

Reproductive anatomy and relationships of *Setchellanthus caeruleus* (*Setchellanthaceae*)

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Summary

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Floral, seed, and fruit anatomy of the unispecific Mexican genus *Setchellanthus* are described. The genus has floral features that are characteristic of some traditionally defined *Capparales* or close allies of an expanded order *Capparales*, viz., a (5-)6(-7)-merous flower with a 3-merous gynoecium and an androecium comprising (5-)6(-7) fascicles of stamens that develop centrifugally; a short androgynophore and well-developed gynophore; a 3-loculed gynoecium with a 3-lobed style and 3 conduplicate valves that separate from the vascular placental column at maturity much as do the valves of *Cleome* or *Brassicaceae*. *Setchellanthus*, however, has straight seeds with a spatulate embryo and a non-fibrous exotegmen; it lacks the reniform seeds with fibrous exotegmen characteristic of the core *Capparales*. Vascular bundles in the fruit wall are amphivasal and show an extensive secondary growth that produces tracheids like those of the secondary xylem of stems; bordered pits are present in the wall of the inner epidermis cells. The floral and seed anatomy as well as the distinctive fruit anatomy support a position of *Setchellanthus* that is near-basal to the core *Capparales*.

Introduction

Setchellanthus Brandege, comprising only the rare *S. caeruleus* Brandege, has been an enigmatic genus with respect to its systematic position (Iltis, 1999; Karol & al., 1999) and was thus in need of extensive studies of its systematic characters. The present paper describes the floral, seed, and fruit anatomy of *Setchellanthus*, which had been little studied. Although material available is limited in quantity and variety of developmental stages, it provides significant morphological information and allows us to evaluate the phylogenetic position of the genus in an "expanded" concept of *Capparales* (Dahlgren, 1975; Rodman & al., 1993), adding to evidence from basic morphology (Iltis, 1999), *rbcL* sequence analysis (Karol & al., 1999), pollen morphology (Tomb, 1999), and wood anatomy (Carlquist & Miller, 1999).

Material and methods

Anatomical structures of flowers and seeds of *Setchellanthus caeruleus* from Cerros Sapioris near Torreón (*Iltis & Lasseigne 100*, *Iltis & al. 31081*, both at WIS), preserved in FAA, were studied by means of transversal and longitudinal microtome sections. For sectioning, several flower buds and mature seeds were dehydrated through a *t*-butyl alcohol series and embedded in Paraplast. Sections cut at 8-12 μm in thickness were stained with Heidenhain's haematoxylin, safranin, and fastgreen FCF, and mounted with Entellan. Fruits (same collections) prepared by Carlquist

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were sectioned at 12 μ m according to usual paraffin techniques. These sections were stained with a safranin-fastgreen combination.

Results

Flowers. – The flowers are actinomorphic and hypogynous (Iltis, 1999: fig. 1D-E), comprising a united calyx of (5-)6(-7) sepals fused into a pointed cap, (5-)6(-7)

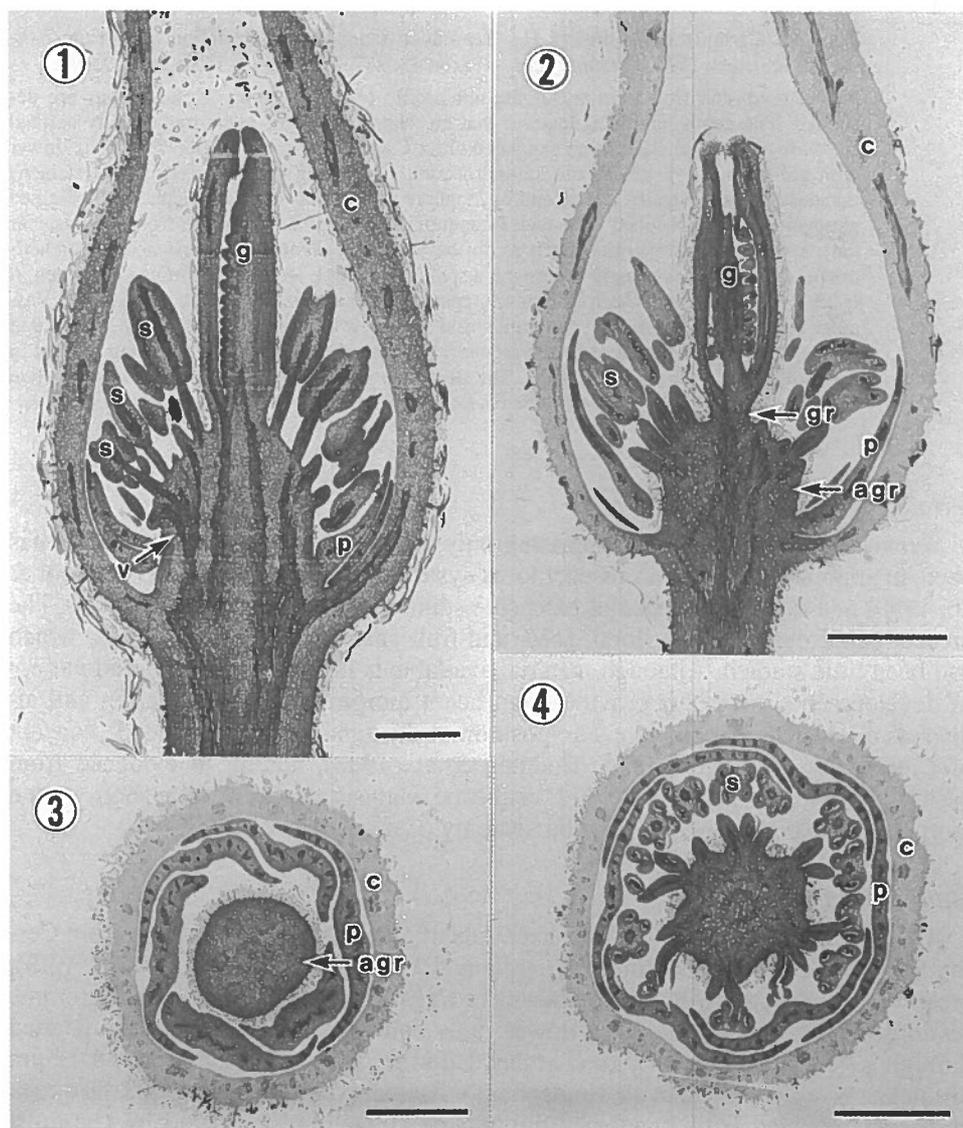


Fig. 1-4. Floral anatomy of *Setchellanthus*. – 1, Longitudinal section (LS) of young flower bud, showing centrifugal development of stamens. 2, LS of flower bud. 3, Transverse section (TS) of flower bud at the level of the androgynophore. 4, TS of flower bud; the stamens form 6 fascicles. – Abbreviations: agr, androgynophore; c, calyx tube; g, gynoecium; gr, gynophore; p, petal; s, stamen; v, vascular supply to stamens. – Scales equal 0.5 mm in Fig. 1 and 1 mm in Fig. 2-4.

free petals, 40-70 stamens, and a 3-locular gynoecium (Fig. 7). The calyx encloses the other floral elements until the flower opens, when it splits along 1 or 2 of the fusion sutures (Fig. 1-6). Its wall is 10-15 cells thick at its base. The flower has a very short androgynophore between the corolla and the androecium, which lengthens

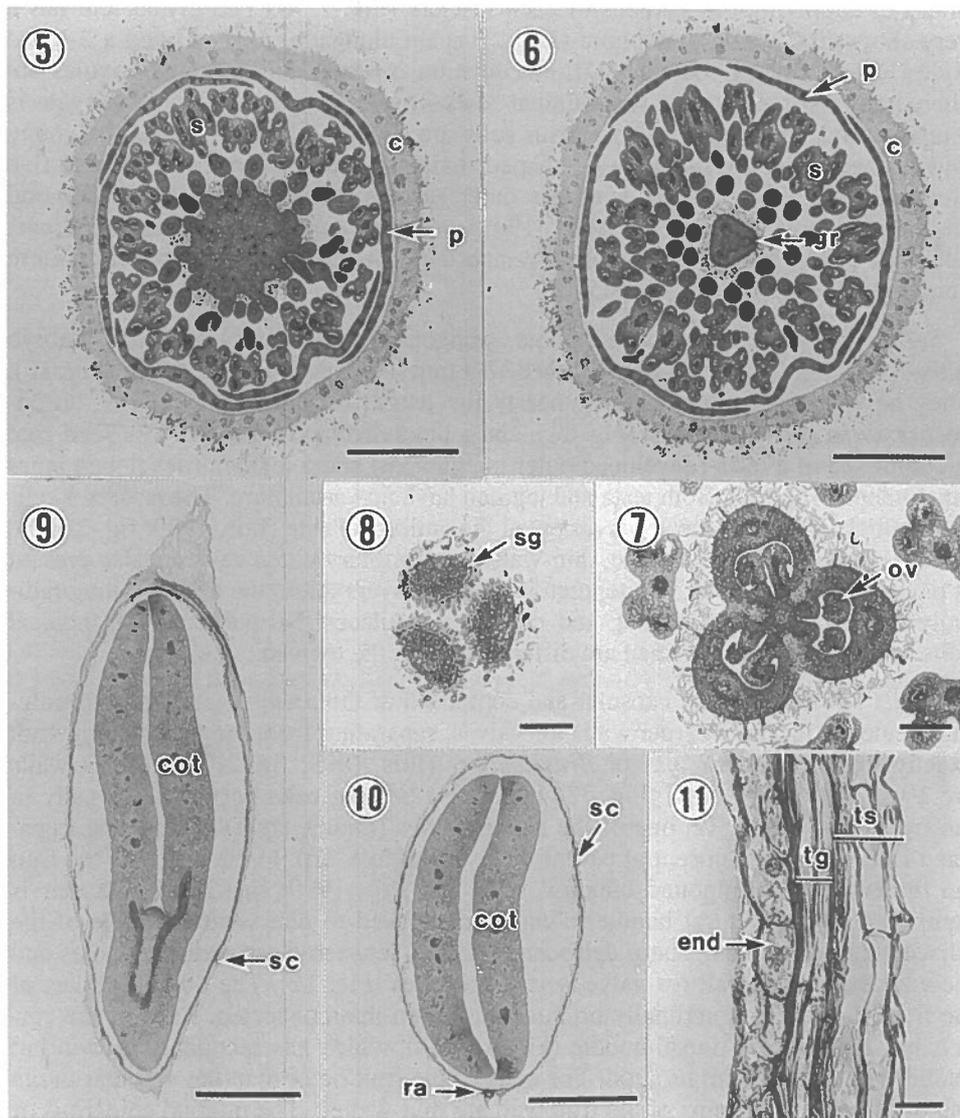


Fig. 5-11. Floral and seed anatomy of *Setchellanthus*. – 5, Transverse section (TS) of flower bud at the upper level of androecium. 6, TS of flower bud at the level of the gynophore. 7, TS of 3-carpellate gynoecium. 8, TS of style branches. 9, Longitudinal section (LS) of mature seed. 10, TS of mature seed. 11, LS of mature seed coat. – Abbreviations: c, calyx tube; cot, cotyledon; end, endosperm; gr, gynophore; ov, ovule; p, petal; ra, raphe; s, stamen; sc, seed coat; sg, stigmatic and style branch; tg, tegmen; ts, testa. – Scales equal 1 mm in Fig. 5, 6, 9, and 10; 0.2 mm in Fig. 7 and 8; 20 μ m in Fig. 11.

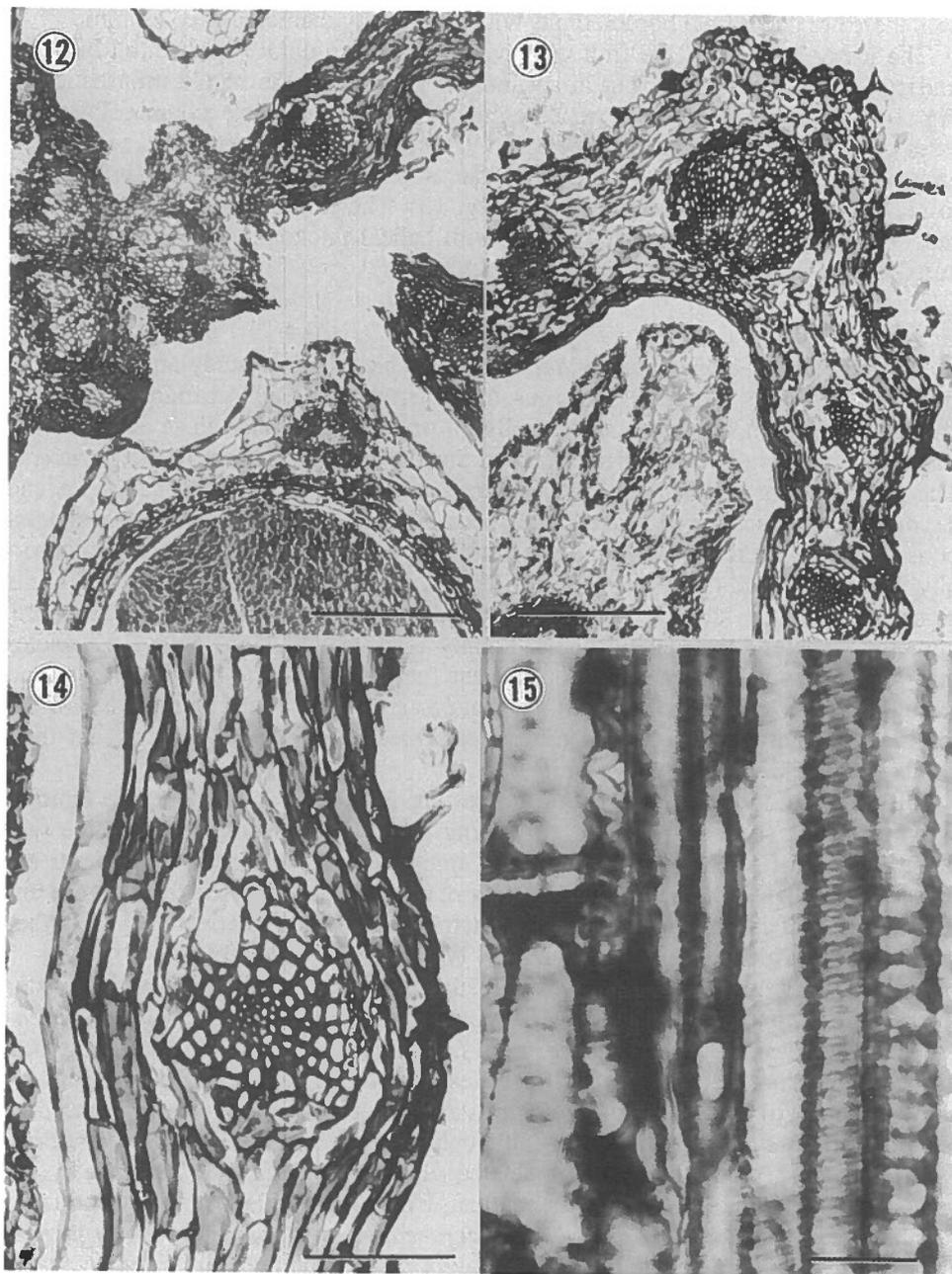
in fruit (Fig. 2; Iltis, 1999: fig. 2E). The stamens develop centrifugally (Fig. 1), and in the flower studied, which was 6-merous, formed six fascicles (Fig. 4). When examined in fruit, these stamens are arranged in (5-)6(-7) longitudinal (radial) double rows (Iltis, 1999: fig. 2E). The androgynophore has (5-)6(-7) vascular bundles arranged in a ring (Fig. 3); each bundle upwardly divides into several vascular branches supplying the stamens of each fascicle (Fig. 1, 4). The gynoecium has a very short stipe, i.e., a gynophore (Fig. 2), again elongating in fruit, and a 3-lobed style (Fig. 8; Iltis, 1999: fig. 2D). Placentation is axile, and numerous ovules are alternately disposed in two longitudinal rows in each locule (Fig. 7). The ovule is bitegmic and anatropous. No myrosin cells are found at least in tissues of young buds. Single-celled Malpighian (T-shaped) hairs with bases formed of four or five elongate epidermal cells occur on the outer surface of the calyx, gynoecium, and androgynophore (Carlquist & Miller, 1999), with the arms of the terminal cell parallel to the long axis of the gynoecium, and the basal cells on the gynoecium more numerous, forming a longer stalk.

Seeds. – Mature seeds are exarillate, straight (Fig. 9), with a spatulate embryo (Iltis, 1999: fig. 2I), bilaterally flattened, 7-9 mm long and 2.5-4 mm wide (Fig. 10). They have a small raphe running nearly the length of the seed (Fig. 10), an endosperm one cell-layer thick (Fig. 11), and a dicotyledonous embryo. The seed coat is comprised of a testa (developed outer integument) and a tegmen (developed inner integument) (Fig. 11). Both testa and tegmen have no vasculature. The testa is 3 cell-layers thick in most of the seeds except at the antiraphal side (Iltis, 1999: fig. 2I); the cells are longitudinally elongate, thin-walled, but solitary pitted cells are also present at places within the testa. The tegmen is 2-3 cell-layers thick; the cells are longitudinally elongate and thin-walled, and collapsed at places. No particular mechanical cells as in a fibrous exotegmen are differentiated in the tegmen.

Fruits. – The fruits are capsular and composed of three united carpels with bulging locules, with the 3 carpel walls, or valves, separating from the placentae in fruit exactly like those of *Cleome* or *Brassicaceae* (Iltis, 1999: fig. 2F). The fruit walls are 10-12 cell layers thick (Fig. 13, 14). Druse-bearing cells occur occasionally in the fruit wall. In Fig. 12, one of the carpel valves (middle right) has become separated from the common central part of the fruit (middle left). In the centre of the fruit are three paired “compound bundles” (Fig. 12; Iltis, 1999: fig. 2G). Each pair is composed of one ventral bundle of one carpel fused to one ventral bundle of the adjacent carpel. A clear, sharp dehiscence occurs between these central bundles and the adjacent carpel wall (or valve) and its bundles (Fig. 12). The 10-13 bundles of the fruit wall are longitudinally oriented and often interconnected. Each of the carpels has a prominent dorsal bundle (Fig. 13, top), which has secondary growth but retains a collateral configuration. The cells of the fruit other than the vascular tissue and the internal epidermis of the fruit wall are thin-walled. The internal epidermis of the fruit wall (Fig. 14) consists of cells that are horizontally elongate and, on drying,

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Fig. 12-15. Fruit anatomy of *Setchellanthus*. – 12, Transverse section (TS) of fruit, showing the three central, compound ventral bundles (middle left) and a portion of a seed with the two cotyledons in TS (bottom). 13, TS of fruit, showing the dorsal bundle of a carpel (top) and other bundles



(right, lower half). 14, A bundle of the fruit wall, showing the radial arrangement of tracheary elements produced by secondary growth and (to the right of the seed portion on the left edge) the inner fruit wall epidermis. 15, Portion of longitudinal section of a bundle in the fruit wall, showing a helically thickened vessel (right), fibriform, pitted vessels (a perforation plate is at bottom centre), and rectangular tracheary elements with bordered pits (left). – Scales equal 300 μm in Fig. 12-13; 100 μm in Fig. 14; and 20 μm in Fig. 15.

produce a very glossy, slippery, finely striate surface. In the walls of these epidermal cell, there are occasional bordered pits with a pit cavity diameter of c. 2.5 μm .

The lesser bundles of the fruit wall (valve), between dorsal and ventral bundles, undergo secondary growth, but in an unusual pattern. As the bundle transection in Fig. 14 shows, the cambium extends around the bundle, adding xylem cells on all sides of the primary xylem. The primary xylem cells mostly have helical wall thickenings (Fig. 15). Secondary growth adds tracheary elements that range from fibriform to rectangular with traverse end walls (Fig. 15). The tracheary elements added by secondary growth are pitted rather than with helical thickenings. The pits are bordered and have a pit cavity diameter of 2-2.5 μm .

Discussion

The flowers of *Setchellanthus caeruleus* available to us for study are presumably basically 6-merous although 5-merous or 7-merous flowers, invariably with a 3-merous gynoecium, do occur occasionally. 3- or 6-merous is found in several *Resedaceae* and sporadically in other members of the *Capparales*, but not in *Capparaceae*. The *Moringaceae* (with parietal placentation), *Akaniaceae*, *Bretschneideraceae*, and *Tropaeolaceae* (with axile placentation), for example, possess a 3-locular, syncarpous gynoecium like *Setchellanthus*, a condition which may constitute a plesiomorphy in the expanded order *Capparales*. *Setchellanthus* is further characterised by its elongating yet very short androgynophore and well developed but short gynophore, numerous stamens that develop centrifugally and are united in (5-)6(-7) fascicles that originate presumably by dedoublement (chorisis) from (5-)6(-7) initials, and axile placentation. Many of these floral features are found in one or the other of the families of Dahlgren's expanded order *Capparales* (Rodman, 1991a, b), but their combination in *Setchellanthus* is unique.

In fruit anatomy, there are several interesting features. For instance, the bundles show extensive secondary growth, producing tracheids much like those of the secondary xylem of stems; the bundles are of amphivasal nature; and bordered pits are present in the walls of the inner epidermis of the fruit wall. These features are unusual in general and indicative of the distinctness of *Setchellanthus*, which is further supported by evidence from wood anatomy (Carlquist & Miller, 1999).

Molecular evidence (Karol & al., 1999) suggests that *Setchellanthus* may be sister to the core *Capparales* (*Bataceae*, *Brassicaceae*, *Gyrostemonaceae*, *Koerberliniaceae*, *Resedaceae*, and *Tovariaceae*) plus *Limnanthaceae*. Seed anatomy supports this interpretation. Reniform seeds (or at least internally reniform, i.e., with an incumbent embryo) with a fibrous exotegmen are characteristic of the core *Capparales* (except *Bataceae* and *Brassicaceae* – although there the embryos are often reniform, with the deep seed coat invagination deleted: Iltis, 1999; Corner, 1976; Tobe & Raven, 1991; and unpublished data). In contrast, like the other glucosinolate-producing families such as *Akaniaceae*, *Bretschneideraceae*, *Limnanthaceae*, *Moringaceae*, and *Tropaeolaceae*, *Setchellanthus* has straight rather than reniform seeds, a spatulate embryo, and a non-fibrous rather than fibrous exotegmen. The reniform seeds with a fibrous exotegmen are probably a specialisation, a synapomorphy of the core *Capparales*. *Setchellanthus*, despite numerous similarities to the latter in floral morphology, appears to be an early offshoot from a common ancestor with the core *Capparales* and close allies. All or part of the unusual fruit anatomical features, like the distinctive wood anatomy, might represent autapomorphies. The most fascinat-

ing question that the mature *Setchellanthus* fruit poses is the nature of its dehiscence: namely, is the separation of the valves from the placental vascular column homologous with the capparaceous (cleomoid) siliqua with its free-falling valves and persistent replum, or has it an independent and analogous origin in the two groups? The fact that each of the three vascular bundles of the central placental column is a fusion product composed of one ventral strand each from two adjoining carpels, and the fact that the androecium is composed of six basic initials, suggest that the former assumption might well be correct.

Acknowledgements

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