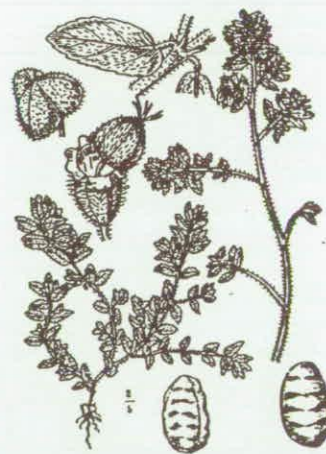
2549. *T. heterophylla* Vent.
It. — 2-4, colt. (Am. bor.).



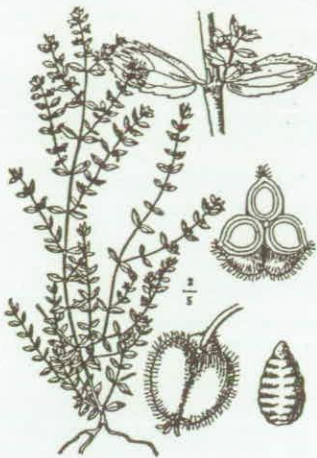
2550. *Tilia tomentosa* Mönch
It. — 2-4, colt. (Eur. or., As. min.).



2551. *Euphorbia nutans* Lag.
It. pen., Elba, Sic. — 2-4, nat. (Am.).



2552. *Euphorbia maculata* L.
Italia — 2-4, nat. (Am. bor.)



2553. *Euphorbia prostrata* Ait.
It. pen., Sic. — 2-3, nat.
(Am. e Afr. trop.).



2554. *Euph. Engelmanni* Boiss.
(Cile).



2555. *Euph. Chamæsyce* L.
Italia — 2-4.



2556. *Euph. humifusa* W.
Italia — 2-4, nat. (As. temp.).



2557. *Euphorbia Peplis* L.
It. — 2-3, lit.



2558. *Euphorbia Lathyris* L.
It. pen., Sard., Cors. — 2-4.



2559. *Euph. palustris* L.
It. pen. (rara al sud) — 2-3.



2560. *Euph. ceratocarpa* Ten.
Puglie, Cal., Sic. — 2.



2561. *Euph. spinosa* L.
It. (escl. bor. p. p.) — 2 e 4.

256
v.
Piem. (al



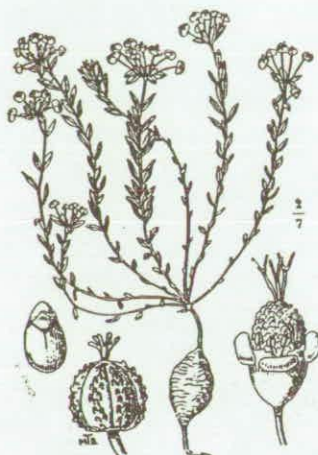
2561. *Euph. v. Bivonae* (Steud.)
Sic., Egadi — 2.



2562. *Euph. epithymoides* L.
v. fragifera (Jan)
Istr., Triest. — 2-7.



2562. *Euph. v. verrucosa* (Jacq.)
It. bor., centr. — 2-5.



2563. *Euphorbia Apios* L.
It. mer. — 2.



2564. *Euph. carniolica* Jacq.
Istr., Alpi or. e centr., Eug. — 4-7.



2565. *Euph. dulcis* L.
It. bor., centr. — 4-5, rr. 2-3.



2566. *Euph. hyberna* L.
v. Gibelliana (Peola)
Piem. (altre var. Lig., Cors., Sard.) — 4



2567. *Euphorbia pilosa* L.
Ven., Piem., Lig. — 4, rr. 3.



2568. *Euph. coralloides* L.
It. centr., mer., Ischia, Sic. — 4-5.



2569. *Euph. pubescens* Vahl
It. (escl. bor.) — 2.



2570. *Euph. akenocarpa* Guss.
Camp., Cal., Sic. — 2.



2571. *Euph. cuneifolia* Guss.
It. centr., mer., ins. — 2.



2572. *Euph. platyphylla* L.
Istr., Pen., Sic., Cors. — 2-5.



2573. *Euph. helioscopia* L.
Italia — 2-5.



2574. *Euph. pterococca* Brot.
Tosc., Puglie, Cal., isole — 2.



2575. *Euph. peplus* L.
Italia — 2-4.



2576. *Euphorbia falcata* L.
Italia — 2-4.



2577. *Euph. sulcata* De Lens
Piem. (rara) — 4.



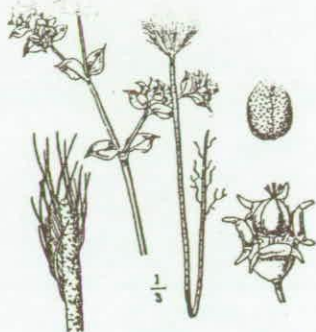
21

2581.
Pie.

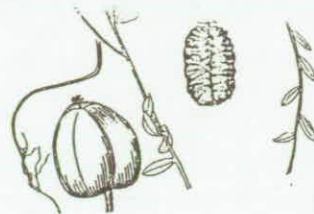
258.



2578. *Euph. exigua* L.
Italia — 2-4.



2579. *Euph. aleppica* L.
Lig., It. mer., Malta, Cors.



2580. *Euph. cernua* Coss. et Dur.



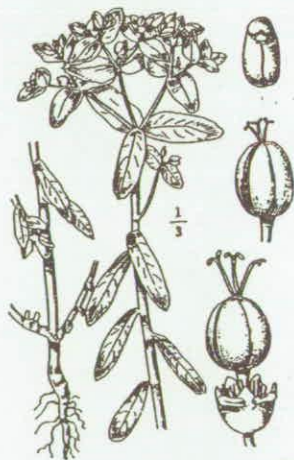
2581. *Euph. taurinensis* All.
Piem., Lig. occ., Nizz. — 4.



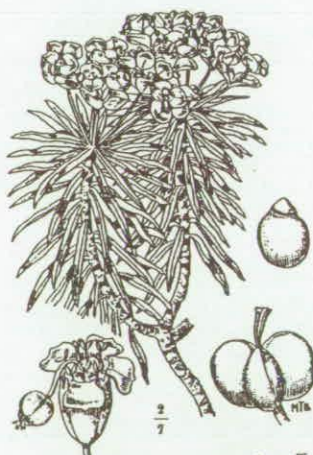
2582. *Euph. segetalis* L.
It. (escl. bor. p. p.) — 2.



2583. *Euph. terracina* L.
It. (escl. bor.) — 2 lit.



2584. *Euph. Lagascae* Spr.
Sard. (rara) — 2.



2585. *Euph. dendroides* L.
Costa occ., It. mer./ins. — 2.



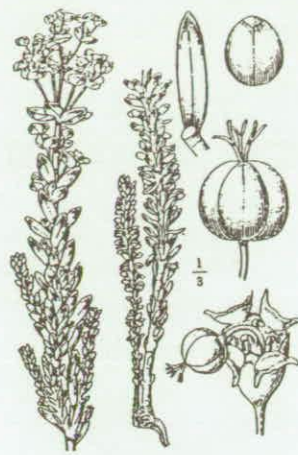
2586. *Euph. biumbellata* Poir.
Lig., Sic., Cors. (rara). — 2.



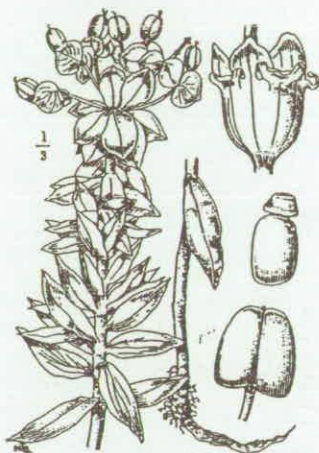
2587. *Euph. Pithyusa* L.
Lig., Livornese, isole — 2 lit.



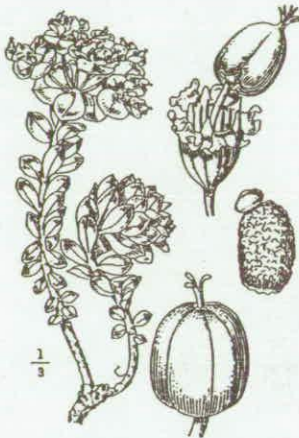
2587.¹ *v. Cupani* (Guss.)
Sic., Sard. — 2.



2588. *Euph. Paralias* L.
Italia — 2 e 3, lit.



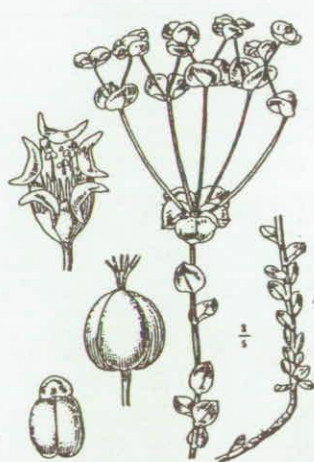
2589. *Euph. biglandulosa* Desf.
Cal., Sic., Malta — 2-5.



2590. *Euph. Myrsinites* L.
Istr., Pen., Sic., Cors. — 5-6.



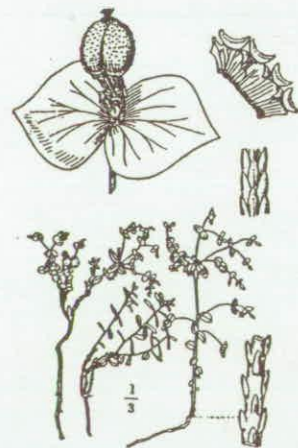
2591. *Euph. Seguieriana* Neck.
Istr. e Pen. — 2-5.



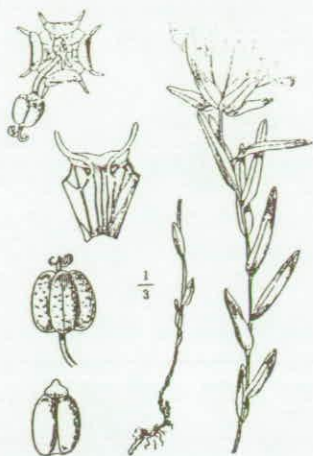
2592. *Euph. Barrelieri* Savi
Costa occ., Pugl., Cal. — 2 e 4.



2593. *Euphorbia Gayi* Salis
Corsica — 2-5.



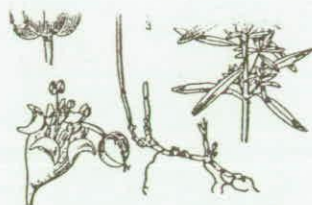
2593.¹ *v. Valliniana* (Belli)
Alpi Cozie (*v. Macra*) — 6-7.



2594. *Euph. variabilis* Ces.
Alpi trent., lomb., Mar. — 4-5.



2595. *Euph. Cyparissias* L.
It. pen. (rara al sud) — 2-7.



2596. *Euph. Esula* L.
It. bor., Tosc. — 2-5.



2597. *Euph. virgata* W. et K.
Triest., Goriz., Tosc. — 4.



2598. *Euph. serrata* L.
C. Tic., Alpi occ., Nap., Sard.,
Pantell. — 2 e 4.



2599. *Euph. amygdaloides* L.
Italia — 2-6



2600. *Euph. Characias* L.
It. (escl. bor. p. p.) — 2 e 3.



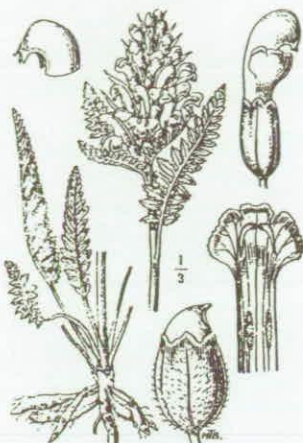
2601. *Andrachne telephioides* L.
Istr., Lig., Pugl., Bas., Sic.,
Malta — 2.



2602. *Chrozophora tinctoria* Raf.
It. (escl. bor. p. p.) — 2, rr. 4.



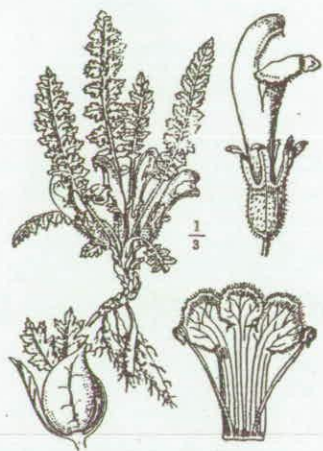
2988. *Pedicul. silvatica* L.
Alpi — 5-7.



2989. *Pedicul. comosa* L.
Alpi, App., Cors. — 4-7.



2990. *Pedicul. petiolaris* Ten.
Istr., App. centr. — 5-7.



2991. *Pedicul. acaulis* Scop.
Fiume, Alpi or. e lomb. — 4-7.



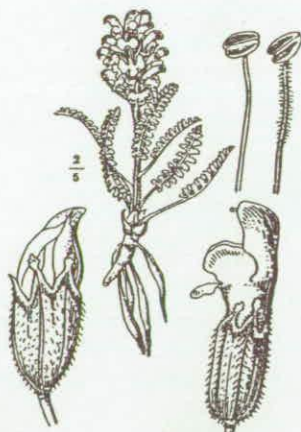
2992. *Pedicul. foliosa* L.
Istr., Alpi, App. — 5-7.



2993. *Pedicul. recutita* L.
Alpi — 5-7.



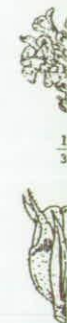
2994. *Pedicul. rosea* Wulf.
Alpi — 5-7.



2995. *Pedicul. Oederi* Vahl
Alpi — 7.



2996. *Orobanche ramosa* L.
Italia — 2-4.



2996.1



2996.2



3002.
Mera:



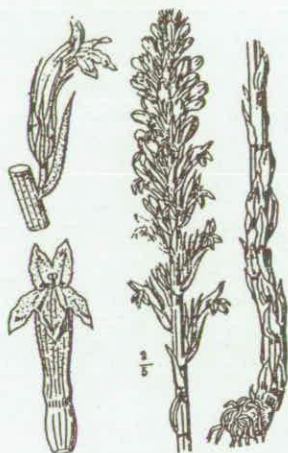
2996. *v. Muteli* (F. Schultz).
Italia — 2-4.



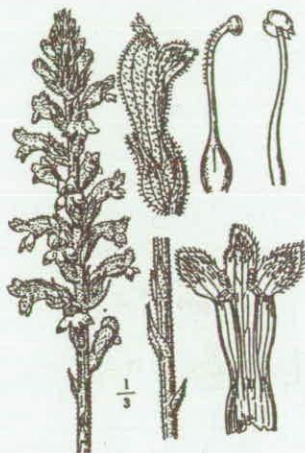
2997. *Orob. aegyptiaca* Pers.
Palermo (M. Gallo) — 2.



2998. *Orob. lavandulacea* Rchb.
Lig., Tosc., Basil., It. ins. — 2.



2999. *Orob. Schultzii* Mutel
v. *stricta* (Moris)
Sic., Eolie, Sard. — 2.



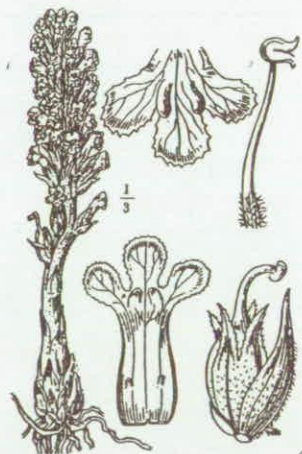
3000. *Orob. purpurea* Jacq.
It. pen., Cors., piccole isole — 2-4?



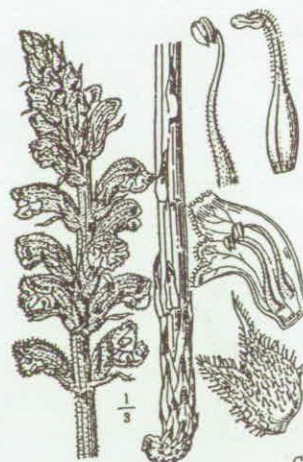
3001. *Orob. arenaria* Borkh.
It. bor., Firenze — 3-5.



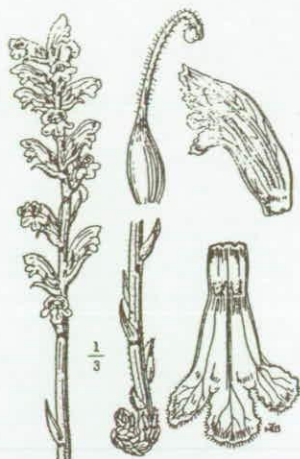
3002. *Orobancha cernua* Loeff.
Merano, Bas., Sic., Eolie, Malta,
Cors. — 2.



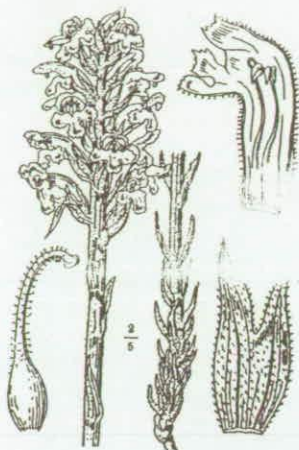
3003. *Orob. caerulea* Steph.
Friuli (scomparsa), Cal. — 2.



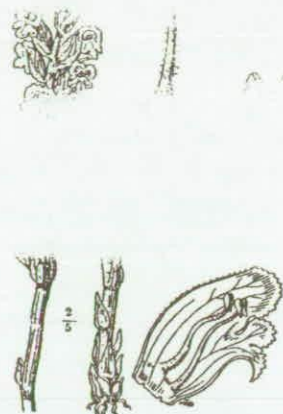
3004. *Orob. caryophyllacea* Sm.
It. (escl. Sard. e Cors.) — 2-4.



3005. *Orob. Teucrii* Hol.
Alpi, A. Apuane — 4.



3006. *Orob. lutea* Baum.
for. *rubens* (Wallr.)
It. pen. — 2-4.



3007. *Orob. gracilis* Sm.
It. pen., Sard., Cors., Elba — 2-5.



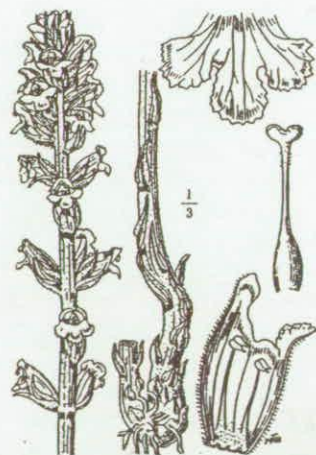
3008. *Orob. variegata* Wallr.
Italia — 2-4.



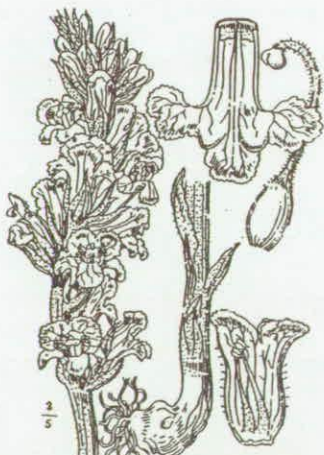
3009. *Orob. sanguinea* Presl
v. *crinita* (Viv.)
Napoli, Bas., It. ins. — 2.



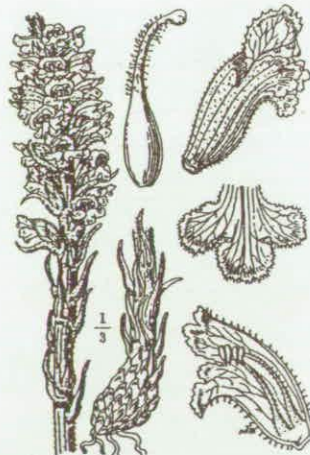
3010. *Orob. alba* Steph.
Istr., It. pen., Sic., Capri — 2-4.



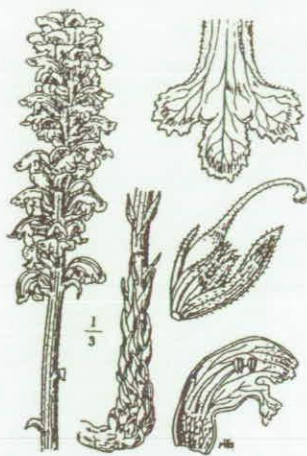
3011. *Orob. reticulata* Wallr.
Alpi, Abr., Cors. — 4-6.



3012. *Orob. crenata* Forsk.
Italia — 2-4.



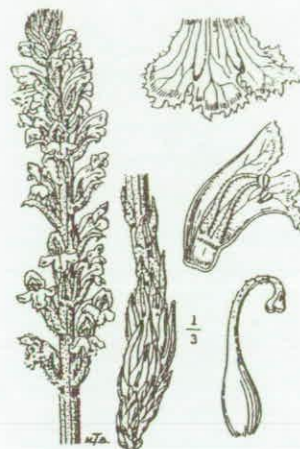
3013. *Orob. major* L.
Cherso, Alto Adige, Trent.,
A. Cozie — 4-5.



3014. *Orob. alsatica* Kirschl.
Istr., Comasco, Lig., Sic. — 2-4.



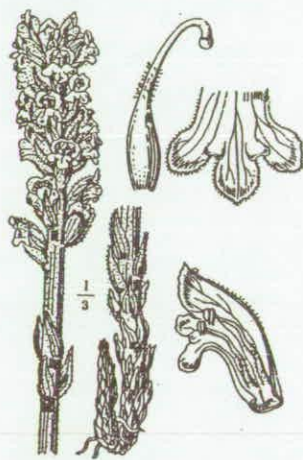
3015. *Orob. denudata* Moris
Sic.?, Sard. — 2-4.



3016. *Orob. flava* Mart.
Alpi or., Comasco — 4-5.



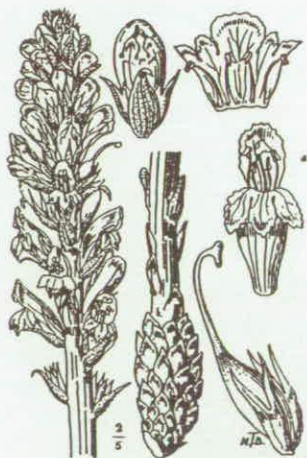
3017. *O. Salviae* F. Schultz
Alpi, App. bor. — 4-5.



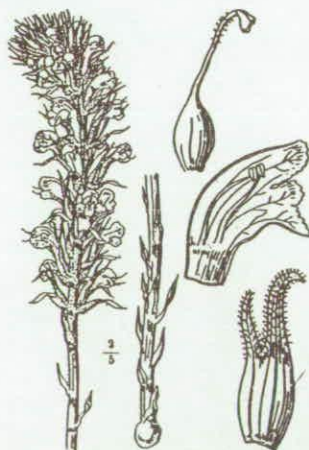
3018. *Orob. lucorum* A. Br.
It. bor., App. bor. ed umbro — 4-5.



3019. *Or. Rapum-Genistae* Thuill.
Italia — 4-5, rr. 3.



3019.¹ *v. rigens* (Lois.)
Sard., Cors. — 2 e 4.



3020. *Orob. amethystea* Thuill.
It. bor., Firenze, Sic., Sard.,
Cors. — 2 e 4.



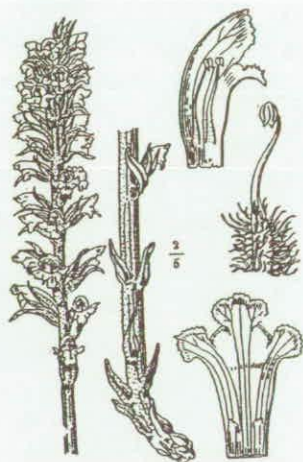
3021. *Orob. loricata* Rehb.
It. bor., centr., ins. — 2-4.



3022. *Orob. barbata* Poir
Italia — 2-4.



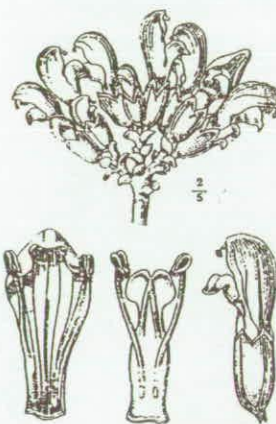
3023. *O. versicolor* F. Schultz
Tosc., Nap., isole — 2.



3025. *Orob. canescens* Presl
Nap., Basil., It. ins. — 2 e 4.



3026. *Lathraea squamaria* L.
Istr., It. pen., Sic. — 3-5.



3027. *Lathraea clandestina* L.
Tosc., Abr., Camp., Cal. — 2-5.



3028. *Catalpa bignonioides* Walt.
It. — 2-4, colt. (Am. bor.).



3029. *Tecoma radicans* Jaume
It. — 2-4, colt. (Am. bor.).



3030. *Ajuga acaulis* Brocchi
App. centr. e mer., Sic. — 4-5.

3036.
Istr

049 -

9676.

A SURVEY OF SURFACE CHARACTERISTICS OF SEEDS OF SCROPHULARIACEAE AND OROBANCHACEAE USING SCANNING ELECTRON MICROSCOPY¹

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&

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Abstract

Seed surface characteristics of 23 species in 11 genera of the Scrophulariaceae and two species in two genera of the Orobanchaceae from the southeastern United States were examined using scanning electron microscopy. All species exhibit a form of reticulation, and three general types are recognized: deeply reticulate, shallowly reticulate, and obscurely reticulate. The internal surface and the ridges of a reticulum may be ornamented or unornamented by either wax deposits or cell outgrowths. In those genera with several species, seed surface characteristics have systematic value.

This study is part of a research effort on the biology of root parasites of the southeastern United States to determine their potential danger as pathogens of commercial forest trees. It sought to characterize the morphology of seeds of 25 species of Scrophulariaceae and Orobanchaceae by scanning electron microscopy. The seeds are small, ranging from 440 to 309,000 per gram, which makes them ideal for SEM study. Such information is useful in the identification of the parasites and has systematic value.

Twenty-three of the 25 species of Scrophulariaceae investigated are hemiparasites. The Orobanchaceae, closely related to the Scrophulariaceae, are represented by two genera of holoparasites.

The value of SEM studies in pollen is well known, but little work has been done on seed surfaces (Tomb, 1974).

Chuang & Heckard (1972) published the first paper on the structure of seeds of a parasitic angiosperm using SEM. They worked on *Cordylanthus*, a root parasite of the Scrophulariaceae closely allied with some of the genera included in this study. Other work on the seeds of parasitic Scrophulariaceae is well summarized by Kuijt (1969) who also presents detailed drawings of seeds of this alliance.

Unfortunately, the terminology needed to adequately describe seed surface characters has not yet been evolved. Therefore, the general terminology used by Chuang & Heckard (1972) is employed here.

Material and Methods

Seeds were collected from various populations throughout the southeastern

SCRO:

Agalini

A. jasc

A. lini

A. obu

A. puri

A. setae

A. tene

A. tena

A. virg

A. virg

A. laeri

A. pedi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

A. virgi

1. Received for publication: June 21, 1976.

The authors thank Gary W. Smith, Dr Floyd G. Manwiller, and Charles M. Stangle for preparing seeds and taking scanning electron micrographs.

TABLE 1 — COLLECTION DATA FOR SPECIES USED FOR SEM STUDY

NAME	LOCALITY	COLLECTOR
SCROPHULARIACEAE		
<i>Agalinis aphylla</i> (Nutt.) Raf.	Savana, near junction of U.S. 31 and Ala. 47, Baldwin County, Alabama	Rich, 226
<i>A. fasciculata</i> (Ell.) Raf.	Dry oak site, Phillips County, Arkansas	No voucher
<i>A. linifolia</i> (Nutt.) Britt.	Roadside ditch, ca. 4 miles north of Calhoun County line, Jackson County, Florida	Rich, 230
<i>A. obtusifolia</i> Raf.	Pine forest at Pine Belt Airport, Jones County, Mississippi	Rich, 206
<i>A. purpurea</i> (L.) Penn.	Pine Plantation ca. 4 miles west of Raleigh, Mississippi	Rich, 203
<i>A. setacea</i> (J. W. Gmelin.) Raf.	Intersection I-20 and U.S. 1, Aiken County, South Carolina	Rich, 312
<i>A. tenella</i> Penn.	Pine plantation near intersection I-20 and U.S. 1, Aiken County, South Carolina	Rich, 313
<i>A. tenuifolia</i> (Vahl.) Raf.	Pine plantation 5 miles north of Sampson County line, Rankin County, Mississippi	Rich, 202
<i>A. virgata</i> Raf.	Sandhill north of Aiken, Aiken County, South Carolina	Rich, 311
<i>Aureolaria flava</i> (L.) Farw.	Stream bank, 2 miles north of Torreya State Park, Liberty County, Florida	Rich, 256
<i>A. laevigata</i> Raf.	Forest opening, Mountain Lake Biological Station, Giles County, Virginia	No voucher
<i>A. pedicularia</i> (L.) Raf.	Sandhill, ca 5 miles west of Darlington County line, Chesterfield County, South Carolina	Musselman and Rich, 4869
<i>A. virginica</i> (L.) Penn.	Oak forest, Crumps Bottom, Summers County, West Virginia	Musselman, 4892
<i>Buchnera americana</i> L.	Roadside, Fla. Hwy. 9 at Oklawaha Canal, Putnam County, Florida	Musselman, 4692
	Meadow, 3 miles west of junction U.S. 1 and Fla. 9, Floyd County, Virginia	Musselman, 4864
	Fla. Hwy.	Rich, 199
<i>glauca</i> Bartr.	Margin of swamp, just south of Angie on Hwy. 21 Washington Parish, Louisiana	Rich, 209
<i>Melampyrum lineare</i> Desr.	Rock outcropping, Wind Rock Overlook, Blue Ridge Parkway, Avery County, North Carolina. (By permit)	No voucher
<i>Pedicularis canadensis</i> L.	Deciduous forest, fire tower near Mountain Lake Geological Station, Giles County, Virginia	Musselman, 4865

TABLE 1 (Cont'd)

NAME	LOCALITY	COLLECTOR
SCROPHULARIACEAE		
<i>Schwalbea americana</i> L.	Savanna, junction of S.C. Hwys. 41 and 99, Berkeley County, South Carolina	Musselman and Rich. 4686
<i>Seymeria cassioides</i> (Walter) Blake	Sandy flatwoods soil, stand of young pines with no overstory, Gulf County, Florida	No voucher
<i>S. pectinata</i> Pursh	Sandy scrub, Mill Dam Recreation area, Ocala National Forest, Marion County, Florida	No voucher
<i>Striga asiatica</i> (L.) Kuntz (= <i>S. lutea</i> Lour.)	Devitalized seeds provided by U.S.D.A. Witchweed Laboratory, Whiteville, North Carolina	No voucher
OROBANCHACEAE		
<i>Conopholis americana</i> (L.) Walp.	Deciduous forest, Crumps Bottom, Summers County, West Virginia	Musselman, 4866
<i>Epifagus virginiana</i> (L.) Bart.	Roadside, Great Dismal Swamp, City of Suffolk, Virginia	Musselman, 4904

United States and immediately sent to the laboratory where they were stored at 5C in sealed containers until ready for examination. Representative populations and voucher specimens are noted in Table 1. Voucher specimens are deposited in the Old Dominion University (ODU) herbarium. Nomenclature of Radford et al. (1968) has been followed. Seeds were selected for uniformity from populations using a binocular microscope.

Seeds were mounted on pin-type stubs using double-stick tape or conductive silver paint, coated with 200 angstroms palladium gold (40%-60%) in a Denton vacuum evaporator, model DV 502 and recoated to eliminate charging of the specimen. An Advanced Metals Re-

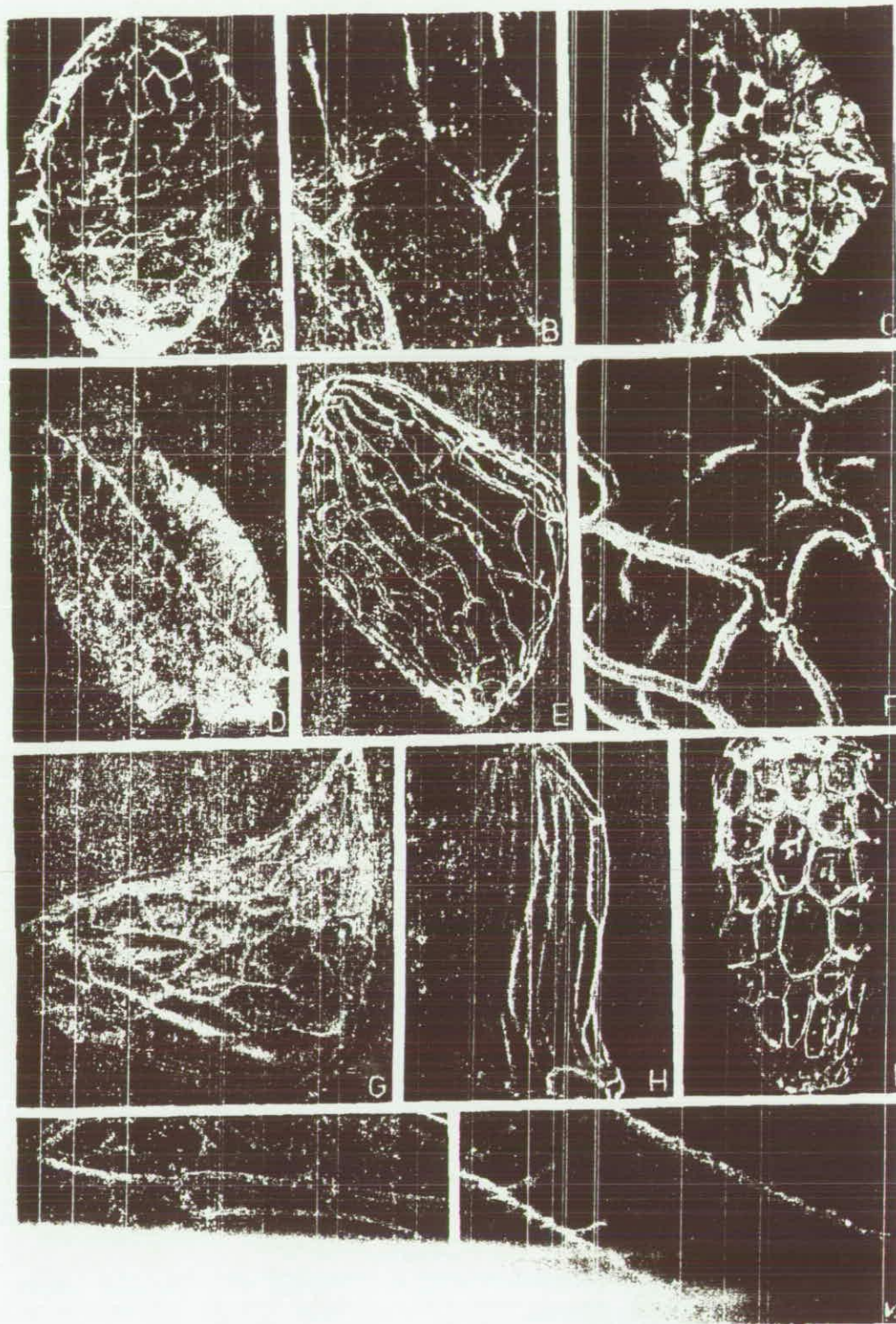
search Corporation 900 scanning electron microscope was used to examine the seeds. A working distance of 12 mm was used. Photographs were taken with an Oscilloscope camera, series 125, f 1.4, 1:1 magnification.

Observations

AGALINIS — It is the largest genus included in this study. Nine species were examined. Relative to seed surface characteristics, these fall into two groups illustrated by *A. tenella* (Fig. 1E, F) and *A. aphylla* (Fig. 1G, J). In the former, the surface of the reticulum is not ornamented (Fig. 1F) although shallow papillae are present, perhaps a result of underlying cells. In *A. aphylla* and

Striga pedicularis
note deep
of seed:

A. Buchnera



CASTILLEJA COCCINEA—The surface of the reticulum ruptures, perhaps as a result of differential growth rates, giving the appearance of shattered glass (Fig. 11). At first it was thought this was an artifact but careful examination of fresh material with the light microscope confirmed the presence of ruptures. This is also involved in some

MELAMPYRUM LINEARE.—This is the smoothest of all seeds examined (Fig. 2G). The surface and ridges of the reticula lack any ornamentation (Fig. 2H). According to Arekal (1963)

2. Remarkably, Tiagi records *Conopholis americana* as growing on *Quercus petraea*, one of the white oaks, in the University Botanical Garden in Copenhagen. In nature, it has been noted repeatedly as being entirely restricted to members of the red oak group of the genus *Quercus*.

Fig. 4A-K—A, B. *Conopholis americana*. A. Roughened portion of seed indicates point of contact with another seed in developing fruit. $\times 93$. B. Wrinkled surface represents sclerified endodermis of integument. $\times 1010$. C. *Dasistoma macrophylla*, seed has a curved, winged testa. D. E. *S. solida*, seed fine network of wax depositions within each reticulum. $\times 48$. D, E. *S. solida* seed in surface view. $\times 210$. E. Outer cells of integument become thickened on top of cells. $\times 1050$. F. *Macranthera flammula*, seed testa is irregularly striate. $\times 41$. G, H. *Macranthera flammula* seed in surface view. $\times 210$. I. Individual reticula represent sclerified outer cells of integument. $\times 1050$. J. *Seymeria* seed in surface view. $\times 52$. K. *Seymeria* seed in surface view of thickenings within reticula. $\times 1050$.

the surface layer of the testa develops by the thickening of the radial and longitudinal walls of the cells of the epidermis of the integument followed by a collapse of these same cells.

PEDICULARIS CANADENSIS — The seeds are round in cross section and uniformly reticulate (Fig. 2I). The reticula are relatively small and quite shallow. Under higher magnification (not illustrated) the surface of the reticula is finely rugose.

SCHWALBEA AMERICANA — The testa is an elongate and loose-fitting structure with a very simple, uniformly reticulate surface (Fig. 3C, D).

SEYMERIA — *S. pectinata* (Fig. 3B) and *S. cassioides* (Fig. 2J) are very different in shape and ornamentation. *S. pectinata* has a prominent crest on its margin and large, deep, reticula with only weak surface thickenings (Fig. 3B), whereas *S. cassioides* lacks a conspicuous crest, has shallow reticula (Fig. 2J) and a prominent network of thickenings on the reticula (Fig. 2K).

STRIGA ASIATICA — The surface of the seed is covered with uniform, elongate reticula which slightly spiral around the body of the seed (Fig. 3A). Superficially, the details of the reticula in this species resemble those of *Buchnera americana* (cf., Figs. 3E and 1K). However, the papillae of the reticula ridges and surfaces are different. Those of *Striga* are more angular whereas those of *Buchnera* are rounded.

Discussion

All the species studied have reticulate surfaces. The characteristics of the

seed surface are as follows, in

cana (Fig. 2A) and *Melampyrum lineare* (Fig. 2G) in which the walls of the outer layer of the integument become exceptionally thick and *Dasistoma macrophylla* (Fig. 2C) with very shallow reticula and narrow, wavy ridges. The surfaces of the reticula may lack ornamentation (e.g., *Schwalbea americana*, Fig. 3C; and *Epifagus virginiana*, Fig. 2D) or have a network composed of either wax deposits (*Aureolaria pedicularia*, Fig. 1B) or actual wall outgrowths (*Buchnera americana*, Fig. 1K; and *Striga asiatica*, Fig. 3E). Species with well-developed crests may have deep (e.g., *Aureolaria flava*, Fig. 1C; and *Macranthera flammea*, Fig. 2F) or shallow (e.g., *Dasistoma macrophylla*, Fig. 2C, and *Seymeria pectinata*, Fig. 3B) reticulations on the crest.

In their studies of the species of *Cordylanthus*, Chuang & Heckard (1972) showed that the surface pattern is due to enlarged epidermal cells of the integument. No doubt many of the species included in this study exhibit a similar pattern of reticulum development, but this must be substantiated by anatomical work. Likewise, the surface feature of the reticula cannot be correctly interpreted without developmental studies. In some species, these thickenings appear to be wax depositions (species of *Aureolaria*; see also Chuang & Heckard, 1972). In *Buchnera americana* and *Striga asiatica*, the thickenings are actual cell outgrowths as revealed by anatomical studies (Rich & Musselman, unpublished).

Chuang & Heckard (1972) found seed surface characteristics to be of systematic value in the genus *Cordylanthus*. While the present study did not include in-depth survey of any one genus, some features of systematic value were found. The species of *Agalinis* with thickenings on the surface of the reticula (Fig. 1G, J)

are related to the section *Purpureae*. Likewise, this study indicates a biological dissimilarity between *Seymeria pectinata* and *S. cassioides* (Fig. 2J). The prominent crest on *S. pectinata* is reticulate unlike *S. cassioides* which places these species in different places. Finally, the surface of *Striga asiatica* is reticulate unlike *Striga pectinatis*;

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MUSSELMAN & MANN - SURFACE CHARACTERISTICS OF SEEDS

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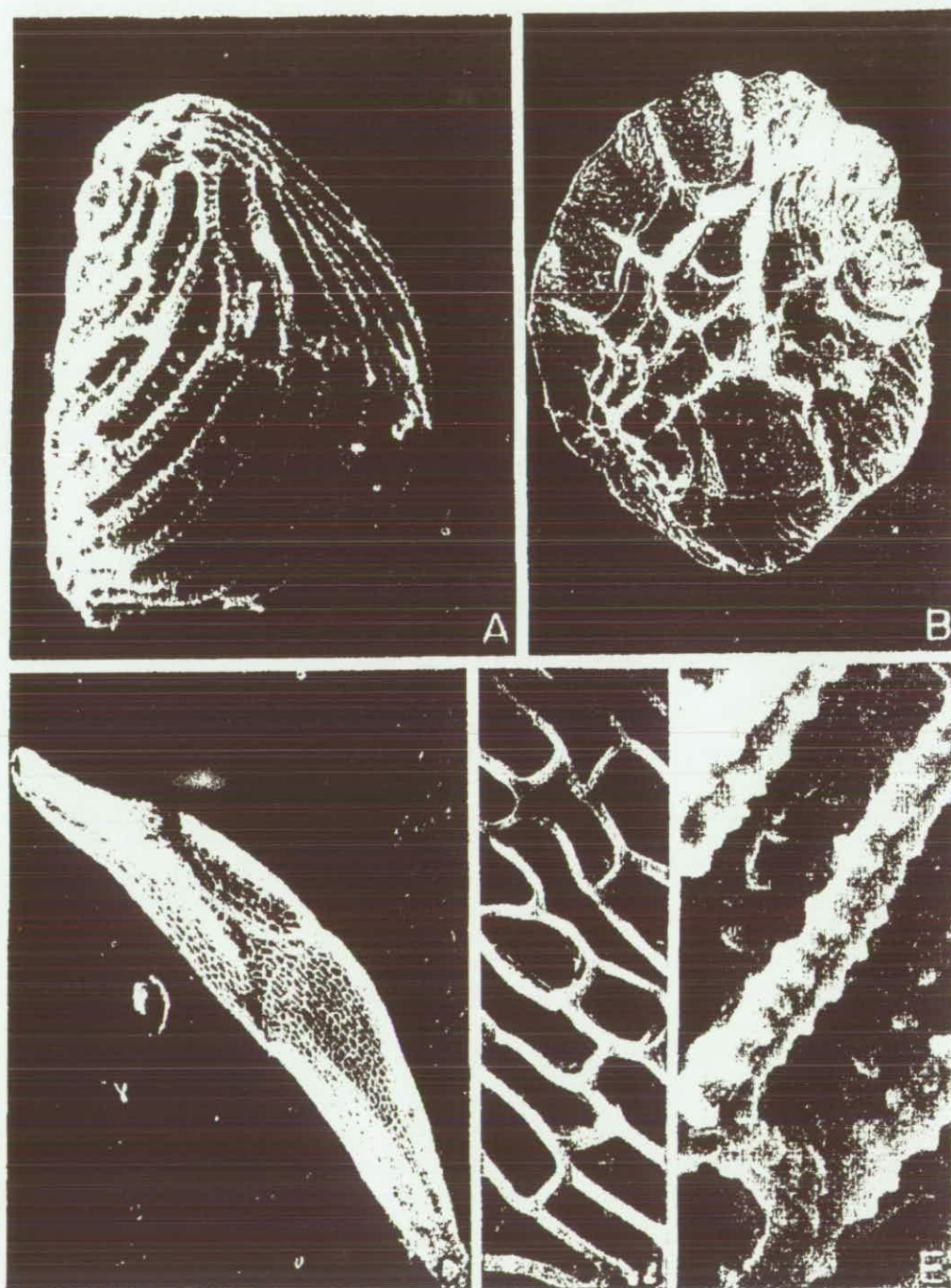


Fig. 3A-E - A. *Stipa asiatica*, entire seed. 468. B. *Securaria pectinata* showing prominent reticula. 120. C, D. *Schwalbea americana*. C. Seed in surface view. 48. D. High magnification view of characteristic crested projections. 1860.

Pennell, 1935) and the three species in the section *Aureolaria* differ in both the amount and the morphology of wax deposition (Fig. 1A, B, C).

While the surface features of seeds may provide information of systematic value, it is very difficult, at present, to interpret the adaptive value for the various patterns revealed in this and other studies. In general, Pennell (1935) has suggested that the smaller seeds with their honeycombed testae are adapted for wind dispersal and the larger, heavier seeds (*Melampyrum lineare* and *Pedicularis canadensis*) are transported by animal vectors. It will be noted that the latter two species as well as *Conopholis americana* (Fig. 3A) have relatively smooth surfaces. In *Conopholis*, however, the unit of diaspore is almost certainly the fleshy fruit. As to the reticulate seeds, Kuijt (1969) has suggested that the reticula are adaptations for water dispersal, by trapping air and aiding in buoyancy. The almost total lack of information on how these seeds behave in nature limits any mean-

ingful interpretation of the adaptive value of seed ornamentation in this group. Almost all of the species of parasitic Scrophulariaceae have stiff, erect fruiting stalks which shake seeds from the capsule. Likewise, the habitat of many of these root parasites (*Aureolaria pedicularia*, *Seymeria cassioides*) on dry, coarse sand would seem to preclude any movement by water over a long distance. The situation in *Conopholis* of the Orobanchaceae has already been referred to; the seeds of *Epifagus* alone are dispersed by water. The fruit forms a sort of "splash cup" where a drop of water will spill the extremely small, light seeds (309,000 per gram; Mann & Musselman, unpublished).

A true understanding of the role of the seed coat in seedling biology must take into account that all of these species are, as far as is known, obligate root parasites. Perhaps the small seed size is an adaptation to filtering through vegetation and litter so as to be positioned as close as possible to a host.

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