

Morphology of fruits, seeds and embryos of Argentinian *Capparis* L. (Capparaceae)

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Embryos, seeds and fruits of four species of *Capparis* L. (Capparaceae) from Argentina are described in this paper: *C. flexuosa* (L.) L. *sensu lato*, *C. retusa* Griseb., *C. speciosa* Griseb. and *C. tweediana* Eichl. Chlorophyllous embryos are found in *C. flexuosa* and *C. retusa*, species with thin seed coats, dehiscent siliques, and somewhat fleshy red endocarps. Nonchlorophyllous embryos are found in the berry-fruited *C. speciosa* and *C. tweediana*, the former with leathery indehiscent fruit wall, the latter with thin-walled dehiscent berries with massive fleshy pulp. The pulp is permeated by seed coat hairs in *C. tweediana*. The embryos of *C. flexuosa*, *C. retusa* and *C. tweediana* belong to the 'Axile Division, Foliate Subdivision, and Folded Type' of the classification devised by A. C. Martin in 1946. Some features of the embryo of *C. speciosa* (which are not considered in Martin's classification), support a new subdivision (Massive) and a new morphological type (Unequal cotyledons), characterized by profound anisocotily, globose shape of the major cotyledon, presence of suberized cells and an undeveloped radicle. Anatomical studies of embryos and seedlings confirm the anisocotily. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, 145, 209–218.

ADDITIONAL KEYWORDS: anisocotily – chlorophyllous embryos – dehiscence – germination – seed coat.

INTRODUCTION

Capparis L. (Capparaceae) is a pantropical genus with c. 200 species (Iltis & Ruiz-Zapata, 1998), seven of which are known from Argentina: *C. atamisquea* Kuntze, *C. flexuosa* (L.) L. *sensu lato*, *C. humilis* Hassl., *C. retusa* Griseb., *C. salicifolia* Griseb., *C. speciosa* Griseb. and *C. tweediana* Eichler.

The New World species of *Capparis* have been the object of several taxonomical and floristic studies (Eichler, 1865; Fawcett & Rendle, 1914; Dugand, 1941; Allen, 1948; Gómez, 1953; Iltis, 1965, 1978, 2001; Legname, 1972; Troncoso, 1987; Zapater, 1992; Iltis *et al.*, 1996; Iltis & Ruiz-Zapata, 1998). Several of these contain detailed descriptions of fruits, seeds and embryos, but none, with the exception of Iltis (2001) (and then only to *C. flexuosa* *s.l.*), refer specifically to any Argentinian species. Except for Iltis (1965), who described and illustrated in detail the seed coat and embryo

structure of *C. pachaca* H.B.K., there are only a handful of studies that deal with the seed anatomy and morphology of these plants (Parisca, 1983; Franceschini, 2002).

Parisca (1983) reported that the genus shows great uniformity in seed morphology: a kidney-shaped, curved embryo with leafy cotyledons which are unequal in size and fold into themselves, enveloping the embryonic axis (i.e. the radicle). On the other hand, she described for *C. coccolobifolia* and *C. flexuosa* a different embryonic model: straight with thick cotyledons and a slightly curved axis. Troncoso (1987) briefly described the embryo of *C. flexuosa*, pointing out its folded (obvolute) cotyledons and long radicle. While Franceschini (2002) mentions the occurrence of marked anisocotily in *C. speciosa*, this interesting character has not until now been confirmed by anatomical studies.

The following arborescent species of *Capparis* native to north-eastern Argentina are discussed in this paper: *C. flexuosa* (L.) L., *s.l.*, *C. retusa* Griseb. [both sect. *Cynophalla* (DC.) Eichler], *C. speciosa* Griseb. [sect. *Capparidastrum* (DC.) Eichler] and

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C. tweediana Eichl. [sect. *Colicodendron* (DC.) Eichler]. In addition to our morphological studies of the fruits, seeds and embryos of these species, the structure of the seed coat of *C. tweediana* is analysed to explain the nature of the fine hairs that permeate the fleshy fruit pulp, and embryo and seedling anatomy and germination are described to clarify the complex and unique morphology of the embryo of *C. speciosa*, confirming its anisocotily.

MATERIAL AND METHODS

Herbarium specimens, fresh material and material fixed in FAA were studied. All the specimens are conserved in CTES. The following taxa were examined.

Capparis flexuosa (sect. *Cynophalla*)

Many 19th-century authors, including Eichler (1865), called *C. flexuosa* s.l. *C. cynophallophora*, and vice versa, causing 'gargantuan nomenclatorial confusion' (Iltis & Ruiz-Zapata, 1998).

ARGENTINA. Prov. Chaco: Department 1° de Mayo, Colonia Benítez, ii.1944, Schulz 4185; idem, Colonia San Miguel, borde del río Guaycurú, xii.1930, Schulz 428. Prov. Corrientes: Department Capital, Molina Punta, 6.iii.1997, De Pompert y Tressens 41; idem, 24.i.1989, Franceschini 41 A y B; idem, 22.i.1972, Quarín 349. Department Itatí, Itatí, 23.i.1972, Krapovickas y Cristóbal 20882. Department Berón de Astrada, 46 km W de Itá Ibaté, Valencia, 15.i.1977, Schinini 13989. Department Mercedes, Lag. Iberá, Paso Picada, Reserva Natural Prov. del Iberá, 24/28.ii.1989, Tressens *et al.* 3556. Department San Martín, Ea. San Agustín, 12 km NE de C. Pellegrini, 18.ii.1976, Krapovickas *et al.* 29450.

Capparis retusa (sect. *Cynophalla*)

ARGENTINA. Prov. Corrientes: Department Capital, Molina Punta, 6.iii.1997, Franceschini y Tressens 2 A y B; ruta 12, 20 km NW de Corrientes, Granja Yatay, 22.i.1976, Schinini 12500. Department San Cosme, Paso de la Patria, 7.iii.1971, Benítez 38; desvío de ruta 12, por camino de tierra a Paso de la Patria, 16.ii.1993, Cabral 602. Department Itatí, ruta nac. 12, 47 km E de Itatí, Ea. Santa Catalina, 26.ii.1977, Ahumada *et al.* 725; ruta 12, 6 km de Itatí, 16.iv.1972, Schinini y Mroginski 4465; Toro Jhú, 8 km S de ruta 12, a 40 km E del desvío a Itatí, 16.ii.1983, Schinini y Carnevali 23257. Department Empedrado, Empedrado, 3.iii.1950, Schwarz 9943; ayo. González, 6.iii.1950, Schwarz 10025. Department San Luis del Palmar, 25 km S de S. L. del Palmar, ruta prov. 6, 27.ii.1972, Quarín *et al.* 535. Department Goya, Goya, camino frente a Sociedad Rural, 700 m E, 19.ii.1970,

Carnevali 4688. Department Esquina, 4 km S de ruta 126, camino de Tres Bocas a Paso Yunque, 13.iii.1975, Krapovickas *et al.* 27662; Colonia Libertador, ayo. Barrancas, 15.iii.1975, Krapovickas *et al.* 27815. Prov. Formosa: Department Pilcomayo, Puente Inglés, ruta 11, 14.ii.1968, Krapovickas *et al.* 13835.

Capparis speciosa (sect. *Capparidastrum*)

ARGENTINA. Prov. Corrientes: Department Capital, Molina Punta, 6.iii.1997, Franceschini y Tressens 1 A y B; ruta 12, 20 km de Corrientes, 20.iii.1975, Arbo *et al.* 759; Molina Punta, 13.xii.1970, Krapovickas y Cristóbal 17279; idem, 11.xii.1976, Martínez Crovetto y Schinini 10641; idem, 3.i.1976, Schinini y Martínez Crovetto 12298; Perichón, 14.xii.1974, Krapovickas 27106. Prov. Salta: Department Santa Ana, 54 km NE de J.V. González, camino a Puerta Blanca, 22.xi.1994, Krapovickas y Cristóbal 46289.

Capparis tweediana (sect. *Quadrella*)

ARGENTINA. Prov. Formosa: Department Maticos, Ing. Juárez, 20.xi.1978, Renvoize 3549. Department Patiño, Gral. Güemes, 11.i.1999, Franceschini 18 A y B. Prov. Chaco: Department Comandante Fernández, El Toba, 8.xi.1999, Chifa 2963; Napenay, 29.xii.1970, Krapovickas y Cristóbal 17293. Department 12 de Octubre, entre Villa Angela y Pinedo, 14.i.1949, Ragonese y Castiglioni 6874. Department 1° de Mayo, Colonia Benítez, xi.1934, Schulz 2484; idem, 13.xii.1942, Schulz 3713. Department Gral. Güemes, Paraje Costa Rica, Proyecto Reserva Ecológica APROMA, 5 km E de 4 de Febrero, 45 m s.n.m., 26.xi.1996, Krapovickas *et al.* 46822 A y B. Prov. Corrientes: Department Capital, Corrientes, cultivada, 3.ii.1999, Franceschini 18.

Serial cross-sections and longitudinal sections of the embryos were made in order to interpret the morphology and relative position of the cotyledons to the embryonic axis. Anatomical studies of embryos and seedlings of *C. speciosa* and analysis of germination were made by placing the seeds on filter paper and cotton in transparent plastic boxes. Development of seedlings was also observed in the field. Serial sections of embryos and cotyledons were obtained with a rotary microtome, following dehydration in a tertiary butyl alcohol series and embedding in paraffin. Sections varied from 10 to 15 µm, were stained with fast green-safranin (Johansen, 1940) and mounted in Canada Balsam. Descriptions and observations were made with a stereomicroscope (Wild M5) and a binocular microscope (Wild M20), and the drawings with their respective camera lucidas. Conventional symbols are used for the diagrams (Metcalfe & Chalk, 1950).

RESULTS

MORPHOLOGICAL DESCRIPTIONS

Fruits

Three types of fruit were found among the studied species: fleshy to dryish dehiscent siliques in *C. flexuosa* and *C. retusa*, dehiscent fleshy berries in *C. tweediana* and indehiscent fleshy berries in *C. speciosa* (Fig. 1).

In *C. flexuosa* and *C. retusa* (both sect. *Cynophalla*), the siliques are characteristically bivalvate, more than five times long as wide, more or less strongly torulose, with the exocarp leathery and greenish-yellow when ripe, and the endocarp fleshy and bright to dark red. In *C. flexuosa* they are 8–35 cm long, with gynophores 4–7 cm long, and contain 3–24 (32) seeds. In *C. retusa* they are 2.2–13 cm long, with gynophores 1.7–4.5 cm long, and contain 1–12 seeds. In both species the siliques open first along one of the sutures and roll up simultaneously over the external face of the carpel, exposing the brilliant red endocarp and embedded snow-white seeds. Later on, the seeds hang free on the funicles, eventually becoming detached; the carpels finally separate along the other suture and unroll. The sutures remain, forming a thin replum (Fig. 2).

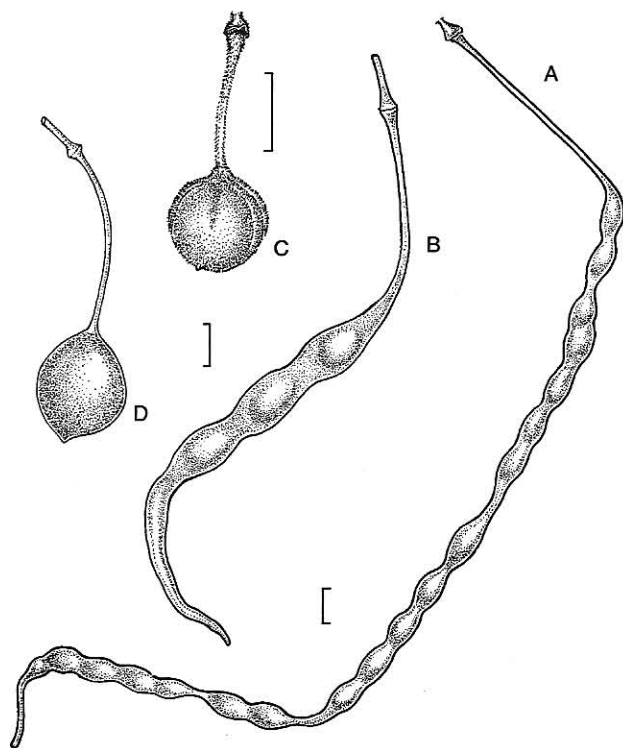


Figure 1. Fruit types of *Capparis*. A, *C. flexuosa*. B, *C. retusa*. C, *C. tweediana*. D, *C. speciosa*. Scale bars = 10 mm.

The berries of *C. tweediana* and *C. speciosa* are pendulous, subglobose to globose and fleshy. In *C. tweediana* they are globose and slightly umbonate at apex, 1–2 cm in diameter, densely covered by rough stellate yellowish hairs, and borne on a gynophore 2–5 cm long. When ripe they open along the 2–4 sutures, with the orange pulp and 3–12 seeds separating from the valves, and fall to the ground. In *C. speciosa* they are glabrous, indehiscent, 2.4–5 cm in diameter, borne on a gynophore 3.5–4.5 cm long. When ripe the pericarp is thick but flexible, greenish and shiny on the outside, with a dark yellow pulp and 4–8 seeds. The fruits' indehiscence, together with their fragrance, suggests dispersal by animals eating a whole fruit at a time.

Seeds

All the species studied have exalbuminous seeds, i.e. lacking endosperm. In *C. flexuosa* and *C. retusa* the seeds are ellipsoid and arillate (dimensions in mm, length × width × thickness), 8–14 × 5–8 × 4–6. The aril

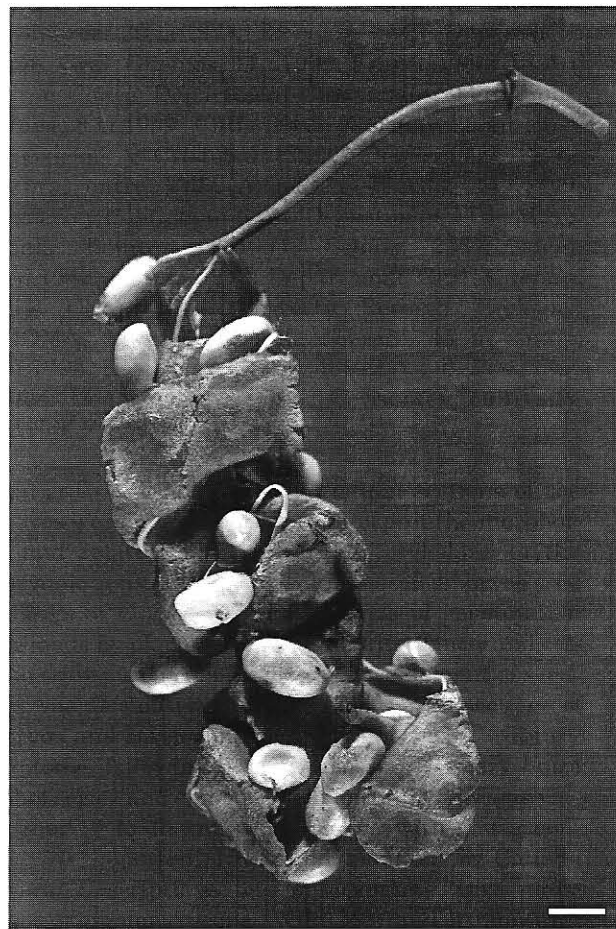


Figure 2. *Capparis flexuosa*. Dehiscent capsule with exposed seeds. Scale bar = 12 mm.

is white and oily, 0.22–0.42 mm thick, and the coat is thin and chartaceous when dry, 0.10 mm thick, ochre coloured and glabrous (Fig. 3A, B). In *C. tweediana* the seeds are somewhat compressed, kidney-shaped, 7×6 – 6.5×4 . In *C. speciosa* they are subglobose, generally with one or more flat faces where they are in contact with other seeds, 6 – 11×8 – 12×6 – 10 (Fig. 3C–E). In both *C. tweediana* and *C. speciosa* they are exarillate with a coriaceous coat. In *C. tweediana* the coat is white-yellow, 0.21 mm thick, covered with many slender unbranched hairs that are short and of unequal (0.23–0.47 mm) length (Fig. 3D). In *C. speciosa* the coat is snow white, 0.14–0.20 mm thick, with a fibrous surface.

Embryo

The colour and shape of the embryo, the size, shape, consistency and position of the cotyledons, and the direction of the axis allow the recognition of three types.

Type 1: C. flexuosa and *C. retusa* (Fig. 4). Embryo ellipsoid, straight, glabrous, chlorophyllous and olive-green, 8 – 13×5 – 6×5 . Cotyledons flat-convex, thick, fleshy, obovulate, asymmetric, with the narrower semilamina in acroscopic position and the wider semilamina covering all or most of the embryonic axis. Axis 2.5–3.5 mm long, straight or slightly curved, with the root apex enfolded except for the very tip.

Type 2: C. tweediana (Fig. 5). Embryo ellipsoid, curved, glabrous, nonchlorophyllous and snow-white, 7×6 – 6.5×4 . Cotyledons foliaceous, asymmetrical, with one cotyledon involute, the other convolute; they embrace each other halfway, with half of each one inside the other's fold. Axis 2–3 mm long, curved, with the root apex uncovered.

Type 3: C. speciosa (Figs 6, 7). Embryo subglobose to globose, glabrous, nonchlorophyllous and white-ivory. The root apex shows itself as a small dark yellow

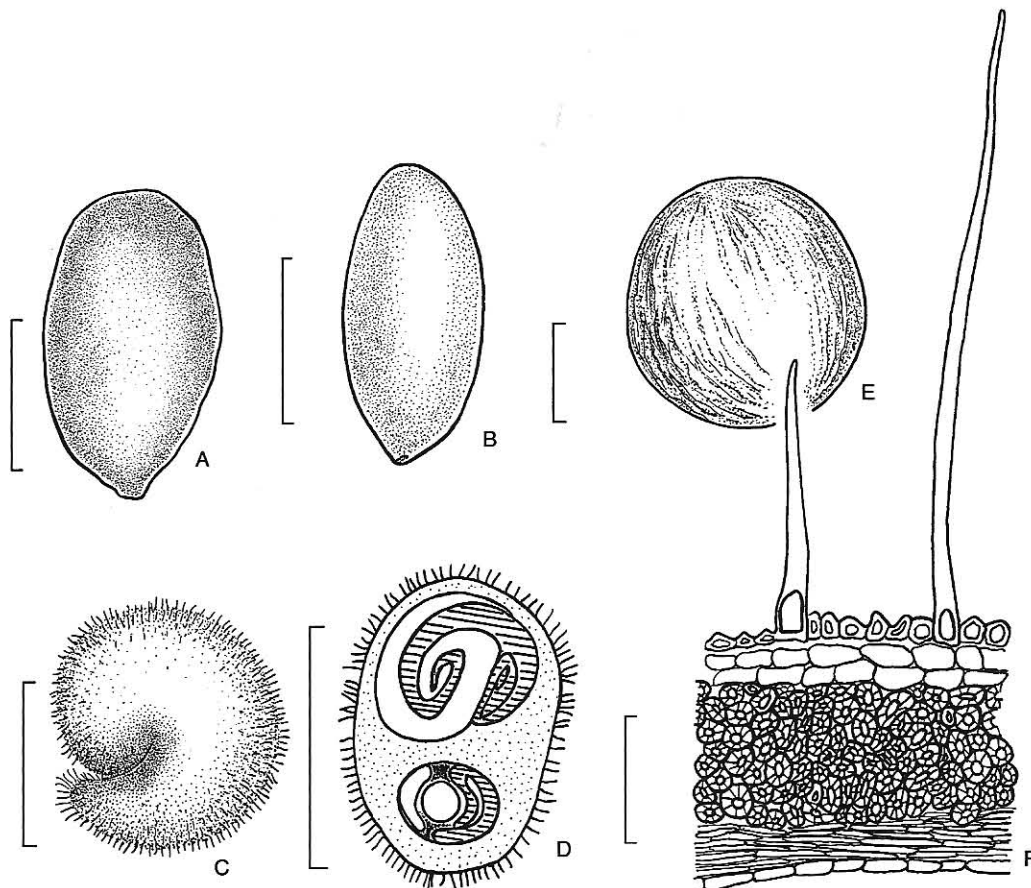


Figure 3. Seeds of *Capparis*. A, *C. flexuosa*. B, *C. retusa*. C–E, *C. tweediana*. C, general view of the seed. D, longitudinal section of seed showing the pulp permeated by hairs of the coat. E, *C. speciosa*. F, detail of the hairs of *C. tweediana*. Scale bars = 5 mm in A–E; 0.1 mm in F.

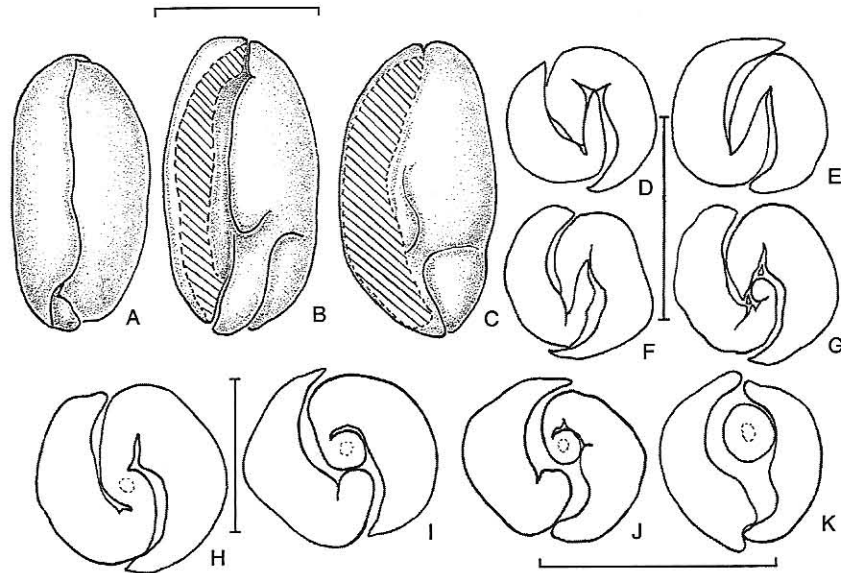


Figure 4. Embryos of *C. flexuosa* and *C. retusa*. A, general view of *C. flexuosa*. B, C, general view of *C. flexuosa* with part of the cotyledons removed, showing the hypocotyl-radicle axis. D–K, cross-section of *C. retusa*. Scale bars = 5 mm.

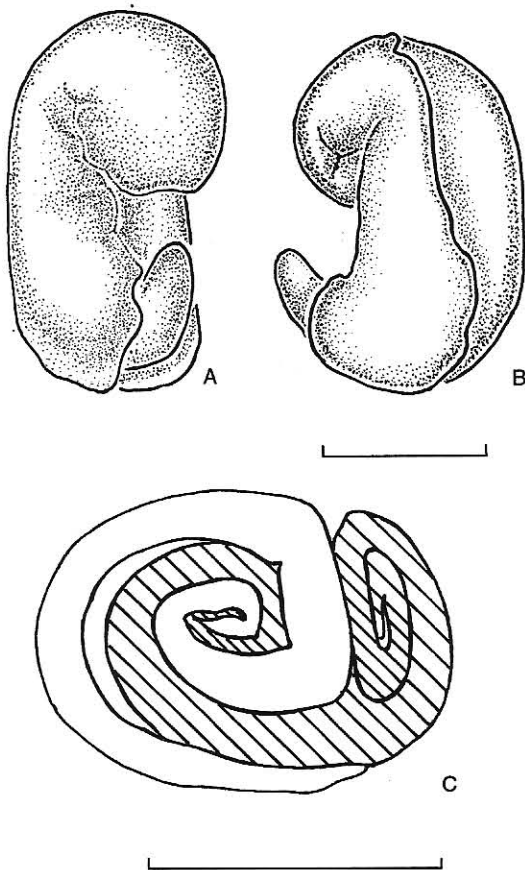


Figure 5. Embryo of *C. tweediana*. A, B, general view. C, cross-section. Scale bars = 3 mm.

protuberance, more or less developed and totally or partially surrounded by a narrow belt of chestnut-brown suberized tissue. Cotyledons notably unequal in size and shape, i.e. strongly anisocotylar (Figs 6A–C, 7A). The larger of the two, constituting the main part of the embryo, is generally subglobose or subellipsoid and sometimes compressed, $4\text{--}10 \times 6\text{--}10 \times 4\text{--}7$, ochre coloured, with a rugose surface interrupted by a narrow smooth region like a belt that partially surrounds the embryo and includes the radicle and the minor cotyledon.

The minor cotyledon varies considerably in size, from $3.5\text{ mm long} \times 1.2\text{ mm wide}$ to $0.5\text{ mm} \times 0.5\text{ mm}$. Sometimes it is absent altogether (Fig. 6C–F). In the latter case, a fold is formed between the radicle and the major cotyledon, wherein the plumule resides. When the minor cotyledon develops, it is located in a depression of the major cotyledon. Its thickness and shape are also variable, with generally triangular outline, acute or rounded apex which is sometimes a little attenuated at the base; in cross-section it is slightly quadrangular, with a convex inner surface, two lateral flat faces and an outer convex one (Fig. 7E). The colour, dark yellow, is similar to that of the root apex. The plumule, deeply seated between the two cotyledons, can be observed only in cross-section or longitudinal sections of the embryo (Fig. 7B, F). Because of the difference in size of the cotyledons, the minor one is displaced so that its axis is almost perpendicular to that of the radicle, a position held also by the plumule, so that the embryonic axis is curved.

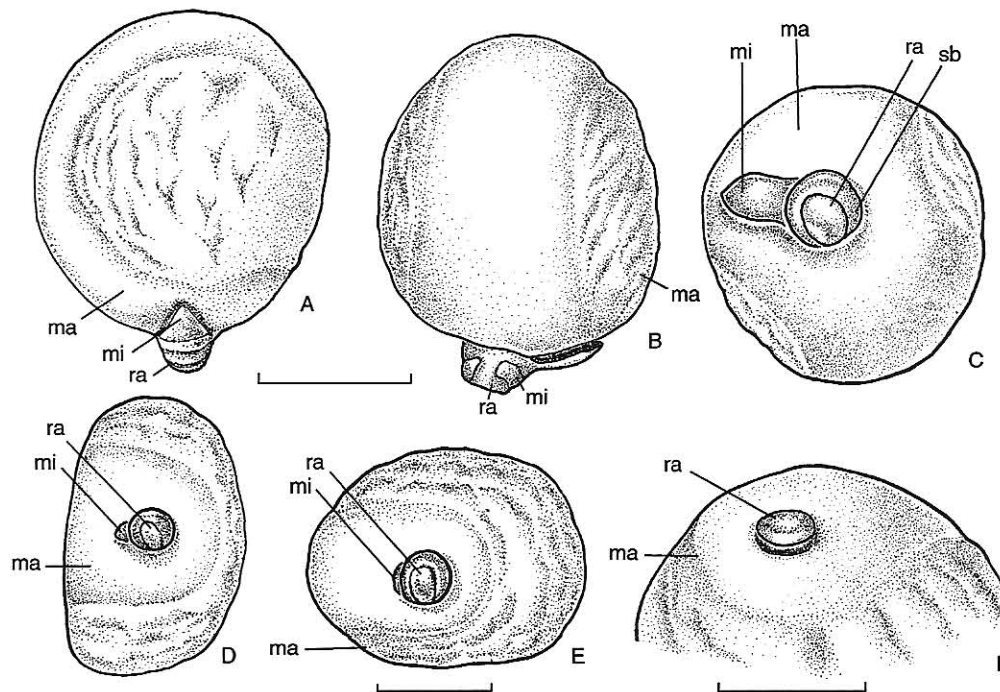


Figure 6. Embryo of *C. speciosa*. A, B, general view. C–E, polar view showing varying sizes of the minor cotyledon. F, embryo without minor cotyledon. Scale bars = 5 mm. *Abbreviations:* ma, major cotyledon; mi, minor cotyledon; ra, radicle; sb, suberized belt.

ANATOMICAL STRUCTURE OF SEED COAT IN *C. TWEEDIANA*

The seed coat is composed of the following layers (inside to out): nonlignified inner epidermis; hypodermal crushed cells; brachysclereids; hypodermal parenchymatous cells; outer epidermis with unicellular hairs which permeate the pulp of the fruit and cause it to be permanently attached to the seed. The cells of the outer epidermis have thick cutinized walls (Fig. 3F).

ANISOCOTYLY IN *C. SPECIOSA*

Anatomy of the embryo

Our study shows the spatial distribution of the radicle and cotyledons and their tissues. The embryo is mainly formed of parenchyma; its cells are filled with grains of starch. Figure 7C–H illustrates a series of sections (see key in Fig. 7B). The suberized cells covering the radicle are shown in Figure 7C. The procambium begins to be evident at this point; above it the vascular tissues form a circle. At the level of the base of the major cotyledon, a small portion of the procambium is deflected into the minor cotyledon (Fig. 7D)

while the provascular tissue forms a continuous cylinder, later fragmenting into bundles (Fig. 7D–H).

Anatomy of the seedling

In our study all the fleshy parts of mature fruits that fell to the ground were eaten by ants. The seeds were left on the soil surface beneath the plant where they germinated. Germination is phanerocotylar semihypogaeal; the hard seed coat breaks open and the cotyledons are exposed to light, turning an intense green colour. The minor cotyledon emerges first, while the major one remains partially covered by the seed coat, which gradually decomposes. The plumule either emerges between them (Fig. 9) or is joined to the major cotyledon when the minor one is absent (Fig. 10). Both cotyledons remain attached to the seedling and suberized areas are produced on their surface; eventually they shrivel and fall off.

The vascular tissue in the fundamental parenchyma is arranged in a semicircle of collateral bundles; these can be seen in cross sections of the minor cotyledon (Fig. 8). There is chlorenchyma within the one-layered epidermis, with its thick cuticle and stomata (Fig. 11). Cork formation starts on the lower surface (Figs 12, 13), slowly extending to cover the whole surface

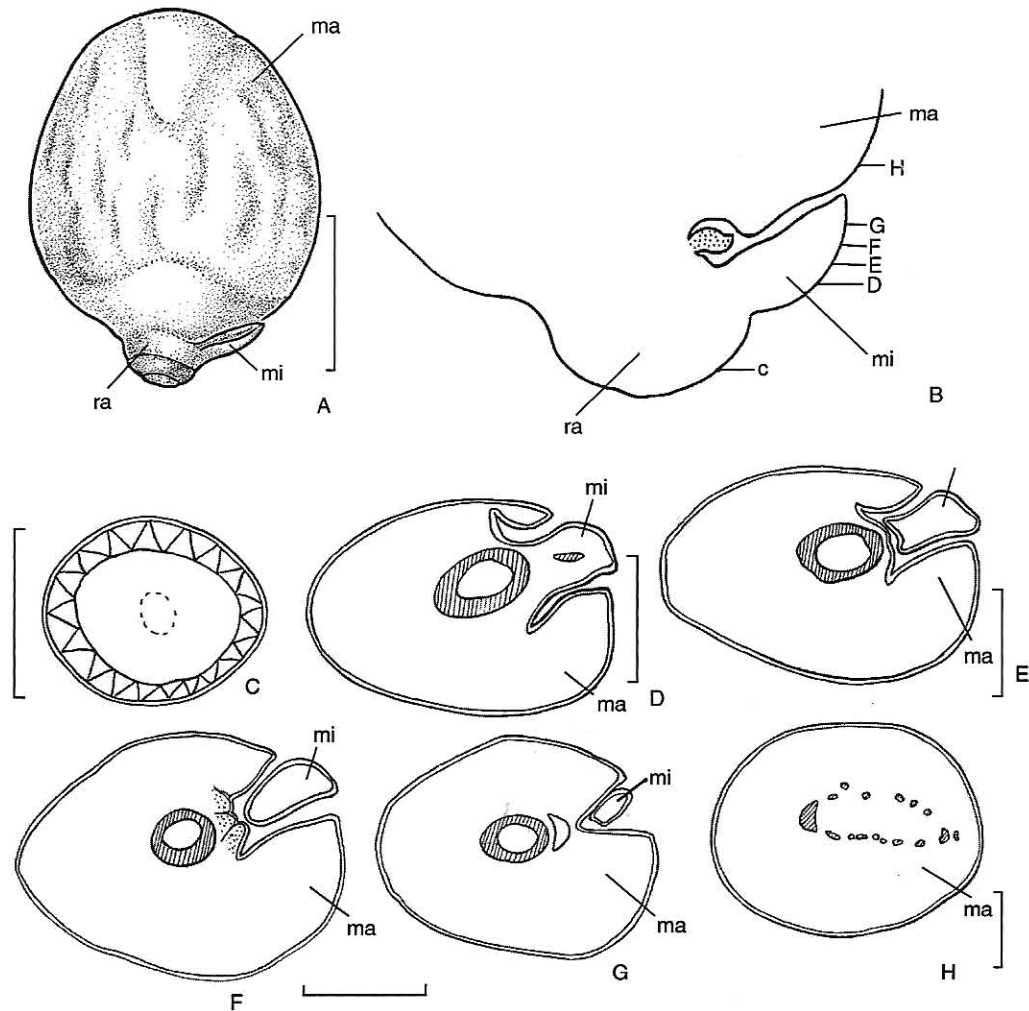
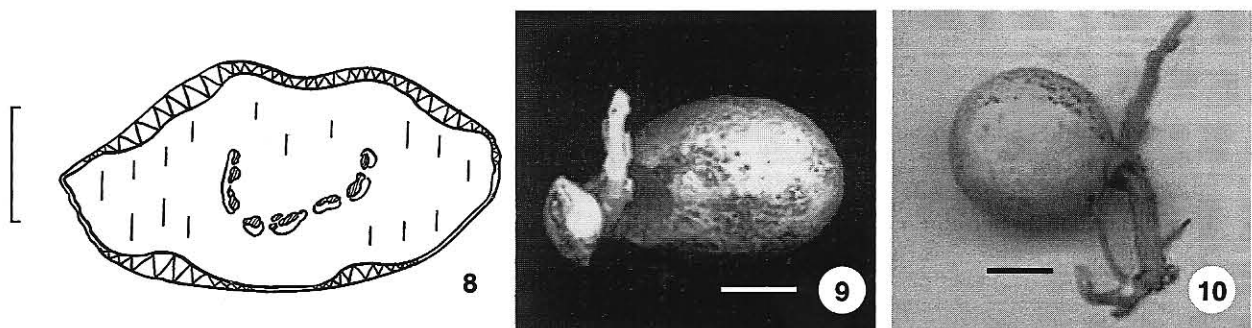
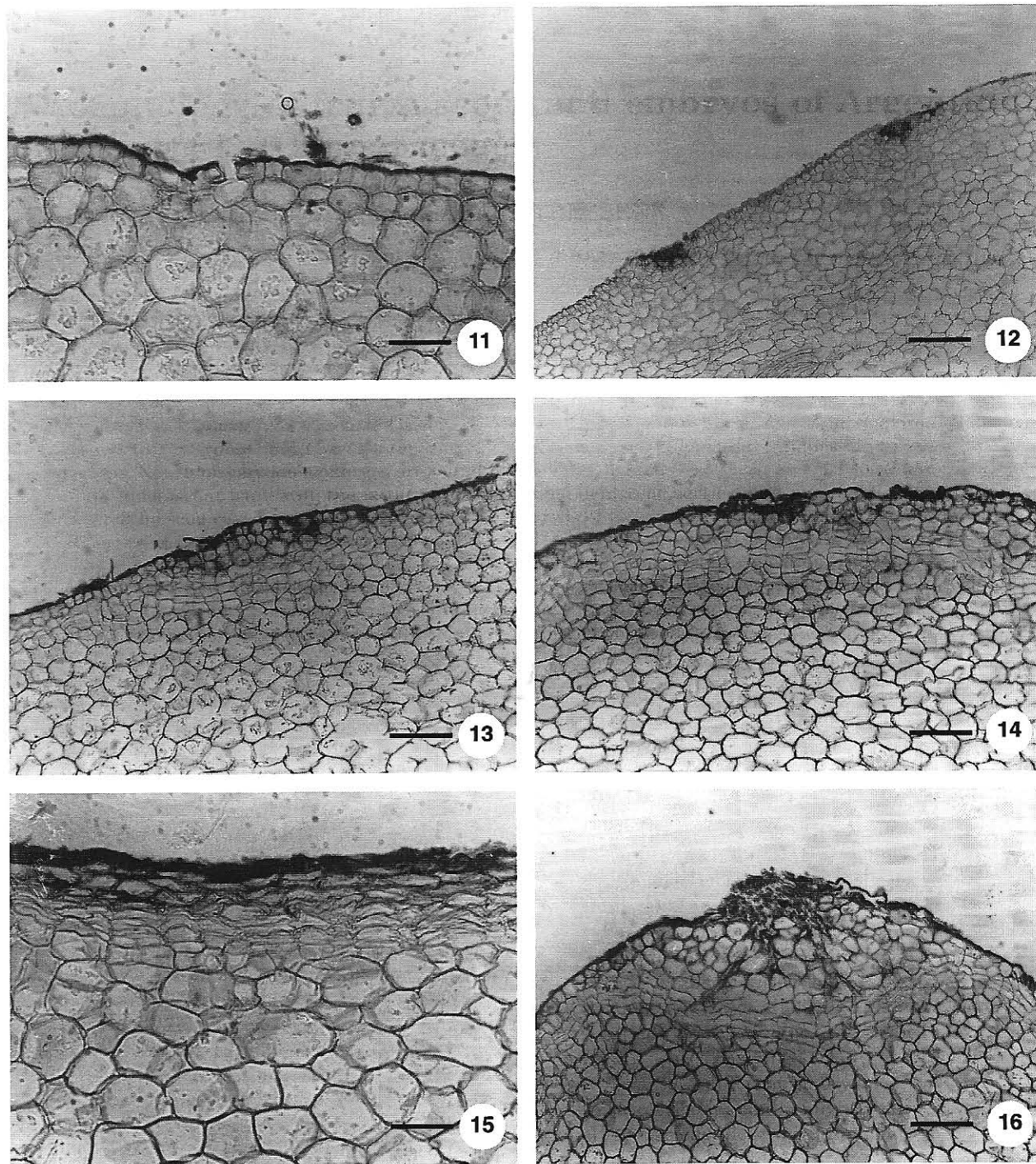


Figure 7. Embryo of *C. speciosa*. A, general view showing the cotyledons and radicle. B, diagram of the sections. C, cross-section of radicle. D–G, cross-sections at different levels of the minor and major cotyledons. H, cross-section at the major cotyledon level. Scale bars = 5 mm in A; 1.5 mm in C–H. Abbreviations per Fig. 6. Plumule dotted in B and F.



Figures 8–10. Seedling of *C. speciosa*. Fig. 8. Cross-section of the minor cotyledon showing arrangement of tissues. Scale bar = 1 mm. Fig. 9. Epicotyle emerging between cotyledons. Scale bar = 5 mm. Fig. 10. Seedling without minor cotyledon. Scale bar = 4 mm. In Figs 9 and 10 the partially decomposed seed coat was removed.



Figures 11–16. Seedling of *C. speciosa*. Partial cross-sections of minor cotyledon. Fig. 11. Epidermis with cuticle and stomata. Scale bar = 37.5 μm . Fig. 12. Zones where suberization begins. Scale bar = 130 μm . Fig. 13. Detail of the beginning of suberized zones. Scale bar = 100 μm . Fig. 14. Continuous cork tissue. Scale bar = 95 μm . Fig. 15. Detail of the suberized tissue. Scale bar = 32.5 μm . Fig. 16. Margin of minor cotyledon showing suberized tissue. Scale bar = 100 μm .

(Figs 14–16). In the minor cotyledon the cork covering begins on the inner surface, then develops on the outer surface and finally completely surrounds it.

DISCUSSION

In *C. flexuosa* and *C. retusa* (both members of sect. *Cynophalla*) the siliques are prominently constricted between the seeds, with the exocarp greenish-yellow when ripe and the endocarp fleshy and bright to dark red. Fruits of Nicaraguan specimens of *C. flexuosa* have been described by Iltis (2001). While the morphological characters of these fruits are similar to those of our Argentinian specimens, the process of dehiscence is somewhat different in that the siliques split open on one side, turning themselves inside out to display the seeds. In other species of sect. *Cynophalla* (e.g. *C. ecuadorica*) the siliques may open by valves as in *C. flexuosa*. However, their fruits are indehiscent or poorly dehiscent, with 2–4 fleshy valves that arch more or less irregularly to expose pendent seeds on long purple threads (Iltis, 1978). We have observed the process of dehiscence in Argentinian specimens of *C. flexuosa* s.l., from initiation to detachment, which is remarkable for the way in which the valves change position. The siliques open along one of the sutures and roll up and over the external face of the carpel; the seeds hang freely on their funiculi, then become detached. Eventually, the carpels separating along the other suture finally unroll and the sutures remain as a thin replum.

The fleshy fruits of *C. speciosa* (sect. *Capparidastrum*) are subglobose to globose, glabrous, greenish and shiny on the outside, fragrant, with a dark yellow pulp. Those of *C. tweediana* (sect. *Quadrella*) are densely covered by rough stellate yellow hairs with orange pulp. With regard to their dehiscence, both have been described simply as berries (Ragonese & Martínez Crovetto, 1947; Gómez, 1953; Legname, 1972; Troncoso, 1987; Zapater, 1992). In fact, the berries of *C. speciosa* are indehiscent, while those of *C. tweediana* open along the sutures at maturity, the orange pulp and enclosed seeds falling together. The valves also come off.

Among the studied species three types of seed are distinguished: (1) ellipsoid, arillate, with thin, chartaceous and glabrous coat (*C. flexuosa* and *C. retusa*); (b) subglobose, exarillate, thick coriaceous fibrous coat (*C. speciosa*); (c) compressed, kidney-shaped, exarillate, with thick, coriaceous, pilose coat (*C. tweediana*).

Fruit pulp is permeated by hairs of the seed coat in *C. tweediana*. The presence of similar hairs was mentioned by Iltis (1965) in *C. pachaca*, sect. *Capparidastrum*.

Three morphological types can be recognized among the embryos: (1) the embryo in *C. tweediana* matches

those described by Parisca (1983) as typical for the genus; (2) the embryos of *C. flexuosa* and *C. retusa* show the morphology mentioned by Parisca (1983) as a different model, with which we agree; (3) *C. speciosa* shows a further, distinctly different, type of embryo, which has, as yet, not been described previously for the genus, one that is specialized for storage and not particularly for postgermination photosynthesis.

Yankovlev & Zhukova (1980) report chlorophyllous embryos for the Capparaceae; these have been often associated with exalbuminous seeds (Dahlgren, 1980). All species studied in this paper have exalbuminous seeds, but only two, *C. flexuosa* and *C. retusa*, have chlorophyllous embryos. Their seeds have a thin coat and are exposed in a dehiscent silique with a relatively thin fleshy red pulp. In *C. speciosa* and *C. tweediana* the embryos are basically white and non-chlorophyllous, the seeds have a leathery seed coat surrounded by fleshy yellow or orange pulp, and are not exposed even though the latter's fruits dehisce along four sutures.

The embryos of *C. flexuosa*, *C. retusa* and *C. tweediana* can be placed in the 'Axile Division, Foliate Subdivision, Folded Type' of Martin's (1946) classification. The cotyledons of the first two species are rather thick but become flat with time, like leaves. The *C. speciosa* embryo can be placed in the 'Axile Division' of Martin's (1946) classification, within which there are three subdivisions: Linear, Miniature and Foliate. Nevertheless, none of the embryo types of Martin's classification show the morphological peculiarities of the embryo of *C. speciosa*, which is characterized by a small radicle and solid cotyledons notably different in size and shape. The minor cotyledon can be severely reduced in size or absent altogether, with the major one filling almost the entire seed.

Taking this into account, we propose adding a new subdivision (Massive) to allow the inclusion of this new type of embryo, which we name here as 'Unequal cotyledons'. Within it we would include those embryos with one or two massive cotyledons which are separate, partially or completely fused, for example the conferruminate embryos of some species of *Eugenia* (Myrtaceae).

Our interpretation of the morphology of the embryo of *C. speciosa* is based on our analyses of its anatomy and germination. The spatial distribution of the procambium differentiates the radicle (with its characteristic provascular cylinder) from the two cotyledons where the provascular tissues separate to form vascular strands. The anatomical structure of the cotyledons is typically foliar, with hypodermal chlorenchyma and colateral bundles. The position of the plumule and green colour of the cotyledons at the initiation of germination corroborate our distinction of 'major' and 'minor' cotyledons, as well as the

occurrence of anisocotily. According to Iltis (pers. comm.; B. Hansen & H. H. Iltis, unpubl. data), similar, often extreme, reduction of the second cotyledon is found in the small woody genus *Forchhammeria* of Mexico and the Antilles, which is usually considered a member of Capparaceae but has recently, based on molecular evidence, been transferred into its own family in a more basal position within the Capparales (Hall, Sytsma & Iltis, 2002). In this case germination is hypogeal, with the cotyledons never leaving the seed coat.

The presence of suberized tissue in the embryo is noteworthy and has not hitherto been mentioned in the literature. Formation of a periderm seems to be frequent in seedlings, particularly when injuries occur. Borger & Kozłowski (1972a, b, c) have reported its occurrence in the hypocotyl; in *C. speciosa*, the periderm arises in the cotyledons.

Further studies of the fruits, seeds and embryos of the other species of *Capparis* are required in order to elucidate evolutionary relationships within the genus.

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