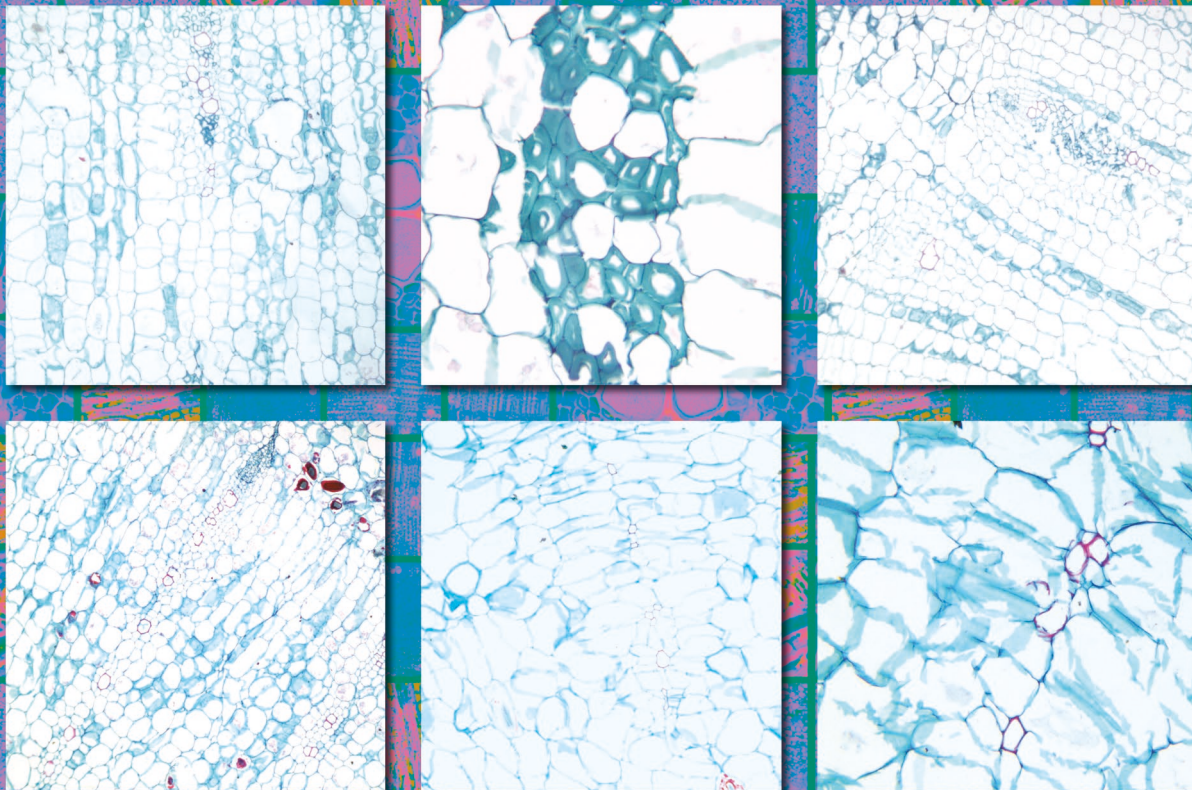


Stem and caudex anatomy of succulent plant species

Giovanna E. ROMERO



DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR*: Bruno David
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / *EDITOR-IN-CHIEF*: Thierry Deroin

RÉDACTEURS / *EDITORS*: Porter P. Lowry II; Zachary S. Rogers

ASSISTANT DE RÉDACTION / *ASSISTANT EDITOR*: Emmanuel Côté (adanson@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT*: Emmanuel Côté

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD*:

P. Baas (Nationaal Herbarium Nederland, Wageningen)
F. Blasco (CNRS, Toulouse)
M. W. Callmander (Conservatoire et Jardin botaniques de la Ville de Genève)
J. A. Doyle (University of California, Davis)
P. K. Endress (Institute of Systematic Botany, Zürich)
P. Feldmann (Cirad, Montpellier)
L. Gautier (Conservatoire et Jardins botaniques de la Ville de Genève)
F. Ghahremaninejad (Kharazmi University, Téhéran)
K. Iwatsuki (Museum of Nature and Human Activities, Hyogo)
A. A. Khapugin (Tyumen State University, Russia)
K. Kubitzki (Institut für Allgemeine Botanik, Hamburg)
J.-Y. Lesouef (Conservatoire botanique de Brest)
P. Morat (Muséum national d'Histoire naturelle, Paris)
J. Munzinger (Institut de Recherche pour le Développement, Montpellier)
S. E. Rakotoarisoa (Millenium Seed Bank, Royal Botanic Gardens Kew, Madagascar Conservation Centre, Antananarivo)
É. A. Rakotobe (Centre d'Applications des Recherches pharmaceutiques, Antananarivo)
P. H. Raven (Missouri Botanical Garden, St. Louis)
G. Tohmé (Conseil national de la Recherche scientifique Liban, Beyrouth)
J. G. West (Australian National Herbarium, Canberra)
J. R. Wood (Oxford)

COUVERTURE / *COVER*:

Réalisée à partir des Figures de l'article/*Made from the Figures of the article*.

Adansonia est indexé dans / *Adansonia is indexed in*:

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Adansonia est distribué en version électronique par / *Adansonia is distributed electronically by*:

- BioOne® (<http://www.bioone.org>)

Adansonia est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Adansonia is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish*: *Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie* sous-sections *Algologie, Bryologie, Mycologie, Comptes Rendus Palevol*

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2022
ISSN (imprimé / *print*): 1280-8571/ ISSN (électronique / *electronic*): 1639-4798

Stem and caudex anatomy of succulent plant species

Giovanna E. ROMERO

Herbario QCA, Escuela de Biología, Facultad de Ciencias Exactas y Naturales,
Pontificia Universidad Católica del Ecuador,
Av. 12 de octubre 3746 y Patria, Quito (Ecuador)
giovanna.e.romero.v@gmail.com

Submitted on 18 May 2021 | accepted on 28 August 2021 | published on 22 March 2022

Romero G. E. 2022. — Stem and caudex anatomy of succulent plant species. *Adansonia*, sér. 3, 44 (10): 81-90.
<https://doi.org/10.5252/adansonia2022v44a10>. <http://adansonia.com/44/10>

ABSTRACT

Succulent angiosperm plants are characterized by the presence of large amounts of water storage tissue as an adaptation to habitats where water is unavailable seasonally or in microhabitats where water is of limited access. In this study, I describe the anatomy of stem and caudex of ten species of succulent plants from eight plant families in the Rosids clade. There are two characteristics of wood among all species with single continuous cambium or successive cambium: 1) extensive parenchyma tissue in ray system and/or axial system; and 2) extensive thin-walled fiber tissue in the axial system. Out of ten species, five present proliferation of the parenchyma tissue in their radial system: *Ceropegia africana* R. Br., *Momordica rostrata* Zimm., *Oxalis megalorrhiza* Jacq., *Adenia glauca* Schinz and *Cyphostemma juttae* (Dinter & Gilg) Desc. Five species were fibrous-wood succulents: *Jatropha curcas* L., *J. macrantha* Müll. Arg., *Adenium obesum* (Forssk.) Roem. & Schult., *Pelargonium carnosum* (L.) L'Hér. and *Moringa drouhardii* Jum. Out of ten, one presents an axial system without visible fibers: *Cyphostemma juttae* (Dinter & Gilg) Desc. Despite to belong to seven different orders, the studied species show structural similarity: extensive parenchyma in the ray system and thin-walled fibers in the axial system. These results suggest multiple independent origins for the anatomical structure of succulence.

KEY WORDS

Succulence,
parenchyma,
fibers,
vascular cambium,
wood.

RÉSUMÉ

Anatomie de la tige et du caudex des espèces de plantes succulentes.

Les plantes angiospermes succulentes sont caractérisées par la présence de grandes quantités de tissu de stockage d'eau comme adaptation aux habitats où l'eau n'est pas disponible de façon saisonnière ou dans les microhabitats où l'eau est d'accès limité. Dans cette étude, je décris l'anatomie de la tige et du caudex de dix espèces de plantes succulentes de huit familles de plantes du clade des Rosides. Il existe deux caractéristiques du bois parmi toutes les essences à cambium continu unique ou à cambium successif: 1) un tissu de parenchyme étendu dans le système des rayons et/ou le système axial; et 2) un tissu fibreux étendu à parois minces dans le système axial. Sur dix espèces, cinq présentent une prolifération du tissu du parenchyme dans leur système radial : *Ceropegia africana* R. Br., *Momordica rostrata* Zimm., *Oxalis megalorrhiza* Jacq., *Adenia glauca* Schinz et *Cyphostemma juttae* (Dinter & Gilg) Desc. Cinq espèces étaient des succulentes à bois fibreux : *Jatropha curcas* L., *J. macrantha* Müll. Arg., *Adenium obesum* (Forssk.) Roem. & Schult., *Pelargonium carnosum* (L.) L'Hér. et *Moringa drouhardii* Jum. Sur les dix, une présente un système axial sans fibres visibles : *Cyphostemma juttae* (Dinter & Gilg) Desc. Bien qu'appartenant à sept ordres différents, les espèces étudiées présentent une similitude structurelle: un parenchyme étendu dans le système des rayons et des fibres à parois minces dans le système axial. Ces résultats suggèrent de multiples origines indépendantes à l'expression anatomique de la succulence.

MOTS CLÉS

Succulence,
parenchyme,
fibres,
cambium vasculaire,
bois.

TABLE 1. — Wood characteristics of stem and caudex in ten succulent plant species. Percentage of axial matrix vs radial matrix. Wood thickness measured from the beginning of the vascular cambium. Abbreviations: **S**, stem; **C**, caudex; **Pa**, parenchymatous wood; **F**, fibrous wood; **NA**, not applicable; **A**, absent; **P**, present. All measurements are in micrometers (μm) unless stated otherwise.

Taxa	Stem (S) Caudex (C)	Presence/ absence	Wood	Axial matrix ~ (%)	Radial matrix ~ (%)	Wood thickness (μm)	Successive cambium	Single continuous cambium
GENTIANALES/APOCYNACEAE								
<i>Adenium obesum</i> (Forssk.) Roem. & Schult.	S C	P P	NA F	NA 73	NA 27	NA 4493	A A	P P
<i>Ceropegia africana</i> R. Br.	S C	P P	NA Pa	NA 13	NA 87	NA 2405	A P	A A
CUCURBITALES/CUCURBITACEAE								
<i>Momordica rostrata</i> Zimm.	S C	P P	Pa Pa	27 33	73 67	2911 3417	P P	A A
MALPIGHIALES/EUPHORBIACEAE								
<i>Jatropha curcas</i> L.	S C	P P	NA F	NA 64	NA 36	NA 2531	A A	P P
<i>Jatropha macrantha</i> Müll. Arg.	S C	P A	F A	63 NA	37 NA	1060 NA	A NA	P NA
GERANIALES/GERANIACEAE								
<i>Pelargonium carnosum</i> (L.) L'Hér.	S C	P A	PF A	58 NA	42 NA	949 NA	A NA	P NA
BRASSICALES/MORINGACEAE								
<i>Moringa drouhardii</i> Jum.	S C	P A	F A	88 NA	12 NA	2025 NA	A NA	P NA
OXALIDALES/OXALIDACEAE								
<i>Oxalis megalorrhiza</i> Jacq.	S C	P A	Pa NA	44 NA	56 NA	1645 NA	A NA	P NA
MALPIGHIALES/PASSIFLORACEAE								
<i>Adenia glauca</i> Schinz	S C	P P	Pa Pa	39 27	61 73	506 6835	A P	P A
VITALES/VITACEAE								
<i>Cyphostemma juttæ</i> (Dinter & Gilg) Desc.	S C	P P	Pa Pa	15 14	85 86	2278 7848	A A	P P

INTRODUCTION

Xerophytes have developed many strategies to stand periods of drought (von Willert 1992; Mauseth 2004a; Srivastava 2002). These adaptations include succulence, carbohydrate storage, and crassulacean acid metabolism among others (Arakaki *et al.* 2011; Evans *et al.* 2014; Spicer 2014). Succulence evolved as an adaptation to limited water resource and, it is defined as the presence of tissue, in any plant organ, for storage of large volumes of water (Eggli & Nyffeler 2009; Arakaki *et al.* 2011; Ogburn & Edwards 2012). It originated independently in several lineages of angiosperms (Nyffeler & Eggli 2010) and has a wide phylogenetic distribution (Ávila-Lovera & Ezcurra 2016). It occurs in 32 orders, 83 families and represents 4% of the total number of angiosperm species (Nyffeler & Eggli 2010). There is high morphological variation of succulence (Evans *et al.* 2014) and sometimes it is not easy to recognize because the tissue is distributed continuously across organs (e.g., root, hypocotyl, epicotyl and shoot; von Willert 1992).

Wood succulence is characterized by proliferation of cells in secondary growth of single vascular cambium or successive cambium (Carlquist 2001). Proliferation is achieved by increasing the volume of individual cells and by increasing the number of cells (e.g., *Fouquieria*, *Adenia*) (Carlquist 2001; Hearn 2006). In single cambium, for example, rayless Crassulaceae has an axial parenchyma that form ground tissue while in *Moringa* (Moringaceae) there are wide bands of vasicentric paratracheal parenchyma. Apotracheal parenchyma with large cells is present in *Bombax*, *Adansonia* and *Chorisia* (Malvaceae) (Mauseth 1988; Carlquist 2001; Stevens 2001). In successive cambium, for example, multiseriate rays and conjunctive tissue have parenchyma that forms ground tissue in *Dendrosicyos socotrona* (Cucurbitaceae), *Adenia* (Passifloraceae), *Avicennia* (Acanthaceae) (Olson 2003; Hearn 2006; Carlquist 2007; Robert *et al.* 2011).

Succulent traits are the result of intricate relationships between morphology, physiology, and the environment (Eggli & Nyffeler 2009). Previous studies of succulent plants have focused on physiological traits (Ávila-Lovera &

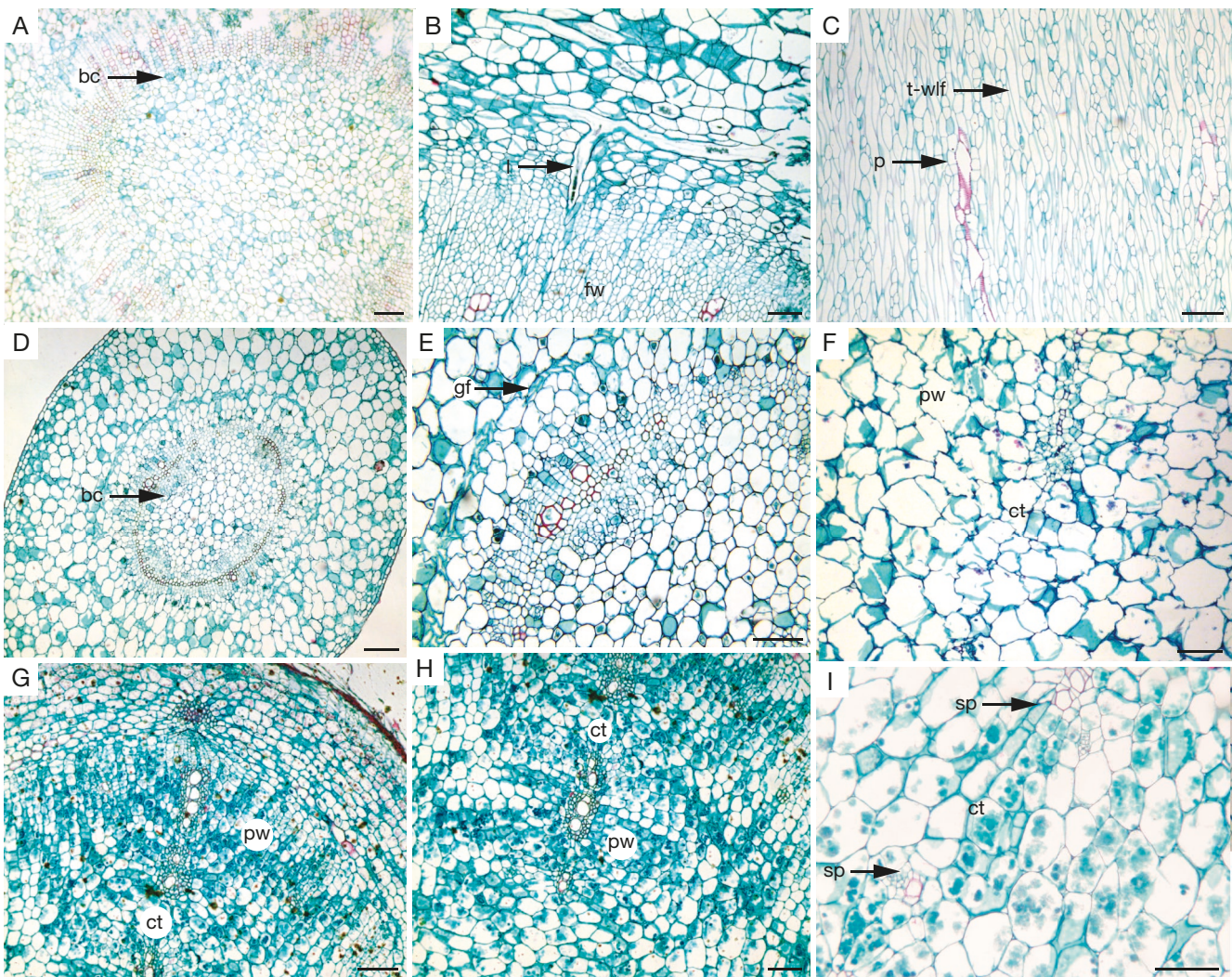


FIG. 1. — Transverse sections of stems and caudices, unless otherwise noted: **A–C**, *Adenium obesum* (Forssk.) Roem. & Schult.; **A**, stem, bicollateral bundle; **B**, caudex, cortex laticifers and fibrous wood; **C**, caudex, fibrous wood, thin-walled libriform fibers, tangential section; **D–F**, *Ceropegia africana* R. Br.; **D**, stem, bicollateral bundles; **E**, stem, extraxylary gelatinous fibers; **F**, caudex, conjunctive tissue, parenchyma cells are proliferated in wood; **G–I**, *Momordica rostrata* Zimm; **G**, stem, wood; **H**, caudex, wood; **I**, caudex, conjunctive tissue bordered by secondary phloem. Abbreviations: **bc**, bicollateral bundle; **l**, laticifer; **p**, parenchyma cells; **gf**, gelatinous fibers; **ct**, conjunctive tissue; **pw**, parenchymatous wood; **fw**, fibrous wood; **sp**, secondary phloem. Scale bars: 50 µm.

Ezcurra 2016; Ogburn & Edwards 2012, 2013), anatomical studies have focused on single families (e.g., Aizoaceae, Caricaceae, Cactaceae, Didiereaceae, Moringaceae) (Landrum 2001; Carlquist 1998; Sajeva & Mauseth 1991; Mauseth & Plemons 1995; Mauseth & Plemons-Rodriguez 1997, 1998; Anderson 2001; Hernandez-Hernandez *et al.* 2011; den Outer & van Veenendaal 1980; Olson & Carlquist 2001), few families (e.g., Cactaceae, Didiereaceae) (Arakaki *et al.* 2011), or genera (e.g., *Adenia*, *Euphorbia*, *Pelargonium*) (Hearn 2006, 2009b; Evans *et al.* 2014; van der Walt *et al.* 1987).

Comprehensive anatomical comparative reviews of angiosperms were presented by (Metcalf & Chalk 1950) and (Carlquist 2001). Comparative studies of the anatomy in non-woody succulents were published by (Mauseth 2004a). The aim of the present study was to describe the anatomy of wood in stems and caudices of ten plant species that belong to seven orders of the Rosids clade.

MATERIAL AND METHODS

PLANT MATERIAL

Taxonomic nomenclature follows IPNI (<https://www.ipni.org>) and Tropicos (<https://www.tropicos.org>). Ten species, representing seven orders of Rosids, were considered for this study (The Angiosperm Phylogeny Group *et al.* 2016) (Table 1). One plantlet specimen of each species was obtained from The Huntington Botanical Garden (California) and voucher specimens were deposited in the Plant Resources Center Herbarium (TEX). The exact age of the specimens was not provided, but it was estimated that they were few years old. Each specimen was dissected following (Mauseth & Plemons 1995; Mauseth 2004b) methodology.

LIGHT MICROSCOPY PREPARATION SAMPLES

The dissected samples were fixed in Navashin's solution, dehydrated through tertiary-butanol series, and embedded in

Paraplast® Plus. Each sample was cut at 12 to 20 µm using a rotary microtome and then mounted on microscope slides. Three voucher slides per cut were stored at James Mauseth laboratory slide collection numbered 401-421, 429 and 439 in University of Texas at Austin. One slide per sample was stained in safranin (1 g safranin, 50 mL 7-methoxyethanol, 7 mL Formalin. 1 g sodium acetate, 50 mL 50% EtOH) for about eight hours, then rinsed in water and treated for 5 min with 1% chromic acid in water. Rinsed in water again and quickly put through a series of dehydration EtOH. Treated for 8 s with Fast Green (0.5 g Fast Green, 50 mL abs EtOH. 25 mL xylene, 25 mL clove oil; stir overnight and filter before use), rinsed in abs EtOH. Then rinsed in a mixture of 25% clove oil, 33% xylene, and 42% abs EtOH. Finally, cleared for 10 min in a mixture of clove oil, xylene, and abs EtOH (2-parts, 1-part, 1-part) (Mauseth *et al.* 1984).

In order to quantify the relative amount of wood in transversal section, I used an ocular scale and then transformed its units to micrometers. Wood extent was measured from the edge of the vascular cambium to the pith; the sections on which the limit between the axial and ray systems was unclear were not measured. An arbitrary threshold of 50 % between axial and ray systems was used to assign wood to two categories: fibrous (> 50% of axial system) or parenchymatous (< 50% of axial system) to qualify the type of wood. These values should be interpreted with caution due to the sampling method and the fact there was only of one plant taken per each species. Also, other authors sample one or few specimens per species based upon availability: one, two, few, some, non-specified (Mauseth 2004b; Olson & Carlquist 2001; Carlquist 2001; Olson 2003; Seago *et al.* 2005; Hearn 2009b; Oladipo & Illoh 2012).

Parenchyma conjunctive tissue is not part of the axial or ray system since it is derived from a master cambium and is not from vascular cambium (Carlquist 2007). Therefore, conjunctive tissue was not measured to estimate the percentage of parenchyma in wood. Stem is defined as the axis of a plant (Mauseth 2003) and caudex is defined a swollen perennial stem at or near ground level (Evans *et al.* 2014).

TERMINOLOGY

In this study, the histological description and terminology of wood follows Mauseth (1988, 2003, 2004a, b) and Carlquist (2001, 2007, 2015).

RESULTS

All specimens had matured primary tissues and were several years old. Out of ten species, six developed caudices. Below I describe the anatomy of each species.

ADENIUM OBESUM (FORSSK.) ROEM. & SCHULT.

Stem cortex has sparse chloroplasts in the outer cells; laticifers are found throughout it and some druses occur in the inner part. Vascular cambium is visible. Wood is formed by some vessels, fibers, and parenchyma cells in the axial matrix. Rays

are multiseriate. There are bicollateral bundles (Fig. 1A). Pith has laticifers and a small number of druses throughout it.

Caudex cortex has sparse laticifers and amyloplasts (Fig. 1B). Cortex cells are proliferating. Wood is fibrous. Axial system is formed by: vasicentric parenchyma cells with mostly scalariform pitting, thin cell wall libriform fibers (Fig. 1B, C). Rays are uniseriate. Few laticifers are located intrusively between ray parenchyma cells. Pith has large parenchyma cells.

CEROPEGIA AFRICANA R. BR.

Stem cortex has chloroplasts in the outer part of cells. Vascular cambium has just formed; therefore, not much wood is present. Vascular cambium shows no distinction between axial and radial systems. Bicollateral bundles are closed to the pith (Fig. 1D). There is an almost uninterrupted ring of extraxylary gelatinous fibers (Fig. 1E). Pith has large parenchyma cells and some laticifers.

Caudex cortex has enlarged parenchyma cells. Wood is parenchymatous and formed by successive cambium. Conjunctive tissue and secondary phloem are characteristic of this type of cambium (Fig. 1F). The axial matrix has mainly parenchyma tissue and few solitary vessels. Multiseriate rays are proliferated. It is difficult to recognize ray or axial system due to proliferation of parenchyma cells in both systems. In addition, some dark granules and latex are found in some parenchyma cells in wood. Pith has an oval shape.

MOMORDICA ROSTRATA ZIMM.

Stem (Fig. 1G) and caudex (Fig. 1H, I) have similar anatomical features. Cortex cells have abundant chloroplasts, and the inner part has a ring of parenchyma cells that are lignified. Wood is parenchymatous, it has large amount of latex and is formed by successive vascular cambium (Fig. 1H, I). The axial matrix has scanty axial parenchyma, libriform, septate fibers (Fig. 2A), and solitary vessels with circular bordered pits (Fig. 2B). Rays are multiseriate and ray cells have undergone proliferation, making them to be confused with the conjunctive tissue. Bands of conjunctive tissue and ray parenchyma have formed a matrix of ground parenchyma. Secondary phloem has some functional cells, and few phloem cells are collapsed.

JATROPHA CURCAS L.

Stem cortex has scattered laticifers. Wood is just formed. Vascular cambium occurs in the entire circumference. Some phloem is visible. Pith has some amyloplasts.

Caudex cortex is chlorenchymatous and it has druses and scattered laticifers. Wood is diffused fibrous. The axial matrix is formed by solitary or two vessels with circular bordered pits (Fig. 2C-E), also it has thin secondary wall libriform fibers (Fig. 2F) and apotracheal unilateral parenchyma with abundant amyloplasts. Ray system is uniseriate with abundant amyloplasts (Fig. 2F). Secondary phloem ray parenchyma has begun to dilatate. Laticifers run parallel to the secondary phloem. Primary phloem fibers are above secondary phloem, these fibers are gelatinous fibers and have formed an incomplete ring around caudex circumference. Pith has large parenchyma cells with abundant amyloplasts.

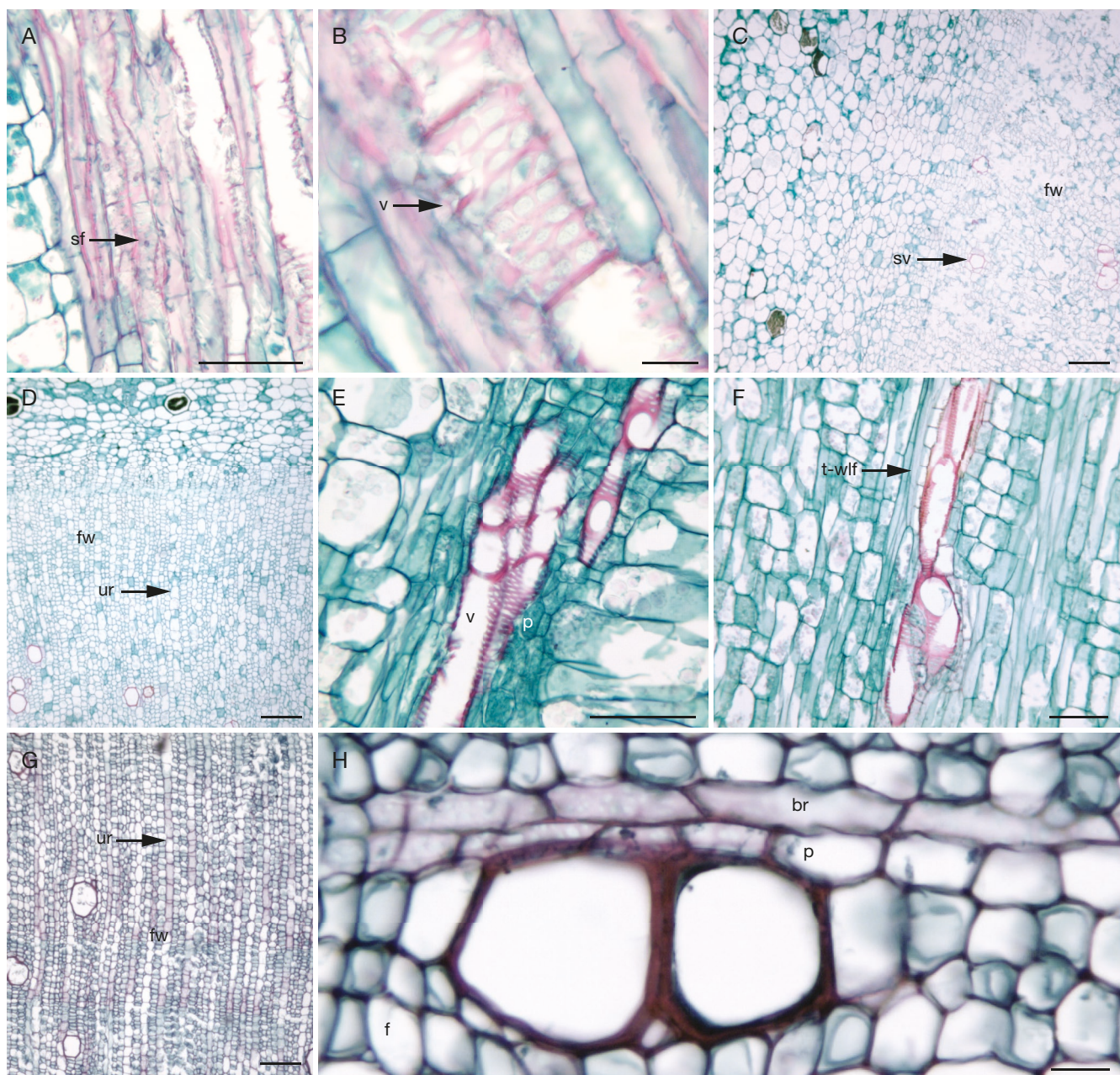


Fig. 2. — Transverse sections of stems and caudices, unless otherwise noted: **A, B**, *Momordica rostrata* Zimm; **A**, caudex, septate fibers, tangential section; **B**, caudex, vessels with bordered pits; **C-F**, *Jatropha curcas* L.; **C**, caudex, solitary vessels, wood; **D**, caudex, fibrous wood; **E**, caudex, vessels, radial section; **F**, caudex, thin-walled libriform fibers, parenchyma with amyloplasts, radial section; **G, H**, *Jatropha macrantha* Müll. Arg.; **G**, stem, diffuse fibrous wood, thin-walled libriform fibers, septate and gelatinous fibers; **H**, stem, axial and ray parenchyma. Abbreviations: **ur**, uniseriate ray; **br**, biseriate ray; **p**, parenchyma; **f**, fibers; **sp**, secondary phloem; **ct**, conjunctive tissue; **sf**, septate fibers; **v**, vessel; **lf**, libriform fibers. Scale bars: A, C-H, 50 µm; B, 10 µm.

JATROPHA MACRANTHA MÜLL. ARG.

Stem cortex cells have druses, tannins and in lesser number mucilage cells. Wood is diffused fibrous. Axial matrix is formed by libriform fibers, gelatinous fibers, septate fibers, scanty vasicentric and apotracheal parenchyma, also vessels with scalariform and circular bordered pitting. (Fig. 2G, H). Ray system is uniseriate. Ray parenchyma cells become lignified when meet the vessels and sometimes when ray cells are not close to vessels. There is little functional phloem and much of collapsed phloem has parenchyma cells and

scattered mucilage cells. Collapsed phloem is distorted due to the dilatation of the axial secondary phloem ray parenchyma. Pith was not fixed.

PELARGONIUM CARNOSUM (L.) L'HÉR.

Stem cortex has abundant tannins and some amyloplasts. Wood is diffused fibrous. Axial matrix is formed by: narrow bands of libriform fibers, wide lumen libriform fibers, apotracheal axial parenchyma, and helical, annular and mostly pseudoscalariform secondary walls with simple

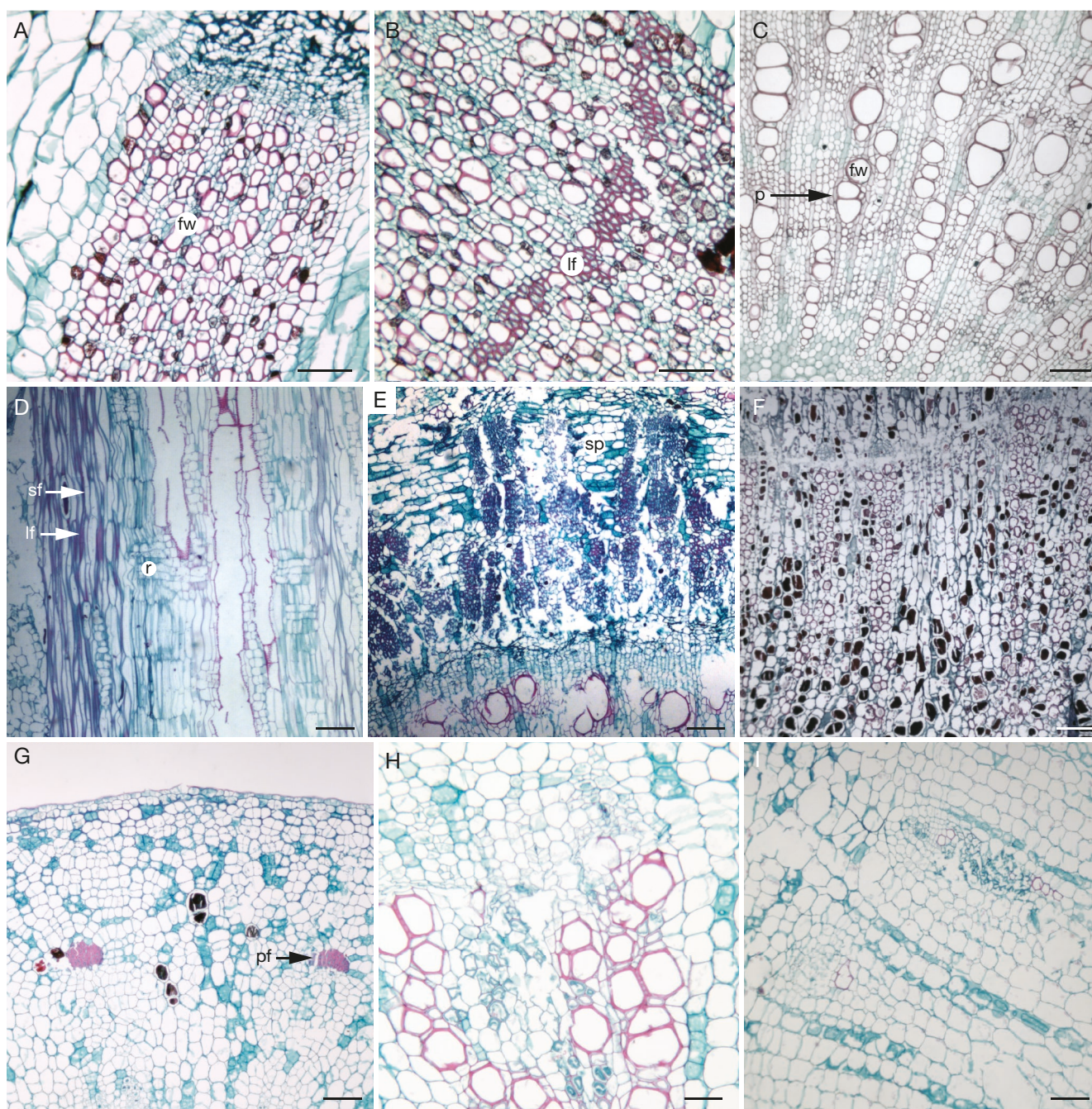


FIG. 3. — Transverse sections of stems and caudices: **A, B**, *Pelargonium carnosum* (L.) L'Hér.; **A**, stem, wood; **B**, stem, bands of libriform fibers; **C-E**, *Moringa drouhardii* Jum.; **C**, stem, diffused fibrous wood, lignification in ray parenchyma cells; **D**, stem, radial section; **E**, stem, secondary phloem dilatated; **F**, *Oxalis megalorrhiza* Jacq., stem, wood; **G-I**, *Adenia glauca* Schinz; **G**, green stem, cortex and phloem fiber caps; **H**, green stem, parenchymatous wood; **I**, caudex, parenchymatous wood. Abbreviations: **lf**, libriform fibers; **r**, rays; **p**, parenchyma cells; **fp**, fiber cap; **sp**, secondary phloem. Scale bars: 50 µm.

perforations vessels. Rays are multiseriate (Fig. 3A, B). Ray secondary phloem parenchyma is distorted. Pith has abundant tannins and few amyloplasts.

MORINGA DROUHARDII JUM.

Stem cortex has chloroplasts, druses and few idioblastic secretory cells. Wood is diffuse fibrous. The axial matrix consists principally of vessels, low secondary cell wall lignification libriform fibers, bands of interspaced scattered septate fib-

ers and bands of axial parenchyma cells. Axial parenchyma can be confused with low lignification libriform and septate fibers (Fig. 3C, D). Rays are uniseriate and certain degree of lignification occurs in ray parenchyma cells where vessels meet them. Axial secondary phloem has only a few rows of functional phloem. Rays of secondary phloem are uniseriate close to the cambium; farther from it, parenchyma rays are dilatated (Fig. 3E). Pith has two ducts lined with epithelium and druses are present.

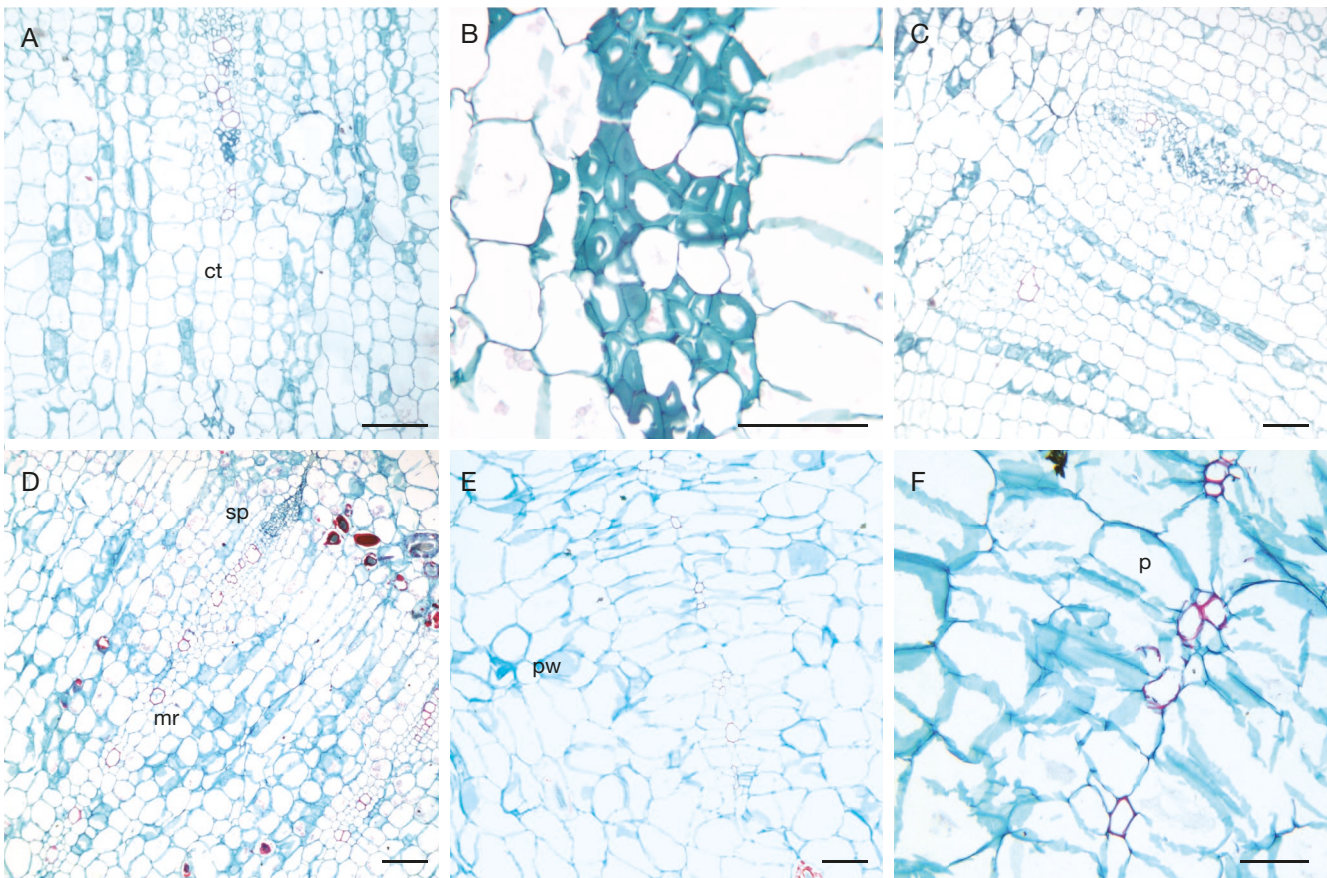


FIG. 4. — Transverse sections of stem and caudices, unless otherwise noted: **A–C**, *Adenia glauca* Schinz; **A**, caudex, conjunctive tissue; **B**, caudex, wood gelatinous fibers; **C**, caudex, parenchymatous wood; **D–E**, *Cyphostemma juttiae* (Dinter & Gilg) Desc.; **D**, stem, multiseriate rays; **E**, caudex, parenchymatous wood; **F**, caudex wood, vasicentric enlarged axial parenchyma. Abbreviations: **mr**, multiseriate rays; **sp**, secondary phloem; **ct**, conjunctive tissue; **p**, enlarged parenchyma cells. Scale bars: 50 µm.

OXALIS MEGALORRHIZA JACQ.

Stem cortex has scattered amyloplasts and ubiquitously tannins are found. Wood is parenchymatous. Axial matrix is formed by vessels, some paratracheal parenchyma cells, few fibers and tannins (Fig. 3F). Rays are multiseriate. Secondary phloem is collapsed. Pith has a star-shape, it has abundant tannins, amyloplasts and few druses.

ADENIA GLAUCA SCHINZ

Stem cortex has chloroplasts (Fig. 3G). Wood is parenchymatous. The axial matrix is formed by sparsely clusters of gelatinous, libriform fibers, parenchyma cells and vessels. Radial system uniseriate and multiseriate. Some uniseriate rays have lignified cells mainly where ray parenchyma cells meet the vessels. Clusters of fiber caps (primary phloem) are above every vascular bundle and appear separated of the vascular bundle due to expansion of parenchyma cells in between them (Fig. 3G, H). Functional secondary phloem is in each bundle. Pith was not fixed.

Caudex cortex has chloroplasts and some amyloplasts. Wood is parenchymatous and formed by successive cambium (Fig. 3I). In between each ring of vascular cambium, conjunctive tissue is present as bands of parenchyma cells (Fig. 4A). Axial system is formed by bands of libriform fibers, septate fibers,

gelatinous fibers (Fig. 4B), axial vasicentric parenchyma and scalariform or circular bordered pitting vessels. Ray system is proliferated multiseriate and amyloplasts are found in it. Some functional secondary phloem and few non-functional are in each vascular bundle (Fig. 4C). Pith was not available.

CYPHOSTEMMA JUTTAE (DINTER & GILG) DESC.

Stem cortex has raphide crystals that occur as idioblasts or in small groups (two to four) of cells. Wood is parenchymatous. Axial matrix is formed by vasicentric paratracheal parenchyma with no visible fibers and small clusters of two to four vessels. Rays are multiseriate. Ray cells have abundant starch grains (Fig. 4D). There is a certain degree of parenchyma cell proliferation in both systems. The secondary phloem rays are wide. Pith has raphide cells.

Caudex cortex has raphide cells that are found mainly as idioblasts near the stele. Wood is parenchymatous (Fig. 4E). Axial matrix is formed by confluent vasicentric parenchyma cells, scalariform vessels mostly solitary or in clusters of two to four cells, and no visible fibers. In the innermost wood, proliferation of vasicentric parenchyma becomes exceptionally larger (diameter of about 607 µm) compared with other paratracheal parenchyma (diameter of about 164 µm), (Fig. 4F). The enlargement of the paratracheal

cells varies from vessel to vessel. Rays are multiseriate. Ray parenchyma cells have abundant amyloplasts especially in areas close to vessels, whereas its abundance diminishes toward the center of the rays and near the pith. Axial and ray parenchyma systems are extremely similar, giving an appearance of a continuous ground tissue of parenchymatous wood. There is collapsed phloem in each bundle. Pith has raphide cells as idioblasts.

DISCUSSION

In this research, I found two wood characteristics in stems and caudices: 1) extensive parenchyma tissue in axial and/or ray system; and 2) extensive thin-walled fiber tissue: libriform, septate, gelatinous fibers and parenchyma in the axial system. Also, six species developed caudex and three of them had successive cambium (*Ceropegia africana*, *Momordica rostrata* and *Adenia glauca*). Below, I discuss the findings.

PARENCHYMA TISSUE

Axial parenchyma

Axial parenchyma is defined as fusiform initials that are derived from vascular cambium and differentiated into living cells with primary cell wall with multiple functions (Mauseth 1988; Carlquist 2001, 2015). All succulent species studied here had parenchyma cells (Table 1). However, the amount of parenchyma tissue varied in stems, and caudices. Only *Cyphostemma juttiae* had axial parenchyma as ground tissue in stem and caudex (Fig. 4D-F).

Ray parenchyma

There were uniseriate and multiseriate rays. Some species had proliferation of multiseriate ray parenchyma cells. Proliferation is defined as the division and enlargement of cells, which makes the tissue to grow larger than others (Carlquist 2001). Wide rays for water storage parenchyma in wood are adaptations to changes in water availability (Carlquist 2001). Wide rays may be formed as extensions of primary rays, aggregate rays, or by conversion of the fusiform initials into ray initials (van der Walt *et al.* 1987; Mauseth 1988; Carlquist 2001). Proliferation of parenchyma cells in stems and caudices for > 50% of wood area were found in *Oxalis megalorhiza* (Stem, Oxalidaceae; Fig. 3F), *Cyphostemma juttiae* (Stem and caudex, Vitaceae; Fig. 4D-F), *Ceropegia africana* (Caudex, Apocynaceae; Fig. 1F), *Momordica rostrata* (Stem and caudex, Cucurbitaceae Fig. 2G-I), and *Adenia glauca* (Caudex, Passifloraceae; Fig. 4A). In general, ray parenchyma tissue defines the type of wood in all species, but *Cyphostemma juttiae* (Table 1).

Successive cambium: conjunctive tissue

Successive cambium is a series of vascular cambia (Robert *et al.* 2011). It could originate from pericycle, cortex cells, and parenchyma phloem cells (Angyalossi *et al.* 2014). According to (Carlquist 2007), when successive cambium arises from cortex cells as part of a master cambium, conjunctive

tissue (fibers and/or parenchyma cells) is formed. Thirty-four angiosperm families grow in stem circumference by successive cambium growth (Hearn 2006; Robert *et al.* 2011; Carlquist 2001, 2007; Angyalossi *et al.* 2014). Successive cambium has multiple origins in angiosperms (Robert *et al.* 2011; Angyalossi *et al.* 2014) and is a polyphyletic character in woody plants (Schnitzer & Bongers 2002). According to Olson (2003) and Hearn (2006, 2009a), successive cambium is an ancestral character to the vine life form of both Cucurbitaceae (*Dendrosicyos*) and Passifloraceae (*Adenia*). This cambium is common in climbing vines and sometimes can be found in trees (Rajput 2017). Successive cambium is found in the caudex of *Ceropegia africana* (Apocynaceae, Fig. 1F), caudex of *Adenia glauca* (Passifloraceae, Fig. 3; 4A-C), stem and caudex of *Momordica rostrata* (Cucurbitaceae, Fig. 1G-I). In these species, successive cambium appears to be an adaptation to achieve succulence instead of flexibility. The evolution of succulence via modifications in successive cambia might be facilitated by the vine life form in the studied species of Cucurbitaceae and Passifloraceae.

FIBERS

Septate, libriform, gelatinous, thin-walled libriform fibers and libriform fibers were found in the axial system of all stems and caudices of all species except one, *Cyphostemma juttiae*. Fibers are derived from fusiform initials, and they generally have thick- or thin-secondary cell walls (Carlquist 2001, 2015). In the examined species, most fibers had thin secondary cell walls. In some cases, it was difficult to discriminate (cross section) between thin-walled libriform fibers, septate fibers, and axial parenchyma (e.g., caudex: *Adenium obesum*, stem: *Pelargonium carnosum* and caudex of *Moringa drouhardii*) (Figs 1B; 3B, C). Fibers were stained pale pink to red (*Adenium obesum*, *Momordica rostrata*, *Pelargonium carnosum* *Moringa drouhardii* (Fig. 1B, C; 2A; 3B-D). According to Mauseth (1988), the deposition of lignin in secondary cell walls of non-conducting sclerenchymatous tissue (fibers and sclereids) varies. Lignin content in wood might vary by cell type in response to environmental pressures or stimulus during development (Zhong & Ye 2015). Thus, the difference of lignin percentage in fibers might be translated into the differences in hues of their secondary cell walls of fibers.

Septate fibers are considered similar in function to parenchyma cells and occur in many flowering plant families (Morris *et al.* 2016; Carlquist 2015). Septate fibers were found in stems of *Momordica rostrata*, *Jatropha macrantha* (Figs 1G-I; 2G, H), *Moringa drouhardii* and the caudex of *Adenia glauca* (Figs 3C, D, I; 4A-C).

Gelatinous fibers lack lignification of the G layer. They are present in tension wood, a type of wood with high content of cellulose that forms in branches and horizontal stems (Mauseth 1988; Evert 2006). Tension wood is generally found in zones with high tension but also occurs in the main stem of *Fagus*, *Populus*, *Prosopis* (Evert 2006), stem of *J. macrantha*, stem of *Moringa drouhardii* and caudex of *Adenia glauca* (Figs 2G; 3C; 4A-C).

The stem and caudex of *Cyphostemma juttae* had no visible fibers. It had vasicentric parenchyma and abundant axial parenchyma (Carlquist 2015). It has been reported that vessels embedded in parenchyma may be safe from cavitation. *Cyphostemma juttae* is a clear example of how vessels avoid embolisms (Fig. 4D-F); (Mauseth 1988; Mauseth & Plemons-Rodriguez 1997).

The examined species belong to seven orders and eight families. My results suggest widespread convergence in the evolution of wood succulence in stems and caudices. Among the examined species, succulence has two alternative paths in stems and caudices. In half of them (*Ceropegia africana*, *Momordica rostrata*, *Oxalis megalorrhiza*, *Adenia glauca* and *Cyphostemma juttae*), there is proliferation of parenchyma tissue in the ray system. In the other half (*Jatropha curcas*, *Jatropha macrantha*, *Adenium obesum*, *Pelargonium carnosum* and *Moringa drouhardii*), succulence was achieved by thin-walled libriform fibers (mainly), septate, gelatinous, libriform fibers and scant parenchyma. Besides, stems and caudexes of *Cyphostemma juttae*, *Jatropha curcas* and *Momordica rostrata* had similar wood pattern (Table 1). It is worth to emphasize that succulent species with successive cambium had parenchymatous wood due to enlarged radial system besides the parenchyma conjunctive tissue. Future studies should focus in analyzing the wood anatomy of succulent plant of other groups to figure out whether there are additional paths for the origin of succulence.

Acknowledgements

James Mauseth and the University of Texas at Austin funded this research. I thank James Mauseth for providing plant specimens, making cross and longitudinal histological sections of all samples and allowing me to use this technique to stain samples. This research was conducted in the laboratory of James Mauseth at the University of Texas at Austin. Special thanks to José Panero for his comments and guidance on this work and Stan Roux for allowing access to use his laboratory equipment to take photographs of tissue slides. At last, thanks to the anonymous referee who helped to improve a previous version of the manuscript.

REFERENCES

- ANDERSON E. F. 2001. — *The cactus Family*. Portland, Or, Timber Press, 776 p.
- ANGYALOSSY V., PACE M. R. & LIMA A. C. 2014. — Liana anatomy: a broad perspective on structural evolution of the vascular system, in SCHNITZER S.A., BONGERS F., BURNHAM R.J. & PUTZ F.E. (eds.), *Ecology of Lianas*. John Wiley & Sons, Ltd., Chichester: 251-287. <https://doi.org/10.1002/9781118392409.ch19>
- ARAKAKI M., CHRISTIN P.-A., NYFFELER R., LENDEL A., EGGLE U., OGBURN R. M., SPRIGGS E., MOORE M. J. & EDWARDS E. J. 2011. — Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences* 108 (20): 8379-8384. <https://doi.org/10.1073/pnas.1100628108>
- ÁVILA-LOVERA E. & EZCURRA E. 2016. — Stem-succulent trees from the Old and New World tropics, in GOLDSTEIN G. & SANTIAGO L.S. (eds.), *Tropical Tree Physiology*. Vol. 6. Springer International Publishing, Cham: 45-65. https://doi.org/10.1007/978-3-319-27422-5_3
- CARLQUIST S. 1998. — Wood and Bark Anatomy of Caricaceae; Correlations with Systematics and Habit. *IAWA Journal* 19 (2): 191-206. <https://doi.org/10.1163/22941932-90001522>
- CARLQUIST S. 2001. — *Comparative Wood Anatomy*. Springer, Berlin, Heidelberg, 448 p. (Springer Series in Wood Science). <https://doi.org/10.1007/978-3-662-04578-7>
- CARLQUIST S. 2007. — Successive cambia revisited: ontogeny, histology, diversity, and functional significance. *The Journal of the Torrey Botanical Society* 134 (2): 301-332. <https://doi.org/ctrqck>
- CARLQUIST S. 2015. — Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function: Axial Parenchyma and Wood Function. *Botanical Journal of the Linnean Society* 177 (3): 291-321. <https://doi.org/10.1111/boj.12247>
- EGGLI U. & NYFFELER R. 2009. — Living under temporarily arid conditions - succulence as an adaptive strategy. *Bradleya* 27 (27): 13-36. <https://doi.org/10.25223/brad.n27.2009.a10>
- EVANS M., AUBRIOT X., HEARN D., LANCIAUX M., LAVERGNE S., CRUAUD C., LOWRY II P. P. & HAEVERMANS T. 2014. — Insights on the Evolution of Plant Succulence from a Remarkable Radiation in Madagascar (Euphorbia). *Systematic Biology* 63 (5): 697-711. <https://doi.org/10.1093/sysbio/syu035>
- EVERT R. F. 2006. — *Esau's Plant Anatomy Meristems, Cells and Tissues of the Plant Body – Their structure, Function and Development*. 3rd ed. John Wiley & Sons. <https://doi.org/10.1002/0470047380>
- HEARN D. J. 2006. — *Adenia* (Passifloraceae) and its Adaptive Radiation: Phylogeny and Growth Form Diversification. *Systematic Botany* 31 (4): 805-821. <https://doi.org/10.1600/036364406779695933>
- HEARN D. J. 2009a. — Descriptive anatomy and evolutionary patterns of anatomical diversification in *Adenia* (Passifloraceae). *Aliso* 27 (1): 13-38. <https://doi.org/10.5642/aliso.20092701.03>
- HEARN D. J. 2009b. — Developmental patterns in anatomy are shared among separate evolutionary origins of stem succulent and storage root-bearing growth habits in *Adenia* (Passifloraceae). *American Journal of Botany* 96 (11): 1941-1956. <https://doi.org/10.3732/ajb.0800203>
- HERNANDEZ-HERNANDEZ T., HERNANDEZ H. M., DE-NOVA J. A., PUENTE R., EGUIARTE L. E. & MAGALLON S. 2011. — Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). *American Journal of Botany* 98 (1): 44-61. <https://doi.org/10.3732/ajb.1000129>
- IPNI 2020. — International Plant Names Index. Available from <https://www.ipni.org/> [accessed 20 April 2020]
- LANDRUM J. V. 2001. — Wide-band tracheids in leaves of genera in Aizoaceae: the systematic occurrence of a novel cell type and its implications for the monophyly of the subfamily Ruschioideae. *Plant Systematics and Evolution* 227 (1-2): 49-61. <https://doi.org/10.1007/s006060170056>
- MAUSETH J. D. 1988. — *Plant anatomy*. Menlo Park, Calif, Benjamin/Cummings Pub. Co. 560 p. (Benjamin/Cummings series in the life sciences).
- MAUSETH J. D. 2003. — *Botany: an introduction to plant biology*. Boston, Jones and Bartlett Publishers. 848 p.
- MAUSETH J. D. 2004a. — Cacti and other succulents: stem anatomy of "other succulents" has little in common with that of cacti. *Bradleya* 22: 131-140. <https://doi.org/10.25223/brad.n22.2004.a10>
- MAUSETH J. D. 2004b. — The structure of photosynthetic succulent stems in plants other than cacti. *International Journal of Plant Sciences* 165 (1): 1-9. <https://doi.org/10.1086/380978>
- MAUSETH J. D. & PLEMONS B. J. 1995. — Developmentally variable, polymorphic woods in cacti. *American Journal of Botany* 82 (10): 1199-1206. <https://doi.org/10.1002/j.1537-2197.1995.tb12652.x>
- MAUSETH J. D. & PLEMONS-RODRIGUEZ B. J. 1997. — Presence of paratracheal water storage tissue does not alter vessel characters in cactus wood. *American Journal of Botany* 84 (6): 815-822. <https://doi.org/10.2307/2445817>

- MAUSETH J. D. & PLEMONS-RODRIGUEZ B. J. 1998. — Evolution of extreme xeromorphic characters in wood: a study of nine evolutionary lines in Cactaceae. *American Journal of Botany* 85 (2): 209-218. <https://doi.org/10.2307/2446308>
- MAUSETH J. D., MONTENEGRO G. & WALCKOWIAK A. M. 1984. — Studies of the holoparasite *Tristerix aphyllus* (Loranthaceae) infecting *Trichocereus chilensis* (Cactaceae). *Canadian Journal of Botany* 62 (4): 847-857. <https://doi.org/10.1139/b84-124>
- METCALFE C. R. & CHALK L. 1950. — *Anatomy of the Dicotyledons*. Vol. 1. *Systematic Anatomy of Leaf and Stem, with a Brief History of the Subject*. Clarendon Press, Oxford, 288 p.
- MORRIS H., BRODERSEN C., SCHWARZE F. W. M. R. & JANSEN S. 2016. — The parenchyma of secondary xylem and its critical role in tree defense against fungal decay in relation to the CODIT model. *Frontiers in Plant Science* 7: 1665. <https://doi.org/10.3389/fpls.2016.01665>
- NYFFELER R. & EGGELI U. 2010. — An up-to-date familial and suprafamilial classification of succulent plants. *Bradleya* 28 (28): 125-144. <https://doi.org/10.25223/brad.n28.2010.a1>
- OGBURN R. M. & EDWARDS E. J. 2012. — Quantifying succulence: a rapid, physiologically meaningful metric of plant water storage: Quantifying succulence. *Plant, Cell & Environment* 35 (9): 1533-1542. <https://doi.org/10.1111/j.1365-3040.2012.02503.x>
- OGBURN R. M. & EDWARDS E. J. 2013. — Repeated Origin of Three-Dimensional Leaf Venation Releases Constraints on the Evolution of Succulence in Plants. *Current Biology* 23 (8): 722-726. <https://doi.org/10.1016/j.cub.2013.03.029>
- OLADIPO O. T. & ILLOH H. C. 2012. — Phytologia Balcanica 18(2)2012 Available from http://www.bio.bas.bg/-phytolbalcan/PDF/18_2/contents.html [accessed 31 July 2021].
- OLSON M. E. 2003. — Stem and leaf anatomy of the arborescent Cucurbitaceae *Dendrosicyos socotrana* with comments on the evolution of pachycauls from lianas. *Plant Systematics and Evolution* 239 (3-4): 199-214. <https://doi.org/10.1007/s00606-003-0006-1>
- OLSON M. E. & CARLQUIST S. 2001. — Stem and root anatomical correlations with life form diversity, ecology, and systematics in *Moringa* (Moringaceae). *Botanical Journal of the Linnean Society* 135 (4): 315-348. <https://doi.org/10.1111/j.1095-8339.2001.tb00786.x>
- OUTER R. W., DEN & VEENENDAAL W. L. H. VAN 1980. — Wood and Bark Anatomy of *Alluaudia* (Didiereaceae) from Madagascar. *IAWA Journal* 1 (3): 133-139. <https://doi.org/10.1163/22941932-90000709>
- RAJPUT K. S. 2017. — Development of inverse cambia and structure of secondary xylem in *Ipomoea turbinata* (Convolvulaceae). *Polish Botanical Journal* 62 (1): 87-97. <https://doi.org/10.1515/pbj-2017-0003>
- ROBERT E. M. R., SCHMITZ N., BOEREN I., DRIESSENS T., HERREMANS K., DE MEY J., VAN DE CASTEELE E., BEECKMAN H. & KOEDAM N. 2011. — Successive cambia: a developmental oddity or an adaptive structure? *PLoS ONE* 6 (1): e16558. <https://doi.org/10.1371/journal.pone.0016558>
- SAJEVA M. & MAUSETH J. D. 1991. — Leaf-like Structure in the Photosynthetic, Succulent Stems of Cacti. *Annals of Botany* 68 (5): 405-411. <https://doi.org/10.1093/oxfordjournals.aob.a088271>
- SCHNITZER S. & BONGERS F. 2002. — The ecology of lianas and their role in forests. *Trends in Ecology & Evolution* 17 (5): 223-230. [https://doi.org/10.1016/S0169-5347\(02\)02491-6](https://doi.org/10.1016/S0169-5347(02)02491-6)
- SEAGO J. L., MARSH L. C., STEVENS K. J., SOUKUP A., VOTRUBOVÁ O. & ENSTONE D. E. 2005. — A re-examination of the root cortex in wetland flowering plants with respect to aerenchyma. *Annals of Botany* 96 (4): 565-579. <https://doi.org/10.1093/aob/mci211>
- SPICER R. 2014. — Symplasmic networks in secondary vascular tissues: parenchyma distribution and activity supporting long-distance transport. *Journal of Experimental Botany* 65 (7): 1829-1848. <https://doi.org/10.1093/jxb/ert459>
- SRIVASTAVA L. M. 2002. — Absciscic acid and stress tolerance in plants, in SRIVASTAVA L. M. (ed.), *Plant Growth and Development*. Academic Press: 381-412. <https://doi.org/10.1016/B978-012660570-9/50158-1>
- STEVENS P. F. 2001. — Angiosperm Phylogeny Website Available from <http://www.mobot.org/MOBOT/research/APweb/> [accessed 20 June 2020]
- THE ANGIOSPERM PHYLOGENY GROUP 2016. — An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181 (1): 1-20. <https://doi.org/10.1111/boj.12385>
- TOMLINSON P. B. & FISHER J. B. 2005. — Development of non-lignified fibers in leaves of *Gnetum gnemon* (Gnetales). *American Journal of Botany* 92 (3): 383-389. <https://doi.org/10.3732/ajb.92.3.383>
- TROPICOS 2020. — Tropicos. Available from <https://tropicos.org/> [accessed 18 May 2020]
- WALT J. J. A. VAN DER, WERKER E. & FAHN A. 1987. — Wood anatomy of *Pelargonium* (Geraniaceae). *IAWA Journal* 8 (2): 95-108. <https://doi.org/10.1163/22941932-90001036>
- WILLERT D. J. VON (ed.) 1992. — *Life Strategies of Succulents in Deserts: with Special Reference to the Namib Desert*. Cambridge University Press, Cambridge, New York, 340 p. (Cambridge studies in ecology).
- ZHONG R. & YE Z.-H. 2015. — Secondary Cell Walls: Biosynthesis, Patterned Deposition and Transcriptional Regulation. *Plant and Cell Physiology* 56 (2): 195-214. <https://doi.org/10.1093/pcp/pcu140>

Submitted on 18 May 2021;
accepted on 28 August 2021;
published on 22 March 2022.