

Atypical fruit of *Talinum triangulare* (Jacq.) Willd., the type species of the genus *Talinum* (Talinaceae, former Portulacaceae)

Tatiana D. Veselova, Khalima K. Dzhalilova & Alexander C. Timonin

Summary: *Talinum triangulare* sharply contrasts to the vast majority of *Talinum* species in explosive dehiscence of its fruits. Distinctively, *Talinum* species have a 3-valvate seed vessel that splits tangentially into outer and inner semi-valves. Such a seed vessel is exemplified by *T. paniculatum*. Its coriaceous outer semi-valves decay while its scarious inner semi-valves separate from the receptacle but remain hanging on mostly fibrous dorsal bundles. The outer semi-valves are traditionally considered epicarp (= exocarp). We have concluded, however, that the outer semi-valves really consist of lignified 1-layered exocarp (= outer epidermis) and unlignified parenchymatous mesocarp. The inner semi-valves consist of heterogeneous obliterated endocarp. Differently shrinking meso- and endocarp interact with a resistant exocarp and dorsal bundles to generate stresses in the seed vessel and cause loculicidal and basal circumscissile dehiscing of the capsule as well as tangential fissuring of the seed vessel. The lignified exocarp of *T. triangulare* is an augmentative homologue of *T. paniculatum*'s one as it consists of an outer epidermis and 1 to 3-layered hypodermis. The unlignified parenchymatous mesocarp of *T. triangulare* is thicker than in *T. paniculatum*, though it corresponds only to the inner part of the latter one (defective homologue). The heterogeneous endocarp of *T. triangulare* is also thicker than in *T. paniculatum*. Besides, it partly obliterates. Thicker endo- and mesocarp coherently shrink to interact with the more resistant thicker exocarp in order to generate higher stresses in the seed vessel. The dorsal and basal circumscissile faults of the seed vessel are flanked by reinforcing lignified tissues to prevent from precocious fissuring of the seed vessel and thus to promote accumulating stresses. The stresses accumulated cause hasty fissuring of the seed vessel and longitudinal bending of each of the 3 resultant valves. It is this hasty bending that induces centrifugal force in the receptacle that pushes the valves away.

Keywords: *Talinum*, Portulacaceae, Talinaceae, capsule, seed vessel, exocarp, mesocarp, endocarp, dehiscence

Seed vessel (= pericarp) structure and fruit dehiscence mode are both considered non-molecular key traits to separate modern *Talinum* Adans. from those Portulacaceae which are regarded to be its relatives or its previous intrageneric segregates (CAROLIN 1987; KIGER 2001; APPLEQUIST 2005; BAIR et al. 2006; NYFFELER & EGGLI 2010). The 3-valvate capsule has been invariably attributed to *Talinum* (ADANSON 1763; DE CANDOLLE 1828; PAX 1889; MCNEILL 1974; KIGER 2001; BAIR et al. 2006; NYFFELER & EGGLI 2010). The seed vessel always consists of distinctly coriaceous epicarp and scarious endocarp (CAROLIN 1987; KIGER 2001; FERGUSON 2001; BAIR et al. 2006; NYFFELER & EGGLI 2010). Prolonged loculicidal dehiscence of the fruit is mostly ascendant (KIGER 2001; FERGUSON 2001; NYFFELER & EGGLI 2010), though descendant dehiscence is also inherent in some species (MCNEILL 1974; NYFFELER & EGGLI 2010). Each fissure leaves dorsal bundles intact and detaches from the seed vessel tissues throughout but their both ends. The loculicidal dehiscence of the capsule is inherently accompanied by peculiar tangential rupturing of the seed vessel which causes every capsule valve to divide into outer semi-valve of epicarp and inner semi-valve of endocarp (GALATI 1986; CAROLIN 1987; KIGER 2001; FERGUSON 2001; NYFFELER & EGGLI 2010). Circumscissile rupturing of the epicarp at the very base of the capsule

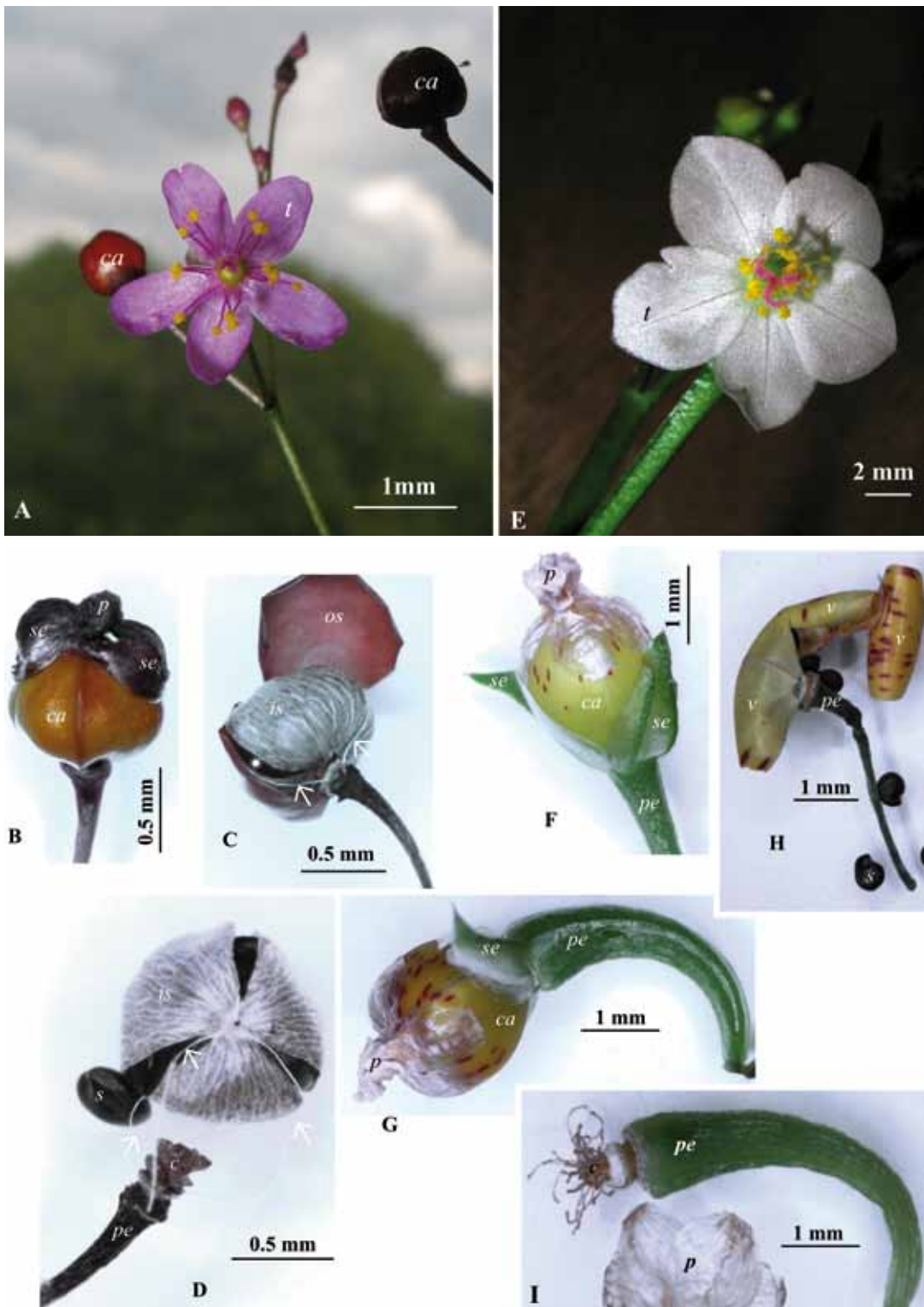


Figure 1. Flowers and fruits of *Talinum paniculatum* (A–D) and *T. triangulare* (E–I). A, E – opened flower; B, G – nearly ripe capsule; F – unripe capsule; C, H – dehiscent capsule; D, I – dehiscent capsule. *c* – column; *ca* – capsule; *is* – inner semi-valve; *os* – outer semi-valve; *p* – perianth; *pe* – pedicel; *s* – seed; *se* – sepaloid; *t* – tepal; *asterisc* – loculicidal fissure; *arrows* – dorsal bundles.

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simultaneously takes place. Combined loculicidal, tangential and circumscissile splitting causes the outer semi-valves to separate completely and to decay. The inner semi-valves remain continuous at their very tops fastened by all 3 dorsal bundles (Fig. 1D). Having separated from the receptacle the inner semi-valves freely hang on these bundles (GALATI 1986; CAROLIN 1987; KIGER 2001; FERGUSON 2001) (Fig. 1D). This complicated dehiscence results in prolonged dissemination (GALATI 1986; CAROLIN 1987). Such a dehiscence is caused by the specific structure of the seed vessel which was outlined by GALATI (l.c.) in *T. paniculatum* (Jacq.) Gaertn.

There are some *Talinum* species, however, which capsule valves do not split tangentially and thus shed off as a whole (KIGER 2001; FERGUSON 2001; NYFFELER & EGGI 2010) and this dehiscence mode was even considered typical of the genus by VON POELLNITZ (1934). Moreover, explosive dehiscence and ballistic dissemination are both inherent in *T. triangulare* (FERGUSON 2001). Fruits of these species are still subject to histological investigations. Seed vessel structure and fruit dehiscence of the latter species are certainly the most intriguing inter alia, because *T. triangulare* has been chosen as the type species of the genus *Talinum* (VON POELLNITZ 1934; McNEILL 1977; BRUMMITT 1978; FERGUSON 2001).

The present investigation is aimed to elucidate the histological structure of the seed vessel and its presumed functioning in the explosive capsule of *T. triangulare* in contrast to the capsule of *T. paniculatum*.

Materials and methods

Plants of *T. paniculatum* and *T. triangulare* were obtained from indoor collections of Komarov Botanical Institute of Russian Academy of Science, St. Petersburg, and Tsitsin Main Botanical Garden of Russian Academy of Science, Moscow, respectively.

Advanced flower buds, opened flowers and fruits at all developmental stages were fixed with FAA fixative (formaldehyde – acetic acid – ethanol) for 24 h. Fixed samples were washed and then dehydrated by means of 70%, 80%, 90%, 100% ethyl alcohol series and moved through 3:1, 1:1, 1:3 ethyl alcohol/xylene mixtures, and 100% xylene to embed into paraffin wax. Samples thus prepared were cut either transversely or longitudinally with rotary microtome MSE (London). About 10 µm thick sections were mounted on microscope slides, deparaffinised through 100% xylene and rehydrated by means of 3:1, 1:1, 1:3 xylene/ethyl alcohol mixtures and 100%, 90%, 80% ethyl alcohol series to pure water. Thereafter, the sections were stained with Rawitz's haematoxylin and aqueous safranin or light green or alcian blue. All stained sections were dehydrated via ethyl alcohol, ethyl alcohol/xylene and xylene series and embedded in Canada balsam.

Digital photos were taken with light microscope Axioplan 2 Imaging equipped with digital camera AxioCam MRc and processed with Corel Photopaint version 11.

Results

Inflorescence and flowers

Talinum paniculatum has multi-nodal close thyrses which bear a great number of pink, hypogynous flowers about 3 mm in diameter (Fig. 1A). *T. triangulare* has mostly trichasial cymoids or rarely 2-nodal thyrses (TIMONIN 2005) and bears much less numerous white hypogynous flowers up to 10 mm in diameter (Fig. 1E). The inflorescence stays in blossom for 1.5 to 2 months in

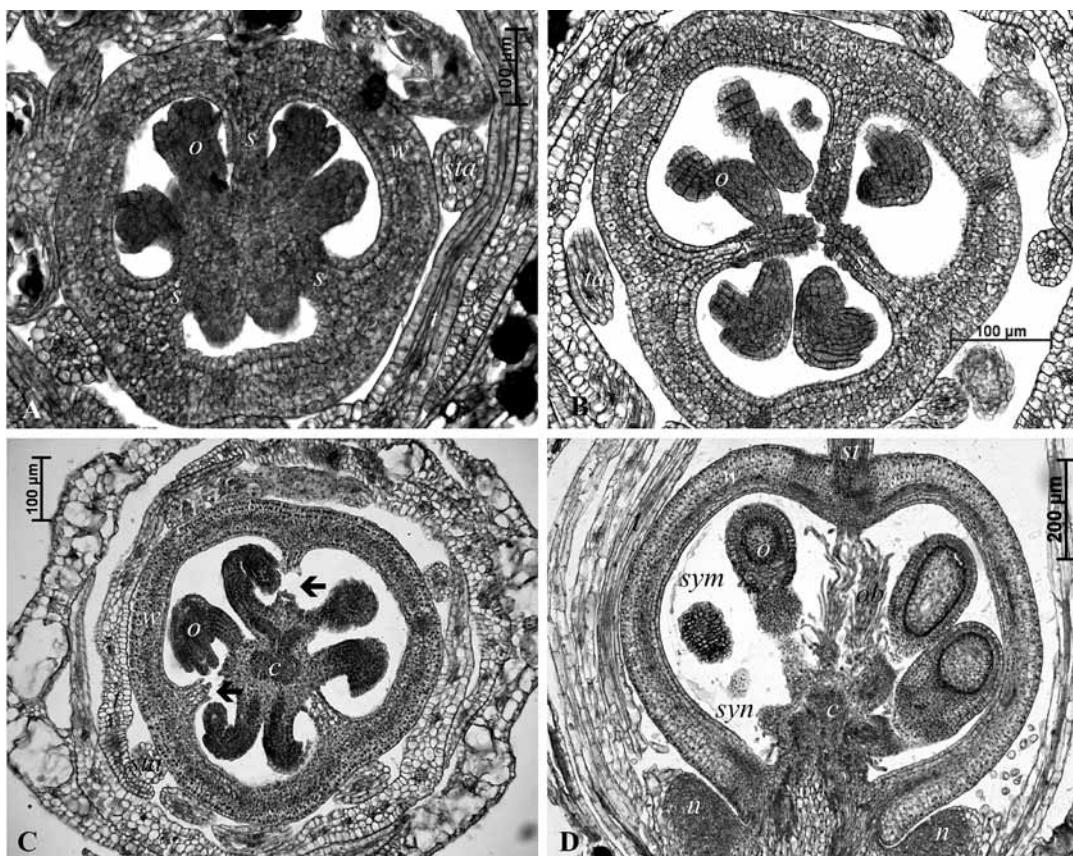


Figure 2. Ovary of *Talinum paniculatum*. A – cross-sectioned synascidiate zone; B – cross-sectioned symplicate zone; C – cross-sectioned destroying septae; D – longitudinally sectioned ovary. *c* – column; *n* – nectary; *o* – ovule; *ob* – obturators; *s* – septa; *st* – style; *sta* – stamen; *sym* – symplicate zone; *syn* – synascidiate zone; *t* – tepal; *w* – ovary wall; *arrow* – destroyed septa.

T. paniculatum and for 3 to 4 weeks in *T. triangulare*. Every flower opens only once for 2 to 3 hours, however, in the afternoon in the former species and by noon in the latter one.

The anthers release their pollen grains just by the flower's opening, but they are distant from the stigmas for the whole period the flower is opened (Fig. 1A, E). When the flower fades, withering tepals tightly envelop the ovary while their tops shrink and press the anthers to the stigmas to cause efficient autogamy. Dried and shrunk perianth breaks away from the receptacle 1 to 2 days after flower fading, but it remains as a scarious cap on the ripening capsule nearly until its dehiscence (Fig. 1B, F, G). Both sepaloids of *T. paniculatum* also break away from the receptacle and cap the capsule (Fig. 1B).

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The 3-merous (occasionally 2- or 4-merous) gynoecium is syncarpous sensu LEINFELLNER (1950), and its distal symplicate zone is twice as long as its basal synascidiate zone (Fig. 2A, B, D). Only the synascidiate zone is fertile, but ovules are lifted by their funiculi to the symplicate zone (Fig. 2B, D). There are 15 to 20 ovules per an ovary and nearly all of them give rise to seeds. The septae start collapsing in both zones when the megasporocytes develop in the ovules (Fig. 2C). Thereof, the central column is arisen. Axile placentation accordingly changes into a free-

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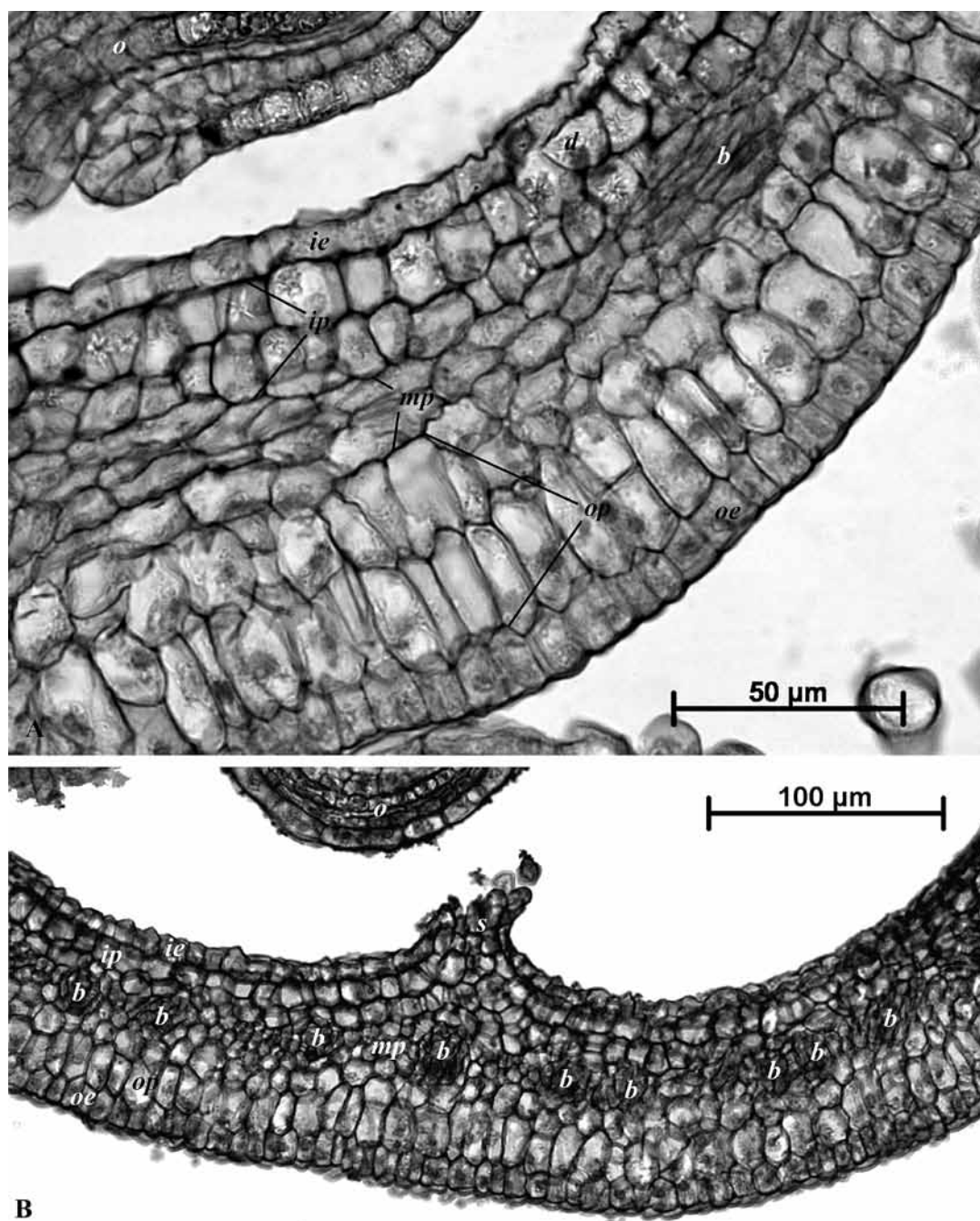


Figure 3. Cross-sectioned ovary wall of *Talinum paniculatum*. A – histological structure; B – vasculature. *b* – vascular bundle; *d* – calcium oxalate druse; *ie* – inner epidermis; *ip* – inner parenchyma; *mp* – middle parenchyma; *o* – ovule; *oe* – outer epidermis; *op* – outer parenchyma; *s* – septa.

central one. Epidermis of the column produces a dense indumentum of uniseriate trichomic obturators which grow upwards to the ovary roof. They intermingle with similar obturators that grow downwards from the ovary soffit just under the style base when the pollination takes place (Fig. 2D). The obturators thus intermingled constitute the continuation of the transmitting tissue of the style.

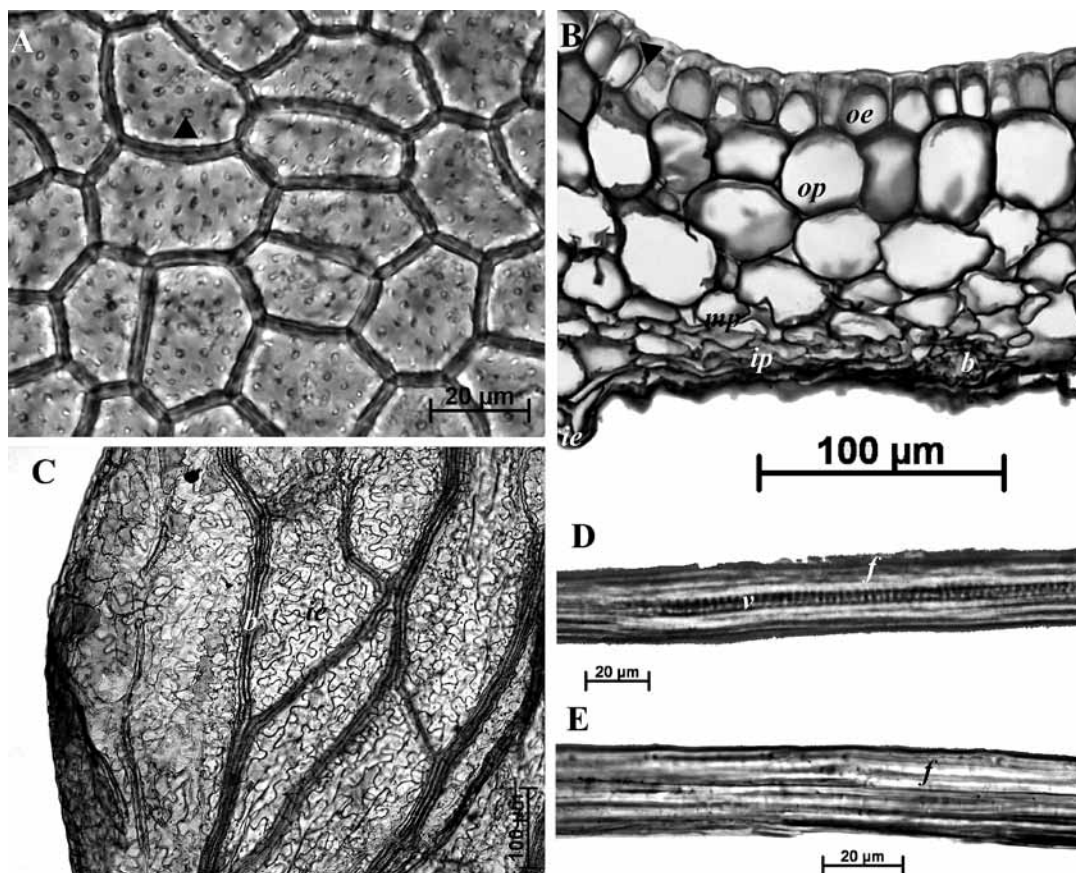


Figure 4. The ripe seed vessel constituents of *Talinum paniculatum*. A – the outer epidermis, appearance; B – cross-sectioned seed vessel; C – the inner epidermis; D, E – separated dorsal bundles. *b* – vascular bundle; *f* – fiber; *ie* – inner epidermis; *ip* – inner parenchyma; *mp* – middle parenchyma; *oe* – outer epidermis; *op* – outer parenchyma; *v* – vessel; arrowhead – pit.

Five anatomical-histological zones are discernible in the ovary wall of the faded flower (Fig. 3A). These are: • outer epidermis; • 2(3)-layered outer parenchyma of larger cells which are a little elongated anticlinally and contain chloroplasts; • 2 to 3-layered middle parenchyma of smaller isodiametric cells containing neither chloroplasts nor calcium oxalate; • 2(3)-layered inner parenchyma of isodiametric cells most of which contain one calcium oxalate druse per cell and • inner epidermis.

The middle parenchyma is traversed by numerous vascular bundles (Fig. 3B). The bundles are highly uniform but the dorsal ones are clearly identifiable due to their position and cell constitution (see below). All zones mentioned drastically change during fruit ripening.

The ripe fruit is a smooth, globular, shining, yellowish brown capsule approximately 1 mm in diameter (Fig. 1A, B). Its outer epidermis consists of tangentially flattened, 5 to 6-gonal lignified cells (Fig. 4A). The latter have strait anticlinal walls and a highly thickened outer wall which bears numerous narrow pits (Fig. 4A, B). The cells die off after being filled with tannin. The cells of the outer parenchyma remain alive and grow rounder to give room for small intercellular spaces (Fig. 4B). On the contrary, the middle and inner parenchyma mostly die off and obliterate and thus displace the bundles towards the inner epidermis (Fig. 4B). The bundles constitute a rather

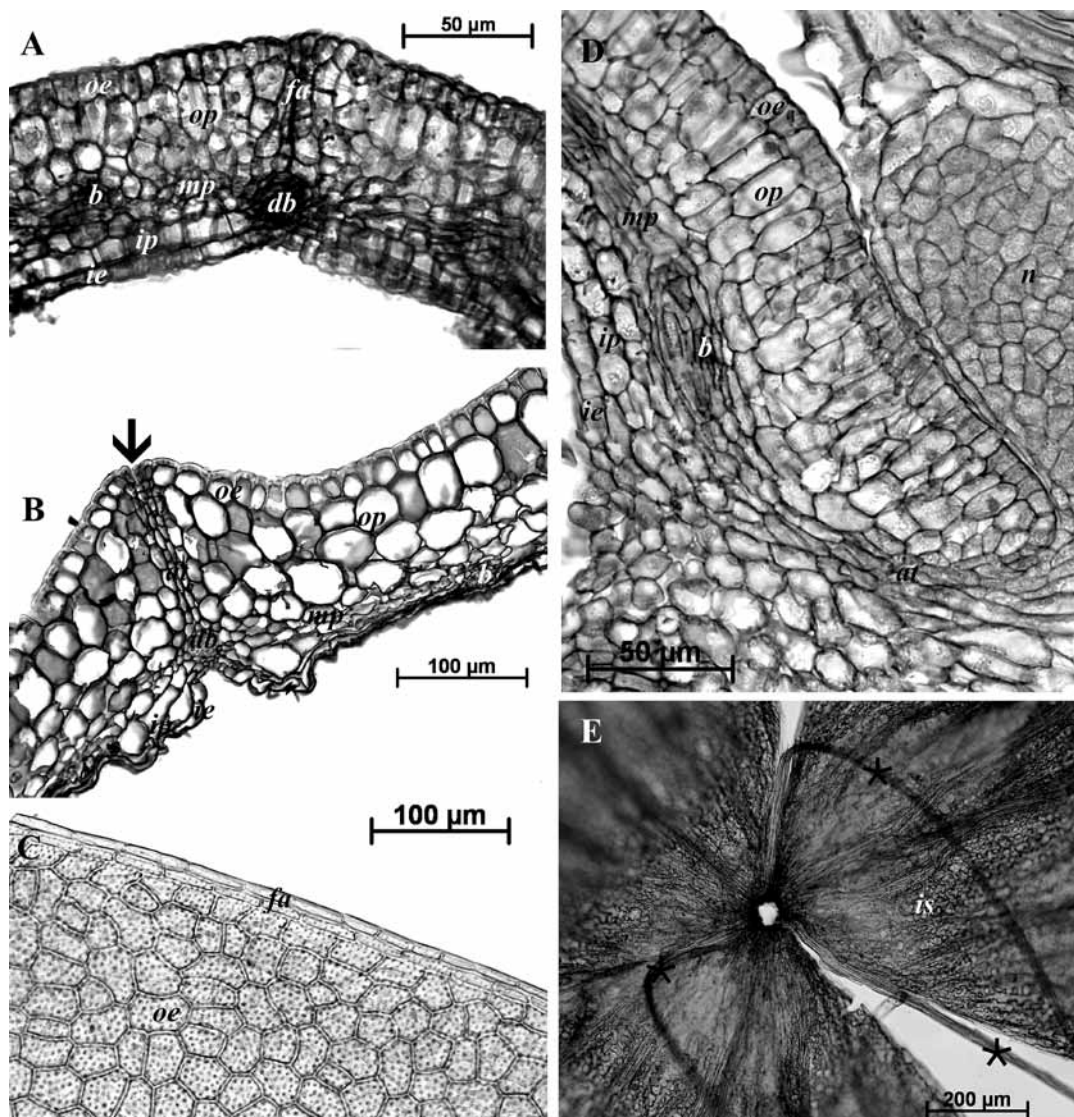
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Figure 5. Dehiscence sites of the seed vessel of *Talinum paniculatum*. A – longitudinal fault; B – split outer epidermis and longitudinal abscission tissue; C – edge of the outer semi-valve, appearance; D – developing circumscissile abscission tissue; E – overhead view of the inner semi-valve. at – abscission tissue; b – vascular bundle; db – dorsal bundle; fa – fault; ie – inner epidermis; ip – inner parenchyma; is – inner semi-valve; mp – middle parenchyma; n – nectary; oe – outer epidermis; op – outer parenchyma; arrow – split outer epidermis; asterisc – separated dorsal bundle.

dense net due to numerous anastomoses (Fig. 4C). The dorsal bundles sharply contrast with the others in having a solitary, mostly discontinuous vessel (Fig. 4D) or even no vessel (Fig. 4E). Instead, these bundles consist of slender long fibers with thickened lignified cell walls and slit-like pits. Lobate cells of the inner epidermis maintain their thin cell walls, though slightly lignified, and die off and tangentially flatten (Fig. 4B, C).

Loculicidal dehiscence of the capsule by means of 3 longitudinal fissures is accompanied by basal circumscissile splitting of the fruit wall. The dehiscence sites are predestinated as seed vessel faults (Fig. 5A) when the embryo sacs are fertilized in the ovules. Three longitudinal stripes 3 to 4 cells wide develop in the outer epidermis along the dorsal bundles. The cells of the stripes

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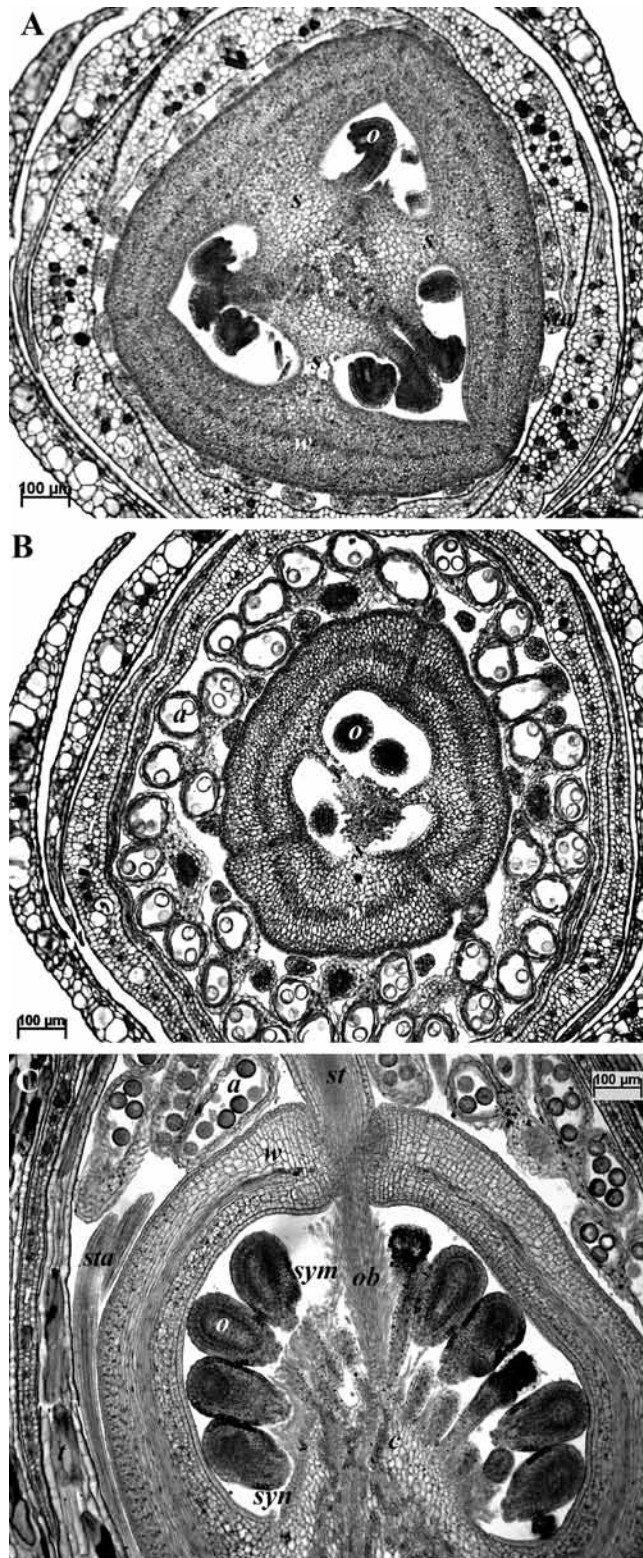


Figure 6. Ovary of *Talinum triangulare*. A – cross-sectioned synascidiate zone; B – cross-sectioned symplicate zone; C – longitudinally sectioned ovary. *a* – anther; *c* – column; *o* – ovule; *ob* – obturators; *s* – septa; *st* – style; *sta* – stamen; *sym* – symplicate zone; *syn* – synascidiate zone; *t* – tepal; *w* – ovary wall.

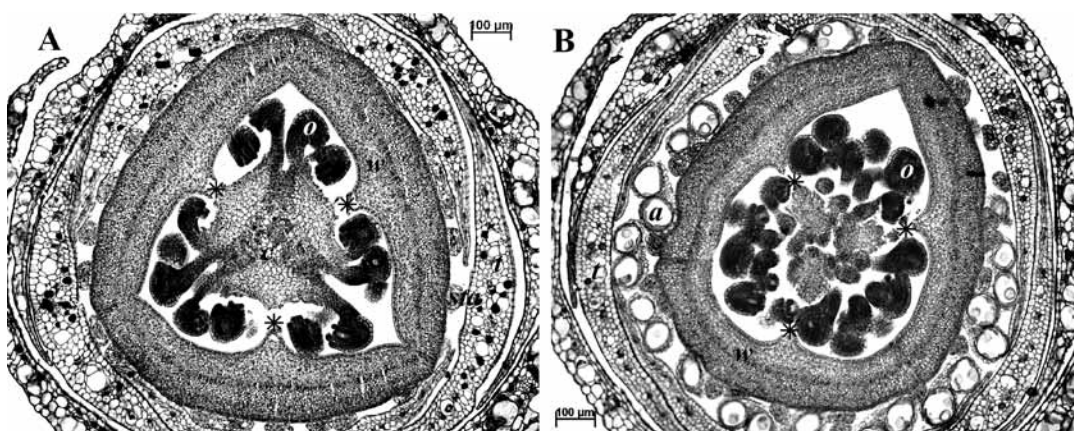
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Figure 7. Decaying septae in the ovary of *Talinum triangulare*. A – synascidiate zone; B – symplicate zone. *a* – anther; *c* – column; *o* – ovule; *sta* – stamen; *t* – tepal; *w* – ovary wall; *asterisc* – destroyed septae.

elongate longitudinally, thicken their outer cell wall, lignify and die off (Fig. 5B, C). Each stripe is underlaid by a 3 to 4 cells thick plate of abscission tissue which is constituted by small anticlinally elongated cells with slightly thickened cell walls (Fig. 5B). Transverse circular plate of similar tissue arises in the outer parenchyma at the very base of the fruit wall (Fig. 5D).

Xerochasy is inherent in *T. paniculatum*. The loculicidal dehiscence is firstly indicated by separating cells of the fault of the outer epidermis due to the destruction of their middle lamellae (Fig. 5B). The fissure thus arisen progresses inwards the abscission tissue also due to the destruction of middle lamellae (Fig. 5B). Having arrived at the dorsal bundle the fissure bifurcates to skirt the dorsal bundle on both sides and thus to loose it from seed vessel tissues (Fig. 5E). Fissuring of the middle and inner parenchyma near the dorsal bundle results from ruptured cells. The inner layer cells of the outer parenchyma rupture tangentially and result in the separation of the outer semi-valve from the inner one. The 3 longitudinal fissures intrude only upon the middle parenchyma of the fruit wall at the very top of the capsule. Thereof, the outer semi-valves completely detach each other while their inner counterparts remain connate (Fig. 5E). The basal circumscissile fissure also develops to the middle parenchyma of the seed vessel. All the fissures, viz 3 longitudinal, tangential and basal circumscissile ones, join and cause shedding the outer semi-valves off (Fig. 1C). The decayed semi-valves slightly bend inwards. Their longitudinal bending resembles the transverse one (Fig. 1C).

The inner semi-valves remain fastened to the receptacle at their connate tops by means of dorsal bundles. They additionally remain directly connate with the receptacle at their bases for a few days (Fig. 1C). Separate seeds mostly stay in the capsule for this period, but a few of them might be disseminated through the loculicidal fissures. Thereafter, the inner semi-valves break off basally from the receptacle and hang on the dorsal bundles (Fig. 1D). Incidentally, they bend longitudinally inwards. As a result, loculicidal fissures get wider and a rather large basal orifice appears while the capsule volume contracts. Gradual dissemination is thus enabled (Fig. 1D).

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The 3-merous gynoecium is syncarpous sensu LEINFELLNER (1950) (Fig. 6). The distal symplicate zone is approximately twice as long as the basal synascidiate one (Fig. 6C). 3 distal longitudinal

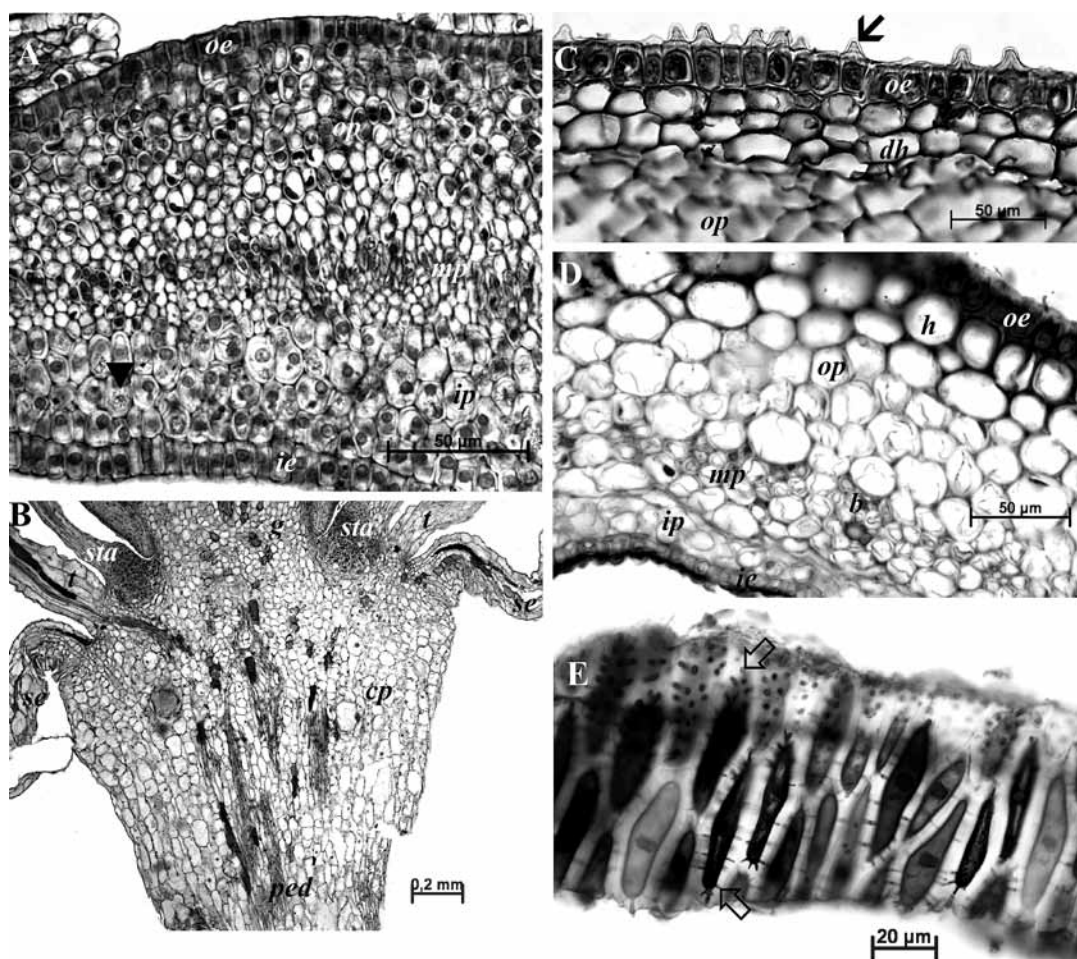


Figure 8. Seed vessel and pedicel of *Talinum triangulare*. A – cross-sectioned ovary wall; B – longitudinally sectioned pedicel; C – cross-sectioned outer epidermis; D – cross-sectioned unripe seed vessel; E – tangentially sectioned outer epidermis of mature capsule. *b* – bundle; *cp* – cortical parenchyma; *dh* – developing hypodermis; *g* – gynoeceum; *h* – hypodermis; *ie* – inner epidermis; *ip* – inner parenchyma; *mp* – middle parenchyma; *oe* – outer epidermis; *op* – outer parenchyma; *ped* – pedicel; *se* – sepaloid; *sta* – stamen; *t* – tepal; *arrowhead* – calcium oxalate druse; *arrow* – papilla; *double arrow* – pit.

shallow dorsal grooves on the ovary surface change downwards into 3 weak basal ridges. Only the synascidiate zone is fertile, but most ovules are lifted upwards to the symplicate zone by their long funiculi (Fig. 6A, C). There are 25 to 65 (rarely up to 90) ovules per ovary. Nearly all of them give rise to seeds. The ovary septae decay in both, the synascidiate (Fig. 7A) and symplicate (Fig. 7B) zones and the central column arises (Fig. 7A) when megasporocytes develop in the ovules. Dense trichomic obturators develop on the column (Fig. 6C). They grow up to the capsule roof to intermix with similar obturators which grow downwards from the ovary soffit just under the style base. The columnar and roof obturators combined continue the transmitting tissue of the style (Fig. 6C).

Five anatomical-histological zones become distinguishable when the embryo sacs are fertilized in ovules. These are (Fig. 8A): • outer epidermis; • 5 to 8-layered larger-celled outer parenchyma; • 5 to 8-layered small-celled middle parenchyma traversed by numerous provascular strands;

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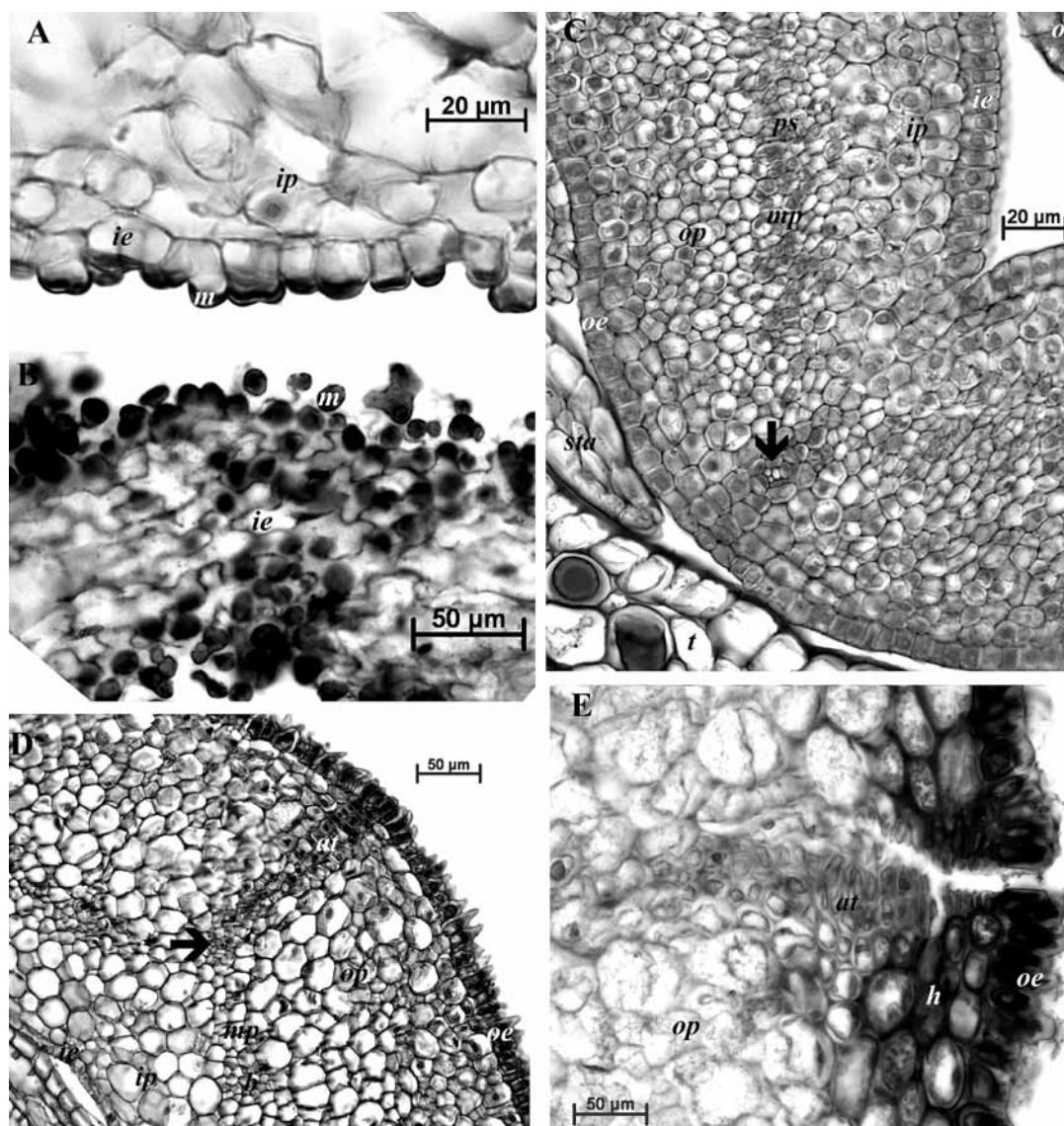


Figure 9. Ovary and seed vessel of *Talinum triangulare*. A – cross-sectioned inner epidermis of nearly ripe seed vessel; B – inner epidermis of nearly ripe seed vessel, appearance; C – underdeveloped ovary wall; D – developing fault of the ovary wall; E – longitudinal fault of the underdeveloped seed vessel. at – abscission tissue; b – bundle; h – hypodermis; ie – inner epidermis; ip – inner parenchyma; m – mamilla; mp – middle parenchyma; o – ovule; oe – outer epidermis; op – outer parenchyma; ps – provascular strand; sta – stamen; t – tepal; arrow – dorsal bundle.

- 3 to 5-layered inner parenchyma which has many cells containing one calcium oxalate druse per cell, and
- inner epidermis.

Fruit ripening coincides with pedicel bending and thickening nearby the capsule (Fig. 1G). The thickening is caused by intensive proliferation of the cortical parenchyma of the pedicel (Fig. 8B). The ripe capsule is globular, 5 to 6 mm in diameter, light yellow, crimson-striate and papillate (Figs 1G, 8C, 9D, E). The outer epidermis remains alive until the capsule dehisces. Its cells are indistinctively 5 to 6-gonal and lignified and have straight anticlinal cell walls (Fig. 8E). The outer cell walls are highly thickened and bear numerous narrow pits (Figs 8E, 9E). One narrow

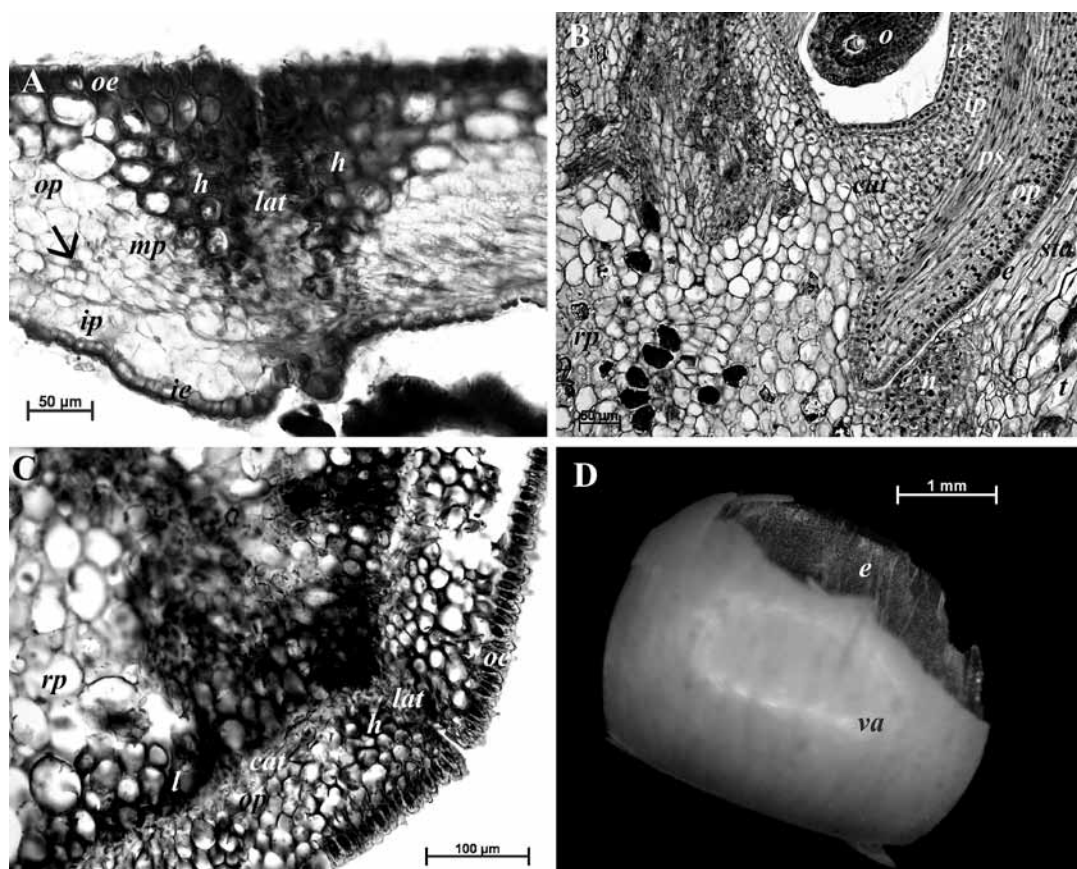


Figure 10. Abscission tissue and artificially split valve in *Talinum triangulare*. A – longitudinal fault; B – developing basal circumscissile abscission tissue; C – joined longitudinal and circumscissile faults; D – tangentially split valve. *cat* – circumscissile abscission tissue; *e* – endocarp; *h* – hypodermis; *ie* – inner epidermis; *ip* – inner parenchyma; *l* – longitudinal resistant tissue of the receptacle; *lat* – longitudinal abscission tissue; *mp* – middle parenchyma; *n* – underdeveloped nectar; *o* – ovule; *oe* – outer epidermis; *op* – outer parenchyma; *ps* – provascular strand; *rp* – receptacle parenchyma; *sta* – stamen; *t* – tepal; *va* – valve; *arrow* – bundle.

conic papilla is situated in the middle of the outer cell wall of epidermal cells (Figs 8C, 9E). Some epidermal cells contain abundant tannin. They constitute the above-mentioned crimson striae. The outer part of the outer parenchyma changes into lignified hypodermis (Fig. 8D) of cells with thickened cell walls. This tissue is 1 to 2-layered nearly throughout but it is distinctly thicker at the seed vessel faults (future loculicidal fissures) (Figs 9E, 10A). Its cells also remain alive until fruit dehiscing. Sub-hypodermal outer parenchyma consists of chloroplast-bearing thin-walled cells (Figs 8C, D, 9E). The middle parenchyma changes a little (Fig. 8D). The provascular strands differentiate into tiny bundles of a few constituents (Fig. 9D). The dorsal bundles develop before the other bundles (Fig. 9C), but they are hardly detectable in more advanced seed vessels (Fig. 9D). The inner parenchyma dies off and obliterates (Figs 9A, 10A). Cells of the inner epidermis become lobate and mammillate and develop a thickened lignified inward cell wall (Fig. 9A, B).

The capsule dehisces loculicidally by means of 3 longitudinal dorsal fissures and a circumscissile basal fissure. Specific longitudinal and basal circumscissile faults of the seed vessel start developing when the megasporocytes arise in the ovules (Figs 9D, 10B). Three stripes of the outer epidermis

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4 to 5 cells wide differentiate in the places of longitudinal faults. Their constituent cells are elongated longitudinally and lignified and they have thickened outer cell walls. The stripes split through middle lamellae long before capsule's dehiscing (Fig. 9E). A 2 to 4 cells thick plate of abscission tissue of small tangentially flattened thin-walled cells develops in the hypodermis and outer parenchyma under each epidermis stripe (Fig. 9D, E). The plates are flanked at both sides by a thickened, multilayered hypodermis (Fig. 10A). The basal abscission tissue consists of anticlinally flattened cells and stretches from the outer epidermis to the inner one (Fig. 10B). Cells of the receptacle tissue that adjoin this abscission tissue thicken and lignify their cell walls during capsule's ripening (Fig. 10C).

Capsule dehiscence is xerochasic. It is caused by destroying the middle lamellae in the outer epidermis and abscission tissue (Fig. 9E) and by rupturing cells of the middle and inner parenchymas and the inner epidermis, respectively. When the capsule has ripened, all the predetermined fissures, viz 3 longitudinal dorsal and one circumscissile, impetuously progress to intersect each other (Fig. 10C) and to separate 3 valves. The latter are thrown out because of their sharp longitudinal inward bending (Fig. 1H) and catapult seeds up to 0.5 m. Massive upper receptacle and column bearing numerous dried funiculi remain after disseminating (Fig. 1J). Tangential splitting of the fruit wall doesn't take place naturally. However, the outer semi-valves can artificially be separated from the inner ones by means of straightening bent valves (Fig. 10D). Such rupturing irregularly progresses through the middle parenchyma. Thereof, this parenchyma and its traversing bundles are partly in the outer semi-valves and partly in the inner semi-valves (Fig. 10D).

Discussion

The ovary wall generally consists of the outer and inner epidermis, a homogeneous parenchyma in between and provascular/vascular bundles up to the period the embryo sacs are fertilized in ovules (ROTH 1977). Both investigated *Talinum* species contrariwise have 5 distinct anatomical-histological zones in their ovary walls already at the stage the megasporocytes develop in the ovules. These zones are provisional, however, and differently change in these species.

Epicarp and endocarp, which separate by fruit dehiscing, are routinely distinguished in the seed vessel of *T. paniculatum* and some other *Talinum* species (CAROLIN 1987; KIGER 2001; FERGUSON 2001; BAIR et al. 2006; NYFFELER & EGGLI 2010) instead of nearly universal recognizing exo-, meso- and endocarp (ROTH 1977). Because the term 'epicarp' completely equals the term 'exocarp' (ROTH 1977; MELIKJAN & DEVJATOV 2001), the fruit of *T. paniculatum* must be considered to have no mesocarp. However, ROTH (l.c.) states that seed vessel always splits tangentially through the interface between the meso- and endocarp. Therefore, the mesocarp must be attributed to the fruit of *T. paniculatum*. Solution of the appeared contradiction is rather complicated because there is no universal concept of the exocarp and endocarp either, so far.

The exocarp is thought (ROTH l.c.) to be either the outer (rarely multilayered) epidermis of the fruit or – more often – the outer epidermis combined with one to several hypodermic layers that are all similar in consistency and jointly form a protective skin of the fruit. The 'epicarp' of *T. paniculatum* is constituted by a lignified, died off outer epidermis and a thin-walled, chloroplast-bearing, live outer parenchyma. Therefore, it certainly does not fit both canonical concepts of the exocarp. Integrity of the 'epicarp' is only caused by distinctive tangential dehiscence of the fruit. As far as we know, dehiscence mode has never been considered a criterion for distinguishing exo-,

meso- and endocarp. There is only the outer epidermis of the *T. paniculatum*'s seed vessel that is worth being considered to be an exocarp irrespectively of the accepted concept of the exocarp.

The endocarp is similarly interpreted as either the inner 1 to multilayered epidermis of the fruit (homogeneous endocarp) or this epidermis combined with some subepidermal layers (ROTH 1977). The latter are similar to the inner epidermis in their consistency or rather different from it but sharply contrast with inner tissues (heterogeneous endocarp) (ROTH l.c.). The inner epidermis, inner and middle parenchymas of the seed vessel of *T. paniculatum* are all similar in consistency because they remain unlignified but die off and obliterate. Due to these traits, the complex of the inner epidermis and inner and middle parenchymas essentially differs from the outer parenchyma which stays intact up to the fruit dehiscence. That is why we consider the whole inner semi-valve to be a heterogeneous endocarp.

The outer parenchyma of the seed vessel constitutes neither exocarp nor endocarp thus identified. This parenchyma zone is worth being interpreted as mesocarp.

We distinguished 3 distinct zones of the seed vessel of *T. paniculatum* on the base of a consistency, not of a generic criterion. If we had prioritized generic criterion, we would have outlined exocarp s. str. (= outer epidermis), endocarp s. str. (= inner epidermis) and mesocarp of 2 quite different zones, viz outer parenchyma and combined middle and inner parenchymas, respectively. We would additionally have elaborated a special term to denote the complex of the inner epidermis (= endocarp) and both inner and middle parenchymas (= part of mesocarp) that is a real structural-functional unit in ripe fruit. We believe such a complicated denotation is unreasonable.

Then, the heterogeneous endocarp of the inner epidermis, inner and middle parenchymas, mesocarp of the outer parenchyma and exocarp of the outer epidermis are worth being recognized in the seed vessel of *T. paniculatum*. The endocarp constitutes the inner semi-valves of the capsule, while mesocarp and exocarp jointly constitute the outer ones. The outer semi-valve should be compared to the epicarp if only the term 'epicarp' is re-defined and considered non-synonymous with the term 'exocarp'. Such a re-comprehending of the term 'epicarp' seems to be unpractical, however.

The consistency criterion must be applied to analyze the seed-vessel structure in *T. triangulare* in order to make results completely comparable to those concerning *T. paniculatum*. The inner and middle parenchymas are more similar to the outer parenchyma in the former species than their counterparts in the latter one. However, they can reasonably be contrasted to the outer parenchyma even in *T. triangulare*. Indeed, the longitudinal plates of the abscission tissue develop only in the outer parenchyma zone (Figs 9D,E, 10A). The dorsal fissures accordingly proceed inwards through middle lamellae of the abscission tissue in the outer parenchyma zone and through tearing cells of the middle and inner parenchymas. Moreover, the seed vessel of *T. triangulare* can artificially be split tangentially by means of forcible straightening of shed, bent valve (Fig. 10D). Such a splitting mostly affects the interface between the outer and the middle parenchymas, though it is less regular in this species than that in *T. paniculatum* (some parts of the middle parenchyma and bundles remain connate with the outer parenchyma). Therefore, we believe that the middle and inner parenchymas and the inner epidermis constitute together the inner unit of the seed vessel which is worth being termed 'heterogeneous endocarp'. The lignified hypodermis is dissimilar from the outer parenchyma in its consistency, but it is similar to the

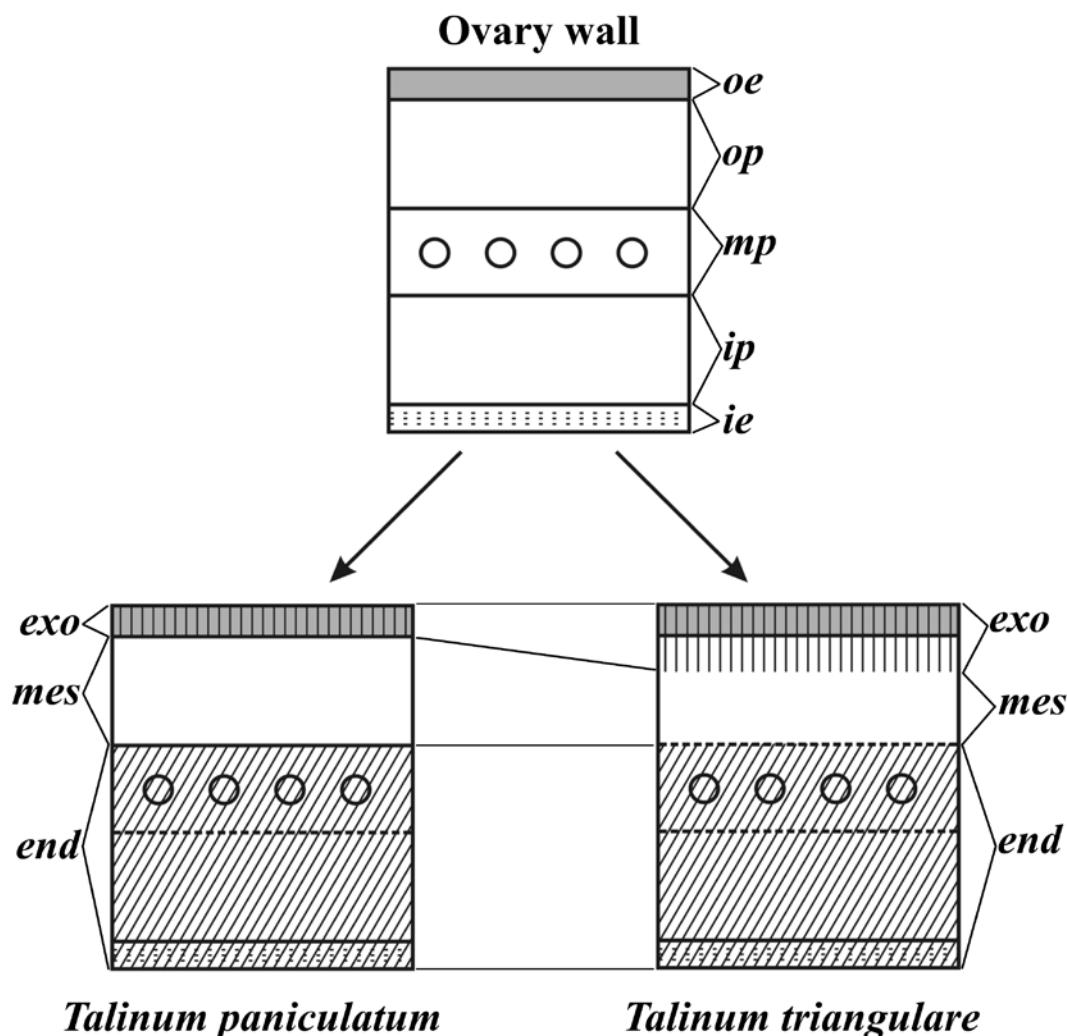
Fruit of *Talinum*

Figure 11. Homologies of the seed vessel constituents of the two *Talinum* species. *end* – endocarp; *exo* – exocarp; *ie* – inner epidermis; *ip* – inner parenchyma; *mes* – mesocarp; *mp* – middle parenchyma; *oe* – outer epidermis; *op* – outer parenchyma.

lignified outer epidermis. Then, the parenchymal mesocarp equals the inner part of the former outer parenchyma of the ovary wall.

The exo-, meso- and endocarp of *T. triangulare* thus considered differently correspond to their counterparts in *T. paniculatum* (Fig. 11). The heterogeneous endocarps of the two species are exactly homologous. The mesocarp of *T. triangulare* is a defective homologue sensu GEGENBAUR (1898) of the mesocarp of *T. paniculatum*. On the contrary, the exocarp of *T. triangulare* is an augmentative homologue sensu GEGENBAUR (l.c.) of the exocarp of *T. paniculatum*.

We believe that the above-mentioned difference between the two investigated species correlates with different modes of their fruit dehiscence. Decayed (semi-)valves show that their inward bending can be a key factor of fruit dehiscing. The necessary forces must be generated by interplay of contractile and resistant tissues due to their uneven deformations of xerochasy (ROTH 1977). We speculatively discuss such interplay as follows (Figs 12–14):

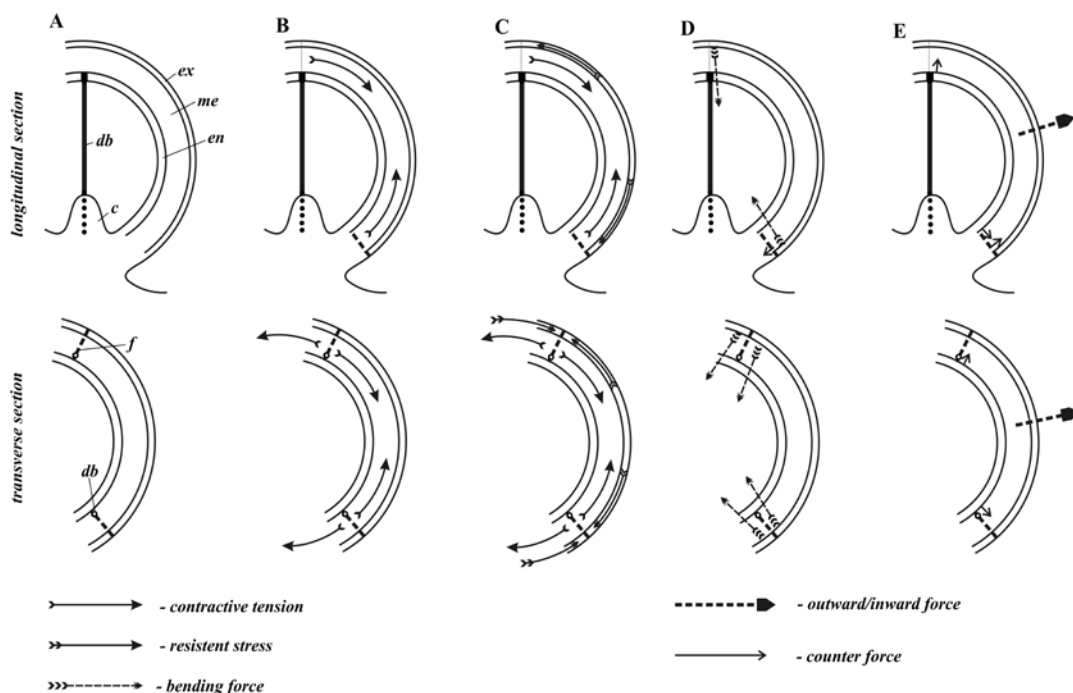


Figure 12. Presumable stresses and forces in the outer semi-valves in *Talinum paniculatum*. A – ripe seed vessel before desiccation; B – contractive tensions in the mesocarp; C – resistant stresses in the exocarp; D – bending forces; E – counter forces of the endocarp and outward force in the outer semi-valves. *c* – column; *db* – dorsal bundle; *en* – endocarp; *ex* – exocarp; *f* – fault; *me* – mesocarp.

In *T. paniculatum*, only 1-layered lignified exocarp is hard enough to be a resistant tissue. Softer unlignified meso- and endocarp are both contractile tissues (Fig. 12A). However, the endocarp of obliterated parenchyma differs in its consistency from the mesocarp of undestroyed parenchyma, so it functions separately from the latter. The meso- and exocarp surely constitute a functional unit.

When the mesocarp shrinks due to desiccation, contractive longitudinal and circular belt tensions arise (Fig. 12B). Counteracting resilient stresses develop reciprocally in the exocarp (Fig. 12C) because the exocarp is much less shrinkable. The preformed faults of splitting exocarp and underlying masses of abscission tissue are weak parts of the seed vessel. The circular belt tension easily exceeds strength of the seed vessel in these sites to separate the future outer semi-valves from each other (Fig. 13E). (As the edge of developing fissure concentrates stress (GORDON 1978), the dorsal fissures thus appeared are provoked to intrude inwards into the endocarp. This intruding is also promoted by the circular belt contractive tension in the endocarp.) The circular belt tension accordingly disintegrates (Fig. 12C). The contractive tension of the mesocarp and the resilient stress of the exocarp summarize to give rise to inward bending forces in the predetermined outer semi-valves (Fig. 12D).

The bending outer semi-valves press mostly on the receptacle and also on the endocarp. This inward pressure must induce counteracting resilient forces which affect the outer semi-valves (Fig. 12E). These forces will later on cause ascendant shedding of the outer semi-valves (Fig. 13E). The bending of semi-valves thus obstructed must also result in outward force (Fig. 12E).

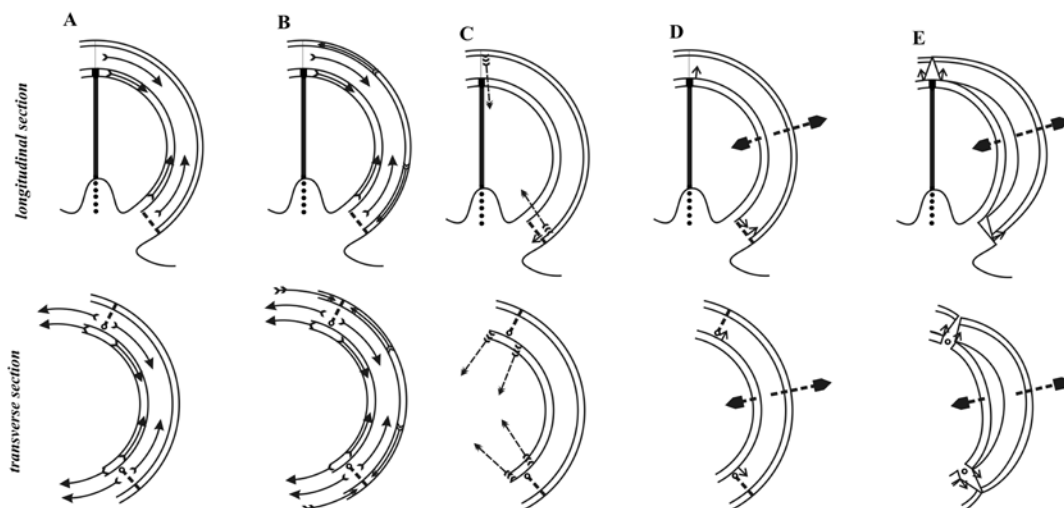
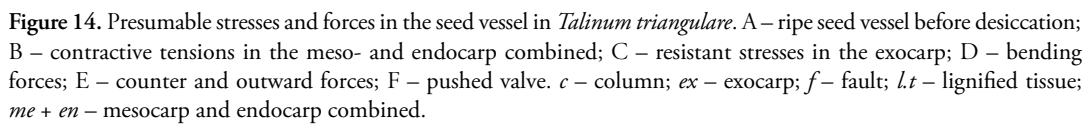
Fruit of *Talinum*

Figure 13. Presumable stresses and forces in the inner semi-valves (endocarp) in *Talinum paniculatum*. A, B – contractive tensions; C – bending forces; D – inward force in the endocarp; E – tangential splitting of the seed vessel; for other explanations see Fig. 12.

The endocarp shrinkage by desiccation causes inner longitudinal and belt tensions (Fig. 13A, B), the latter promoting loculicidal splitting of the endocarp into 3 fragments. The inward bending forces arise in the endocarpic fragments (Fig. 13C). These fragments are probably not able to participate coherently in seed vessel bending, however, because they remain fixed at their bases and tops. Instead, the longitudinal shrinking of the endocarp can rather cause a tendency towards flattening. Inward force must be generated in the endocarp by its flattening (Fig. 13D). The inward force in the inner endocarpic proto-semi-valve and the outward one in the outer mesocarpic proto-semi-valve are likely to provoke a tangential rupturing of the seed vessel (Fig. 13E). Advancing shrinkage of the inner semi-valves after decaying of the outer semi-valves could subsequently make them break off the receptacle.

In *T. triangulare*, the exocarp also functions as resistant tissue and the meso- and endocarp act as contractile tissues, but force patterns in the seed vessel seem to be less complicated (Fig. 14). In the heterogeneous endocarp, only the former inner parenchyma mostly obliterates while the former middle parenchyma remains alive. This parenchyma is thus similar but not identical in its consistency and strength with the mesocarpic parenchyma. Besides, there are neither rigid dorsal bundles that fix the endocarp's top nor a continuous endocarp's top. The endo- and mesocarp are thereof able to deform coherently and to contribute to generalized contractive forces (Fig. 14B). The lignified exocarp withstands these forces (Fig. 14C). As a result, the seed vessel tends to inward bending (Fig. 14D). 3 dorsal faults in the seed vessel make the belt stress discontinuous and enable the proto-valves to bend inwards separately (Fig. 14B–E).

The explosive xerochasic dehiscence of the fruit needs accumulated stress in the seed vessel in advance (ROTH 1977). Such an accumulated stress discharges by means of instantaneously rupturing of the seed vessel just after the stress has surpassed the strength of its tissues. The structure of the seed vessel of *T. triangulare* is certainly suited to accumulating stress. Only the former inner parenchyma obliterates in the endocarp of this species. The former middle parenchyma of the endocarp remains alive and is rather similar in its consistency to the mesocarp's



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parenchyma. Besides, there are no rigid dorsal bundles in the endocarp. Then, the endocarp and the mesocarp can both act jointly as contractile tissue. The endo- and mesocarps in *T. triangulare* are thicker than their counterparts in *T. paniculatum*. Therefore, their coherent shrinkage causes tensions in the seed vessel of *T. triangulare* that must be higher than those in the seed vessel of *T. paniculatum*. The exocarp of *T. triangulare* is thicker and more resistant than the exocarp of *T. paniculatum*. Thicker contractile and resistant tissues in the former species surely induce higher stress in the seed vessel. A thickened exocarp, which flanks 3 longitudinal faults of the seed vessel, is likely to prevent premature loculicidal dehiscing and thus enables stress to be accumulated. The lignified tissue that adjoins the basal circular abscission tissue also promotes stress accumulation (Fig. 14C). Additionally, it concentrates the stress in this abscission tissue because it withstands the seed vessel thinning of desiccation.

Accumulated stresses generate inward bending forces in the seed vessel of *T. triangulare* (Fig. 14D) which seem to be much higher than those in the seed vessel of *T. paniculatum*. The transverse bending forces mostly cause separation of the valves from each other. The longitudinal bending forces cause separations of the valves from the receptacle and induce counter force in the latter (Fig. 14E). This counter force is necessary to push the valves away (Fig. 14E, F). That is why the longitudinal bending of the valves completely suppresses the transverse one (Fig. 1H).

Tangentially rupturing of the seed vessel is a scanty character of the angiosperms (ROTH 1977), but it is typical of a few segregates of the former Portulacaceae (CAROLIN 1987). These segregates are rather distant relatives. Therefore, tangentially rupturing of the seed vessel is not a synapomorphic trait of traditional Portulacaceae. Hence, the ancestor of Portulacaceae s. ampl. did not have such a character. *Talinum* is a basalmost portulacaceous member, so it is expected to retain ancestral traits of the fruit dehiscence. Then, the seed vessel structure of *T. triangulare* tempts a botanist to consider it plesiomorphic, because the seed vessel does not split tangentially under natural conditions.

However, the distinctive dorsal bundles in the seed vessel of *T. paniculatum* must be a key agent of dehiscence mode of the species. Such bundles unlikely evolved from highly reduced ones which are inherent in *T. triangulare*. On the contrary, the seed vessel structure of *T. triangulare* can be derived from that of *T. paniculatum*. There is close correspondence between both species in developmental pathways of their endocarps though only the inner parenchyma obliterates and the middle one remains alive in the seed vessel of *T. triangulare*. Partially obliterated endocarp must be less expedient for generating distinctive stress patterns in the seed vessel that is necessary for explosive dehiscence of the capsule. Then, obliteration of the inner parenchyma of the endocarp in *T. triangulare* is worth being considered rather a trace of the structure of ancestor's seed vessel than an adaptation to dehiscence mode of its fruit. The fruit of the ancestor of *T. triangulare* thus must have had a tangentially splitting seed vessel similar to the seed vessel of modern *T. paniculatum*.

The dorsal bundles certainly do not play a role in explosive dehiscence of the capsule. On the contrary, rigid dorsal bundles would make such a dehiscence difficult. Therefore, highly reduced dorsal bundles in *T. triangulare* are a quite natural result of evolving explosive dehiscence of its fruit. Reduction of these bundles seems to have been facilitated by having nearly lost their conductive function in favor of a mechanical one in the presumed ancestor's fruit which could be likened to the fruit of modern *T. paniculatum*.

We believe that seed vessel structure of *T. triangulare* is advanced and derivable from that of *T. paniculatum* and very many *Talinum* species, but not vice versa. Advancement of the *T. triangulare* fruit is also confirmed by molecular phylogeny of the genus *Talinum* (APPLEQUIST et al. 2006; NYFFELER 2007; NYFFELER & EGGLI 2010). *T. paniculatum* must retain ancestral design of the seed vessel and dehiscence mode, both fitting to passive prolonged dissemination. Ballistic dissemination probably evolved in *T. triangulare* and caused changes of its seed vessel structure, viz thickening of the seed vessel, decreasing obliteration of the endocarp, thickening of the resistant exocarp by means of inclusion of the outer mesocarp, reducing of the dorsal bundles, coherent shrinkage of the meso- and endocarp and reinforcement of the seed vessel faults by lignified tissue. All changes must have resulted in preventing from tangential rupturing of the seed vessel, in accumulating stress in the seed vessel and in explosive 3-valvate dehiscing of the capsule.

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Address of the authors:

Dr Tatiana D. Veselova
Khalima Kh. Dzhililova
Prof. Dr Alexander C. Timonin
Department of Higher Plants
Faculty of Biology
Lomonosov Moscow State University
Vorobyevy Gory 1 (12)
119992 Moscow
Russia
E-mail: timonin58@mail.ru

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