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Stapfia	80	311-322	5.7.2002

Floral development and morphology in *Cuscuta reflexa* ROXB. (*Convolvulaceae*)

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A b s t r a c t : PRENNER G., DEUTSCH G. & P. HARVEY (2002): Floral development and morphology in *Cuscuta reflexa* ROXB. (*Convolvulaceae*). — Stapfia **80**: 311-322.

The floral development, morphology and anatomy of *Cuscuta reflexa* ROXB. is described and illustrated. All floral organs are initiated in acropetal direction: The sepals are initiated helically in clockwise or counter clockwise direction. Two lateral adaxial sepals are initiated first, grow faster than the remaining three sepals and act like bracteoles. The petals are initiated simultaneously and remain free over a long period. Along with the connecting filaments they form a prominent corolla-filament tube. Very late in floral ontogeny the petals fuse above the stamen to a 0,5 mm long corolla tube. Stamens and petals are more or less simultaneously initiated. Filament scales are formed at the base of stamens not before the anther development is finished. The gynoecium is open over a longer period. It consists of two carpels, which are divided incompletely by a median outgrowth of the ovular walls. Stomata at the base of the gynoecium exude nectar, which is held in the flower by the staminal scales. These scales are seen as secondary nectar receptacles. *Cuscuta reflexa* has a wide host range. It was possible to grow it on several tested plants of different families. Only on *Lycopersicon esculentum* and on *Hibiscus sinensis* it was found to be unable to form haustoria.

Z u s a m m e n f a s s u n g : PRENNER G., DEUTSCH G. & P. HARVEY (2002): Blütenentwicklung und –morphologie bei *Cuscuta reflexa* ROXB. (*Convolvulaceae*). — Stapfia **80**: 311-322.

Die Blütenentwicklung, -morphologie und -anatomie von *Cuscuta reflexa* ROXB. wird beschrieben und dargestellt. Alle Blütenorgane werden akropetal angelegt. Die Kelchblätter werden entweder in einer Links- oder einer Rechtsschraube angelegt. Zwei laterale Sepalen werden zuerst gebildet, wachsen schneller und verhalten sich vorblattartig. Die Anlage der Kronblätter erfolgt synchron. die Petalen bleiben über längere Zeit voneinander frei und bilden gemeinsam mit den Filamenten der fünf Staubblätter einen prominenten Kron-Filament-Tubus. Die Kronblätter verwachsen erst sehr spät in der Blütenentwicklung zu einem ca. 0,5mm langen Krontubus. Die Staubblätter werden fast zugleich mit den Petalen synchron angelegt. Schuppen am Grunde der Staubblätter werden erst nach der Anlage der Antheren als Auswüchse der Filamente gebildet. Diese Schuppen bedecken während der Anthese den basalen Teil des Gynoeceums und dienen als Safthalter. Das Gynoeceum wird als letztes Organ angelegt und bleibt über einen längeren Zeitraum offen. Es besteht aus zwei Fruchtblättern, die durch eine mediane Scheidewand unvollständig getrennt sind. An der Basis des reifen Gynoeceums finden sich Spaltöffnungen, über die Nektar sezerniert wird. *Cuscuta reflexa* hat eine breites Wirtsspektrum. Es war möglich die Pflanze auf mehreren Vertretern unterschiedlicher Familien zu kultivieren. Lediglich an *Lycopersicon esculentum* und *Hibiscus sinensis* wurden keine Haustorien gebildet.

K e y w o r d s : *Cuscuta reflexa*, *Convolvulaceae*, floral development, host specificity.

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Introduction

The genus *Cuscuta* consists of about 145 cosmopolitan chlorophyll-less parasites (MABBERLY 1997). Taxonomically the genus is treated either under *Convolvulaceae* or as a separate family *Cuscutaceae*.

The giant dodder *Cuscuta reflexa* ROXB. (Fig. 1) is native to South Asia (ENCKE et al. 1994: 217), but is also introduced to some parts of California (SCHOENIG 2000). In E-India and neighbouring islands the dodder is cultivated on *Pelargonium* because of its flowers similar to *Convallaria* (HEGI 1966: 2090).

Fig. 1: *C. reflexa* cultivated on *Ficus benjamina*. **a,** vegetative shoot system. **b,** inflorescence. **c,** flowers.

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Also in India, seeds of the giant dodder, which are called "Armabel", are sometimes used pharmaceutically as Anthelminthicum and Laxans (HEGNAUER 1964: 554, 559).

Studies on floral development in the genus are rather rare and only a common corolla-filament-tube and the absence of sympetaly was found (ERBAR 1991, ERBAR & LEINS 1996, NISHINO 1983). NISHINO (1983) and recently KUOH & LIAO (1993) studied floral initiation and development of *Cuscuta australis*. JOHRI & TIAGI (1952) worked on floral morphology and seed formation in *C. reflexa*. TIAGI (1966) worked on the floral morphology of *C. reflexa* and *C. lupuliformis* and gave a brief review of literature on the genus *Cuscuta*. Studies on morphology and embryology of *C. hyalina* and *C. planiflora* were done by TIAGI (1951).

Studies of IHL et al. (1988) on *C. reflexa* showed that *Lycopersicon esculentum* developed a defense mechanism against the parasite.

Cuscuta reflexa is a right hand twiner like all members of *Convolvulaceae* (see TEPPNER (1981) on twining; twining to the right hand for *Cuscuta gronovii*).

Material and Methods

The investigated clone of *Cuscuta reflexa* ROXB. was obtained from Dr. Anrdzey JANKUN, Kraków on 17.11.1999, growing on *Pelargonium* sp. The Polish plants originated from the Botanical Garden Halle, Germany (JANKUN, personal communication), where two clones are cultivated (JACOB 1966: 559). Since spring 2000 it is cultivated on *Ficus benjamina* L. in the temperate house of the new greenhouses at the Botanical Garden of the Institute of Botany, Karl-Franzens-University Graz. Although the plant flowers abundantly during wintertime, no fruit set was observed ever.

For scanning electron microscopy (SEM), buds of different size and age were collected and immediately fixed in FAA (5 parts formalin-5 parts acetic acid-90 parts 70% ethyl alcohol) and stored in 70% ethanol. Floral parts were dissected in alcohol of the same concentration under a Zeiss stereomicroscope. Bracts, sepals, petals or anthers were removed by fine tweezers and insect needles.

Afterwards, specimen were dehydrated in formalindimethylacetal (FDA, after GERSTBERGER & LEINS 1978: 382) for at least 24 hours and critical-point dried with liquid CO_2 in a Polaron 7010 CPD. Dried specimens were mounted on aluminium stubs with nail polish and dissection was completed on the stubs. The buds were coated with gold in an Agar sputter coater. Micrographs were taken in a Philips XL 30 ESEM at 20 kV at the Institute of Plant Physiology, Karl-Franzens-University Graz.

The photographs show buds oriented always with the bract abaxially (lowermost).

For microtome sections, paraffin methods after JOHANSEN (1940) were implemented. Sections, 13 µm thick, were made with a "C" knife on a sliding microtome from C. Reichert, Vienna. The sections were stained with safranin and fast green. Digital photographs of the sections were taken on a Zeiss Axiophot microscope with a Zeiss Axio Cam.

In outdoor experiments during May to September 2000 host specificity of *Cuscuta reflexa* was tested in a private garden in Graz, Mariatrost.

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Following plants were infected with the parasite by putting shoots of about 40-50 cm in length on shoots or leafs of the possible host:

Cornus sericea (*Cornaceae*), *Euphorbia* sp. (*Euphorbiaceae*), *Ficus benjamina* (*Moraceae*), *Hibiscus sinensis* (*Malvaceae*), *Lycopersicon esculentum (Solanaceae), Origanum vulgare* (*Lamiaceae*), *Parthenocissus inserta* (*Vitaceae*), *Petroselinum crispum* (*Apiaceae*), *Philadelphus coronarius* (*Hydrangeaceae*), *Syringa vulgaris* (*Oleaceae*), *Weigelia* sp. (*Caprifoliaceae*).

Results

Initiation and development of sepals: Sepals are initiated helically in clockwise or counterclockwise direction (Figs. 2b, c). Initiation starts with one lateral, adaxial sepal either to the left or to the right of the median plane. It is followed immediately by the second, lateral, adaxial sepal (Fig. 2a). According to the first initiated sepal the third sepal is initiated abaxially either on the right or on the left side of the median plane. The fourth initiated sepal is always the adaxial sepal in median position and the last initiated sepal is again, either the right or the left abaxial sepal.

The two first initiated sepals grow faster than the remaining three sepals and they overtake bud protection in bracteole manner (Fig. 2d). Finally calyx aestivation is quincuncial and at a length of about 3-4 mm the calyx is pressed open by the elongating corolla-filament-tubus.

Initiation and development of petals: Shortly after all five sepals are initiated the growing point becomes pentagonal and at the angles five petal primordia are initiated more or less simultaneously and separate from each other (Fig. 2c). The petals grow very slowly (Figs. 2e, f) and only when the development of the anthers is almost finished and the gynoecium is closing, the petals begin to grow faster and bend over these organs (Fig. 3c). The five pepals are connected with each other by bridges of the developing filaments of the stamens and a long corolla-filament tube is formed (Fig. 3a).

Late in ontogeny adjacent petals fuse laterally (Fig. 3d) so that at the tip of the corolla-filament-tube a c. 0,5 cm long corolla-tube is visible (Figs. 5c-f).

Initiation and development of stamen: Alternating with the petals the five stamens are initiated immediately after initiation of the petals. The initiation of stamens appears to be simultaneous (Fig. 2e), although sometimes one or two stamens may be initiated a little bit earlier and differences in the size of the primordia are observed frequently (Figs. 2e, f). Especially the initiation of the adaxial stamen is of interest, because sometimes it seems to be in connection with the developing gynoecium (Fig. 2e).

Scale initiation and development: Only when all floral organs are initiated and the development of the anthers is finished, scales are formed at the base of the filaments of each stamen (Figs. 3e, f; 5c). In the mature flower the scales are about 1,5 mm long and 0,7 mm broad with hairs at their rim (Fig. 5c). The scales hold

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nectar in the flower, which is secreted at the gynoecium base and are therefore seen as secondary nectar receptacles.

Initiation and development of the gynoecium: Initiation of the gynoecium starts almost simultaneously with the initiation of the stamens, where a bulge is visible in the center of the flower (Fig. 2e). At the beginning, the primordium is somewhat pentagonal (Fig. 2f) and the two stigmas are initiated successively (Figs. 3a, b; 4a). The gynoecium remains open for a longer period so that a horizontal division is visible inside (Figs. 4a, b). Two outgrowths (one larger than the other) arise from the walls of the ovary along the median line of symmetry. They are opposite to each other and partially separate the ovary into two compartments (Figs. 4c-f).

Finally two papillate cone-shaped stigmas are formed which are sitting almost without a style on the ovary (Fig. 5a). Several stomata are visible at the base of the ovary, which secrete nectar (Fig. 5b).

Floral Anatomy: The tips of the petals are flapped outwards, thus the tips of the anthers are nearly protruding out of the urceolate corolla tube (Figs. 1b, c). The petals form a short corolla tube with no vascular bundle trace (Figs. 5c, f). This corolla-tube goes over into a corolla-filament tube (Figs. 5c, e). Likewise, the sepals unite at the base to form a small sepal tube.

The petals consist of four cell layer-thick parenchymatous tissue sandwiched between the two epidermis layers, which have square cells with cuticle striations.

The anthers are dithecous and tetrasporangiate with longitudinal deshiscence (Figs. 5d, f) which takes place by means of a longitudinal slit, extending from the tip to the bottom of the two thecas. The septa, which seperates the two microsporangia, is strongly reduced at dehiscence of the anthers, that the stub, often wrongly called "placenta", disappears. The anthers appear to bear oil globules in locules, presumably to facilitate sticking of the pollen on the pollinator. These oil globules originate from the tapetum and most probably serve as nutrition for the growing pollen mother cells as well. The independent filament is deeply grooved at the base. The filament part builds a ridge in the corolla-filament tube.

The scales (Safthalter) are at the base of the stamens. The bifid stigma along with the looped scales form a partition, which shields the nectar at the base of the corolla (Fig. 6a). For the larger part the corolla-filament tube is largely pentagonal. But at the point of connection of the scales to the tube, the edges become more convolute, protruding out between the tips of the sepals. The short style ends at this level and the ovary begins. The scales unite with each other at the bottom to form a pentagonal ring (Fig. 6b).

Host plants of *Cuscuta reflexa*: The investigated clone of *Cuscuta reflexa* was obtained as a parasite growing on *Pelargonium*. To make greenhouse-culture of this parasitic plant easier, a more durable host was needed, and in *Ficus bejamina* a most suitable host was found (TEPPNER, experimental data). On a 2 m tall plant of *Ficus benjamina*, this dodder grows since 2 years without any visible damage to its host (Figs. 1a-c).

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In outdoor experiments members of different families were tested as host plants. Nearly all tested plants showed positive results. Only with *Hibiscus sinensis* (*Malvaceae*) and *Lycopersicon esculentum (Solanaceae)* it was impossible to establish proper parasitic relationship and no haustoria were formed. On all other investigated plants the dodder was able to form typical haustoria and a healthy rate of growth was visible.

Discussion

In *C. europaea* ERBAR (1991: 427, Figs. 43-44) did not find sympetaly. Here the small interprimoridial region between two adjacent petals does not unite. So the tube is formed exclusively by the fused petals and filaments. NISHINO (1983) states for *C. australis*, that the tube formation resembles that of *Dichondra repens* (*Convolvulaceae*) and that the tube is considered "only as the common structure of petals and stamens". According to these two reports the "*Cuscutaceae*" are treated as having no corolla tube by ERBAR (1991) and ERBAR & LEINS (1996). The current study on *C. reflexa* shows that in *Cuscutaceae* like in *Convolvulaceae* the occurrence of both, late sympetaly and lack of a corolla tube can be found. This supports the trend to lump the family *Cuscutaceae* with *Convolvulaceae*. On the basis of NEYLAND (2001) reduction or loss of sympetaly could be interpreted as a derived character in *Convolvulaceae*. But further studies are necessary.

While KUOH & LIAO (1993) state helical succession in sepal initiation for *C. australis* only, in the present study clockwise as well as counter clockwise direction of initiation could be shown for *C. reflexa*. Also the striking precociousity of the two lateral sepals found in *C. reflexa* is not mentioned for *C. australis*. The authors did not go into details of tube formation, but it seems that *C. australis* does not have a distinct corolla tube (cf. KUOH & LIAO 1993: 102, Fig. 14).

No clear host specificity was found for *C. reflexa*. This dodder is able to parasite on a wide range of hosts. Like in IHL et al. (1988) *C. reflexa* was not able to parasite on *Lycopersicon esculentum* and also no haustoria were formed on *Hibiscus sinensis*.

Through its ability to parasite on a wide range of host plants, *C. reflexa* is a serious pest on *Citrus*, *Coffea* and *Litchi* not only in Asia but also in the New World. The giant dodder, *C. reflexa*, was introduced in California and classified there as noxious weed ("A" rated) in the CDFA weed list of the California Department of Food and Agriculture, USA (SCHOENIG 2000).

Acknowledgements

We wish to thank Dr. Anrdzey JANKUN, Krakòw, Poland for providing us with the clone of *C. reflexa*. We are deeply grateful to Dr. Edith STABENTHEINER, Institute of Plant Physiology, Karl-Franzens-University Graz, for allowing us to make the SEM-studies in her laboratory. Many thanks to Dr. Wolfgang WETSCHNIG for the possibility to use his microscope for digital photography.

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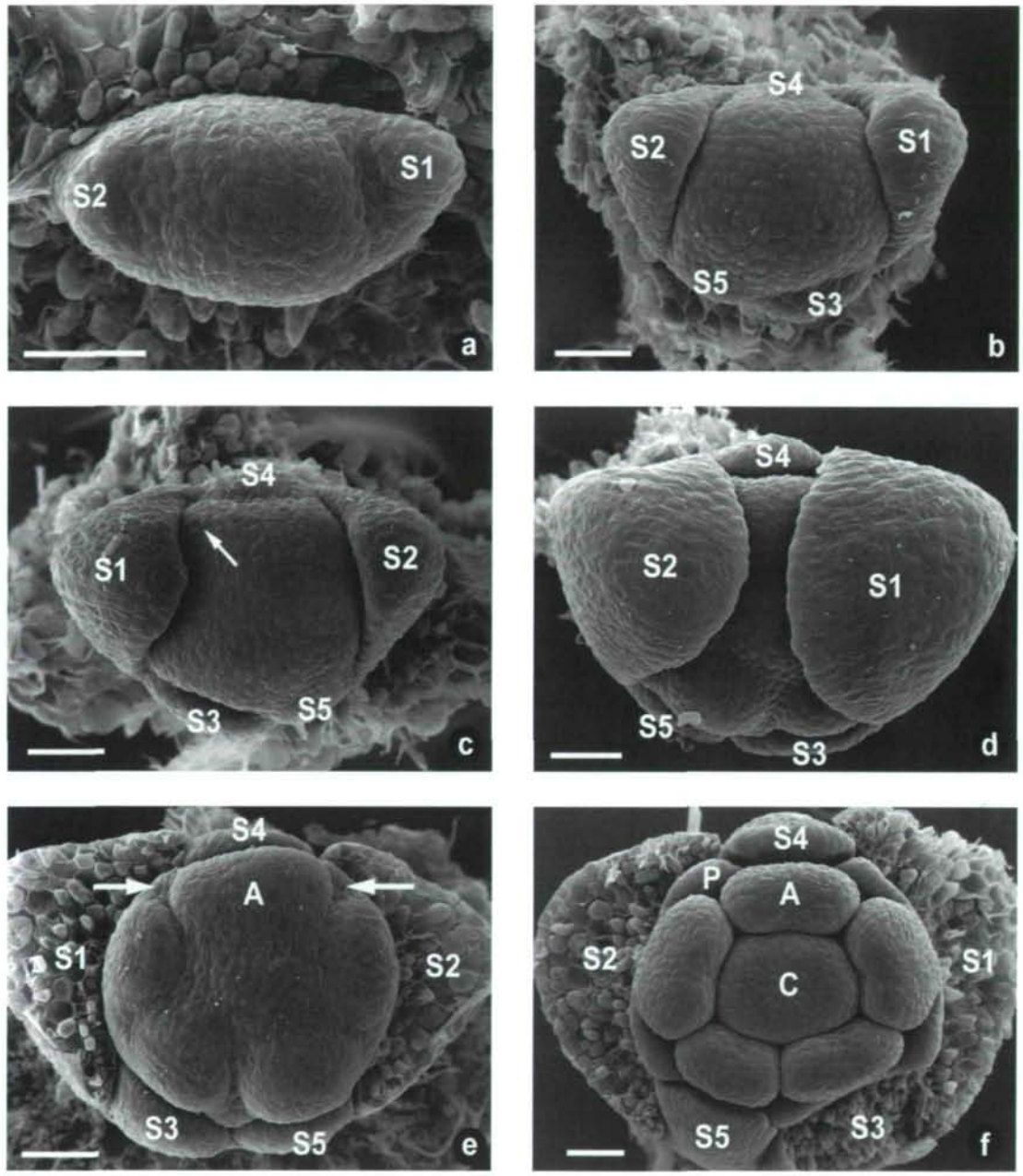

Fig. 2: Flower development in *C. reflexa*. **a,** initiation of two lateral sepals S1 and S2. **b,** Counter-clockwise initiation of sepals S1-5. **c,** Clockwise initiation of sepals S1-5, initiation of petals (arrow). **d,** enlargement of sepals S1 and S2. **e,** initiation of petals (arrows) and stamens (A), sepal S1 and S2 removed. **f,** initiation of the carpel C, sepals S1-3 removed. (Abbreviations: S1-5 = sepals in order of initiation, P = petal, A = stamen, C = carpel. Bar = 100 µm).

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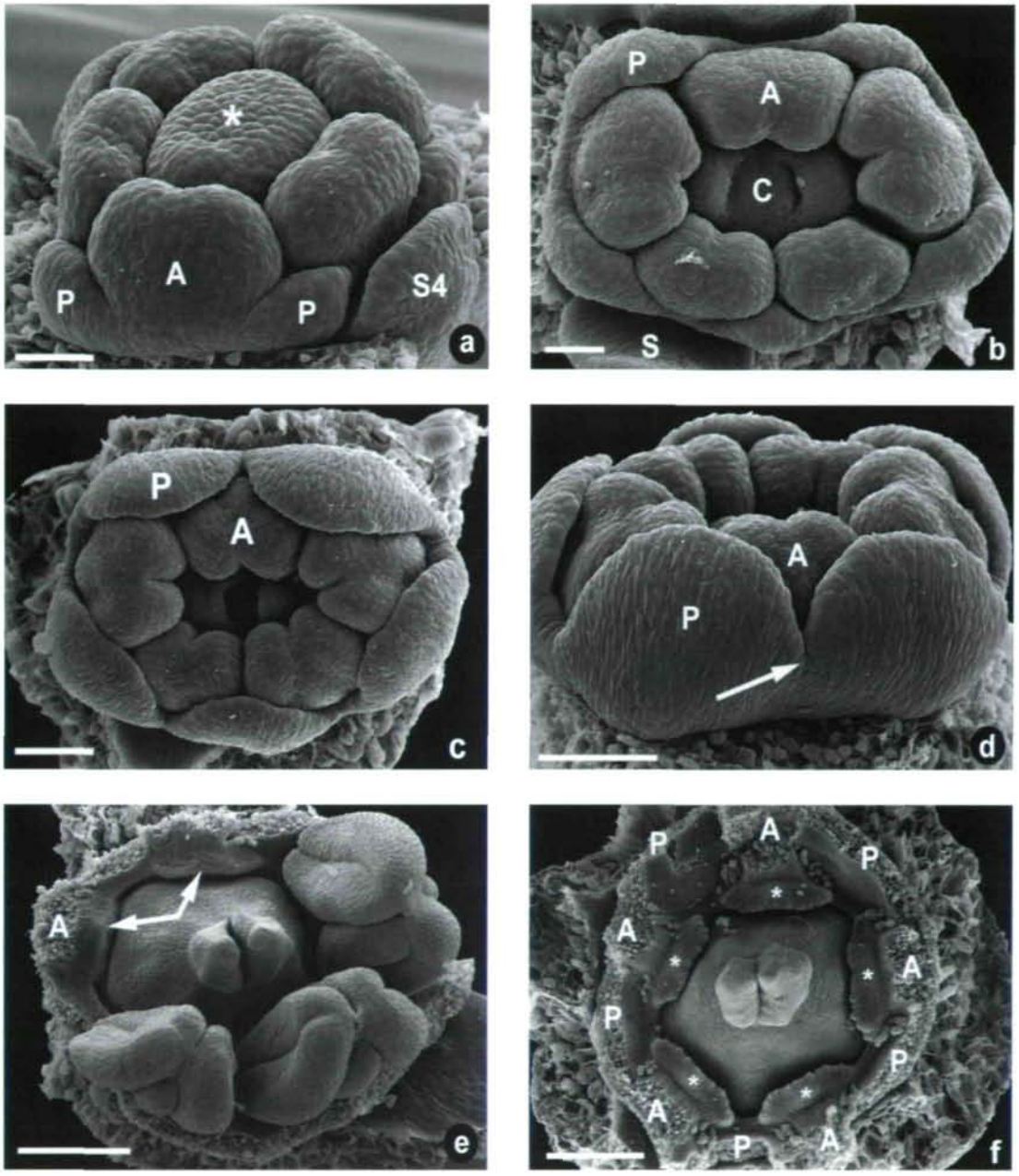

Fig. 3: Flower development in *C. reflexa*. **a,** lateral view of Fig. 2f; beginning depression of the carpel (asterisk), petals p distinctly separated by the anther A. **b,** development of petals, stamens with anther formation and carpel with formation of the two lateral stigmas; sepals removed. **c,** enlargement of petals P, development of stamens A and carpel; sepals removed. **d,** view of Fig. 3a from abaxial side; beginning fusion of petals P (arrow). **e,** development of nectar scales (arrows) at the base of the stamens, perianth and two stamens removed. **f,** development and enlargement of nectar scales (asterisks); sepals, petals and stamens removed. (Abbreviations: S = sepal, P = petal, A = stamen, C = carpel. Bar in a, b = 100 µm, in c, d = 200

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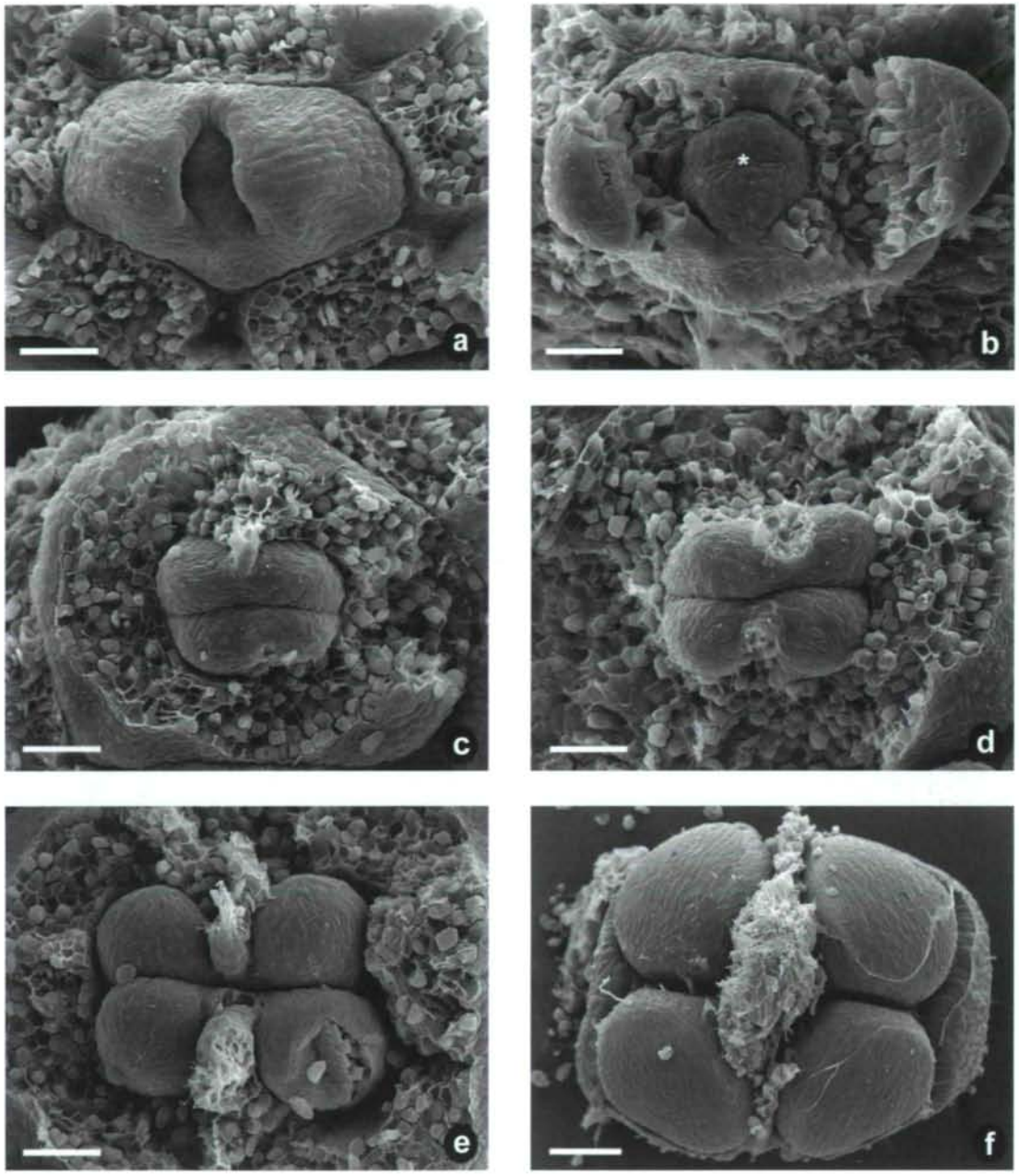

Fig. 4: Flower development in *C. reflexa*. **a,** young, still open ovary. **b,** dissected ovary of Fig. 4a with ovule initials, horizontal constriction (asterisk). **c,** four ovule initials, beginning of median outgrowth. **d,** proceeding growth of median outgrowth. **e,** four ovules uncompletely separated. **f,** fully developed ovules with median outgrowth from the walls of the ovary, separating it partially in two compartments. (Bar in a-ev= 100 μm, in f = 200 μm).

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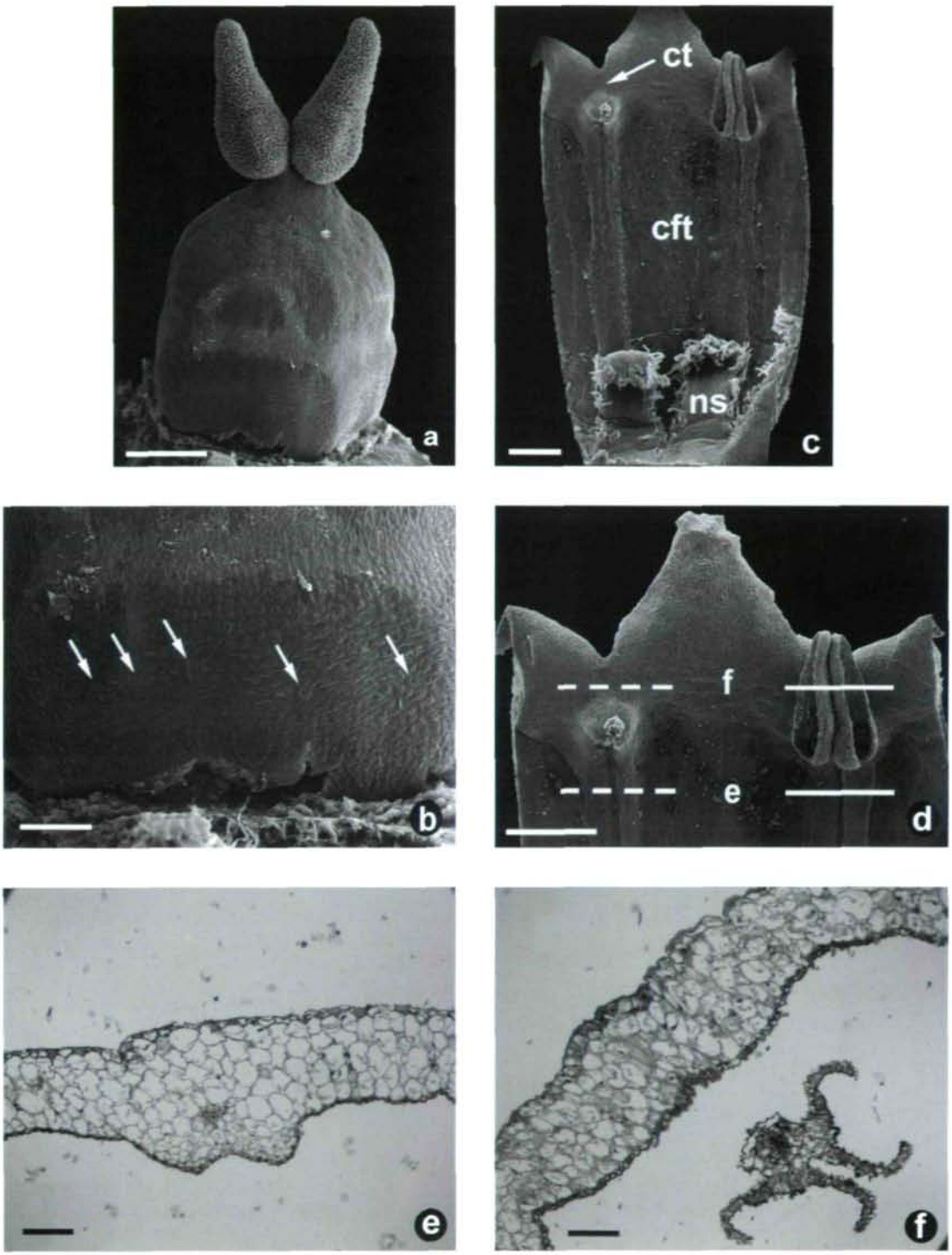

Fig. 5: Flower development in *C. reflexa*. **a,** unripe fruit with persistent stigmas. **b,** base of the carpel with visible stomata (arrows, detail of Fig. 5a). **c,** part of the corolla of a mature flower, with basal hodded nectar scales (ns), a prominent corolla-filament tube (cft) and with a short corolla tube. (arrow). **d,** detail of Fig. 5c, with direction of sections shown in Figs. e and f. **e,** transverse section of the corolla-filament tube (plane e in Fig. 5d) with vascular bundle visible. **f,** transverse section of the corolla tube (plane f in Fig. 5d) with no vascular bundle visible and with upper part of the anther. (Abbreviations: ns = nectar scale, cft = corolla-filament tube, ct = corolla tube. Bar in a = 500 µm, in b = 200 µm, in c, d = 1 mm, in e, f = 200 µm).

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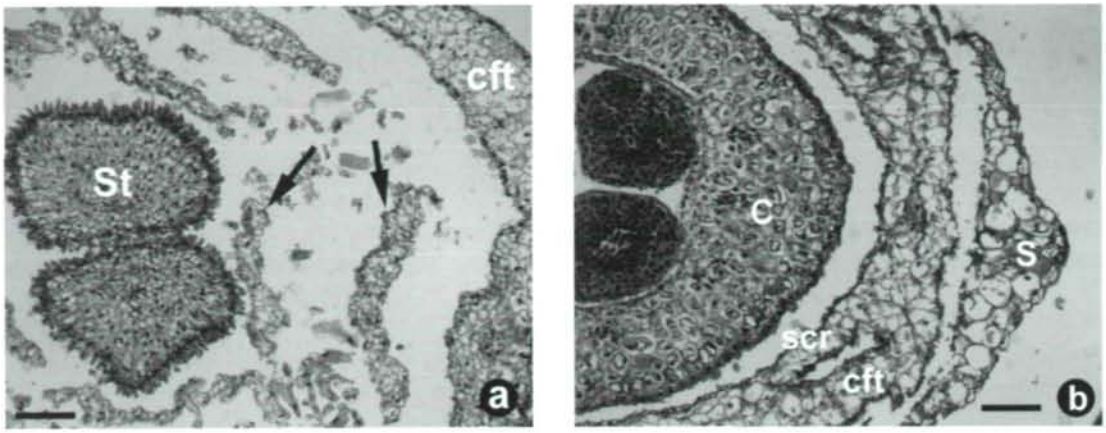

Fig. 6: Flower development in *C. reflexa*. **a,** transverse section passing through the corolla-filament tube (cft), hood of the scales (arrows) and the two stigma lobes (St). The latter two form a partition blocking the free accession to the nectar collected at the base. **b**, transverse section passing through the ovary (c), scale ring (scr), corolla-filament tube (cft) and a free sepal tip (s). The free arms of the nectar scales unite at the bottom to form a scale ring (scr). (Bar in a-b = 200 μm).

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Jahr/Year: 2002

Band/Volume: 0080

Autor(en)/Author(s): Prenner Gerhard, Deutsch Gerfried, Harvey Pramodchandra

Artikel/Article: Floral development and morphology in Cuscuta reflexa ROXB. (Convolvulaceae). 311-322