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David J. Hearn
University of Arizona, Tucson

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DESCRIPTIVE ANATOMY AND EVOLUTIONARY PATTERNS OF ANATOMICAL DIVERSIFICATION IN *ADENIA* (PASSIFLORACEAE)

DAVID J. HEARN

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA
(*dhearn@email.arizona.edu*)

ABSTRACT

To understand evolutionary patterns and processes that account for anatomical diversity in relation to ecology and life form diversity, anatomy of storage roots and stems of the genus *Adenia* (Passifloraceae) were analyzed using an explicit phylogenetic context. Over 65,000 measurements are reported for 47 quantitative and qualitative traits from 58 species in the genus. Vestiges of lianous ancestry were apparent throughout the group, as treelets and lianous taxa alike share relatively short, often wide, vessel elements with simple, transverse perforation plates, and alternate lateral wall pitting; fibriform vessel elements, tracheids associated with vessels, and libriform fibers as additional tracheary elements; and well-developed axial parenchyma. Multiple cambial variants were observed, including anomalous parenchyma proliferation, anomalous vascular strands, successive cambia, and a novel type of intraxylary phloem. Successive cambia, trichomes, dermal features, and intraxylary phloem were synapomorphic for particular clades, whereas most traits were homoplastic. Several anatomical features of *Adenia* are consistent with xeromorphy. Repeated loss and gain of cuticularized, photosynthetic mature stems, narrow vessel elements, highly aggregated vessels, and other features indicative of xeromorphy reveal labile evolution of ecologically significant anatomical features, whereas features that are characteristic of the liana life form reveal evolutionary conservation despite diversification of life form within *Adenia*.

Key words: *Adenia*, anatomy, conservation, evolution, growth form, lability, Passifloraceae, phylogeny.

INTRODUCTION

The rates of evolutionary processes (tempo) and the patterns of evolutionary change (mode) have been foci of evolutionary research since Simpson's (1944) seminal contribution to the Modern Synthesis. The recent availability of phylogenetic hypotheses (Hearn 2006), coupled with the dramatic diversity of growth habits, of members of the genus *Adenia* Forssk. (Passifloraceae) afford the opportunity to examine the interplay between evolutionary lability and conservation of anatomy in relation to life form diversification and ecology to decipher the mode of evolution in this group. The group was ancestrally lianous (Hearn 2006), and pachycaul and caudiciform succulents, as well as vines, succulent multi-branched shrubs, and geophytic herbs evolved from this ancestral liana. Moreover, succulent stems and storage roots, in particular, appear to have evolved ca. 4 and 6–8 times, respectively (Hearn 2006). With between 80 and 100 species in *Adenia* distributed throughout the Old World tropics, and more species likely to be discovered (Hearn 2007), habitat use diversity is also astonishing. Some species occur in the driest deserts in southwestern Africa, and others live in the wettest rainforests in Asia. Here, I provide a description of 47 anatomical and morphological features of 58 species of *Adenia*, and I examine basic patterns of anatomical diversification in a phylogenetic context.

Research concerning anatomy of *Adenia* spans more than a century, but prior studies focused on a limited set of species (e.g., one in Obaton 1960, and four in Janse van Vuuren 1970). Without a comprehensive survey of taxa and an explicit phylogenetic hypothesis of species relationships, it is difficult to discern recurrent features of anatomical evolution. Ayensu and Stern (1964) provided the first and only comprehensive

anatomical survey in Passifloraceae, but they did not consider phylogeny explicitly. Although they investigated 44 species in Passifloraceae, they characterized the anatomy of only one species of *Adenia* (*A. lobata*).

Studies by Ayensu and Stern (1964) and others (Baccarini 1908; Claverie 1908; Stern and Brizicky 1958; Obaton 1960; Janse van Vuuren 1970) highlight the preponderance of anomalous anatomical features in Passifloraceae in general and *Adenia* in particular. Vascular arrangements that differ from the typical single secondary vascular cambium, which produces xylem to its interior and phloem to its exterior in a circular band around the stem, are rare in the woody eudicots as a whole. Successive cambia are known from 34 families of which 15 have lianoid representatives (Carlquist 2001: 277), interxylary phloem is recognized in 19 families (Carlquist 2001: 282), and furrowed xylem is recognized in 7 families (Carlquist 2001: 286). Ayensu and Stern (1964) characterized three types of anomalous secondary growth for Passifloraceae alone: dispersed type, successive cambia (interrupted type), and included phloem (patches of phloem embedded in the xylem cylinder). Surprisingly, Harms (1893; as cited in De Wilde 1971a), who worked extensively on the anatomy of Passifloraceae, did not report cambial variants in the family.

Baccarini (1908) was the first to highlight cambial variants in *Adenia*: the proliferation of parenchyma in *A. venenata*, which corresponds roughly to the dispersed type of Ayensu and Stern (1964), which they defined as “irregularly shaped, disoriented strands of xylem and phloem associated with fragments of vascular cambium spread throughout a parenchymatous matrix.” Janse van Vuuren (1970) also reported similar proliferation of parenchyma and anomalous vascular bundles in three species of succulent *Adenia* (*A. fruticosa*, *A. glauca*, *A. spinosa*) and proliferation of parenchyma in the

liana, *A. gummifera*, all from South Africa. Similarly, Claverie (1908) reported vascular bundles in the storage parenchyma that were not found in lianescent portions of the stem of the Malagasy pachycaul, *A. firingalavensis*. More recently, Stern and Brizicky (1958) reported that *Passiflora multiflora* L. from the Florida Keys has the dispersed type of anomalous secondary growth. In addition to vascular bundles and parenchyma proliferation, Obaton (1960) observed successive cambia in *A. cissampeloides* (Planch. ex Hook.) Harms that are similar to those observed by Janse van Vuuren (1970) in *A. gummifera*.

Like cambial variants, wide vessels relative to angiosperms as a whole [as characterized by Metcalfe and Chalk (1983)] are widespread throughout Passifloraceae. Ayensu and Stern (1964) concluded that wide vessels are a consequence of lianous origins of *Passiflora* L. Anatomical innovation can be tightly coupled to growth habit, and lianas provide a classic example (Carlquist 1975). Lianas have very long but narrow stems compared to other growth forms, and they must transport water up these relatively narrow stems. A general solution to water conduction in lianas is to develop wide vessels; wide vessels have much greater conductivity (as stated explicitly by the Hagen-Poiseuille law; see, e.g., Zimmermann 1983) than narrow vessels (Carlquist 1975: 180).

In other respects, xylem characters of Passifloraceae are, in general, derived or specialized relative to the evolutionary polarization of traits provided by Bailey and Tupper (1918), Frost (1930a,b, 1931), and Kribs (1935, 1937). Traits that are considered derived include wide, circular, simple perforations in vessel elements, shortened vessel elements, alternate lateral wall pitting in vessels, transverse end walls (Bailey and Tupper 1918; Frost 1930), and abundant axial parenchyma (Kribs 1937). In general, Passifloraceae possess these traits, woods are diffuse porous, and they lack storied structures (Ayensu and Stern 1964).

A possible exception to the specialized state of vascular tissues in Passifloraceae is the presence of scalariform perforation plates in *Paropsia* Noronha ex Thou. (Paropsieae). These plants are trees and shrubs with highly lignified secondary xylem; the tribe Paropsieae includes no scandent representatives (De Wilde 1971b). In contrast, members of tribe Passifloreae tend to be vines and lianas (De Wilde 1974). Some authors therefore rejected inclusion of *Paropsia* in Passifloraceae (e.g., Harms 1925; as cited in De Wilde 1971a). *Paropsia*, however, shares similar patterns of axial parenchyma and fibriform vessel elements with other Passifloraceae. Fibriform vessel elements were first documented in Passifloraceae (Woodworth 1934, 1935). They are essentially irregularly perforate tracheids or fiber tracheids (Ayensu and Stern 1964).

With this historical backdrop of anatomical description and discovery in Passifloraceae, I focus on anatomical and morphological features in *Adenia* and discuss plesiomorphic and synapomorphic traits in relation to life form and ecology. Detailed measurements, variances, and sample sizes are provided in Tables 4–6. Using molecular sequence data from the nuclear ribosomal internal transcribed spacer region (ITS1 + 5.8S + ITS2) from Hearn (2006), I reconstruct both the phylogenetic relationships of 52 of the 58 taxa that have no missing anatomical data used in comparative analyses, as well as the evolutionary history of anatomical and morphological

characters. I discuss patterns of lability and conservation of these traits in relation to phyletic diversity and ecology to discern the mode of anatomical and life form evolution in *Adenia*.

MATERIALS AND METHODS

Taxon and Specimen Sampling

Anatomy of one mature stem, one juvenile stem, and one storage root (when present) were characterized for each of 58 species of *Adenia*, one of *Deidamia*, one of *Paropsia*, and two of *Passiflora* (Table 1). Sampling storage roots generally kills the plant, and injured stems of the succulent species tend to rot, often resulting in whole plant death. Variation, therefore, was considered within individuals and across species rather than among individuals of species. Plants were either field collected or cultivated (Table 1). Tissue samples were cut to expose radial, tangential, and transverse surfaces.

Anatomical Preparation

Detailed protocols that describe the fixation, preparation, paraffin embedding, sectioning, staining, and mounting of tissues are provided by Hearn (2004). Tissue samples included radial, tangential, and cross sections, as well as macerations of mature stems (see Hearn 2004 for details). In general, sectioning, staining, and mounting of specimens followed the standard paraffin embedding and staining protocols used in the anatomy lab at the Rancho Santa Ana Botanic Garden (RSA), as the majority of anatomical preparation occurred there. I did not have tissue samples of young *A. karibaensis*, *A. metamorpha* Hearn, *A. penangiana*, and *A. repanda*, or mature *A. heterophylla*, and *A. penangiana* storage root during my work at RSA, so these samples were later hand-sectioned and stained with safranin to make anatomical measurements. A duplicate set of all slides is available at RSA.

Despite efforts to soften wood by immersing tissues in a 10% solution of ethylene diamine (Kukachka 1977; Carlquist 1982) for 1–3 weeks, some tearing of sections was unavoidable. Cambial regions were particularly prone to tearing. To reduce tearing, sections were cut thicker than would be optimal for microscopy. Thus, some longitudinal sections (radial and tangential) were difficult to interpret because of their thickness. In two species (*A. ellenbeckii*, *A. hastata*), the transverse sections of new growth were torn. Cells could be measured, but some qualitative measurements and measurements of larger structures were not possible for these two species.

Digital Imaging and Anatomical Characterization

Digital images were taken of every slide, and areas, lengths, angles, and counts of anatomical features were recorded using an image measurement software tool described in detail in Hearn (2004). Forty-seven characters were quantified or qualitatively characterized. For the majority of characters, measurement and characterization conventions were those described by Carlquist (2001). Macromorphological data were gathered from plants growing in the field, from plants growing in the University of Arizona greenhouses, or from descriptions in the monograph (De Wilde 1971a).

In total, more than 65,000 quantitative measurements were made in addition to qualitative observations. Tables 2–3

Table 1. List of *Adenia* species and outgroup used for anatomical analyses, with collection and voucher information of wild and cultivated plants (collection numbers prefixed by “cult”), region of origin, habit modified from Hearn (2006) (V = vine/geophyte, L = liana, P = pachycaul, S = succulent shrub, t = tendrillate), and storage root presence (x = present, occ. = occasional).

Taxa	Collection	Origin	Habit
<i>Adenia aculeata</i> (Oliv.) Engl.	Hearn cult1 (ARIZ)	Ethiopia	P,t,x
<i>A. acuta</i> De Wilde	Hearn Mad007 (ARIZ)	Madagascar	L,t
<i>A. boivinii</i> De Wilde	Hearn Mad023 (ARIZ)	Madagascar	P,t,x
<i>A. aff. cissampeloides</i> (Planch. ex Hook.) Harms	Hearn 211119 (ARIZ)	Tanzania	L,t,x
<i>A. cladosepala</i> (Baker) Harms	Hearn Mad011 (ARIZ)	Madagascar	L,t,x
<i>A. densiflora</i> (Baker) Harms	Hearn Mad040 (ARIZ)	Madagascar	L,t,x
<i>A. digitata</i> (Harv.) Engl.	Hearn 1040 (ARIZ)	South Africa	V,t,x
<i>A. elegans</i> Perr.	Hearn Mad053 (ARIZ)	Madagascar	V,t,x
<i>A. ellenbeckii</i> Harms	Hearn cult5 (ARIZ)	Kenya	S,x
<i>A. fasciculata</i> De Wilde	Hearn Mad002 (ARIZ)	Madagascar	L,t
<i>A. firingalavensis</i> Harms	Specks 3601 (ARIZ)	Madagascar	P,t
<i>A. fruticosa</i> Burtt Davy	Hearn 1029 (ARIZ)	South Africa	P,t,x
<i>A. glauca</i> Schinz	Hearn 1035 (ARIZ)	South Africa	P,t
<i>A. globosa</i> Engl.	HBG 78550 (ARIZ)	Kenya	P
<i>A. goetzei</i> Harms	Hearn cult8 (ARIZ)	Tanzania	V,x
<i>A. gummifera</i> (Harv.) Harms	Hearn 1015 (ARIZ)	South Africa	L,t,x
<i>A. hastata</i> Schinz	Hearn 1008 (ARIZ)	South Africa	V,t,x
<i>A. heterophylla</i> (Bl.) Kds. subsp. <i>australis</i> (R.Br. ex DC.) De Wilde	Hearn cult11 (ARIZ)	Australia	L,t
<i>A. hondala</i> (Gaertn.) De Wilde	Hearn cult12 (ARIZ)	India	P,t,x
<i>A. inermis</i> (Oliv.) De Wilde	Hearn cult13 (ARIZ)	Ethiopia	V,t,x
<i>A. isaloensis</i> (Perr.) De Wilde	Hearn Mad046 (ARIZ)	Madagascar	V,t,x
<i>A. karibaensis</i> De Wilde	Hearn cult14 (ARIZ)	Zimbabwe	P,t,x
<i>A. keramanthus</i> Harms	Hearn 201116 (ARIZ)	Tanzania	S,x
<i>A. kirkii</i> (Mast.) Engl.	Hearn 261131 (ARIZ)	Tanzania	V,t,x
<i>A. lanceolata</i> Engl. subsp. <i>scheffleri</i> (Engl. & Harms) De Wilde	Hearn 201115 (ARIZ)	Tanzania	V,t,x
<i>A. lapiazicola</i> Bardot-Vaucoulon	Hearn Mad26 (ARIZ)	Madagascar	S
<i>A. letouzeyi</i> De Wilde	Meise 39–1490 (BR)	unknown	L,t
<i>A. lindiensis</i> Harms	Hearn 181110 (ARIZ)	Tanzania	V,t,x
<i>A. litoralis</i> Hearn	Hearn Mad031 (ARIZ)	Madagascar	P,t,x
<i>A. lobata</i> (Jacq.) Engl.	De Wilde 873 (BR)	West Africa	L,t
<i>A. longestipitata</i> De Wilde	Hearn Mad042 (ARIZ)	Madagascar	L,t
<i>A. mannii</i> (Mast.) Engl.	L. Escobar 92–38 (ARIZ)	Africa	V,t
<i>A. mcdadiana</i> Hearn	Hearn Mad029 (ARIZ)	Madagascar	L,t
<i>A. metamorpha</i> Hearn	Hearn Mad025 (ARIZ)	Madagascar	P,t,x
<i>A. metriosiphon</i> De Wilde	Hearn cult18 (ARIZ)	Tanzania	V,t,x
<i>A. monadelphica</i> Perr.	Hearn Mad050 (ARIZ)	Madagascar	P,t,x
<i>A. olaboensis</i> Claverie	Hearn Mad016 (ARIZ)	Madagascar	P,t
<i>A. pachyphylla</i> De Wilde	Hearn cult20 (ARIZ)	Madagascar	L,t
<i>A. pachuili</i> (Engl.) Harms	Hearn cult21 (ARIZ)	Namibia	P,x
<i>A. peltata</i> (Baker) Schinz	Hearn cult22 (ARIZ)	Madagascar	P,t
<i>A. penangiana</i> (Wall. ex G.Don) De Wilde	Hearn T6 (ARIZ)	Thailand	V,t,x
<i>A. perrieri</i> Clav.	Hearn Mad048 (ARIZ)	Madagascar	P,t,x
<i>A. pyromorpha</i> (Perr.) De Wilde	Hearn Mad061 (ARIZ)	Madagascar	V,x
<i>A. racemosa</i> De Wilde	Hearn 261132 (ARIZ)	Tanzania	V,t,x
<i>A. refracta</i> (Tul.) Schinz	Hearn Mad008 (ARIZ)	Madagascar	V,t,x
<i>A. repanda</i> (Burch.) Engl.	Hearn 1023 (ARIZ)	Namibia	V,t,x
<i>A. rumicifolia</i> Engl. & Harms	Hearn 41241 (ARIZ)	Tanzania	L,t
<i>A. aff. schliebenii</i> Harms	Hearn cult24 (ARIZ)	Tanzania	L,t,x
<i>A. schweinfurthii</i> Engl.	Hearn cult25 (ARIZ)	unknown	V,t,x
<i>A. sphaerocarpa</i> Clav.	Hearn cult26 (ARIZ)	Madagascar	L,t
<i>A. spinosa</i> Burtt Davy	Hearn 1022 (ARIZ)	South Africa	P,t
<i>A. stenodactyla</i> Harms	Hearn 3515 (ARIZ)	Tanzania	V,t
<i>A. stylosa</i> (Drake ex Jumelle) Hearn	Hearn cult28 (ARIZ)	Madagascar	P,t
<i>A. subsessilifolia</i> Perr.	Hearn Mad051 (ARIZ)	Madagascar	V,t,x
<i>A. venenata</i> Forssk.	Hearn cult29 (ARIZ)	Kenya	P,t
<i>A. volkensii</i> Harms	Hearn cult30 (ARIZ)	Kenya	S,x
<i>A. wightiana</i> (Wall ex W. & A.) Engl. subsp. <i>africana</i> De Wilde	Hearn 18119 (ARIZ)	Tanzania	V,t
<i>A. wilmsii</i> Harms	Hearn 1028 (ARIZ)	South Africa	V,x
<i>Deidamia bicolor</i> Perr.	Hearn Mad06 (ARIZ)	Madagascar	L,t
<i>Paropsia madagascarensis</i> (Baill.) Perr.	Hearn Mad037 (ARIZ)	Madagascar	tree
<i>Passiflora caerulea</i> L.	K. Hansen 16 (TEX)	Paraguay	L,t
<i>P. foetida</i> L.	Hearn cult32 (ARIZ)	United States	V,t

Table 2. Qualitative anatomy characters used in Tables 4–7. General legend: NA = not applicable; m = missing.

Abbreviation	Description	Legend
AngV	Vessels angular in cross section?	+ = yes – = no
AxPar	Type of axial parenchyma	0 = wood parenchymatized 0a = 0 with scanty vasicentric lignification 1 = 0 with chainlike clusters of vessels surrounded by scanty lignified tissue 1' = 1 with wide bands interrupting chains 2 = apotracheal parenchyma, lignified tissue in strips from pith to vc, with ray-adjacent parenchyma 2a = 2 with wide bands 3 = apotracheal diffuse 3a = 3 to absent cp = parenchyma proliferation in cortex ip = intraxylary n = normal cambia sc = successive cambia
CambV	Type of cambial variant (future work will provide details of anomalous vascular strands and parenchyma proliferation outside the cortex)	a = absent e = elongate f = flattened i = irregular mi = minute s = spherical sp = sparse/spaces between cells sq = square
EpiDesc	Epidermal cell description	+ = yes – = no ± = sparingly so a = epidermis absent s = simple a = absent g = cells indistinguishable from ground parenchyma h = homocellular p = procumbent pI = similar to paedomorphic type I pII = similar to paedomorphic type II pIII = similar to paedomorphic type III sq = square u = upright ++ = very many + = present – = absent ± = few
EpiMS	Epidermis multiseriate?	a = absent p = periderm ph = phloem vc = vascular cambium
Plate	Perforation plate type	+ = yes – = no
RayH	Ray histology	a = alternate h = helical n = none/very small o = opposite p = pseudoscalariform
Starch	Presence of starch plastids	
Storied	Location of storied structure	
Tyl	Presence of tyloses	
VELW	Vessel element lateral wall pit type	

provide a list of abbreviations of characters, and Tables 4–6 provide means, standard deviations, and sample sizes of quantitative characters.

Phylogenetic Analyses and Character Reconstruction

The ITS1 + 5.8S + ITS2 sequence data of Hearn (2006) were used to infer phylogenetic relationships among the taxa analyzed in this study. These taxa represent a subset of the

67 species of *Adenia* investigated by Hearn (2006). Fifty-two of the species were used in phylogenetic analyses. Limitations were imposed by software that requires complete character data to infer ancestral states or perform comparative analyses. Due to lack of comparative data [missing character(s) listed in parentheses], the following species were not included: *A. cissampeloides* (storage root, VELW, imperfW, imperfL, VEPit), *A. cladosepala* (storage root), *A. letouzeyi* (VELW, imperfL, VEPit), *A. lindiensis* (tuber perW, perL, perThick,

Table 3. Quantitative anatomy characters used in Tables 4–7: means, standard deviations, and number of measurements.

Abbreviation	Description	Units
1°Xyl	Length of tail of primary xylem	$\mu\text{m} \pm \text{SD (N)}$
2°PW	Width of secondary phloem in storage root	$\mu\text{m} \pm \text{SD (N)}$
BundAng	Phloem fiber bundles per arc of 1°	number/degree $\pm \text{SD (N)}$
BundL	Length of phloem fiber bundle	$\mu\text{m} \pm \text{SD (N)}$
BundW	Width of phloem fiber bundle	$\mu\text{m} \pm \text{SD (N)}$
CrysD	Diameter of crystal	$\mu\text{m} \pm \text{SD (N)}$
CtxW	Width of cortex	$\mu\text{m} \pm \text{SD (N)}$
CutW	Cuticle thickness	$\mu\text{m} \pm \text{SD (N)}$
HypW	Width of hypodermis	$\mu\text{m} \pm \text{SD (N)}$
ImperfL	Length of narrow tracheary elements	$\mu\text{m} \pm \text{SD (N)}$
ImperfW	Width of narrow tracheary elements	$\mu\text{m} \pm \text{SD (N)}$
LibL	Length of libriform fiber	$\mu\text{m} \pm \text{SD (N)}$
LibW	Diameter of libriform fiber	$\mu\text{m} \pm \text{SD (N)}$
MaxVEDiam	Maximal diameter of vessel element lumen	μm
MaxVEL	Maximal length of vessel element	μm
MinVEDiam	Minimal diameter of vessel element lumen	μm
MinVEL	Minimal length of vessel element	μm
Par2°P	Diameter of parenchyma in secondary phloem in storage root	$\mu\text{m} \pm \text{SD (N)}$
ParAx	Diameter of xylem parenchyma	$\mu\text{m} \pm \text{SD (N)}$
ParCor	Diameter of cortex parenchyma	$\mu\text{m} \pm \text{SD (N)}$
ParCort%	Percent parenchyma in cortex	%
ParPith	Diameter of pith parenchyma	$\mu\text{m} \pm \text{SD (N)}$
ParXyl%	Percent parenchyma in xylem	%
PerL	Length of periderm cell	$\mu\text{m} \pm \text{SD (N)}$
PerThick	Periderm thickness	$\mu\text{m} \pm \text{SD (N)}$
PerW	Width of periderm cell	$\mu\text{m} \pm \text{SD (N)}$
PithR	Radius of pith	$\mu\text{m} \pm \text{SD (N)}$
PlateAng	Perforation plate angle	angle in degrees $\pm \text{SD (N)}$
RayW	Ray width	$\mu\text{m} \pm \text{SD (N)}$
SEDiam	Sieve element diameter	$\mu\text{m} \pm \text{SD (N)}$
Stone	Stone cell diameter	$\mu\text{m} \pm \text{SD (N)}$
Tannin	Diameter of tannin cell	$\mu\text{m} \pm \text{SD (N)}$
VCW	Width of vascular cambium	$\mu\text{m} \pm \text{SD (N)}$
VE#/mm	Vessel element number per mm ²	number/mm ² $\pm \text{SD (N)}$
VEAgg	Number of vessels per aggregation	number/aggregation $\pm \text{SD (N)}$
VEDiam	Diameter of vessel element lumen	$\mu\text{m} \pm \text{SD (N)}$
VEL	Length of vessel element	$\mu\text{m} \pm \text{SD (N)}$
VEPit	Vessel element lateral wall pit size	$\mu\text{m} \pm \text{SD (N)}$
VEW	Vessel element wall width	$\mu\text{m} \pm \text{SD (N)}$

SEDiam, rayW, tannin, VCW, VEL, VE#/mm, stone), *A. longestipitata*, and *A. metriosiphon* (libL, plateAng, VEL, VEPit). Similar phylogenetic methods as in Hearn (2006) were employed. In summary, MrBayes vers. 3.1.2 (Ronquist and Huelsenbeck 2003) performed a Bayesian analysis of phylogeny under a GTR + I + G model of sequence evolution, with two runs of 10,000,000 MCMC iterations each, sampled every 1000 iterations. The *allcompat* consensus tree was constructed based on a sample of 5000 trees from the (post-burn-in) posterior distribution. The *allcompat* tree reports an amalgam of those clades having highest posterior probability. Using the *allcompat* consensus tree, which is a fully resolved tree with branch lengths, the evolutionary histories of anatomical features were reconstructed using unordered parsimony for discrete characters and squared-change parsimony for continuous characters as implemented in Mesquite vers. 2.01 (Maddison and Maddison 2007).

RESULTS

Anatomical Measurements and Characterization

General features of Adenia.—Wood of most *Adenia* is best described as parenchymatous diffuse porous. Growth rings were absent in *Adenia*, even though all members of *Adenia* are perennial.

Developmental association between stems and tubers.—Tuberous storage roots in *Adenia* are developmentally derived from the radicle and hypocotyl. Rooted cuttings of many species develop storage roots from fibrous roots, e.g., most Malagasy taxa with tubers (see Table 1 for geographic origins), *A. ellenbeckii*, *A. fruticosa*, *A. goetzei*, *A. keramanthus*, *A. schweinfurthii*, and *A. stricta* (Mast.) Engl. Originating from hypocotyl and/or radicle tissue, tuberous roots in *Adenia* lack features of stems (nodes, buds or eyes, leaves and leaf scars, anatomical patterning of stele, maintenance of cortex).

Table 4. Storage root anatomy. See Tables 2 and 3 for column abbreviations.

Taxa	Starch	AngV	RayH	Stored	2°PW	CrysD	Par2°P	ParAx
<i>A. aculeata</i>	+	+	g	p	819 ± 42 (5)	39 ± 17 (15)	67 ± 24 (50)	63 ± 22 (50)
<i>A. boivinii</i>	—	—	pII	a	1741 ± 106 (7)	33 ± 10 (17)	77 ± 30 (30)	51 ± 20 (38)
<i>A. densiflora</i>	+	±	g	vc	1887 ± 210 (6)	31 ± 8 (7)	43 ± 21 (54)	54 ± 22 (48)
<i>A. digitata</i>	+	+	g	p	1256 ± 70 (6)	29 ± 5 (5)	75 ± 47 (38)	48 ± 21 (40)
<i>A. elegans</i>	±	+	g	p	m	0	m	161 ± 78 (88)
<i>A. ellenbeckii</i>	+	+	g	p	1221 ± 146 (7)	53.49 (1)	77 ± 45 (54)	48 ± 26 (82)
<i>A. fruticosa</i>	±	+	g	p	863 ± 147 (5)	33 ± 9 (21)	48 ± 22 (84)	63 ± 25 (68)
<i>A. goetzei</i>	—	+	g	a	601 ± 23 (8)	0	65 ± 43 (56)	74 ± 26 (48)
<i>A. gummifera</i>	+	+	g	p	563 ± 120 (10)	40.63 (1)	38 ± 14 (40)	53 ± 16 (56)
<i>A. hastata</i>	—	+	g	m	m	0	m	116 ± 45 (44)
<i>A. inermis</i>	—	+	pI(u),g	p,vc	749 ± 131 (10)	32 ± 6 (17)	32 ± 15 (28)	47 ± 24 (56)
<i>A. isaloensis</i>	+	+	g	a	3780 ± 110 (5)	0	41 ± 19 (48)	54 ± 23 (50)
<i>A. karibaensis</i>	+	+	g	p,vc	1482 ± 107 (6)	33 ± 6 (5)	42 ± 19 (54)	49 ± 16 (48)
<i>A. keramanthus</i>	+	+	s,u,g	p,vc	1253 ± 82 (5)	33 ± 6 (12)	39 ± 18 (60)	75 ± 27 (38)
<i>A. kirkii</i>	+	+	g	p	1310 ± 38 (4)	33 ± 10 (6)	41 ± 14 (40)	55 ± 25 (78)
<i>A. lanceolata</i>	+	+	g	m	978 ± 133 (8)	28 ± 5 (10)	37 ± 22 (34)	36 ± 22 (36)
<i>A. lindiensis</i>	+	+	g	m	m	0	m	72 ± 22 (34)
<i>A. metamorpha</i>	+	+	g	p	2375 ± 67 (5)	52 ± 15 (18)	62 ± 24 (62)	56 ± 19 (52)
<i>A. metriosiphon</i>	+	+	g	p,vc	2038 ± 188 (4)	34 ± 15 (11)	86 ± 30 (50)	91 ± 31 (84)
<i>A. monadelph</i>	+	+	g	a	1774 ± 53 (6)	43 ± 11 (18)	57 ± 25 (84)	71 ± 30 (50)
<i>A. pachuili</i>	—	+	g	p,vc	1918 ± 39 (5)	0	60 ± 19 (72)	44 ± 19 (62)
<i>A. penangiana</i>	+	+	g	a	976 ± 44 (6)	0	49 ± 9 (12)	15 ± 4 (8)
<i>A. perrieri</i>	—	+	pII,g	p	1890 ± 97 (7)	52 ± 16 (2)	52 ± 21 (40)	39 ± 15 (52)
<i>A. pyromorpha</i>	+	+	s	m	2093 ± 100 (5)	56 ± 2 (2)	47 ± 31 (52)	69 ± 38 (36)
<i>A. racemosa</i>	+	+	g	p,ph	2087 ± 244 (4)	33 ± 13 (19)	41 ± 19 (38)	63 ± 20 (30)
<i>A. refracta</i>	+	+	g	p,vc	548 ± 34 (8)	33 ± 7 (10)	44 ± 19 (28)	47 ± 18 (50)
<i>A. repanda</i>	+	—	g	a	1374 ± 88 (4)	44 ± 12 (11)	55 ± 20 (48)	45 ± 26 (58)
<i>A. schliebenii</i>	+	+	pII(s,u,p)	p	2594 ± 28 (5)	31 ± 9 (96)	61 ± 33 (52)	50 ± 25 (52)
<i>A. schweinfurthii</i>	—	+	g	p	2822 ± 197 (5)	52 ± 16 (16)	55 ± 20 (54)	83 ± 34 (46)
<i>A. stenodactyla</i>	+	+	g	p	2565 ± 888 (4)	25 ± 6 (19)	36 ± 10 (52)	51 ± 23 (64)
<i>A. subsessilifolia</i>	—	+	g	p	1761 ± 157 (6)	43 ± 7 (2)	m	m
<i>A. volkensii</i>	+	+	pII(s,u)	p	2149 ± 45 (6)	0	75 ± 46 (46)	55 ± 21 (44)
<i>A. wilmsii</i>	±	+	g	p,vc	m	0	43 ± 21 (72)	27 ± 10 (46)

	PerL	PerW	PerThick	SEDiam	RayW	Tannin	Stone
<i>A. aculeata</i>	75 ± 34 (9)	13 ± 4 (9)	119 ± 35 (10)	44 ± 10 (7)	1150 ± 474 (3)	34 ± 6 (4)	81.56 (1)
<i>A. boivinii</i>	74 ± 25 (18)	15 ± 4 (18)	149 ± 24 (13)	26 ± 6 (11)	285 ± 62 (4)	0	0
<i>A. densiflora</i>	41 ± 17 (12)	21 ± 5 (12)	m	22 ± 4 (10)	457 ± 323 (4)	41 ± 18 (34)	46 ± 15 (9)
<i>A. digitata</i>	75 ± 27 (26)	22 ± 6 (26)	130 ± 32 (15)	25 ± 4 (9)	1043 ± 134 (2)	0	0
<i>A. elegans</i>	m	m	164 ± 40 (12)	m	m	0	70 ± 27 (8)
<i>A. ellenbeckii</i>	97 ± 29 (11)	19 ± 6 (11)	113 ± 46 (8)	16 ± 4 (3)	417 ± 182 (4)	85 ± 38 (21)	0
<i>A. fruticosa</i>	61 ± 17 (21)	16 ± 5 (21)	306 ± 89 (11)	23 ± 12 (9)	591 ± 265 (4)	38 ± 20 (21)	0
<i>A. goetzei</i>	90 ± 27 (17)	22 ± 8 (17)	129 ± 11 (15)	21 ± 8 (6)	608 ± 525 (3)	0	0
<i>A. gummifera</i>	m	m	m	22 ± 6 (11)	2503.46 (1)	0	63 ± 13 (8)
<i>A. hastata</i>	m	m	m	m	m	39 ± 12 (2)	0
<i>A. inermis</i>	28 ± 10 (11)	17 ± 8 (11)	256 ± 20 (13)	24 ± 9 (10)	398 ± 321 (4)	31 ± 12 (41)	55 ± 16 (11)
<i>A. isaloensis</i>	51 ± 15 (12)	21 ± 4 (12)	183 ± 74 (9)	21 ± 3 (13)	261 ± 106 (6)	52 ± 18 (18)	63 ± 16 (13)
<i>A. karibaensis</i>	64 ± 19 (15)	28 ± 16 (15)	144 ± 30 (17)	20 ± 4 (17)	262 ± 143 (5)	0	0
<i>A. keramanthus</i>	55 ± 23 (22)	16 ± 5 (22)	150 ± 27 (10)	14 ± 6 (12)	563.08 (1)	34 ± 18 (21)	0
<i>A. kirkii</i>	45 ± 14 (26)	9 ± 3 (26)	145 ± 44 (10)	15 ± 5 (8)	932 ± 537 (3)	26 ± 9 (3)	0
<i>A. lanceolata</i>	m	m	m	m	m	54 ± 14 (2)	0
<i>A. lindiensis</i>	m	m	m	m	m	m	m
<i>A. metamorpha</i>	74 ± 24 (18)	19 ± 6 (18)	222 ± 47 (9)	39 ± 8 (3)	336 ± 181 (4)	0	0
<i>A. metriosiphon</i>	53 ± 18 (20)	12 ± 3 (20)	263 ± 51 (11)	21 ± 5 (9)	460.85 (1)	0	0
<i>A. monadelph</i>	52 ± 21 (18)	16 ± 5 (18)	118 ± 35 (22)	17 ± 7 (3)	499 ± 276 (3)	0	0
<i>A. pachuili</i>	65 ± 22 (21)	17 ± 5 (21)	167 ± 33 (15)	24 ± 7 (14)	590 ± 210 (3)	0	0
<i>A. penangiana</i>	41 ± 11 (13)	24 ± 7 (13)	363 ± 66 (7)	29 ± 15 (9)	1662 ± 791 (2)	0	0
<i>A. perrieri</i>	59 ± 20 (23)	22 ± 5 (23)	208 ± 72 (13)	32 ± 7 (19)	118 ± 69 (8)	0	0
<i>A. pyromorpha</i>	m	m	70 ± 45 (10)	15 ± 6 (20)	94 ± 45 (8)	51 ± 6 (2)	69 ± 21 (18)
<i>A. racemosa</i>	75 ± 21 (26)	14 ± 4 (26)	339 ± 28 (14)	45 ± 16 (7)	1128.88 (1)	0	0
<i>A. refracta</i>	54 ± 22 (28)	18 ± 5 (28)	171 ± 20 (12)	23 ± 6 (10)	525 ± 145 (2)	34 ± 15 (18)	0
<i>A. repanda</i>	NA	NA	NA	16 ± 4 (10)	572 ± 235 (3)	0	0

Table 4. Continued.

	PerL	PerW	PerThick	SEDiam	RayW	Tannin	Stone
<i>A. schliebenii</i>	47 ± 32 (23)	14 ± 5 (23)	144 ± 39 (13)	22 ± 6 (23)	162 ± 64 (9)	66 ± 33 (32)	0
<i>A. schweinfurthii</i>	51 ± 16 (40)	20 ± 8 (40)	176 ± 34 (14)	24 ± 6 (3)	847 ± 456 (3)	0	0
<i>A. stenodactyla</i>	39 ± 10 (20)	11 ± 4 (20)	116 ± 23 (17)	41 ± 11 (2)	m	0	61 ± 17 (27)
<i>A. subsessilifolia</i>	51 ± 15 (27)	18 ± 4 (27)	234 ± 30 (16)	20 ± 4 (12)	566 ± 162 (3)	0	47 ± 9 (18)
<i>A. volkensii</i>	48 ± 17 (21)	24 ± 11 (21)	150 ± 22 (15)	23 ± 5 (8)	436 ± 148 (4)	57 ± 19 (4)	0
<i>A. wilmsii</i>	50 ± 18 (22)	21 ± 5 (22)	253 ± 71 (15)	15 ± 4 (26)	230 ± 102 (6)	35 ± 17 (4)	0

	VCW	VEDiam	VEL	VE#/mm	VEAgg	VEW
<i>A. aculeata</i>	155 ± 80 (4)	44 ± 15 (33)	m	6 ± 11 (6)	3 ± 6 (30)	3 ± 1 (3)
<i>A. boivinii</i>	0	69 ± 24 (51)	315 ± 159 (12)	9 ± 9 (6)	2 ± 1 (29)	5 ± 3 (5)
<i>A. densiflora</i>	45 ± 2 (2)	74 ± 40 (27)	162 ± 59 (11)	2 ± 3 (4)	2 ± 1 (32)	4 ± 2 (4)
<i>A. digitata</i>	101 ± 29 (9)	38 ± 9 (17)	102 ± 35 (6)	11 ± 15 (2)	2 ± 1 (18)	3 ± 1 (6)
<i>A. elegans</i>	0	98 ± 73 (15)	178 ± 68 (9)	2 ± 1 (2)	3 ± 3 (8)	10 ± 7 (6)
<i>A. ellenbeckii</i>	37.27 (1)	55 ± 13 (46)	177 ± 66 (18)	6 ± 6 (4)	2 ± 1 (32)	5 ± 2 (9)
<i>A. fruticosa</i>	48 ± 11 (3)	68 ± 27 (35)	213 ± 98 (3)	7 ± 8 (4)	3 ± 2 (27)	5 ± 3 (5)
<i>A. goetzei</i>	30 ± 8 (5)	52 ± 14 (16)	149 ± 62 (7)	4 ± 4 (2)	2 ± 1 (38)	5 ± 3 (7)
<i>A. gummifera</i>	40.54 (1)	89 ± 32 (34)	m	9 ± 12 (2)	2 ± 1 (23)	5 ± 3 (4)
<i>A. hastata</i>	m	78 ± 28 (16)	118 ± 55 (10)	9 ± 10 (2)	2 ± 1 (19)	4 ± 1 (2)
<i>A. inermis</i>	36 ± 9 (6)	50 ± 13 (32)	206 ± 98 (18)	12 ± 16 (4)	2 ± 2 (62)	6 ± 3 (8)
<i>A. isaloensis</i>	38 ± 7 (8)	72 ± 30 (35)	164 ± 81 (8)	10 ± 12 (2)	1 ± 1 (36)	5 ± 3 (5)
<i>A. karibaensis</i>	22 ± 6 (6)	50 ± 10 (24)	132 ± 38 (10)	7 ± 7 (4)	2 ± 1 (25)	4 ± 2 (8)
<i>A. keramanthus</i>	18 ± 3 (3)	33 ± 12 (26)	165 ± 44 (3)	0.27 (1)	2 ± 1 (17)	4 ± 1 (3)
<i>A. kirkii</i>	19 ± 1 (2)	44 ± 12 (56)	113 ± 40 (8)	8 ± 10 (4)	2 ± 1 (42)	4 ± 3 (7)
<i>A. lanceolata</i>	19.12 (1)	46 ± 14 (38)	99 ± 49 (16)	15 ± 21 (2)	2 ± 1 (23)	3 ± 1 (10)
<i>A. lindiensis</i>	m	25 ± 2 (2)	m	m	2 (1)	3 (1)
<i>A. metamorpha</i>	26 ± 6 (5)	139 ± 48 (43)	206 ± 45 (6)	7 ± 13 (6)	2 ± 1 (34)	6 ± 4 (10)
<i>A. metriosiphon</i>	28 ± 9 (6)	38 ± 10 (14)	135 ± 20 (5)	2 ± 2 (4)	2 ± 1 (9)	3 ± 3 (5)
<i>A. monadelphica</i>	31 ± 12 (2)	51 ± 24 (50)	118 ± 37 (11)	5 ± 6 (2)	3 ± 2 (27)	5 ± 2 (5)
<i>A. pachuëlii</i>	38 ± 11 (6)	33 ± 12 (40)	138 ± 71 (22)	12 ± 16 (2)	m	4 ± 1 (13)
<i>A. penangiana</i>	0	62 ± 32 (9)	m	11 ± 5 (2)	1 (10)	5 ± 8 (2)
<i>A. perrieri</i>	39 ± 14 (11)	55 ± 15 (18)	204 ± 68 (8)	14 ± 19 (2)	2 ± 1 (19)	3 ± 3 (5)
<i>A. pyromorpha</i>	37 ± 14 (16)	52 ± 20 (43)	130 ± 31 (4)	4 ± 4 (2)	2 ± 1 (23)	4 ± 2 (11)
<i>A. racemosa</i>	35 (2)	41 ± 9 (13)	28 ± 14 (20)	3 ± 4 (2)	1 ± 1 (11)	5 ± 1 (2)
<i>A. refracta</i>	22 ± 1 (3)	43 ± 19 (26)	146 ± 71 (18)	1 ± 1 (2)	1 ± 1 (27)	4 ± 2 (4)
<i>A. repanda</i>	18 ± 3 (4)	25 ± 9 (46)	m	13 ± 15 (4)	3 ± 2 (25)	3 ± 1 (9)
<i>A. schliebenii</i>	67 ± 21 (11)	53 ± 18 (44)	175 ± 61 (15)	10 ± 13 (2)	2 ± 1 (24)	4 ± 2 (17)
<i>A. schweinfurthii</i>	36 ± 13 (9)	54 ± 24 (41)	166 ± 80 (6)	14 ± 19 (2)	3 ± 2 (33)	5 ± 2 (19)
<i>A. stenodactyla</i>	m	49 ± 15 (28)	105 ± 26 (29)	9 ± 12 (2)	2 ± 1 (16)	4 ± 2 (4)
<i>A. subsessilifolia</i>	26 ± 6 (11)	27 ± 7 (34)	142 ± 61 (6)	10 ± 13 (6)	5 ± 3 (15)	2 ± 1 (9)
<i>A. volkensii</i>	28.94 (1)	44 ± 12 (39)	182 ± 87 (16)	16 ± 20 (4)	2 ± 1 (49)	4 ± 1 (10)
<i>A. wilmsii</i>	38 ± 9 (5)	37 ± 13 (30)	185 ± 31 (9)	7 ± 9 (4)	2 ± 1 (34)	3 ± 1 (9)

Other macromorphological features.—Tendrils are a conspicuous feature of *Adenia* plants. Plants of the majority of species employ tendrils to attach to supportive structures; no stems of *Adenia* species twine. Inflorescences typically develop from tendrillate branches. Tendrils have been secondarily modified or lost in a number of species, in which case inflorescences appear on short axillary shoots. In *A. globosa* and *A. spinosa*, two pachycauls, tendrils have been modified into thorns. In *A. spinosa*, juvenile tendrils are functional and can attach to other objects. As tendrils mature, the base of the tendril stiffens and the tip degenerates, leaving a sharp point. Thorns of *A. globosa* are never functional tendrils and are recognizable as tendrils only through positional homology. These thorns are thick and conical. *Adenia pachuëlii* has no vestiges of tendrils, but the tips of stems undergo necrosis, thereafter functioning as spines.

Dermal tissue.—New growth of all species develops a cuticularized epidermis that can persist in mature stems

(Table 5: cutW; Fig. 1–6). The epidermis (Table 5: epiDesc) consists of round (Fig. 5), radially elongate (Fig. 1), or flattened cells (Fig. 2), and it is uniseriate (Fig. 1, 3, 5) or with multiple layers of cells in parts of the epidermis (Fig. 2; Table 5: epiMS); in old stems, the cells of the epidermis can become highly variable in shape and size (Fig. 2). The stem epidermis can be smooth (e.g., *A. spinosa*), wrinkled (e.g., *A. keramanthus*), regularly tubercled (*A. lobata*, *A. rumicifolia*), or irregularly warty (*A. globosa*), and there is evidence for both periclinal and anticlinal divisions in epidermal cells (see Fig. 1 for anticlinal divisions). Preparations of stem sections did not always successfully maintain epicuticular waxes, but they can become encrusting (Fig. 2). In contrast to many lianas (Fig. 1–4) and most pachycauls, stems of geophytes develop a periderm when they perennate (e.g., *A. digitata*, *A. kirkii*; Fig. 7).

Specialization of epidermal cells includes stomata and trichomes (Fig. 1, 3–6). These soft to hispid trichomes are

Table 5. Anatomy data for stems with extensive secondary growth. See Tables 2 and 3 for column abbreviations.

Taxa	Starch	AngV	CambV	EpiDesc	EpiMS	VELW	AxPar	Plate	RayH	Storied	Tyl
<i>A. aculeata</i>	+	+	cp	s	—	a,p	1	s	g	p	+
<i>A. acuta</i>	+	—	cp	f	±	a	2a	s	pI,u	a	—
<i>A. boivinii</i>	—	—		a	a	a	2a	s	pII	p	—
<i>A. cissampeloides</i>	++	—	sc	e,sp	±	m	2a	s	pII,u,sq	a	—
<i>A. cladosepala</i>	+	—	n	e	—	a	2a	s	pI	ph	+
<i>A. densiflora</i>	+	—	cp	a	a	a	2a	s	pII,u,sq	a	+
<i>A. elegans</i>	—	—	n	e	—	a	2	s	pI	a	+
<i>A. ellenbeckii</i>	+	+	cp	f,mi	±	a,p	1	s	g	a	+
<i>A. fasciculata</i>	—	—		i	—	a	2a	s	pII,sq	a	+
<i>A. firingalavensis</i>	±	—		i	—	a,p	2a	s	pII,u,sq,g	ph	+
<i>A. fruticosa</i>	±	+	cp	mi	±	o,p	0a	s	g	a	—
<i>A. glauca</i>	+	+	cp	i,mi	±	p	0a	s	g	a	+
<i>A. globosa</i>	—	+	cp	f	±	a,o	0a,1	s	g	a	—
<i>A. gummifera</i>	+	—	sc	e	—	a	2a	s	pII,u	a	+
<i>A. heterophylla</i>	—	—	n	a	a	a,p	2	s	pII,u,sq	p	—
<i>A. hondala</i>	—	+	cp	a	a	a	1	s	g	p	+
<i>A. karibaensis</i>	±	+	cp	mi,i	—	o,a	0a,1	s	g	a	—
<i>A. keramanthus</i>	+	+	cp	sp,i	—	a	0,1'	s	g	vc	—
<i>A. lapiazicola</i>	+	+	cp	a	a	a,p	1	s	u,sq,g	p	+
<i>A. letouzeyi</i>	—	—	n	e	—	m	2a	s	g	vc	+
<i>A. litoralis</i>	+	—		a	a	a,p	0	s	g	p	+
<i>A. lobata</i>	+	—	n	e,sp	—	a	2a	s	pII	a	+
<i>A. longestipitata</i>	+	—		e	±	a	2	s	pI,sq,u	vc	+
<i>A. mcdadiana</i>	+	—		f	—	a	2,2a	s	pI,g	vc	+
<i>A. metamorpha</i>	—	—		a	a	a	2,2a	s	pII,sq,u	p	+
<i>A. monadelphpha</i>	+	+		a	a	a	1	s	pII,u,sq	p	+
<i>A. olaboensis</i>	+	—	cp	f	—	a	2	s	g	p,vc	+
<i>A. pachyphylla</i>	—	—	n	e	—	m	2a	s	pII,u,sq	a	—
<i>A. pechuëlii</i>	—	+	cp	i	±	a,p	0,1	s	g	a	+
<i>A. peltata</i>	+	+		a	a	a,o	0a	s	pII,u,sq	p,vc	+
<i>A. perrieri</i>	+	—		a	a	a	0a,1'	s	pII,u	p	—
<i>A. rumicifolia</i>	+	—		i,sp	—	a,p	2,2a	s	pII,sq,u,p	a	+
<i>A. schweinfurthii</i>	—	+		a	a	a	2	s	g	a	+
<i>A. sphaerocarpa</i>	+	—		f,mi	±	a	2a	s	pII,sq,u	a	+
<i>A. spinosa</i>	—	+	cp	m	m	a,o,p	0,0a	s	g	a	—
<i>A. stylosa</i>	+	—		a	a	a,p	0a	s	g	p	—
<i>A. venenata</i>	—	+	cp	i,f	±	a	2a	s	pII,u,g	a	+
<i>A. volkensii</i>	—	+	n (juv.)	f,i	±	a,p	2	s	pII,u	a	+
<i>Deidamia</i>	±	—	n	a	a	m	2a	s	pI	p	+
<i>Paropsia</i>	+	—	n	a	a	m	3a	s	pIII	a	+
<i>Passiflora caerulea</i>	—	—	n	a	a	m	3a	s	h	a	—
<i>Passiflora foetida</i>	—	—	n	sq	—	m	3a?	s	a	a	—

	CtxW	CrysD	CutW	ImperfL	ImperfW	HypW	LibL
<i>A. aculeata</i>	2417 ± 764 (5)	49 ± 15 (10)	5 ± 1 (9)	563 ± 209 (9)	23 ± 18 (8)	0	1168 ± 283 (10)
<i>A. acuta</i>	1655 ± 70 (7)	37 ± 5 (16)	17 ± 3 (13)	245 ± 111 (4)	25 ± 25 (3)	92 ± 22 (13)	986 ± 150 (7)
<i>A. boivinii</i>	2962 ± 336 (5)	45 ± 8 (12)	0	644 ± 180 (5)	43 ± 21 (4)	0	1888 ± 427 (10)
<i>A. cissampeloides</i>	1760 ± 37 (6)	37 ± 9 (9)	27 ± 4 (16)	m	m	0	m
<i>A. cladosepala</i>	3339 ± 192 (5)	38 ± 7 (3)	30 ± 7 (14)	750 ± 357 (13)	71 ± 32 (3)	0	2208 ± 269 (10)
<i>A. densiflora</i>	3011 ± 193 (8)	38 ± 10 (13)	29 ± 9 (8)	740 ± 164 (7)	39 ± 11 (4)	0	1182 ± 518 (6)
<i>A. elegans</i>	1220 ± 56 (7)	32 (1)	23 ± 8 (24)	1064 ± 453 (5)	36 ± 13 (5)	0	2205 ± 509 (9)
<i>A. ellenbeckii</i>	1000 ± 74 (8)	35 ± 10 (31)	5 ± 1 (9)	302 ± 164 (3)	m	45 ± 8 (18)	795 ± 310 (10)
<i>A. fasciculata</i>	1335 ± 117 (8)	32 ± 5 (9)	26 ± 8 (24)	495 ± 157 (11)	33 ± 9 (11)	105 ± 12 (6)	1752 ± 599 (5)
<i>A. firingalavensis</i>	3083 ± 68 (6)	33 ± 5 (19)	8 ± 4 (10)	380 ± 143 (12)	27 ± 8 (4)	100 ± 53 (4)	1032 ± 302 (7)
<i>A. fruticosa</i>	2108 ± 70 (7)	35 ± 8 (23)	8 ± 4 (14)	634 ± 192 (13)	27 ± 18 (8)	0	864 ± 187 (9)
<i>A. glauca</i>	3072 ± 664 (2)	28 ± 10 (4)	6 ± 3 (30)	493 ± 177 (18)	25 ± 7 (9)	64 ± 19 (16)	819 ± 168 (2)
<i>A. globosa</i>	2298 ± 256 (4)	32 ± 6 (12)	0	595 ± 274 (5)	36 ± 12 (5)	0	2249 ± 300 (9)
<i>A. gummifera</i>	695 ± 76 (7)	25 ± 4 (19)	9 ± 4 (18)	436 ± 178 (21)	26 ± 9 (12)	0	672 ± 510 (12)
<i>A. heterophylla</i>	2614 ± 10 (3)	24 ± 6 (24)	0	1063 ± 499 (12)	28 ± 16 (7)	0	1458 ± 537 (11)
<i>A. hondala</i>	2845 ± 125 (4)	39 ± 11 (24)	0	482 ± 189 (8)	30 ± 12 (5)	0	2478 ± 762 (7)
<i>A. karibaensis</i>	1614 ± 49 (8)	40 ± 9 (34)	9 ± 3 (8)	433 ± 146 (11)	30 ± 7 (6)	0	807 ± 142 (13)
<i>A. keramanthus</i>	1793 ± 64 (6)	31 (1)	12 ± 6 (9)	591 ± 331 (22)	35 ± 10 (6)	0	1267 ± 367 (15)

Table 5. Continued.

	CtxW	CrysD	CutW	ImperfL	ImperfW	HypW	LibL
<i>A. lapiazicola</i>	3586 ± 104 (5)	34 ± 8 (30)	0	249 (1)	m	0	653 ± 391 (5)
<i>A. letouzeyi</i>	2056 ± 301 (7)	26 ± 9 (20)	8 ± 2 (12)	242 ± 41 (4)	m	0	10 ± 3 (7)
<i>A. litoralis</i>	1364 ± 97 (4)	25 ± 5 (29)	0	365 ± 152 (5)	28 ± 3 (3)	0	625 ± 188 (10)
<i>A. lobata</i>	1991 ± 160 (5)	23 ± 6 (27)	7 ± 4 (17)	273 ± 174 (10)	38 ± 35 (10)	0	962 ± 359 (6)
<i>A. longestipitata</i>	1828 ± 149 (6)	33 ± 13 (3)	11 ± 3 (30)	541 ± 228 (12)	24 ± 4 (6)	0	1186 ± 372 (11)
<i>A. mcdadiana</i>	3528 ± 96 (4)	42 ± 8 (29)	12 ± 4 (14)	520 ± 193 (21)	47 ± 19 (19)	76 ± 33 (16)	1062 ± 273 (16)
<i>A. metamorpha</i>	2350 ± 167 (6)	29 ± 6 (52)	0	683 ± 208 (8)	30 ± 9 (2)	78 ± 12 (6)	1754 ± 579 (10)
<i>A. monadelpha</i>	2290 ± 139 (6)	38 ± 8 (21)	0	488 ± 83 (18)	38 ± 24 (17)	126 ± 22 (11)	1437 ± 628 (13)
<i>A. olaboensis</i>	3895 ± 365 (3)	38 ± 12 (14)	0	314 ± 134 (11)	24 ± 5e+00 (5)	0	1668 ± 218 (9)
<i>A. pachyphylla</i>	619 ± 101 (10)	31 (1)	11 ± 5 (14)	352 ± 102 (2)	m	103 ± 25 (12)	17 ± 4 (4)
<i>A. pachuëlii</i>	1977 ± 31 (5)	31 ± 8 (21)	7 ± 2 (11)	705 ± 305 (9)	32 ± 10 (7)	61 ± 26 (19)	958 ± 210 (11)
<i>A. peltata</i>	1013 ± 50 (7)	33 ± 7 (33)	0	502 ± 328 (9)	42 ± 14 (6)	173 ± 39 (7)	2124 ± 581 (13)
<i>A. perrieri</i>	1072 ± 65 (5)	35 ± 8 (42)	0	511 ± 238 (18)	41 ± 16 (9)	0	1071 ± 107 (7)
<i>A. rumicifolia</i>	2351 ± 626 (4)	40 ± 9 (17)	13 ± 4 (18)	642 ± 292 (21)	28 ± 7 (2)	0	692 ± 274 (10)
<i>A. schweinfurthii</i>	2754 ± 59 (6)	36 ± 11 (29)	0	381 ± 166 (15)	20 ± 6 (8)	0	773 ± 118 (8)
<i>A. sphaerocarpa</i>	1809 ± 80 (7)	35 ± 6 (13)	13 ± 4 (17)	562 ± 112 (12)	30 ± 10 (8)	0	1560 ± 208 (2)
<i>A. spinosa</i>	2979 ± 781 (4)	0	m	300 ± 147 (26)	32 ± 6 (10)	0	719 ± 193 (5)
<i>A. stylosa</i>	3707 ± 20 (2)	0	0	504 ± 333 (6)	27 ± 18 (2)	0	930 ± 218 (10)
<i>A. venenata</i>	1620 ± 54 (5)	31 ± 6 (47)	9 ± 3 (19)	464 ± 200 (18)	34 ± 18 (9)	0	628 ± 691 (19)
<i>A. volkensii</i>	1749 ± 130 (6)	47 ± 15 (5)	m	471 ± 183 (15)	42 ± 13 (9)	68 ± 16 (19)	973 ± 222 (9)
<i>Deidamia</i>	1482 ± 57 (4)	38 (1)	0	581 ± 448 (4)	m	0	29 ± 8 (6)
<i>Paropsia</i>	703 ± 41 (8)	28 ± 6 (8)	0	m	m	0	23 ± 5 (4)
<i>Passiflora caerulea</i>	1284 ± 64 (4)	0	0	m	m	0	m
<i>Passiflora foetida</i>	459 ± 79 (14)	19 ± 6 (11)	10 ± 3 (13)	m	m	38 ± 12 (13)	10 ± 1 (8)

	LibW	ParCor	ParAx	ParPith	PlateAng	PerL	PerW
<i>A. aculeata</i>	12 ± 2 (10)	42 ± 18 (40)	48 ± 14 (46)	66 ± 17 (58)	81 ± 21 (13)	42 ± 12 (15)	11 ± 4 (15)
<i>A. acuta</i>	19 ± 5 (7)	36 ± 10 (8)	39 ± 12 (78)	44 ± 14 (38)	42 ± 13 (6)	0	0
<i>A. boivinii</i>	27 ± 7 (10)	55 ± 25 (34)	48 ± 31 (28)	31 ± 9 (22)	67 ± 25 (9)	48 ± 12 (9)	25 ± 6 (9)
<i>A. cissampeloides</i>	m	37 ± 15 (40)	42 ± 19 (28)	75 ± 16 (28)	89 ± 8 (9)	0	0
<i>A. cladosepala</i>	26 ± 5 (10)	47 ± 12 (36)	37 ± 24 (76)	63 ± 24 (71)	82 ± 10 (9)	0	0
<i>A. densiflora</i>	24 ± 8 (6)	35 ± 12 (36)	26 ± 8 (50)	55 ± 18 (68)	67 ± 13 (4)	28 ± 10 (16)	12 ± 4 (16)
<i>A. elegans</i>	18 ± 4 (9)	40 ± 17 (42)	37 ± 19 (66)	26 ± 10 (46)	74 ± 8 (4)	0	0
<i>A. ellenbeckii</i>	148 ± 398 (10)	47 ± 17 (68)	31 ± 9 (58)	48 ± 14 (50)	67 ± 14 (18)	0	0
<i>A. fasciculata</i>	24 ± 5 (5)	36 ± 15 (50)	46 ± 13 (70)	52 ± 17 (60)	81 ± 15 (20)	0	0
<i>A. firingalavensis</i>	23 ± 3 (7)	38 ± 15 (50)	27 ± 16 (52)	44 ± 16 (60)	90 ± 7 (10)	17 ± 6 (18)	8 ± 3 (18)
<i>A. fruticosa</i>	14 ± 3 (9)	52 ± 21 (66)	66 ± 23 (70)	NA	58 ± 28 (12)	0	0
<i>A. glauca</i>	21 ± 1 (2)	35 ± 13 (50)	35 ± 12 (58)	66 ± 17 (62)	72 ± 16 (12)	0	0
<i>A. globosa</i>	23 ± 8 (9)	40 ± 19 (48)	58 ± 16 (42)	NA	57 ± 24 (7)	0	0
<i>A. gummifera</i>	432 ± 660 (11)	30 ± 14 (62)	19 ± 6 (30)	43 ± 14 (64)	84 ± 10 (14)	0	0
<i>A. heterophylla</i>	25 ± 11 (11)	46 ± 14 (16)	23 ± 9 (20)	44 ± 13 (34)	88 ± 7 (7)	32 ± 9 (9)	14 ± 3 (9)
<i>A. hondala</i>	19 ± 8 (7)	58 ± 23 (116)	m	68 ± 22 (62)	63 ± 18 (11)	45 ± 16 (20)	16 ± 4 (20)
<i>A. karibaensis</i>	20 ± 6 (13)	41 ± 15 (76)	54 ± 22 (46)	NA	70 ± 22 (11)	0	0
<i>A. keramanthus</i>	24 ± 6 (15)	60 ± 26 (56)	72 ± 32 (60)	NA	81 ± 10 (23)	0	0
<i>A. lapiazicola</i>	11 ± 10 (5)	38 ± 17 (26)	35 ± 20 (70)	NA	77 ± 14 (29)	39 ± 15 (20)	13 ± 3 (20)
<i>A. letouzeyi</i>	10 ± 3 (7)	37 ± 19 (72)	24 ± 5 (42)	27 ± 12 (102)	76 ± 17 (13)	0	0
<i>A. litoralis</i>	14 ± 5 (10)	30 ± 14 (35)	25 ± 10 (50)	32 ± 17 (54)	68 ± 21 (6)	29 ± 6 (18)	8 ± 4 (18)
<i>A. lobata</i>	21 ± 6 (6)	41 ± 16 (30)	33 ± 11 (48)	49 ± 14 (54)	70 ± 21 (19)	0	0
<i>A. longestipitata</i>	19 ± 4 (11)	31 ± 12 (40)	28 ± 11 (44)	54 ± 14 (50)	79 ± 7 (4)	0	0
<i>A. mcdadiana</i>	22 ± 7 (16)	38 ± 16 (56)	37 ± 18 (38)	52 ± 13 (50)	87 ± 5 (12)	0	0
<i>A. metamorpha</i>	14 ± 3 (10)	40 ± 20 (56)	23 ± 9 (54)	34 ± 8 (34)	80 ± 13 (27)	40 ± 16 (20)	11 ± 4 (20)
<i>A. monadelpha</i>	17 ± 4 (13)	62 ± 19 (56)	30 ± 9 (36)	75 ± 28 (56)	64 ± 26 (22)	33 ± 15 (19)	13 ± 7 (19)
<i>A. olaboensis</i>	12 ± 3 (9)	39 ± 10 (62)	37 ± 20 (42)	44 ± 12 (56)	80 ± 11 (12)	31 ± 8 (16)	10 ± 5 (16)
<i>A. pachyphylla</i>	18 ± 5 (3)	24 ± 9 (42)	20 ± 7 (36)	47 ± 24 (74)	74 ± 13 (23)	0	0
<i>A. pachuëlii</i>	21 ± 3 (11)	33 ± 15 (66)	44 ± 25 (60)	m	73 ± 15 (10)	0	0
<i>A. peltata</i>	12 ± 5 (13)	41 ± 15 (52)	41 ± 15 (56)	49 ± 18 (46)	77 ± 23 (12)	40 ± 14 (10)	14 ± 3 (10)
<i>A. perrieri</i>	20 ± 3 (7)	51 ± 26 (50)	38 ± 18 (68)	49 ± 20 (48)	73 ± 21 (15)	38 ± 11 (29)	19 ± 7 (29)
<i>A. rumicifolia</i>	13 ± 6 (10)	36 ± 12 (58)	32 ± 25 (28)	53 ± 18 (70)	87 ± 10 (10)	0	0
<i>A. schweinfurthii</i>	16 ± 4 (8)	48 ± 20 (98)	47 ± 27 (46)	19 ± 6 (30)	65 ± 20 (14)	34 ± 13 (29)	18 ± 6 (29)
<i>A. sphaerocarpa</i>	20 ± 5 (2)	41 ± 14 (68)	46 ± 19 (88)	56 ± 17 (48)	75 ± 13 (13)	0	0
<i>A. spinosa</i>	15 ± 2 (5)	53 ± 20 (72)	53 ± 20 (42)	NA	57 ± 17 (12)	0	0
<i>A. stylosa</i>	13 ± 7 (10)	42 ± 15 (36)	42 ± 12 (48)	NA	81 ± 16 (12)	36 ± 13 (16)	15 ± 5 (16)

Table 5. Continued.

	LibW	ParCor	ParAx	ParPith	PlateAng	PerL	PerW
<i>A. venenata</i>	848 ± 789 (19)	29 ± 10 (40)	53 ± 21 (86)	NA	89 ± 8 (10)	0	0
<i>A. volkensii</i>	23 ± 4 (9)	73 ± 23 (64)	m	85 ± 30 (58)	42 ± 15 (9)	0	0
<i>Deidamia</i>	29 ± 6 (6)	m	21 ± 4 (34)	31 ± 10 (74)	80 ± 8 (11)	26 ± 9 (14)	12 ± 4 (14)
<i>Paropsia</i>	25 ± 4 (3)	28 ± 13 (42)	NA	38 ± 11 (46)	m	34 ± 9 (10)	18 ± 8 (10)
<i>Passiflora caerulea</i>	m	23 ± 15 (20)	m	m	80 ± 9 (15)	m	m
<i>Passiflora foetida</i>	9 ± 2 (7)	19 ± 6 (24)	m	50 ± 20 (48)	m	0	0

	PerThick	BundL	BundW	SEDiam	PithR	RayW
<i>A. aculeata</i>	349 ± 69 (8)	NA	NA	31 ± 6 (11)	617 ± 459 (15)	650 ± 240 (5)
<i>A. acuta</i>	0	172 ± 23 (2)	67 ± 32 (2)	26 ± 8 (20)	474 ± 124 (4)	512 ± 55 (3)
<i>A. boivinii</i>	256 ± 21 (8)	NA	NA	38 ± 10 (14)	159 ± 24 (5)	175 ± 104 (3)
<i>A. cissampeloides</i>	0	249 ± 35 (2)	161 ± 18 (2)	44 ± 11 (30)	1545 ± 390 (4)	175 ± 90 (7)
<i>A. cladosepala</i>	0	244 ± 59 (2)	158 ± 13 (2)	43 ± 11 (28)	1532 ± 283 (3)	122 ± 47 (3)
<i>A. densiflora</i>	317 ± 153 (18)	NA	NA	27 ± 7 (26)	1268 ± 133 (3)	77 ± 35 (10)
<i>A. elegans</i>	0	144 ± 32 (4)	122 ± 44 (4)	34 ± 9 (32)	291 ± 51 (5)	88 ± 62 (3)
<i>A. ellenbeckii</i>	0	138 ± 61 (9)	108 ± 59 (9)	17 ± 4 (27)	1474 ± 141 (5)	156 ± 61 (20)
<i>A. fasciculata</i>	0	156 ± 2 (2)	89 ± 4 (2)	22 ± 6 (21)	750 ± 142 (5)	419 ± 319 (4)
<i>A. firingalavensis</i>	98 ± 22 (12)	NA	NA	30 ± 6 (26)	1002 ± 75 (2)	59 ± 31 (3)
<i>A. fruticosa</i>	0	316 (1)	182 (1)	27 ± 6 (9)	NA	676 ± 606 (2)
<i>A. glauca</i>	0	321 ± 42 (2)	156 ± 15 (2)	33 ± 10 (8)	NA	m
<i>A. globosa</i>	0	82 (1)	97 (1)	24 ± 4 (5)	NA	872 (1)
<i>A. gummifera</i>	0	NA	NA	46 ± 12 (40)	552 ± 19 (3)	68 ± 54 (4)
<i>A. heterophylla</i>	325 ± 119 (11)	235 (1)	95 (1)	30 ± 4 (16)	798 ± 102 (6)	126 ± 23 (2)
<i>A. hondala</i>	215 ± 31 (15)	233 (1)	159 (1)	27 ± 7 (11)	1881 ± 219 (3)	624 ± 153 (3)
<i>A. karibaensis</i>	0	NA	NA	22 ± 6 (27)	NA	352 ± 175 (2)
<i>A. keramanthus</i>	0	178 (1)	155 (1)	28 ± 7 (13)	NA	405 ± 59 (3)
<i>A. lapiazicola</i>	205 ± 68 (18)	NA	NA	21 ± 5 (24)	NA	415 ± 115 (3)
<i>A. letouzeyi</i>	0	80 ± 10 (5)	73 ± 13 (5)	28 ± 6 (25)	948 ± 45 (3)	77 ± 29 (7)
<i>A. litoralis</i>	110 ± 22 (12)	NA	NA	36 ± 9 (6)	m	123 ± 77 (13)
<i>A. lobata</i>	0	146 ± 54 (3)	85 ± 14 (3)	29 ± 9 (34)	569 ± 56 (10)	146 ± 35 (2)
<i>A. longestipitata</i>	0	209 ± 56 (3)	160 ± 35 (3)	31 ± 7 (21)	857 ± 88 (8)	99 ± 26 (4)
<i>A. mcdadiana</i>	0	258 (1)	105 (1)	29 ± 8 (30)	2033 ± 454 (2)	156 ± 112 (5)
<i>A. metamorpha</i>	216 ± 18 (15)	102 ± 21 (2)	76 ± 34 (2)	26 ± 7 (41)	465 ± 18 (4)	312 ± 85 (5)
<i>A. monadelphica</i>	149 ± 22 (18)	NA	NA	22 ± 4 (25)	1771 ± 161 (4)	124 ± 38 (5)
<i>A. olaboensis</i>	87 ± 17 (13)	275 (1)	187 (1)	33 ± 8 (60)	2001 ± 411 (4)	156 ± 2 (2)
<i>A. pachyphylla</i>	0	165 ± 18 (6)	106 ± 16 (6)	19 ± 4 (19)	988 ± 132 (5)	69 ± 36 (8)
<i>A. pechuëlii</i>	0	255 (1)	189 (1)	20 ± 4 (12)	NA	688 ± 340 (3)
<i>A. peltata</i>	153 ± 43 (19)	171 ± 65 (3)	62 ± 4 (3)	30 ± 9 (20)	906 ± 139 (5)	170 ± 62 (8)
<i>A. perrieri</i>	167 ± 32 (17)	110 ± 59 (2)	65 ± 18 (2)	23 ± 6 (28)	1255 ± 303 (4)	205 ± 131 (6)
<i>A. rumicifolia</i>	0	NA	NA	31 ± 9 (35)	1234 ± 206 (5)	451 ± 258 (3)
<i>A. schweinfurthii</i>	225 ± 19 (12)	152 ± 32 (5)	115 ± 20 (5)	20 ± 6 (21)	547 ± 244 (8)	237 ± 144 (15)
<i>A. sphaerocarpa</i>	0	121 ± 28 (2)	55 ± 7 (2)	24 ± 6 (28)	1229 ± 255 (4)	195 ± 177 (14)
<i>A. spinosa</i>	0	NA	NA	30 ± 12 (3)	NA	266 (1)
<i>A. stylosa</i>	102 ± 22 (11)	93 (1)	67 (1)	16 ± 3 (10)	NA	m
<i>A. venenata</i>	0	170 (1)	130 (1)	21 ± 3 (8)	NA	178 ± 227 (3)
<i>A. volkensii</i>	0	216 ± 105 (10)	178 ± 39 (10)	21 ± 5 (24)	1530 ± 379 (3)	179 ± 82 (11)
<i>Deidamia</i>	188 ± 39 (8)	220 (1)	133 (1)	21 ± 4 (22)	884 ± 42 (4)	28 (1)
<i>Paropsia</i>	351 ± 36 (12)	NA	NA	17 ± 5 (21)	1150 ± 210 (5)	14 ± 4 (4)
<i>Passiflora caerulea</i>	223 ± 33 (6)	NA	NA	27 ± 9 (50)	m	32 ± 17 (11)
<i>Passiflora foetida</i>	0	142 ± 34 (18)	57 ± 15 (18)	14 ± 4 (15)	585 ± 111 (6)	NA

	Tannin	Stone	VCW	VEDiam	VEL	VE#/mm
<i>A. aculeata</i>	0	0	45 ± 3 (5)	56 ± 23 (37)	147 ± 58 (17)	14 ± 25 (5)
<i>A. acuta</i>	54 ± 18 (32)	27 ± 7 (15)	36 ± 8 (12)	75 ± 46 (44)	232 ± 154 (15)	9 ± 10 (4)
<i>A. boivinii</i>	0	74 ± 20 (31)	26 ± 3 (3)	135 ± 69 (69)	166 ± 121 (11)	11 ± 12 (4)
<i>A. cissampeloides</i>	51 ± 18 (24)	54 ± 9 (4)	60 ± 18 (20)	232 ± 82 (31)	240 ± 80 (17)	7 ± 7 (6)
<i>A. cladosepala</i>	47 ± 17 (41)	59 ± 23 (32)	61 ± 23 (6)	270 ± 109 (22)	258 ± 90 (20)	10 ± 9 (4)
<i>A. densiflora</i>	38 ± 14 (62)	44 ± 12 (23)	17 ± 7 (10)	142 ± 64 (46)	168 ± 85 (13)	15 ± 17 (4)
<i>A. elegans</i>	35 ± 12 (26)	64 ± 24 (36)	49 ± 20 (7)	139 ± 50 (27)	160 ± 76 (12)	6 ± 6 (8)
<i>A. ellenbeckii</i>	46 ± 13 (22)	0	55 ± 11 (7)	45 ± 13 (36)	181 ± 77 (16)	12 ± 16 (12)
<i>A. fasciculata</i>	47 ± 14 (27)	32 ± 8 (18)	41 ± 8 (8)	85 ± 33 (39)	205 ± 62 (23)	14 ± 17 (4)

Table 5. Continued.

	Tannin	Stone	VCW	VEDiam	VEL	VE#/mm
<i>A. firingalavensis</i>	39 ± 10 (40)	44 ± 20 (27)	55 ± 12 (3)	155 ± 91 (49)	259 ± 95 (29)	11 ± 13 (4)
<i>A. fruticosa</i>	0	0	67 (1)	95 ± 30 (34)	495 ± 219 (9)	14 ± 16 (2)
<i>A. glauca</i>	0	58 ± 17 (6)	0	96 ± 40 (17)	143 ± 104 (18)	30 ± 1 (2)
<i>A. globosa</i>	0	58 ± 17 (14)	0	45 ± 10 (56)	241 ± 169 (16)	19 ± 26 (2)
<i>A. gummifera</i>	37 ± 11 (43)	61 ± 31 (22)	20 (1)	202 ± 109 (66)	165 ± 67 (46)	17 ± 19 (2)
<i>A. heterophylla</i>	0	64 ± 14 (7)	69 ± 31 (6)	148 ± 78 (61)	200 ± 95 (14)	33 ± 39 (2)
<i>A. hondala</i>	27 ± 6 (5)	0	59 ± 18 (10)	73 ± 22 (52)	209 ± 65 (22)	9 ± 11 (4)
<i>A. karibaensis</i>	0	0	50 ± 16 (5)	56 ± 20 (46)	210 ± 105 (40)	9 ± 11 (4)
<i>A. keramanthus</i>	0	0	18 ± 4 (5)	69 ± 19 (61)	169 ± 74 (55)	13 ± 15 (4)
<i>A. lapiazicola</i>	0	58 ± 5 (3)	21 ± 6 (10)	88 ± 32 (92)	179 ± 58 (33)	14 ± 20 (4)
<i>A. letouzeyi</i>	52 ± 36 (7)	0	25 ± 8 (8)	121 ± 68 (62)	180 ± 76 (19)	25 ± 31 (2)
<i>A. litoralis</i>	0	52 ± 10 (13)	25 ± 6 (6)	79 ± 38 (78)	255 ± 136 (24)	8 ± 10 (2)
<i>A. lobata</i>	31 ± 13 (37)	50 ± 16 (13)	41 ± 10 (8)	110 ± 54 (44)	141 ± 64 (21)	10 ± 11 (4)
<i>A. longestipitata</i>	41 ± 17 (18)	0	45 ± 19 (7)	99 ± 56 (56)	157 ± 60 (11)	19 ± 20 (6)
<i>A. mcdadiana</i>	0	50 ± 12 (14)	60 ± 15 (12)	204 ± 69 (22)	124 ± 51 (20)	13 ± 14 (2)
<i>A. metamorpha</i>	28 ± 9 (7)	0	29 ± 14 (6)	109 ± 42 (109)	243 ± 71 (24)	51 ± 67 (2)
<i>A. monadelphica</i>	0	0	26 ± 8 (3)	53 ± 21 (93)	140 ± 88 (77)	39 ± 46 (4)
<i>A. olaboensis</i>	39 ± 14 (33)	67 ± 24 (33)	36 ± 14 (9)	186 ± 66 (34)	219 ± 57 (15)	20 ± 20 (2)
<i>A. pachyphylla</i>	41 ± 19 (35)	34 ± 9 (25)	22 ± 3 (4)	90 ± 45 (36)	173 ± 63 (26)	9 ± 11 (4)
<i>A. pachuili</i>	0	0	40 ± 2 (3)	35 ± 14 (82)	129 ± 58 (44)	18 ± 25 (4)
<i>A. peltata</i>	0	0	19 ± 5 (7)	54 ± 18 (26)	204 ± 125 (8)	11 ± 13 (2)
<i>A. perrieri</i>	0	0	41 ± 9 (4)	93 ± 31 (37)	228 ± 85 (27)	21 ± 27 (2)
<i>A. rumicifolia</i>	0	47 ± 12 (24)	25 ± 9 (8)	201 ± 113 (34)	138 ± 60 (25)	22 ± 26 (4)
<i>A. schweinfurthii</i>	0	0	31 ± 8 (14)	41 ± 19 (47)	195 ± 56 (18)	23 ± 31 (2)
<i>A. sphaerocarpa</i>	0	0	51 ± 20 (20)	75 ± 31 (106)	214 ± 122 (45)	19 ± 26 (2)
<i>A. spinosa</i>	0	59 ± 17 (22)	36 ± 4 (2)	40 ± 13 (48)	169 ± 87 (21)	8 ± 11 (2)
<i>A. stylosa</i>	36 ± 19 (15)	0	0	72 ± 33 (16)	191 ± 116 (11)	4 ± 4 (4)
<i>A. venenata</i>	0	0	23 ± 4 (4)	45 ± 15 (23)	233 ± 94 (29)	11 ± 12 (4)
<i>A. volkensii</i>	40 ± 3 (2)	0	55 ± 27 (8)	62 ± 17 (47)	218 ± 81 (32)	10 ± 14 (4)
<i>Deidamia</i>	33 ± 8 (37)	43 ± 11 (11)	0	185 ± 105 (27)	491 ± 173 (13)	7 ± 7 (4)
<i>Paropsia</i>	37 ± 10 (40)	39 ± 14 (11)	15 ± 4 (4)	42 ± 14 (33)	m	63 ± 87 (2)
<i>Passiflora caerulea</i>	0	0	37 ± 5 (7)	42 ± 30 (92)	197 ± 47 (25)	64 ± 89 (2)
<i>Passiflora foetida</i>	20 ± 9 (13)	0	27 ± 10 (19)	62 ± 25 (40)	m	25 ± 35 (2)

	VEPit	VEAgg	VEW	ParCort%	ParXyl%	Max VEDiam	Max VEL	Min VEDiam	Min VEL
<i>A. aculeata</i>	7 ± 2 (26)	4 ± 4 (21)	3 ± 2 (7)	100 (1)	94 (1)	117	228	24	51
<i>A. acuta</i>	5 ± 1 (9)	2 ± 1 (26)	4 ± 2 (5)	100 (1)	79 (1)	187	583	15	28
<i>A. boivinii</i>	8 ± 2 (18)	2 ± 1 (37)	6 ± 3 (10)	92 (1)	51 (1)	371	324	33	45
<i>A. cissampeloides</i>	m	1 ± 1 (33)	5 ± 4 (11)	98 (1)	61 (1)	407	388	101	120
<i>A. cladosepala</i>	4 ± 1 (12)	1 (37)	11 ± 4 (4)	84 (1)	46 (1)	467	458	74	90
<i>A. densiflora</i>	6 (10)	1 ± 1 (56)	7 ± 4 (11)	91 (1)	68 (1)	275	337	25	56
<i>A. elegans</i>	6 ± 2 (27)	1 ± 1 (52)	6 ± 2 (8)	64 (1)	23 (1)	237	296	51	23
<i>A. ellenbeckii</i>	8 ± 1 (8)	3 ± 3 (28)	3 ± 2 (20)	98 (1)	75 (1)	78	310	16	35
<i>A. fasciculata</i>	6 ± 2 (26)	2 ± 1 (37)	4 ± 3 (7)	98 (1)	80 (1)	154	362	26	87
<i>A. firingalavensis</i>	6 ± 3 (36)	1 ± 1 (35)	6 ± 3 (9)	77 (1)	72 (1)	386	458	33	75
<i>A. fruticosa</i>	10 ± 4 (33)	2 ± 1 (53)	7 ± 5 (9)	99 (1)	93 (1)	182	809	41	96
<i>A. glauca</i>	9 ± 4 (34)	3 ± 2 (13)	5 ± 3 (16)	97 (1)	99 (1)	209	413	44	50
<i>A. globosa</i>	8 ± 3 (34)	2 ± 1 (38)	3 ± 3 (3)	98 (1)	92 (1)	75	603	28	72
<i>A. gummifera</i>	6 ± 1 (26)	2 ± 1 (72)	6 ± 3 (20)	88 (1)	40 (1)	492	369	45	55
<i>A. heterophylla</i>	7 ± 2 (33)	1 ± 1 (42)	5 ± 2 (7)	97 (1)	38 (1)	327	346	18	35
<i>A. hondala</i>	5 ± 1 (26)	2 ± 1 (38)	5 ± 2 (4)	99 (1)	86 (1)	126	340	37	104
<i>A. karibaensis</i>	13 ± 4 (25)	2 ± 1 (31)	5 ± 2 (10)	95 (1)	96 (1)	121	573	25	63
<i>A. keramanthus</i>	8 ± 2 (36)	2 ± 2 (34)	4 ± 1 (8)	99 (1)	85 (1)	127	365	29	43
<i>A. lapiazicola</i>	7 ± 3 (37)	2 ± 2 (77)	4 ± 2 (10)	100 (1)	85 (1)	161	321	34	83
<i>A. letouzeyi</i>	m	1 ± 1 (54)	3 ± 2 (8)	100 (1)	54 (1)	356	321	31	37
<i>A. litoralis</i>	4 ± 2 (16)	1 ± 1 (112)	4 ± 2 (16)	93 (1)	69 (1)	189	520	19	34
<i>A. lobata</i>	8 ± 2 (59)	1 ± 1 (75)	6 ± 4 (11)	95 (1)	43 (1)	215	330	31	58
<i>A. longestipitata</i>	8 ± 3 (43)	2 ± 1 (112)	5 ± 2 (15)	73 (1)	42 (1)	249	237	20	73
<i>A. mcdadiana</i>	5 ± 2 (50)	1 (27)	7 ± 3 (4)	99 (1)	63 (1)	353	254	104	46
<i>A. metamorpha</i>	9 ± 3 (26)	2 ± 1 (113)	5 ± 3 (26)	98 (1)	53 (1)	200	368	27	133
<i>A. monadelphica</i>	6 ± 2 (37)	4 ± 3 (54)	4 ± 2 (14)	98 (1)	35 (1)	110	401	18	22
<i>A. olaboensis</i>	6 ± 2 (60)	1 ± 1 (44)	9 ± 5 (8)	97 (1)	71 (1)	308	345	50	132

Table 5. Continued.

	VEPit	VEAgg	VEW	ParCort%	ParXyl%	Max VEDiam	Max VEL	Min VEDiam	Min VEL
<i>A. pachyphylla</i>	9 (1)	1 ± 1 (35)	3 ± 1 (8)	88 (1)	47 (1)	201	280	30	45
<i>A. pechuëlii</i>	8 ± 2 (36)	2 ± 2 (55)	3 ± 1 (8)	99 (1)	93 (1)	80	223	15	28
<i>A. peltata</i>	5 ± 2 (59)	2 ± 2 (48)	4 ± 2 (8)	99 (1)	82 (1)	93	416	25	21
<i>A. perrieri</i>	6 ± 1 (42)	1 ± 1 (96)	4 ± 2 (17)	96 (1)	83 (1)	146	376	32	103
<i>A. rumicifolia</i>	7 ± 2 (37)	1 ± 1 (62)	5 ± 3 (15)	90 (1)	55 (1)	475	271	39	35
<i>A. schweinfurthii</i>	4 ± 1 (21)	2 ± 1 (66)	4 ± 2 (9)	100 (1)	82 (1)	122	338	10	109
<i>A. sphaerocarpa</i>	8 ± 2 (27)	2 ± 2 (75)	3 ± 1 (22)	99 (1)	76 (1)	152	603	20	18
<i>A. spinosa</i>	4 ± 2 (20)	2 ± 2 (27)	4 ± 2 (5)	97 (1)	98 (1)	74	399	17	47
<i>A. stylosa</i>	7 ± 3 (30)	1 ± 1 (20)	3 ± 3 (5)	100 (1)	96 (1)	127	445	36	35
<i>A. venenata</i>	11 ± 4 (37)	2 ± 2 (25)	3 ± 2 (12)	98 (1)	92 (1)	90	442	27	50
<i>A. volkensii</i>	8 ± 4 (28)	3 ± 2 (75)	4 ± 2 (20)	97 (1)	57 (1)	103	393	27	66
<i>Deidamia</i>	m	1 (36)	6 ± 6 (6)	84 (1)	28 (1)	455	911	59	264
<i>Paropsia</i>	m	4 ± 3 (44)	5 ± 2 (10)	87 (1)	8 (1)	69	m	20	m
<i>Passiflora caerulea</i>	m	2 ± 1 (50)	4 ± 2 (9)	62 (1)	42 (1)	239	276	11	91
<i>Passiflora foetida</i>	m	1 ± 1 (47)	4 ± 2 (5)	95 (1)	60 (1)	120	m	18	m

Table 6. Anatomy of stems with little secondary growth when mature. See Tables 2 and 3 for abbreviations.

Taxa	AxPar	CambV	Plate	Starch	VELW	ImperfL	ImperfW
<i>A. digitata</i>	3	ip	s	—	a	740 ± 164 (7)	18 ± 5 (8)
<i>A. goetzei</i>	3a		s	—	h,n	949 ± 387 (6)	32 ± 12 (9)
<i>A. hastata</i>	m		s	—	p	211 ± 76 (4)	19 ± 5 (3)
<i>A. inermis</i>	3a		s	—	m	221 ± 1 (2)	m
<i>A. isaloensis</i>	m		s	—	a	427 ± 112 (14)	24 ± 8 (8)
<i>A. kirkii</i>	3a	ip	s	—	a	453 ± 217 (6)	19 ± 13 (5)
<i>A. lanceolata</i>	3a	ip	s	—	a	527 ± 234 (18)	m
<i>A. mannii</i>	2a		s	—	m	390 (1)	m
<i>A. metriosiphon</i>	2		s	—	m	m	m
<i>A. penangiana</i>	m		s	+	a	672 ± 247 (9)	m
<i>A. pyromorpha</i>	3a		s	—	o,a	390 ± 184 (16)	26 ± 11 (12)
<i>A. racemosa</i>	3a		s	—	a	413 ± 113 (15)	24 ± 7 (9)
<i>A. refracta</i>	2–3a		s	—	a	898 ± 533 (20)	45 ± 15 (10)
<i>A. repanda</i>	m		s	+	a,p	392 ± 156 (16)	28 ± 7 (11)
<i>A. schliebenii</i>	3a		s	—	a,p	706 ± 351 (14)	36 ± 11 (7)
<i>A. stenodactyla</i>	1		s	—	a	1152 ± 453 (7)	36 ± 12 (6)
<i>A. subsessilifolia</i>	3a		s	+	a	396 ± 140 (13)	24 ± 5 (4)
<i>A. wilmsii</i>	3a		s	—	a	355 ± 115 (8)	19 ± 6 (4)

	LibL	LibW	PlateAng	VEL	VEPit	ParCort%	ParXyl%
<i>A. digitata</i>	1054 ± 506 (9)	15 ± 4 (9)	78 ± 11 (8)	195 ± 99 (13)	7 ± 2 (17)	94 (1)	31 (1)
<i>A. goetzei</i>	1658 ± 901 (8)	24 ± 4 (8)	66 ± 25 (4)	1015 ± 329 (4)	m	79 (1)	0 (1)
<i>A. hastata</i>	2093 ± 1400 (2)	21 ± 16 (2)	44 ± 6 (2)	128 ± 23 (3)	10 ± 4 (34)	m	10 (1)
<i>A. inermis</i>	273 (1)	3 (1)	82 ± 15 (7)	m	6 ± 2 (19)	89 (1)	0 (1)
<i>A. isaloensis</i>	757 ± 227 (10)	26 ± 7 (10)	72 ± 21 (4)	209 ± 105 (12)	4 ± 1 (44)	84 (1)	0 (1)
<i>A. kirkii</i>	1630 ± 655 (10)	12 ± 4 (10)	81 ± 9 (12)	170 ± 94 (21)	4 ± 2 (46)	88 (1)	0 (1)
<i>A. lanceolata</i>	1218 ± 488 (14)	16 ± 3 (14)	70 ± 18 (6)	276 ± 139 (5)	7 ± 2 (32)	89 (1)	16 (1)
<i>A. mannii</i>	m	8 ± 1 (3)	59 ± 19 (8)	258 ± 59 (10)	10 ± 2 (7)	98 (1)	43 (1)
<i>A. metriosiphon</i>	m	13 ± 2 (11)	m	m	m	94 (1)	58 (1)
<i>A. penangiana</i>	2219 ± 802 (10)	20 ± 4 (10)	66 ± 20 (9)	359 ± 88 (12)	3 ± 1 (22)	88 (1)	0 (1)
<i>A. pyromorpha</i>	1427 ± 381 (16)	15 ± 3 (16)	63 ± 7 (5)	60 ± 22 (12)	5 ± 1 (26)	78 (1)	0 (1)
<i>A. racemosa</i>	940 ± 236 (8)	12 ± 3 (8)	72 ± 12 (6)	211 ± 144 (11)	4 ± 1 (38)	89 (1)	34 (1)
<i>A. refracta</i>	1313 ± 437 (9)	14 ± 4 (9)	81 ± 14 (17)	320 ± 160 (13)	6 ± 2 (33)	91 (1)	30 (1)
<i>A. repanda</i>	1139 ± 322 (10)	21 ± 3 (10)	45 ± 18 (14)	252 ± 130 (24)	5 ± 2 (43)	85 (1)	63 (1)
<i>A. schliebenii</i>	1280 ± 581 (5)	18 ± 3 (5)	82 ± 15 (7)	209 ± 83 (12)	7 ± 2 (46)	94 (1)	0 (1)
<i>A. stenodactyla</i>	1160 ± 330 (5)	21 ± 9 (5)	76 ± 10 (9)	204 ± 59 (12)	7 ± 3 (46)	99 (1)	55 (1)
<i>A. subsessilifolia</i>	1634 ± 1006 (14)	17 ± 5 (14)	63 ± 41 (2)	247 ± 108 (5)	6 ± 2 (40)	94 (1)	64 (1)
<i>A. wilmsii</i>	558 ± 162 (9)	16 ± 6 (9)	50 ± 18 (8)	m	5 ± 2 (17)	86 (1)	26 (1)

located on leaves and stems (Fig. 5). Waxy epidermal projections have been noticed on stems of *A. elegans* and *A. inermis*. The dermal projections of *A. aculeata* (sister to *A. inermis*) develop into sclerified prickles. Stem trichomes are not known in other species, but in *A. cladosepala*, whitish, waxy appendages are present on leaf undersides.

Although no special tissue preparations were made to observe stomata, epidermal peels with stomata were present in macerations (Fig. 4, 6), and guard cells were visible in stem cross sections (Fig. 1, 3, 5). Even though the epidermal peels represent neither an exhaustive taxon sample, nor a representative sample, many stomatal variants were observed that ranged from paracytic to cyclocytic. Stomata were not generally located in pits or fissures but were occasionally associated with substomatal chambers (Fig. 3). *Adenia pachyphylla*, a wet forest species, had stomata in grooves (Fig. 1). No palisade cortical parenchyma was associated with stomata, but spongy tissue was occasionally present beneath stomata (Fig. 3).

Periderm cells were uniformly lengthened tangentially (Tables 4, 5, 7: perL), narrow axially (Tables 4, 5, 7: perW), and they were often storied (Fig. 9–10; Tables 4, 5: storied). All tubers had periderms (Table 4), with the possible exception of those of *A. repanda*. However, the tuber that was examined of *A. repanda* was young and may not have initiated periderm development yet.

Cortex.—Cortical tissue consists of collenchyma and parenchyma of the ground meristem (Tables 5–7: parCor, parCort%) located between the dermal and vascular tissue of stems (Esau 1977). The hypodermis immediately proximal to the dermis (Tables 5, 7: hypW) was detected by the presence of collenchyma whose cell walls are irregularly thickened near the periphery of the stem (Fig. 3, 5, 12). Young plants frequently had a hypodermis, but as the plant aged, the hypodermis became less visible.

Bundles of thick-walled, libriform fibers (Tables 5–7: bundL, bundW) were in distal regions of primary phloem (e.g., Fig. 7, 9, 11) of stems of all species except *A. monadelpha*; these bundles remained distal in secondary phloem in mature stems (Fig. 7, 9, 11–13, 20, 21). The number of bundles in cross section varied from species to species (Table 7: bundAng). In *A. digitata* and other geophytes of Clade IV, additional bundles developed as the stem aged (Fig. 7–8). These fiber bundles associated with phloem were absent from storage roots.

Anomalous proliferation of cortical parenchyma was observed in several species (Fig. 11; Tables 5–6: camV), resulting in increases in girth of the cortex. The relative width of the cortex varied interspecifically among similarly aged juvenile stems (Tables 5, 7: ctxW). No cortical vascular bundles were observed. A unique cortical tissue type was present in stems that emerge from the storage trunk of the pachycaul, *A. globosa* (Fig. 12). This tissue consisted of large, thin-walled, irregular parenchyma cells with extensive air spaces between them. As well, crushed phloem was present interior to cortices of mature stems in species that produced secondary growth (e.g., bands in the cortex of Fig. 7). Lastly, lysigenous secretory cavities were observed in the cortex of *A. lobata* (Fig. 13). The chemical constituents of these cavities are unknown.

Inclusions and other cellular contents.—Inclusions (Fig. 14–19) considered here were brachysclereids (stone cells; Table 5: stone; Fig. 19), crystals (Fig. 14–15; Tables 4, 5, 7: crysD), and tanniferous (or possibly resin) cells (Fig. 16–17; Tables 4, 5, 7: tannin). Stone cells and tanniferous cells were frequent near the surfaces of both storage roots and stems.

Druses were common and ranged from occupying nearly every parenchymatous cell (Fig. 14–15) to being absent. They developed in the pith, rays, cortex, and occasionally in the periderm of nearly every species in new and old stems and storage roots but were not observed in lignified tissue. Their highest densities were in the pith and cortex, and they were occasionally present in most cells that subtended the epidermis (Fig. 14).

Secretory cells included what were interpreted as tanniferous cells (*sensu* De Wilde 1971a). These were distributed throughout parenchymatous cells in storage roots and stems. They were numerous (Fig. 16–17) to absent or rare (e.g., Fig. 7). In cross section, tanniferous cells appeared similar to other parenchyma cells (Fig. 17). In longitudinal section, however, they were often elongate (Fig. 16).

Phloem and vascular cambium including cambial variants.—Phloem was not exhaustively characterized. Sieve element diameter was the sole phloem character quantified (Tables 5, 7: SEDiam). At a larger scale, regions containing sieve elements were separated by wide rays in the phloem (e.g., Fig. 21). Within the secondary phloem, scattered fibers often developed. The vascular cambium was characterized as the region between phloem and xylem, often consisting of regularly arrayed rectangular cells (in cross section) that were thin walled and undifferentiated (Tables 4, 5, 7: VCW).

Adenia had four distinct cambial variants (Tables 5, 6: cambV), including successive cambia of the *Atriplex*-type to *Securidaca*-type (*sensu* Carlquist 2001; Fig. 21), ground tissue proliferation and vascular strands (to be discussed in detail elsewhere), and a novel type, intraxylary phloem (Fig. 7–8). Successive cambia were observed in *A. gummifera* and *A. cissampeloides* (Fig. 21). They were also observed in a specimen of a related species that could not be identified with confidence but was potentially *A. stoltzii* Harms (*Hearn 26-11-35* [ARIZ]).

Rays and axial parenchyma.—According to IAWA Committee on Nomenclature (1964), a ray is “a ribbon-like aggregate of cells extending radially in the xylem and phloem”. This general definition permits a wide range of cell patterns to be rays. Using this definition, rays in *Adenia* were very wide (Table 5: rayW; Fig. 23–30); their heights were not determinable from longitudinal sections. In longitudinal section, lignified tissue appeared to be embedded in a matrix of parenchyma.

Ray and axial parenchyma (Tables 5, 6: parXyl%) consisted of thin-walled, non-lignified cells of varying types (Fig. 23–30; Tables 4, 5: rayH, parAx). Wood of *Adenia* is so highly parenchymatized, that it was difficult to distinguish ray, axial, and ground parenchyma. When ray cells could be distinguished from axial parenchyma, the axial parenchyma cells were smaller (Fig. 24–25, 27, 29). Lignified tissue frequently formed aliform bundles in a matrix of abundant, apotracheal parenchyma (Fig. 25, 27–28; Table 6: axPar). Both wide and narrow axial parenchyma bands were frequent around bundles of thick-walled libriform fibers in lianas and many pachycauls

Table 7. Anatomy of juvenile stems. See Tables 2 and 3 for abbreviations.

Taxa	AngV	EpiDesc	EpiMS	Plate	1°Xyl	CtxW	CrysD	CutW	HypW
<i>A. aculeata</i>	+	s	±	s	102 ± 20 (9)	292 ± 55 (15)	0	0	53 ± 14 (11)
<i>A. acuta</i>	—	e,sq	—	s	174 ± 49 (6)	511 ± 82 (14)	0	12 ± 2 (18)	0
<i>A. boivinii</i>	—	s	—	s	97 ± 25 (10)	253 ± 47 (11)	43 ± 12 (12)	10 ± 1 (13)	66 ± 19 (16)
<i>A. cissampeloides</i>	—	e	—	s	153 ± 49 (21)	583 ± 71 (18)	47 (1)	13 ± 3 (12)	0
<i>A. cladosepala</i>	—	s	±	s	146 ± 65 (17)	411 ± 58 (20)	29 ± 7 (13)	11 ± 2 (14)	0
<i>A. densiflora</i>	—	e	—	s	165 ± 93 (10)	774 ± 49 (12)	28 ± 5 (19)	16 ± 6 (18)	91 ± 11 (10)
<i>A. digitata</i>	+	s	—	s	123 ± 14 (7)	173 ± 21 (17)	0	5 ± 1 (9)	25 ± 6 (16)
<i>A. elegans</i>	+	s	—	s	47 ± 8 (5)	222 ± 31 (23)	33 ± 21 (2)	5 ± 1 (14)	0
<i>A. ellenbeckii</i>	—	f	—	s	73 ± 24 (4)	172 ± 45 (5)	0	0	56 ± 15 (14)
<i>A. fasciculata</i>	—	e	—	s	98 ± 16 (15)	309 ± 56 (21)	25 ± 7 (19)	9 ± 2 (7)	80 ± 24 (17)
<i>A. firingalavensis</i>	—	s,mi	±	s	139 ± 25 (20)	284 ± 27 (24)	26 (1)	0	77 ± 6 (22)
<i>A. fruticosa</i>	+	sq	—	s	177 ± 45 (16)	289 ± 41 (15)	27 ± 5 (6)	4 ± 2 (12)	55 ± 13 (19)
<i>A. glauca</i>	+	s	—	s	157 ± 44 (7)	314 ± 44 (13)	0	4 ± 2 (10)	51 ± 14 (22)
<i>A. globosa</i>	+	f,mi	±	s	111 ± 33 (13)	639 ± 32 (9)	22 ± 4 (12)	0	45 ± 9 (15)
<i>A. goetzei</i>	—	f	±	s	65 ± 21 (9)	247 ± 38 (20)	0	7 ± 2 (13)	26 ± 7 (25)
<i>A. gummifera</i>	+	s	—	s	98 ± 20 (12)	172 ± 26 (14)	12 (1)	3 ± 1 (6)	50 ± 6 (24)
<i>A. hastata</i>	—	s	—	s	63 ± 23 (14)	112 ± 18 (6)	0	0	35 ± 10 (15)
<i>A. heterophylla</i>	—	s	—	s	80 ± 16 (8)	174 ± 15 (19)	15 ± 4 (2)	3 ± 1 (10)	41 ± 5 (13)
<i>A. hondala</i>	+	s,e	—	s	193 ± 36 (15)	379 ± 37 (17)	37 ± 9 (5)	0	0
<i>A. inermis</i>	—	i	±	s	88 ± 30 (9)	219 ± 53 (16)	27 ± 5 (2)	5 ± 1 (14)	42 ± 8 (14)
<i>A. isaloensis</i>	—	e	—	s	189 ± 96 (11)	498 ± 58 (15)	0	6 ± 3 (13)	0
<i>A. karibaensis</i>	—	s	±	s	245 ± 94 (5)	245 ± 75 (7)	0	5 ± 2 (3)	38 ± 8 (12)
<i>A. keramanthus</i>	+	i	—	s	215 ± 52 (8)	734 ± 93 (21)	0	0	83 ± 20 (15)
<i>A. kirkii</i>	+	i,s,f	—	s	114 ± 29 (7)	387 ± 115 (18)	22 (1)	12 ± 5 (14)	37 ± 6 (18)
<i>A. lanceolata</i>	+	i	—	s	133 ± 41 (10)	347 ± 64 (15)	0	10 ± 2 (15)	23 ± 9 (11)
<i>A. lapiazicola</i>	+	a	a	s	368 ± 90 (7)	1269 ± 212 (4)	22 ± 9 (28)	0	0
<i>A. letouzeyi</i>	+	s	—	s	80 ± 36 (10)	368 ± 51 (22)	24 ± 3 (7)	5 ± 1 (10)	46 ± 10 (11)
<i>A. lindiensis</i>	+	s,sq	—	s	82 ± 13 (13)	160 ± 37 (8)	23 (1)	7 ± 1 (12)	22 ± 7 (18)
<i>A. litoralis</i>	+	f,sq	±	s	124 ± 16 (7)	241 ± 31 (11)	0	0	29 ± 10 (12)
<i>A. lobata</i>	—	mi	—	s	97 ± 34 (12)	477 ± 110 (17)	23 ± 4 (11)	7 ± 3 (18)	37 ± 16 (14)
<i>A. longestipitata</i>	+	e,sp	—	s	91 ± 48 (11)	251 ± 43 (24)	23 ± 5 (9)	7 ± 2 (29)	100 ± 34 (12)
<i>A. mannii</i>	+	sq	—	s	71 ± 14 (9)	276 ± 46 (27)	0	8 ± 2 (11)	39 ± 9 (20)
<i>A. mcladadiana</i>	—	s	±	s	91 ± 18 (16)	268 ± 41 (11)	30 (1)	0	64 ± 7 (13)
<i>A. metamorpha</i>	+	s	—	s	95 ± 34 (6)	302 ± 48 (17)	20 ± 9 (17)	5 ± 1 (9)	40 ± 15 (30)
<i>A. metriosiphon</i>	—	f	—	s	77 ± 19 (4)	483 ± 50 (13)	19 ± 6 (20)	11 ± 4 (17)	70 ± 20 (11)
<i>A. monadelpha</i>	+	f	±	s	127 ± 39 (3)	573 ± 117 (9)	24 ± 4 (11)	7 ± 1 (7)	140 ± 31 (14)
<i>A. olaboensis</i>	+	i	—	s	174 ± 14 (2)	m	23 ± 2 (6)	5 ± 1 (7)	55 ± 8 (17)
<i>A. pachyphylla</i>	+	sq,e	—	s	64 ± 21 (8)	237 ± 28 (12)	18 ± 5 (26)	0	65 ± 12 (20)
<i>A. pachuili</i>	+	s,f	—	s	260 ± 121 (10)	1426 ± 86 (12)	28 ± 6 (9)	7 ± 2 (4)	46 ± 15 (26)
<i>A. peltata</i>	+	sq,s	—	s	81 ± 21 (13)	182 ± 15 (17)	0	0	32 ± 6 (16)
<i>A. penangiana</i>	+	f,s	—	s	221 ± 53 (8)	377 ± 28 (16)	32 ± 8 (21)	9 ± 3 (11)	73 ± 18 (15)
<i>A. perrieri</i>	—	f,sq	—	s	72 ± 10 (10)	170 ± 25 (18)	18 ± 7 (6)	8 ± 1 (11)	39 ± 5 (28)
<i>A. pyromorpha</i>	+	i	±	s	50 ± 16 (9)	263 ± 37 (14)	31 ± 6 (3)	0	41 ± 9 (25)
<i>A. racemosa</i>	+	f	±	s	71 ± 13 (6)	415 ± 98 (15)	0	0	34 ± 9 (19)
<i>A. refracta</i>	—	f	—	s	54 ± 9 (13)	298 ± 69 (29)	21 ± 6 (9)	7 ± 2 (11)	m
<i>A. repanda</i>	+	s	—	s	194 ± 6 (5)	452 ± 58 (8)	36 ± 13 (28)	8 ± 2 (6)	89 ± 23 (18)
<i>A. rumicifolia</i>	+	sq,e	—	s	59 ± 10 (8)	284 ± 46 (25)	22 (1)	4 ± 1 (8)	0
<i>A. schliebenii</i>	—	s	±	s	151 ± 32 (13)	496 ± 49 (16)	31 ± 4 (2)	8 ± 2 (9)	58 ± 9 (22)
<i>A. schweinfurthii</i>	+	s	±	s	68 ± 24 (12)	622 ± 38 (17)	33 ± 7 (9)	0	59 ± 13 (29)
<i>A. sphaerocarpa</i>	—	s	±	s	82 ± 18 (13)	322 ± 40 (13)	0	0	67 ± 17 (26)
<i>A. spinosa</i>	—	mi	±	s	88 ± 22 (15)	474 ± 43 (13)	26 (1)	5 ± 2 (11)	58 ± 14 (33)
<i>A. stenodactyla</i>	—	mi,sp	—	s	116 ± 28 (6)	622 ± 69 (10)	30 ± 4 (13)	13 ± 2 (18)	60 ± 20 (11)
<i>A. stylosa</i>	—	s,sp	—	s	63 ± 16 (6)	117 ± 18 (26)	0	8 ± 2 (15)	0
<i>A. subsessilifolia</i>	+	s,f	±	s	53 ± 16 (7)	327 ± 36 (20)	25 ± 6 (17)	3 ± 1 (10)	30 ± 13 (33)
<i>A. venenata</i>	+	sq	—	s	133 ± 24 (16)	295 ± 37 (20)	0	5 ± 1 (7)	25 ± 6 (22)
<i>A. volkensii</i>	—	s	—	s	171 ± 49 (9)	429 ± 40 (17)	41 ± 9 (4)	0	71 ± 15 (26)
<i>A. wightiana</i>	—	f,s	—	s	110 ± 23 (11)	1056 ± 169 (15)	44 ± 7 (2)	10 ± 2 (11)	62 ± 17 (19)
<i>A. wilmsii</i>	+	f	±	s	168 ± 25 (14)	491 ± 76 (16)	0	5 ± 2 (4)	50 ± 13 (42)
<i>Deidamia</i>	—	s	—	s	134 ± 29 (14)	210 ± 31 (16)	0	5 ± 1 (12)	0
<i>Paropsia</i>	—	s	—	s	190 ± 50 (5)	279 ± 56 (22)	37 ± 15 (7)	0	0
<i>Passiflora caerulea</i>	+	s	—	s	109 ± 31 (6)	198 ± 27 (18)	15 ± 6 (6)	9 ± 3 (16)	26 ± 11 (26)
<i>Passiflora foetida</i>	—	sq,e	—	s	121 ± 9 (7)	189 ± 36 (21)	17 ± 4 (17)	3 ± 2 (8)	0

Table 7. Continued.

	ParCor	ParAx	ParPith	PerL	PerW	PerThick	BundAng	BundL
<i>A. aculeata</i>	22 ± 8 (34)	NA	24 ± 7 (26)	0	0	0	0.09 (1)	67 ± 31 (31)
<i>A. acuta</i>	48 ± 18 (34)	NA	144 ± 40 (46)	0	0	0	0.06 (1)	275 ± 99 (12)
<i>A. boivinii</i>	30 ± 13 (24)	NA	42 ± 10 (26)	0	0	0	0.06 (1)	176 ± 78 (21)
<i>A. cissampeloides</i>	27 ± 9 (56)	NA	54 ± 18 (38)	0	0	0	0.09 (1)	124 ± 34 (24)
<i>A. cladosepala</i>	27 ± 6 (38)	NA	43 ± 11 (50)	0	0	0	0.10 (1)	117 ± 32 (32)
<i>A. densiflora</i>	27 ± 7 (48)	18 ± 3 (16)	32 ± 9 (44)	0	0	0	0.13 (1)	133 ± 49 (20)
<i>A. digitata</i>	16 ± 5 (44)	NA	28 ± 10 (50)	0	0	0	0.06 (1)	100 ± 24 (12)
<i>A. elegans</i>	32 ± 10 (40)	NA	19 ± 7 (52)	0	0	0	0.03 (1)	81 ± 7 (9)
<i>A. ellenbeckii</i>	20 ± 5 (42)	NA	27 ± 6 (46)	0	0	0	m	123 ± 17 (4)
<i>A. fasciculata</i>	17 ± 5 (34)	NA	32 ± 9 (56)	0	0	0	0.10 (1)	160 ± 63 (14)
<i>A. firingalavensis</i>	10 ± 2 (20)	NA	27 ± 10 (58)	0	0	0	0.12 (1)	99 ± 18 (9)
<i>A. fruticosa</i>	22 ± 6 (38)	NA	41 ± 16 (50)	0	0	0	0.07 (1)	128 ± 31 (16)
<i>A. glauca</i>	18 ± 6 (48)	NA	25 ± 8 (56)	0	0	0	0.03 (1)	247 ± 69 (12)
<i>A. globosa</i>	19 ± 5 (20)	NA	38 ± 11 (52)	0	0	0	0.08 (1)	61 ± 15 (21)
<i>A. goetzei</i>	24 ± 10 (64)	NA	42 ± 13 (44)	0	0	0	0.04 (1)	176 ± 59 (14)
<i>A. gummifera</i>	15 ± 5 (40)	NA	28 ± 9 (58)	0	0	0	0.05 (1)	132 ± 29 (15)
<i>A. hastata</i>	16 ± 4 (22)	NA	18 ± 5 (20)	0	0	0	m	m
<i>A. heterophylla</i>	12 ± 5 (20)	NA	29 ± 10 (66)	0	0	0	0.07 (1)	111 ± 21 (7)
<i>A. hondala</i>	24 ± 8 (54)	NA	34 ± 14 (70)	0	0	0	0.07 (1)	168 ± 42 (19)
<i>A. inermis</i>	13 ± 4 (43)	NA	18 ± 6 (58)	0	0	0	0.05 (1)	93 ± 33 (16)
<i>A. isaloensis</i>	23 ± 6 (30)	NA	40 ± 14 (98)	0	0	0	0.05 (1)	343 ± 145 (16)
<i>A. karibaensis</i>	28 ± 4 (10)	NA	35 ± 17 (24)	0	0	0	0.07 (1)	190 ± 41 (12)
<i>A. keramanthus</i>	39 ± 12 (46)	NA	58 ± 20 (82)	0	0	0	0.06 (1)	131 ± 31 (12)
<i>A. kirkii</i>	18 ± 7 (32)	NA	30 ± 8 (42)	0	0	0	0.08 (1)	140 ± 68 (23)
<i>A. lanceolata</i>	19 ± 9 (32)	NA	23 ± 8 (36)	0	0	0	0.12 (1)	153 ± 77 (31)
<i>A. lapiazicola</i>	35 ± 14 (50)	22 ± 5 (26)	44 ± 16 (66)	36 ± 12 (10)	16 ± 6 (10)	150 ± 41 (10)	m	72 (1)
<i>A. letouzeyi</i>	28 ± 8 (40)	NA	36 ± 10 (58)	0	0	0	0.07 (1)	79 ± 31 (13)
<i>A. lindiensis</i>	14 ± 5 (22)	NA	20 ± 4 (24)	0	0	0	0.07 (1)	96 ± 19 (4)
<i>A. litoralis</i>	19 ± 6 (41)	NA	34 ± 10 (46)	0	0	0	0.08 (1)	126 ± 41 (15)
<i>A. lobata</i>	27 ± 8 (30)	NA	24 ± 5 (30)	0	0	0	0.09 (1)	108 ± 39 (15)
<i>A. longestipitata</i>	23 ± 7 (30)	NA	22 ± 6 (48)	0	0	0	0.06 (1)	92 ± 34 (20)
<i>A. mannii</i>	24 ± 7 (32)	NA	32 ± 10 (26)	0	0	0	0.06 (1)	101 ± 39 (14)
<i>A. mcdadiana</i>	16 ± 5 (38)	NA	35 ± 9 (44)	0	0	0	0.11 (1)	95 ± 23 (9)
<i>A. metamorpha</i>	24 ± 6 (30)	13 ± 5 (18)	38 ± 6 (36)	0	0	0	0.09 (1)	110 ± 39 (33)
<i>A. metriosiphon</i>	34 ± 9 (26)	19 ± 8 (22)	41 ± 8 (40)	0	0	0	0.04 (1)	183 ± 53 (13)
<i>A. monadelpha</i>	71 ± 25 (58)	NA	63 ± 18 (58)	0	0	0	NA	NA
<i>A. olaboensis</i>	26 ± 9 (50)	NA	26 ± 8 (38)	0	0	0	0.08 (1)	96 ± 38 (22)
<i>A. pachyphylla</i>	13 ± 3 (40)	NA	26 ± 8 (60)	0	0	0	0.07 (1)	73 ± 23 (8)
<i>A. pechuëlii</i>	32 ± 11 (38)	NA	NA	0	0	0	0.04 (1)	184 ± 30 (11)
<i>A. peltata</i>	14 ± 4 (66)	NA	NA	0	0	0	0.07 (1)	98 ± 20 (11)
<i>A. penangiana</i>	30 ± 12 (20)	NA	46 ± 14 (38)	0	0	0	0.05 (1)	188 ± 66 (14)
<i>A. perrieri</i>	23 ± 9 (38)	23 ± 9 (30)	35 ± 12 (54)	0	0	0	0.08 (1)	112 ± 35 (11)
<i>A. pyromorpha</i>	17 ± 4 (32)	NA	18 ± 5 (42)	0	0	0	34.36 (1)	165 ± 56 (11)
<i>A. racemosa</i>	27 ± 13 (38)	NA	28 ± 6 (30)	0	0	0	0.06 (1)	126 ± 34 (11)
<i>A. refracta</i>	26 ± 7 (36)	NA	27 ± 8 (42)	0	0	0	0.07 (1)	86 ± 29 (16)
<i>A. repanda</i>	26 ± 6 (18)	21 ± 4 (10)	48 ± 10 (20)	0	0	0	0.04 (1)	202 ± 54 (14)
<i>A. rumicifolia</i>	15 ± 5 (32)	NA	30 ± 9 (52)	0	0	0	0.05 (1)	94 ± 21 (16)
<i>A. schliebenii</i>	31 ± 11 (40)	NA	45 ± 13 (44)	0	0	0	0.06 (1)	167 ± 53 (18)
<i>A. schweinfurthii</i>	28 ± 7 (38)	NA	24 ± 5 (50)	0	0	0	0.06 (1)	97 ± 37 (20)
<i>A. sphaerocarpha</i>	18 ± 5 (32)	NA	29 ± 7 (44)	0	0	0	0.11 (1)	98 ± 48 (21)
<i>A. spinosa</i>	24 ± 7 (34)	NA	34 ± 8 (42)	0	0	0	0.08 (1)	144 ± 52 (19)
<i>A. stenodactyla</i>	29 ± 10 (48)	NA	45 ± 15 (56)	0	0	0	0.10 (1)	247 ± 131 (8)
<i>A. stylosa</i>	12 ± 4 (18)	NA	28 ± 7 (32)	0	0	0	0.08 (1)	75 ± 21 (18)
<i>A. subsessilifolia</i>	26 ± 10 (40)	NA	24 ± 10 (32)	0	0	0	0.04 (1)	54 ± 12 (8)
<i>A. venenata</i>	14 ± 3 (22)	NA	35 ± 10 (40)	0	0	0	0.08 (1)	131 ± 38 (19)
<i>A. volkensii</i>	32 ± 9 (52)	NA	38 ± 10 (38)	0	0	0	0.07 (1)	128 ± 32 (25)
<i>A. wightiana</i>	37 ± 10 (38)	NA	49 ± 16 (38)	0	0	0	0.05 (1)	106 ± 18 (7)
<i>A. wilmsii</i>	44 ± 14 (32)	NA	49 ± 17 (52)	0	0	0	0.04 (1)	242 ± 73 (14)
<i>Deidamia</i>	24 ± 6 (24)	NA	50 ± 14 (54)	0	0	0	0.07 (1)	202 ± 50 (21)
<i>Paropsia</i>	19 ± 7 (50)	NA	46 ± 16 (74)	0	0	0	0.08 (1)	154 ± 108 (17)
<i>Passiflora caerulea</i>	13 ± 3 (28)	NA	NA	0	0	0	0.08 (1)	98 ± 21 (10)
<i>Passiflora foetida</i>	13 ± 3 (36)	NA	29 ± 8 (32)	0	0	0	0.06 (1)	100 ± 32 (21)

Table 7. Continued.

	BundW	SEDiam	PithR	Tannin	VCW	VEDiam	VEAgg	VEW
<i>A. aculeata</i>	55 ± 29 (31)	16 ± 6 (21)	391 ± 79 (9)	0	33 ± 13 (19)	53 ± 22 (25)	2 ± 1 (11)	2 ± 2 (10)
<i>A. acuta</i>	125 ± 36 (12)	41 ± 12 (7)	713 ± 120 (7)	103 ± 47 (2)	93 ± 26 (13)	142 ± 30 (5)	1 (5)	6 ± 4 (7)
<i>A. boivinii</i>	85 ± 21 (21)	34 ± 10 (14)	298 ± 42 (5)	0	30 ± 8 (11)	77 ± 26 (26)	2 ± 1 (17)	5 ± 3 (7)
<i>A. cissampeloides</i>	69 ± 14 (24)	23 ± 4 (14)	900 ± 127 (6)	39 ± 13 (41)	34 ± 8 (15)	43 ± 12 (30)	1 ± 1 (33)	3 ± 1 (7)
<i>A. cladosepala</i>	70 ± 17 (32)	16 ± 4 (14)	504 ± 98 (9)	34 ± 11 (33)	39 ± 9 (11)	130 ± 31 (23)	1 (21)	3 ± 2 (8)
<i>A. densiflora</i>	110 ± 42 (20)	20 ± 7 (16)	798 ± 129 (8)	32 ± 11 (28)	42 ± 16 (12)	68 ± 36 (40)	4 ± 8 (27)	3 ± 2 (10)
<i>A. digitata</i>	62 ± 19 (12)	14 ± 3 (9)	279 ± 89 (10)	0	28 ± 4 (11)	48 ± 8 (28)	2 ± 1 (23)	1 ± 1 (8)
<i>A. elegans</i>	42 ± 7 (9)	13 ± 3 (18)	123 ± 39 (7)	0	26 ± 4 (10)	46 ± 10 (8)	1 (7)	3 ± 2 (6)
<i>A. ellenbeckii</i>	52 ± 12 (4)	14 ± 3 (4)	230 ± 56 (9)	18 ± 6 (15)	0	108 ± 11 (3)	1 (2)	0
<i>A. fasciculata</i>	93 ± 23 (14)	23 ± 7 (25)	480 ± 49 (7)	28 ± 10 (15)	28 ± 7 (12)	50 ± 15 (25)	1 (13)	3 ± 2 (8)
<i>A. firingalavensis</i>	62 ± 16 (9)	14 ± 4 (30)	647 ± 69 (8)	21 ± 7 (36)	24 ± 6 (10)	47 ± 12 (7)	1 (4)	2 ± 1 (7)
<i>A. fruticosa</i>	79 ± 20 (16)	15 ± 3 (11)	470 ± 48 (7)	0	39 ± 5 (15)	55 ± 12 (8)	1 (7)	2 ± 1 (6)
<i>A. glauca</i>	156 ± 33 (12)	13 ± 4 (22)	292 ± 59 (9)	26 ± 6 (39)	33 ± 8 (4)	38 ± 10 (16)	6 ± 5 (9)	2 ± 1 (7)
<i>A. globosa</i>	69 ± 19 (21)	14 ± 3 (16)	1033 ± 316 (5)	0	35 ± 6 (13)	35 ± 8 (11)	1 (2)	2 ± 1 (7)
<i>A. goetzei</i>	75 ± 22 (14)	15 ± 4 (25)	304 ± 64 (7)	21 ± 6 (24)	25 ± 5 (21)	34 ± 8 (10)	1 (6)	3 ± 2 (15)
<i>A. gummifera</i>	57 ± 9 (15)	17 ± 4 (26)	348 ± 48 (7)	20 ± 6 (41)	34 ± 9 (7)	56 ± 9 (5)	1 (5)	2 ± 1 (7)
<i>A. hastata</i>	m	11 ± 3 (4)	364 ± 65 (5)	0	m	46 ± 13 (10)	2 ± 1 (8)	6 ± 23 (7)
<i>A. heterophylla</i>	47 ± 7 (7)	12 ± 3 (18)	341 ± 22 (8)	32 (1)	14 ± 3 (12)	31 ± 9 (7)	1 (1)	4 ± 1 (4)
<i>A. hondala</i>	92 ± 22 (19)	15 ± 5 (32)	860 ± 79 (7)	0	37 ± 7 (20)	43 ± 7 (10)	3 ± 1 (25)	3 ± 1 (10)
<i>A. inermis</i>	53 ± 16 (16)	13 ± 4 (33)	230 ± 50 (12)	19 ± 6 (13)	13 ± 5 (6)	56 ± 14 (11)	2 ± 1 (10)	3 ± 2 (8)
<i>A. isaloensis</i>	196 ± 54 (16)	19 ± 4 (35)	538 ± 106 (8)	34 ± 12 (41)	24 ± 8 (14)	66 ± 15 (12)	2 ± 1 (8)	6 ± 3 (17)
<i>A. karibaensis</i>	86 ± 22 (12)	10 ± 1 (6)	751 ± 143 (8)	0	0	30 ± 11 (15)	m	2 ± 1 (3)
<i>A. keramanthus</i>	135 ± 27 (12)	14 ± 4 (23)	1647 ± 205 (5)	37 ± 14 (32)	35 ± 7 (33)	33 ± 6 (22)	4 ± 4 (22)	4 ± 1 (10)
<i>A. kirkii</i>	93 ± 44 (23)	28 ± 9 (27)	460 ± 62 (6)	0	32 ± 8 (7)	119 ± 29 (25)	1 (22)	6 ± 4 (5)
<i>A. lanceolata</i>	108 ± 45 (31)	19 ± 6 (46)	805 ± 164 (6)	0	36 ± 16 (18)	119 ± 37 (29)	1 (23)	4 ± 2 (9)
<i>A. lapiazicola</i>	69 (1)	11 ± 3 (23)	1439 ± 548 (3)	0	16 ± 3 (5)	37 ± 9 (64)	3 ± 2 (31)	4 ± 3 (13)
<i>A. letouzeyi</i>	49 ± 12 (13)	15 ± 3 (23)	433 ± 62 (7)	24 ± 7 (8)	23 ± 6 (22)	31 ± 11 (4)	2 ± 1 (4)	2 ± 1 (6)
<i>A. lindiensis</i>	38 ± 6 (4)	10 ± 3 (15)	254 ± 22 (8)	0	26 ± 5 (9)	56 ± 19 (10)	1 ± 1 (10)	2 ± 1 (9)
<i>A. litoralis</i>	81 ± 25 (15)	16 ± 4 (19)	593 ± 72 (7)	0	18 ± 4 (15)	52 ± 10 (17)	2 ± 2 (16)	3 ± 3 (10)
<i>A. lobata</i>	69 ± 15 (15)	14 ± 4 (17)	324 ± 40 (9)	0	20 ± 6 (7)	58 ± 14 (12)	1 (12)	3 (5)
<i>A. longestipitata</i>	56 ± 19 (20)	10 ± 2 (22)	310 ± 25 (9)	26 ± 9 (28)	14 ± 2 (4)	37 ± 9 (19)	1 (17)	2 ± 1 (5)
<i>A. mannii</i>	45 ± 20 (14)	15 ± 3 (17)	366 ± 48 (7)	0	24 ± 7 (15)	44 ± 11 (5)	1 (3)	3 ± 2 (2)
<i>A. mcdadiana</i>	51 ± 10 (9)	16 ± 3 (12)	756 ± 76 (8)	0	18 ± 7 (8)	45 ± 10 (21)	1 ± 1 (10)	2 ± 1 (10)
<i>A. metamorpha</i>	89 ± 24 (33)	18 ± 4 (21)	382 ± 49 (8)	0	23 ± 10 (14)	46 ± 24 (57)	1 (63)	3 ± 1 (2)
<i>A. metriosiphon</i>	67 ± 19 (13)	22 ± 5 (27)	468 ± 69 (8)	0	21 (1)	75 ± 28 (52)	2 ± 1 (31)	4 ± 1 (6)
<i>A. monadelphina</i>	NA	18 ± 5 (55)	NA	0	21 ± 4 (12)	26 ± 8 (34)	7 ± 6 (28)	3 ± 2 (8)
<i>A. olaboensis</i>	49 ± 16 (22)	17 ± 5 (25)	331 ± 44 (9)	0	29 ± 5 (10)	73 ± 22 (31)	2 ± 1 (53)	4 ± 2 (6)
<i>A. pachyphylla</i>	38 ± 8 (8)	10 ± 3 (15)	214 ± 28 (7)	22 ± 6 (10)	15 ± 4 (9)	23 ± 11 (5)	2 ± 1 (4)	2 ± 1 (2)
<i>A. pachuëlii</i>	197 ± 54 (11)	20 ± 7 (21)	358 ± 45 (5)	0	30 ± 10 (8)	32 ± 10 (33)	3 ± 2 (30)	3 ± 2 (12)
<i>A. peltata</i>	38 ± 3 (11)	10 ± 4 (13)	333 ± 29 (12)	0	10 ± 3 (7)	39 ± 7 (11)	2 ± 1 (6)	2 ± 1 (12)
<i>A. penangiana</i>	72 ± 25 (14)	15 ± 3 (14)	497 ± 72 (11)	0	44 ± 29 (10)	33 ± 8 (21)	2 ± 1 (26)	2 ± 1 (7)
<i>A. perrieri</i>	43 ± 9 (11)	18 ± 6 (19)	364 ± 56 (8)	0	26 ± 7 (8)	45 ± 18 (20)	1 (18)	3 ± 1 (6)
<i>A. pyromorpha</i>	94 ± 25 (11)	12 ± 3 (34)	212 ± 54 (10)	27 ± 10 (14)	5 ± 2 (12)	44 ± 11 (12)	2 ± 1 (15)	2 ± 1 (9)
<i>A. racemosa</i>	62 ± 15 (11)	21 ± 6 (32)	292 ± 36 (7)	0	34 ± 10 (13)	91 ± 36 (21)	1 ± 1 (18)	3 ± 1 (3)
<i>A. refracta</i>	48 ± 18 (16)	24 ± 5 (36)	265 ± 40 (9)	0	19 ± 4 (9)	86 ± 46 (33)	2 ± 2 (19)	4 ± 2 (5)
<i>A. repanda</i>	144 ± 24 (14)	15 ± 4 (10)	456 ± 50 (6)	0	0	38 ± 10 (33)	2 ± 2 (9)	3 ± 2 (4)
<i>A. rumicifolia</i>	46 ± 10 (16)	15 ± 5 (28)	260 ± 38 (7)	0	21 ± 5 (14)	58 ± 19 (10)	1 (11)	2 ± 1 (7)
<i>A. schliebenii</i>	84 ± 19 (18)	22 ± 5 (28)	766 ± 81 (7)	33 ± 6 (15)	36 ± 11 (15)	68 ± 20 (11)	1 ± 1 (8)	4 ± 2 (12)
<i>A. schweinfurthii</i>	71 ± 25 (20)	19 ± 4 (18)	339 ± 52 (8)	0	21 ± 5 (12)	35 ± 8 (29)	3 ± 1 (18)	2 ± 1 (11)
<i>A. sphaerocarpa</i>	71 ± 23 (21)	16 ± 3 (26)	591 ± 82 (8)	0	36 ± 8 (23)	31 ± 5 (3)	1 (5)	2 ± 1 (7)
<i>A. spinosa</i>	120 ± 43 (19)	17 ± 5 (20)	558 ± 97 (8)	28 ± 8 (20)	29 ± 8 (19)	47 ± 15 (37)	1 ± 1 (25)	2 ± 1 (5)
<i>A. stenodactyla</i>	143 ± 68 (8)	19 ± 5 (20)	913 ± 48 (4)	0	44 ± 19 (8)	57 ± 25 (32)	2 ± 1 (20)	3 ± 2 (12)
<i>A. stylosa</i>	40 ± 12 (18)	10 ± 3 (19)	339 ± 26 (6)	14 ± 4 (20)	19 ± 2 (12)	79 ± 35 (26)	1 (70)	2 ± 1 (6)
<i>A. subsessilifolia</i>	78 ± 25 (8)	10 ± 2 (22)	276 ± 47 (9)	38 ± 11 (20)	19 ± 5 (6)	32 ± 15 (7)	1 (5)	1 ± 1 (5)
<i>A. venenata</i>	97 ± 23 (19)	15 ± 3 (23)	684 ± 18 (6)	0	26 ± 6 (12)	48 ± 14 (11)	2 ± 2 (7)	3 ± 1 (14)
<i>A. volkensii</i>	89 ± 14 (25)	14 ± 3 (21)	615 ± 110 (8)	35 ± 16 (9)	30 ± 6 (30)	30 ± 9 (45)	3 ± 2 (12)	2 ± 1 (14)
<i>A. wightiana</i>	79 ± 19 (7)	20 ± 5 (40)	570 ± 101 (7)	0	28 ± 7 (6)	83 ± 30 (46)	1 ± 1 (43)	4 ± 2 (8)
<i>A. wilmsii</i>	151 ± 37 (14)	18 ± 5 (53)	688 ± 123 (8)	0	42 ± 10 (23)	50 ± 25 (20)	1 ± 1 (11)	3 ± 1 (14)
<i>Deidamia</i>	50 ± 11 (21)	18 ± 3 (20)	570 ± 74 (9)	38 ± 10 (30)	23 ± 6 (18)	m	1 (4)	3 ± 1 (9)
<i>Paropsia</i>	43 ± 13 (17)	10 ± 3 (16)	500 ± 41 (8)	28 ± 9 (29)	17 ± 2 (2)	29 ± 6 (24)	8 ± 6 (28)	3 ± 1 (10)
<i>Passiflora caerulea</i>	44 ± 21 (10)	16 ± 4 (24)	415 ± 38 (6)	0	16 ± 7 (10)	22 ± 8 (11)	3 ± 1 (8)	4 ± 1 (6)
<i>Passiflora foetida</i>	58 ± 14 (21)	8 ± 2 (28)	251 ± 47 (8)	18 (1)	13 ± 3 (10)	15 ± 4 (18)	m	3 ± 1 (7)

Fig. 1–6. Epidermal features of *Adenia* stems.—1. Stomatal complex in groove of *A. pachyphylla*. Anticlinal divisions (AD) in epidermal cells are visible.—2. Layered epicuticular wax of mature *A. fasciculata* with some regions of multiple files of epidermal cells (MS).—3. Substomatal chamber (SSC) of *A. venenata*.—4. Epidermal peel of *A. fruticosa* showing stomata.—5. Uniseriate trichome of young *A. keramanthus* with isodiametric epidermal cells.—6. Epidermal peel of *A. stylosa* showing cyclocytic stomata. Key: AD = anticlinal divisions; C = cuticle; E = epidermis; ECW = epicuticular waxes; H = hypodermis; MS = multiseriate regions; PFB = phloem fiber bundle; T = trichome; () = stomata. (Scale bars: Fig. 1–4, 6 = 0.1 mm; Fig. 5 = 0.4 mm).

(Fig. 23–24), particularly in pachycauls of Clade V (see Hearn 2006 for listing of pachycaul species). The secondary growth in stems of several lianas had large regions of parenchyma with bands of vascularized tissue (Fig. 28).

Perforate tracheary elements.—Perforate tracheary elements (Fig. 31–40) were dimorphic following usage of Carlquist (2001). In *Adenia*, fibriform vessel elements intergraded with imperforate tracheary elements (e.g., Fig. 38), and the lengths provided for “imperforate” elements therefore include both fibriform vessel elements and the tracheids associated with vessels (Tables 5, 6: imperfL, imperfW). Although it was difficult to distinguish these two cell types, other perforate vessel members were wide and easily distinguishable (e.g., Fig. 31–33). Measurements for vessel elements are of these wider cells (Tables 4–7: maxVEDiam, maxVEL, minVEDiam, minVEL, VEDiam, VEL). Fibriform vessel elements had oblique, caudate tips in most species, but in some geophytes, they had transverse ends and few lateral wall pits (e.g., Fig. 40).

Wide vessels were solitary or aggregated (Fig. 23–30; Tables 4, 5, 7: VEAgg). Vessels tended to be more aggregated in succulents (e.g., Fig. 26, 29), and the highest level of aggregation was in storage roots (Fig. 30). In some species, aggregations were oriented radially (Fig. 30), tangentially (Fig. 26), or there was no discernable pattern (Fig. 27, 29). Densities of vessels in stems (Tables 4, 5: VE#/mm²) averaged 12 vessels per mm² and ranged from less than one to greater than 50 vessels per mm². Perforation plate angles in wide elements (Tables 5, 6: plateAng, angV) ranged from transverse (Fig. 31–32) to oblique in secondary xylem (Fig. 36). Perforation plates were uniformly simple and unbordered (Fig. 31–40;

potentially weakly bordered; see Baas 1976; Tables 5–7: Plate), with no trebectulae observed. Tyloses (Table 5: Tyl) were frequent in vessels of the older portions of stems (Fig. 18).

Lateral wall pits (Tables 5–6: VELW, VEPit) in both the wide vessel elements and the fibriform elements were bordered or weakly bordered and were not vested (Fig. 31–33, 36, 39). Vessel lateral surfaces lacked helical thickenings and had alternate (Fig. 31), irregularly alternate (Fig. 32), or approaching pseudoscalariform pits (Fig. 33).

Imperforate tracheary elements.—Imperforate tracheary elements in xylem consisted of both tracheids and libriform fibers (Fig. 34–35, 37–38). Libriform fibers tended to be thick-walled and narrow (Fig. 35; Tables 5, 6: libW), but in some, both thick- and thin-walled fibers were present (Fig. 34). Some contained septa (Fig. 34; e.g., *A. karibaensis*). The average length of all fibers (Tables 5, 6: libL) was relatively short (1.2 mm), but averages within species varied between 444 μ m (*A. inermis*) and 2.5 mm (*A. hondala*). Pitting and shapes of tracheids closely resembled those of fibriform vessel elements. Lengths (Tables 5, 6: imperfL, imperfW) of the tracheids and fibriform vessel elements averaged 0.5 mm, but they ranged between 0.2 and 1.2 mm.

Pith.—Pith consisted primarily of large-celled, thin-walled parenchyma (Tables 5, 7: parPith, pithR). Pith in proximity to primary xylem was lignified as is visible when viewed in relation to protoxylem (Fig. 8, 20, 28). Both tannin cells and druse crystals were present in the pith of many species. Medullary bundles, as discussed in depth elsewhere (D. Hearn, unpubl.), were prominent features of mature succulent stems.

Phylogenetic Analysis

The consensus phylogeny (Fig. 41–42 present the Bayesian *allcompat* tree) resulting from the taxon sample of 52 taxa was similar to that presented by the more thorough taxon sampling of Hearn (2006). It maintained Clades I–V that were strongly supported by both morphological and molecular data in Hearn (2006), although Clade V, with the limited taxon sample here, had weaker support (Fig. 41a, 42a). The consensus phylogeny differed from that of Hearn (2006) in the placement of *A. perrieri* and *A. schweinfurthii*. *Adenia perrieri* was sister to *A. boivinii*, *A. lapiazicola*, *A. litoralis*, *A. metamorpha*, *A. monadelphae*, and *A. refracta* in this analysis, whereas it was sister to *A. lapiazicola*, *A. litoralis*, and *A. metamorpha* in Hearn (2006). *Adenia hondala* was sister to *A. schweinfurthii* in the current analysis, whereas these taxa formed a paraphyletic grade in Hearn (2006). Positions of *A. glauca* + *A. spinosa*, *A. pachuëlii*, *A. repanda*, and *A. sphaerocarpa* + *A. mcdadiana* were unresolved here and in Hearn (2006).

Examination of reconstructed character histories revealed that evolutionary transitions in quantitative traits tended to be labile and that repeated loss and gain of discrete features is the rule rather than the exception. Dermal characters, for example, display great lability. Evolutionary transitions between taxa with stems that develop secondary dermal tissues (periderm) and those that maintain an epidermis throughout life (Tables 4, 5, 7: perL, perW, perThick) occurred a minimum of nine times (Fig. 42b). A cuticularized epidermis in mature stems is the ancestral condition in *Adenia* (Fig. 42b), although this condition is lost in multiple lineages. Uniseriate, epidermal

Fig. 7–19. Anatomical features of *Adenia*.—7. Stem cross section of *A. digitata*, a geophytic vine. Thick periderm and numerous, proliferating phloem fiber bundles.—8. Close up of boxed region in Fig. 7 with anomalous phloem between pith and primary xylem.—9. Stem periderm and cortex of *A. schweinfurthii*, a liana.—10. Highly storied storage root periderm of *A. densiflora*, a liana.—11. Cortex of *A. venenata* highlighting zone of proliferation.—12. Collapsible storage parenchyma in *A. globosa*.—13. Lysigenous cavities in cortex of *A. lobata*.—14. Druses and prismatic crystals in cells beneath the epidermis of *A. ellenbeckii* under polarized light.—15. Plentiful druses (white dots) in cortex of *A. lapiazicola* under polarized light.—16. Longitudinal section through a young stem of *A. cladosepala* showing tanniferous cells.—17. Close up of cross section through tanniferous cells in *A. acuta*.—18. Tyloses in stem vessel of *A. densiflora*. Tanniferous bodies are also present in the cellular tyloses.—19. Mature stem of *A. elegans* with extensive stone cells. Key: 1°X = primary xylem; 2°P = secondary phloem; C = cuticle; CSP = crushed secondary phloem; DC = druse crystal; E = epidermis; H = hypodermis; LC = lysigenous cavity; LF = libriform fiber; M = pith [medulla]; MX = metaxylem; PC = prismatic crystal; PD = periderm; PFB = phloem fiber bundle; PGT = proliferating ground tissue; SC = stone cell; T = tracheid; TC = tanniferous cell; VE = vessel element; () = stomata. (Scale bars: Fig. 7, 15 = 0.5 mm; Fig. 8, 14, 17–19 = 0.1 mm; Fig. 9–10, 12–13 = 0.4 mm; Fig. 11 = 0.25 mm; Fig. 16 = 0.2 mm).

trichomes are a uniquely derived epidermal feature of one lineage (Fig. 5), the “trichome clade” (Hearn 2006; *A. ellenbeckii*, *A. keramanthus*, *A. schliebenii*, *A. stricta*, *A. volkensii*), and rapid transition from juvenile epidermis to periderm was characteristic of the clade dubbed the “warty-gland clade” (*A. lapiazicola* through *A. peltata* in Fig. 2e) by Hearn (2006) for the irregular extra-floral nectaries found in this group.

Like uniseriate trichomes in the “trichome clade”, successive cambia evolved once and present a synapomorphy for Clade I of Hearn (2006: Fig. 21; *Adenia* sect. *Ophiocaulon* [De Wilde 1968]). *Adenia wightiana* is a member of this clade, but it never developed substantial secondary growth, and thus did not exhibit the successive cambia of the thick-stemmed lianas (e.g., *A. cissampeloides* and *A. gummifera*). Another anatomical synapomorphy is the anomalous intraxylary phloem (Fig. 7–8) that is restricted to Clade IV (all geophytes; Fig. 41–42). This anomalous anatomy consists of phloem with phloem fiber bundles that are embedded within the primary xylem and lignified pith regions (Fig. 8).

Fibriform vessel elements, libriform fibers, tracheids, and prolific axial parenchyma were shared by all members of *Adenia*. Few other traits were uniform in measurement or occurrence; more frequently, repeated convergent or parallel evolution was apparent. For example, wide, lianous stems were lost a minimum of two times, and regained around six times (Fig. 42a), whereas caducous leaves were gained around 4 times (Fig. 42c). Other traits, such as vessel dimensions (Fig. 41a), parenchyma diameters (Fig. 41b), or vessel aggregation sizes (Fig. 41c) varied from one clade to the next.

DISCUSSION

Patterns of Evolutionary Conservation and Innovation in Anatomical Evolution

The evolutionary history of stem anatomy in *Adenia* is dominated by both evolutionary conservation and innovation. Plesiomorphic, constant traits fit well with anatomical syndromes associated with lianas, and data now available for

Fig. 20–22. Anatomy of *A. cissampeloides* and close relative, *A. gummifera*.—20. Cross section through young stem of *A. cissampeloides*.—21. Storage root of *A. gummifera*. Vessels are narrow, and anatomy is very different from stem. Storage root was unavailable for *A. cissampeloides*.—22. Fairly young stem of *A. cissampeloides* with successive cambia. Key: 1°X = primary xylem; 2°P = secondary phloem; 2°X = secondary xylem; CT = conjunctive tissue; M = pith

labile traits (Tables 4–7) are poised for future investigation of associations between climate, habit, and anatomy using an explicit phylogenetic framework.

Signs of (tendrillate) lianous origins of *Adenia* (Hearn 2006) are indicated throughout the genus, and lianous vestiges influence patterning of wood anatomy in *Adenia* across all growth habit categories. Moreover, and as discussed below, anatomical patterning matches prior expectations that relate anatomy, habit, and ecology. Hearn (2006) categorized four major growth habit types (summarized in Table 1): (1) geophytes and tuberous vines with subterranean perennating storage roots and (usually) short-lived stems with minimal secondary growth, (2) lianas, with perennial climbing stems having extensive secondary growth, (3) caudiciform and pachycaul succulents (see Rowley 1987), some with massive water storage stems reaching over two meters in diameter, and (4) stem succulents with many thick cylindrical branches and no, or limited, vining stems. With the exception of a few geophytes and some stem succulents that lack them, tendrils fix branches of *Adenia* to other plants for support (Hearn 2006).

In addition to the presence of tendrils throughout the first three growth habit types, features that are characteristic of lianas are found in all four habit categories, even those lacking tendrils. Fibriform vessel elements were uniformly present in all taxa observed. Since the initial discovery of fibriform vessel elements in Passifloraceae over 70 yr ago (Woodworth 1934, 1935), these lengthened, narrow perforate tracheary elements have since been observed in diverse families including Euphorbiaceae and, in particular, families with scandent plants (Carlquist 1981, 1985a; Carlquist and Hanson 1991; Steinmann 2001). In some groups such as *Ipomoea* L. (Carlquist and Hanson 1991), fibriform vessel elements intergrade with imperforate tracheary elements, as they do in *Adenia* (e.g., Fig. 38).

Ayensu and Stern (1964) apply the term fiber-tracheid to non-libriform imperforate elements in Passifloraceae. In cross and longitudinal section, it is difficult to distinguish non-libriform imperforate elements from fibriform vessel elements as clear indications of perforation plates can be missing in sections with fibriform vessel elements. Macerations revealed that there are, indeed non-libriform, imperforate elements in *Adenia* and other anatomists (e.g., Metcalfe and Chalk 1983; Carlquist 1985b, 1986) have referred to similar elements as vascular tracheids or vascentric tracheids (Fig. 23–29). Metcalfe and Chalk's (1983: 13) definition of a vascular tracheid as “an imperforate cell resembling in form and position a small vessel element” fits well with the description of non-libriform imperforate elements in *Adenia* (e.g., Fig. 34–35), but because of the difficulty in distinguishing these types, I will refer to them simply as tracheids. The pitting and the shapes of these elements closely resemble those of the fibriform vessel elements.

Unlike Ayensu and Stern (1964), who found no libriform fibers in Passifloraceae as a whole, libriform fibers were universally present in species of *Adenia*, so they may provide a

←

[medulla]; PFB = phloem fiber bundle; PGT = proliferating ground tissue; R = ray; VB = vascular bundle; VC = vascular cambium; filled black circle = stem center. (Scale bars: Fig. 20–21 = 0.8 mm; Fig. 22 = 0.25 mm).

Fig. 23–30. Axial and ray parenchyma, including vessel aggregation patterns. Double-headed arrows oriented radially.—23. Wide and narrow apotracheal bands in *A. litoralis*. Islands of libriform fibers are abundant between rays and bands.—24. Close up of Fig. 23. Tracheids and/or fibriform vessel elements are next to vessel. Other lignified tissue is composed of thick-walled libriform fibers.—25. Axial parenchyma and rays in *A. rumicifolia*, a canopy liana. Rays are relatively narrow and interrupted by the large, mostly solitary, intrusive vessels. Rays consist of radially elongate cells. Other cells are the abundant apotracheal axial parenchyma.—26. Tangentially oriented vessel aggregations of *A. ellenbeckii*, a succulent shrub. Ray cells are indistinguishable from ground parenchyma.—27. Anatomy of stem of *A. boivinii*, a pachycaul. Vessel multiples are oriented irregularly. Axial parenchyma cells are distinctly smaller than ray cells (upper left corner). Both tracheids (and/or fibriform vessel elements) and libriform fibers are present.—28. Wide bands that lack vessels in the liana, *A. letouzeyi*.—29. Irregular vessel aggregations in the stem of *A. monadelphica*, a pachycaul. Adjacent parenchyma cells are irregularly shaped and sized.—30. Radial multiples in storage root of *A. subsessilifolia*, a sub-shrub. Apart from the narrow band of vessels, the secondary growth is composed of irregularly shaped and sized parenchyma. Key: AP = axial parenchyma; IFC = interfascicular cambium; LF = libriform fibers; PGT = proliferating ground tissue; R = ray; VC = vascular cambium; VE = vessel element; T = tracheids. (Scale bars = 0.2 mm).

synapomorphy for *Adenia*. Every species except *A. monadelphica* had prominent libriform fiber bundles distal to the phloem in stems (e.g., Fig. 7, 9, 1–13), as well as clusters of libriform fibers scattered in axial parenchyma in lianas and other growth habits with secondary growth (Fig. 26, 29). The extensive axial

parenchyma, libriform fiber bundles, and tracheids are all characteristic features of lianas (Carlquist 1985a), and their vestigial presence in all growth habits having extensive secondary growth hints at functional and phylogenetic conservatism of these traits.

Apart from the plesiomorphic features that are universally present in *Adenia* (i.e., wide and fibriform vessel elements, prolific axial parenchyma, libriform fibers, and tracheids), few other features were universally present, or synapomorphic, for large clades in *Adenia*. Indeed, most quantitative and qualitative traits analyzed here were labile (Fig. 41–42). For example, following the size classification of Metcalfe and Chalk (1983: 120), average diameters (Tables 4, 5: VEDiam) of the wide (i.e., not fibriform) vessel elements ranged from small (32 μ m) to large (204 μ m), with the maximal vessel sizes occurring in the lianas *A. gummifera* (Fig. 21) and *A. rumicifolia* (Fig. 27). Vessels whose lumina have diameters that are 204 μ m in diameter are in the tail of the distribution of vessel sizes for angiosperms and 32 μ m are smaller than average (Metcalfe and Chalk 1983: 120). Mean vessel element lengths across all *Adenia* (217 μ m; Tables 4–6: VEL) were considerably smaller on average than is typical for dicots (Metcalfe and Chalk 1983: 121), and species averages ranged between 60 μ m and 1 mm.

Despite the evolutionary lability of most traits, two types of anomalous secondary growth are unique innovations of (synapomorphies for) two of the clades identified by Hearn (2006). Clade I (see Fig. 41–42), a clade of lianas and vines, is the only clade in *Adenia* with successive cambia. Successive cambia in *Adenia* were first reported by Obaton (1960) for *A. cissampeloides* and here for *A. gummifera* (Fig. 20–22; see also Janse van Vuuren 1970) and *A. aff. stolzii*, all members of Clade I.

Like successive cambia for Clade I, intraxylary phloem (Fig. 8) associated with primary xylem is another innovation, and is synapomorphic for Clade IV (Fig. 41–42). Carlquist and Hanson (1991) report that intraxylary phloem is present in Convolvulaceae, another predominantly scandent group. In *Adenia*, this anomalous vascular condition presents phloem and phloem fibers differentiating *within* the lignified pith and primary xylem near the pith (Fig. 7). I am not aware of any other plant lineages with this type of anomalous growth.

Few other anatomical features provide synapomorphies for particular lineages. *Adenia lapiazicola*, *A. litoralis*, *A. metamorpha*, *A. monadelphica*, *A. peltata*, *A. perrieri*, and *A. refracta* comprise a lineage of Malagasy species, the “warty gland clade” (Hearn 2006), in which there is an abrupt transition in the juvenile stem between a photosynthetic epidermis and a periderm. In contrast, the majority of succulent taxa in other lineages have photosynthetic stems. Uniseriate trichomes (Fig. 5) are restricted to the trichome clade, and they provide a synapomorphy for this group, as well.

Ecological Considerations

Thus far, I have focused on patterns of phyletic diversification and conservation. Several of the patterns observed fit nicely with previously reported syndromes connecting functional aspects of habit, climate, and anatomy. Future work will rigorously examine associations between transitions in anatomy, climate, and habit. Here, however, I focus on functional aspects of plesiomorphic features, or features that evolved only

Fig. 31–40. Vascular cellular structure in maceration.—31. Vessels of *A. cladosepala*. This liana has uniformly alternate lateral wall pitting, transverse plates, and wide vessels.—32. Vessels of *A. gummifera*. Arrow highlights contact pits.—33. Mixed pitting of *A. fruticosa*, a pachycaul.—34. Septate, thin-walled libriform fiber of *A. karibaensis*, a pachycaul tree.—35. Wide, non-septate libriform fibers of *A. isaloensis*, a storage root-bearing shrub.—36. Caudate tips of vessel of *A. acuta*, a small liana.—37. Fibriform vessel element adjacent to septate libriform fiber (right) and axial parenchyma (left).—38. Irregular fibriform vessel elements and tracheids of *A. cladosepala*, a liana.—39. Close up of perforation in fibriform vessel element of *A. cladosepala*.—40. Close up of perforation of fibriform vessel element of *A. goetzei*. Lateral wall pits appear to be minutely bordered, minute themselves, and sparse. Key: LF = libriform fiber; P = parenchyma cell; PP = perforation plate; S = septa; VE = vessel element. (Scale bars: 0.1 mm).

once or twice within *Adenia* or its ancestors. These features are not amenable to standard phylogenetically informed comparative tests because such tests require variation in traits in order to establish a sample size that is sufficient to detect correlated patterns of trait evolution. Thus, the approach I adopt to discuss invariant and infrequent traits is to relate them, as anecdotes, to a larger body of literature, and in so doing, add additional examples that strengthen proposed functional hypotheses.

Tracheary elements.—Carlquist initiated the field of ecological wood anatomy (1966, 1975, 1984, 1985a,b, 1986, 1989, 2001) and multiple other authors have continued its development, including Baas (1973, 1976), Baas et al. (1983), Zimmermann (1983), Tyree and Sperry (1989), Mauseth and Sajeve (1992), Mauseth (1993, 2000, 2006), Mauseth and Plemons-Rodriguez (1998), Olson and Carlquist (2001), and Olson (2003). Much of this work considered putative tradeoffs between conduction, mechanical support, and aspects of climate, such as water availability and ambient temperature. Considerations of vessel conduction failure and its avoidance were launching points for much of this work. Carlquist (1985a,b) argued that xylem arrangements with wide vessels surrounded by narrower vasicentric tracheids promote conduction safety; if a wide vessel became embolized, the surrounding narrow tracheary elements could provide a detour for water flow without

catastrophic failure (Carlquist 1985a). Lianous members of *Adenia* with their tracheids associated with vessels and dimorphic vessel elements appear to fit this syndrome (Fig. 23–40). The (on-average) shortened vessel elements in *Adenia* are also indicative of lianous origins, in which perforation plates are hypothesized to act as strengthening girdles, and shorter elements permit a greater density of these girdles in vessels (Carlquist 2001).

Plants in xeric habitats often have large negative water potentials, which increase the likelihood of cavitation and embolism (Salisbury and Ross 1991: Chapter 5), so mechanisms to reduce cavitation are likely to be advantageous in water-stressed environments. Similar to vasicentric tracheids, Carlquist (1984, 1987, 2001) argued that dense vessels and vessel aggregates are to be expected in plants living in xeric habitats, as adjacent vessels in aggregations provide alternate conduits if one of the vessels becomes blocked. Both radial and tangential aggregates have been reported in other Passifloraceae (Ayensu and Stern 1964) and were found in *Adenia* as well (Fig. 23–30). Densities of vessels in stems (Tables 4, 5: VE#/mm) averaged 12 vessels per mm² and ranged from <1 to >50 vessels per mm². These values are particularly low for xerophytes (Carlquist 2001: 54) but are not unexpected due to the preponderance of parenchyma in stems of *Adenia*. The above mechanisms of conductive safety in *Adenia* (i.e., tracheids and fibriform vessel elements associated with wider vessels and vessel aggregates) are all indicative of xeromorphy, and indeed, *Adenia* species tend to live in seasonally dry habitats, and some species live in deserts (e.g., *A. aculeata*, *A. ballyi* Verdc., *A. pechuëlii*).

Parenchyma and succulence.—Extensive axial parenchyma with bundles of libriform fibers scattered throughout stems of lianas (e.g., Fig. 25) have been hypothesized to ease torsion in liana stems, and provide water and starch storage tissue (Carlquist 2001: 207; Olson 2003). Olson (2003) and Janse van Vuuren (1970) proposed that the extensive axial parenchyma of lianas can be co-opted during evolution for water storage. The evolutionary expansion through co-option can generate pachycaul habits. Needless to say, water storage tissue is widely acknowledged as an adaptation to water stressed habitats (e.g., Schwinning 2001). Once again, patterns of axial parenchyma and stem succulence evolution in *Adenia* match these prior expectations concerning abundance of axial parenchyma in lianas and evolutionary origin of pachycauls within lianous clades.

Even modifications to vessel wall pitting appear to relate to the dominance of axial parenchyma. Within the same vessel element, pitting sizes (Tables 4–6: VELW, VEPit) can vary depending on whether pits are adjacent to other tracheary elements (intervascular pits) or to parenchyma (contact pits). Intervascular pits tend to be smaller than contact pits (Fig. 32–33). This pit size difference is somewhat unusual as Frost (1931) claims that 85% of “dicots” show no difference. Wider pits neighboring parenchyma potentially aid water and nutrient transfer. Carlquist (2001: 76) describes pseudoscalariform pitting as a relatively rare condition, most prevalent in succulent woods (Carlquist 1962), in which pits span the lateral wall face. Some pits in *Adenia* (Fig. 33) verge on pseudoscalariform pits, but they do not traverse the length of the lateral wall, so might best be called wide, alternate pits.

41A

41B

41C

Dermal layers and stem photosynthesis.—In addition to auxiliary tracheary elements that may reduce damage from embolism, and extensive water storage tissue in stems and storage roots, additional features of *Adenia* fit other patterns observed in xerophytic plants. Green epidermises are retained throughout the life of stems of several *Adenia* taxa (Fig. 1–6), stomata are present in green stems (Fig. 1, 3–6), and caducous leaves and/or reduced leaves evolved in several desert taxa (*A. globosa*, *A. pachuëlii*, *A. subsessilifolia*; Fig. 42c). Retention of a photosynthetic epidermis has been described as an adaptation by xerophytic lineages to limited water availability (e.g., Janse van Vuuren 1970; Steinmann 2001). Leaves can be shed when water becomes scarce, and stems can continue to photosynthesize at a slower rate using water present in succulent storage tissue. Succulents generally exhibit low transpiration rates with moderate negative partial pressures for conduction; they are able to rapidly take up water on a seasonal basis, but persist with a slow and steady rate of transpiration (Carlquist 2001: 208).

Unlike other xerophytes (Felger and Henrickson 1997; Steinmann 2001), stomata in *Adenia* are not typically associated with grooves or pits in which relative humidity can remain high to reduce water loss through stomata. Stomata are in stem grooves in *A. pachyphylla*; this species (Fig. 1), however, is found in humid forests, so it is unclear that the need to maintain a humid boundary layer is important. Stem stomata are not associated with palisade parenchyma either, unlike stomata of some other succulent taxa, such as *Euphorbia* L. spp. (Steinmann 2001).

In addition to a retained epidermis and storage parenchyma, many *Adenia* plants have thick cuticles and epicuticular waxes in mature stems (Fig. 2), which presumably reduce water loss from stems (Steinmann 2001). Such waxes are recorded in certain species as occasionally becoming encrusting (Jumelle 1907; De Wilde 1971a), although my preparations did not reveal this for many taxa.

Cortices.—Unusual cortical parenchyma was observed in *A. globosa* (Fig. 12). Structurally, this tissue closely resembles the cortical tissue of some cacti, where it was inferred to provide collapsible water storage tissue (Mauseth 1995). By analogy, it is suggested to serve a similar function in *Adenia*. However, the extensive aerenchyma suggests the cortex of *A. globosa* may be involved in respiration, so physiological work is required to distinguish these functions. This tissue type appears to be uniquely derived in *A. globosa* and putatively in its sister species, *A. ballyi* (anatomy not analyzed due to rarity of plants).

In addition to mechanical support (potentially reducing damage from shear stresses) that is likely to be provided by cortical phloem fiber bundles, the cortex can also store water. As in succulent *Euphorbia* (Steinmann 2001), Cactaceae, and other succulents (Mauseth and Sajeve 1992; Mauseth 2004), the relative width of the cortex varies interspecifically among

similarly aged juvenile stems in *Adenia*, and the thickness of the cortex presumably relates to storage capacity.

Defense.—Thirsty herbivores may be attracted to water storage stems, and many African pachycauls (*A. aculeata*, *A. ballyi*, *A. globosa*, *A. pachuëlii*, *A. spinosa*) possess thorns or prickles, presumably in defense. Thorns and prickles are derived from tendrils (*A. globosa*, *A. spinosa*), necrosed stem tips (*A. pachuëlii*), or dermal projections (*A. aculeata*). Additional defensive innovations include crystals (Fig. 14–15; Franceschi and Nakata 2005) and secondary chemistry. Some of the most toxic of angiosperm compounds, such as the toxalbumin, modeccin, are known from *Adenia* (e.g., Gasperi-Campani et al. 1978). The current work also found evidence of extensive tannin cells (Fig. 16–17), and lysigenous secretory cavities with unknown contents (Fig. 13; also observed by Janse van Vuuren 1970, more universally). Tannins and other phenolics precipitate proteins and reduce digestion efficiency in herbivores (Boettcher and Targett 1993; Heiska et al. 2007).

Anomalous secondary growth and cambial variants.—I identified four types of anomalous secondary growth in *Adenia*. The functional and evolutionary significance of anomalous proliferation of parenchyma and anomalous vascular bundles is discussed elsewhere (D. Hearn, unpubl.). The preponderance of successive cambia in lianas suggests they may have a functional association with the lianous habit. Indeed, Carlquist (2001, 2007) emphasized that the supportive, concentric cables of vascular tissue alternating with spongy conjunctive tissue may reduce the chance of physical disruption of vessels, and provide relief from stem torsion.

Carlquist (2001: 290–295) also proposed that anomalous secondary tissue may facilitate nutrient transfer. Similar to several dry forest species of trees and shrubs (Janzen 1967), most species in *Adenia* lose leaves during dry periods, and flowering often commences before leafing and seasonal rains (pers. obs. in *A. digitata*, *A. lanceolata*, *A. spinosa*). When rains come, plants burst into leaf. Anomalous secondary growth may play a pivotal role in waking from dormancy; Carlquist (2001: 290–295) proposed that anomalous cambia can rapidly mobilize nutrients for rapid growth. The intraxylary phloem of geophytes in Clade IV (Fig. 7–8) may accelerate starch transport from storage roots to developing shoots. Amyloplasts are a common occurrence in conjunctive tissue of both storage roots and stems (Tables 4–5: Starch). The proximity of these water and starch storage cells to anomalous secondary growth may facilitate water and nutrient mobilization. However, detailed physiological work remains to investigate experimentally whether anomalous cambia are associated with increased metabolic capacity in *Adenia*.

Summary

The mode of anatomical evolution in *Adenia* reveals a story of both conservatism and innovation. Conservatism of

Fig. 41. Bayesian *allcomp* consensus tree with ancestral states reconstructed for continuous-valued traits mapped using squared-change parsimony.—A. Phylogeny with posterior probabilities, five clades (I–V) identified by Hearn (2006), and evolutionary history of average vessel element diameter reconstructed. Legend shows average vessel lumen diameter in mm.—B. Reconstructed evolutionary history of average parenchyma diameter in axial system. Legend shows average cell diameter in mm.—C. Reconstructed evolutionary history of average vessel aggregation size. Legend shows average number of vessels per aggregation.

42A

42B

42C

ancestral habit (liana) traits appears to be the rule, whereas other anatomical traits of ecological importance present a great deal of evolutionary lability. *Adenia* species share the specialized woods that are generally possessed by members of Passifloraceae (wide and short vessels with simple, transverse perforation plates, little storring, extensive axial parenchyma, and fibriform vessel elements). Quantitative traits such as vessel measurements vary widely among species, and other traits relating to xeromorphy and water conduction are conserved throughout the genus. Some anatomical features of *Adenia* are not known to occur in other Passifloraceae, such as successive cambia and a distinctive type of intraxylary phloem. Although anatomy of storage roots in Passifloraceae had not been investigated prior to this study, storage roots in *Adenia* are uniformly parenchymatized, and libriform fibers are scattered throughout the parenchyma.

Patterns of anatomical evolution and innovation fit well with preexisting observations concerning wood anatomy and its functional association to habit and climate. I provide functional descriptions of anatomical features that did not vary in *Adenia* or that were uniquely derived within particular sub-clades. Future work will examine correlated patterns of evolutionary change in a phylogenetic comparative framework. The climatic and evolutionary factors responsible for repeated origins of different growth habits, storage roots (e.g., see Hearn 2006 in which storage roots are called “tubers”), and different sizes and distributions of anatomical features are still unclear. In particular, the conditions responsible for the multiple origins of storage roots are unknown. Interest in storage root and tuber evolution is growing (e.g., Mauseth and Stone-Palmquist 2001; Olson and Carlquist 2001; Yesson and Culham 2006; Conran 2008), yet there are few studies that provide explanations for their anatomical features and their repeated origins throughout the angiosperms. The current work provides anatomical data for storage roots and multiple other features of *Adenia* for future research to investigate storage root evolution and anatomical evolution more generally.

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LITERATURE CITED

- AYENSU, A. S. AND W. L. STERN. 1964. Systematic anatomy and ontogeny of the stem in Passifloraceae. *Contr. U.S. Natl. Herb.* **34**: 45–73.
- BAAS, P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. *Blumea* **21**: 193–258.
- . 1976. Some functional and adaptive aspects of vessel member morphology. *Leiden Botanical Series* **3**: 157–181.
- , E. WERKER, AND A. FAHN. 1983. Some ecological trends in vessel characters. *IAWA Bull. NS* **4**: 141–159.
- BACCARINI, P. 1908. Notize sulla struttura anatomica della *Modecca abyssinica*. *Bull. Soc. Bot. Ital.* **40**: 40–50.
- BAILEY, I. W. AND W. W. TUPPER. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. *Proc. Amer. Philos. Soc.* **54**: 149–204.
- BOETTCHER, A. A. AND N. M. TARGETT. 1993. Role of polyphenolic molecular size in reduction of assimilation efficiency in *Xiphister mucosus*. *Ecology* **74**: 891–903.
- CARLQUIST, S. 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorphology* **12**: 30–45.
- . 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. *Aliso* **6**(2): 25–44.
- . 1975. Ecological strategies of xylem evolution. University of California Press, Berkeley, USA. 257 p.
- . 1981. Wood anatomy of Nepenthaceae. *Bull. Torrey Bot. Club* **108**: 324–330.
- . 1982. The use of ethylenediamine in softening hard plant structures for paraffin sectioning. *Stain Technol.* **57**: 311–317.
- . 1984. Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. *Aliso* **10**: 505–525.
- . 1985a. Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. *Aliso* **11**: 139–157.
- . 1985b. Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions: review of vasicentric tracheids. *Aliso* **11**: 37–68.
- . 1986. Terminology of imperforate tracheary elements. *IAWA Bull. NS* **7**: 75–81.
- . 1987. Diagonal and tangential vessel aggregations in wood: function and relationship to vasicentric tracheids. *Aliso* **11**: 451–462.
- . 1989. Wood anatomy of *Cercidium* (Fabaceae), with emphasis on vessel wall sculpture. *Aliso* **12**: 235–255.
- . 2001. Comparative wood anatomy: systematic, ecological and evolutionary aspects of dicotyledon wood, 2nd ed. Springer-Verlag, Berlin, Germany. 448 p.
- . 2007. Successive cambia revisited: ontogeny, histology, diversity, and functional significance. *J. Torrey Bot. Soc.* **134**: 301–332.
- AND M. A. HANSON. 1991. Wood and stem anatomy of Convolvulaceae: a survey. *Aliso* **13**: 51–94.
- CLAVERIE, P. 1908. Contribution a l'étude anatomique et histologique des plantes textiles exotiques (Passiflorées, Musacées, Palmiers, Aroïdées, Cypéracées). *Annales du musée colonial de Marseille* **2**: 7–72.

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Fig. 42. Bayesian *allcompat* consensus tree with ancestral states reconstructed for binary traits mapped using unordered parsimony. The most parsimonious reconstruction implying the fewest origins of the trait is presented.—A. History of lianous stem evolution.—B. The evolution of cuticle presence in mature stems is reconstructed.—C. The evolutionary origins of leaves that are shed rapidly under dry conditions (caducous leaves) are presented. Legend: White branches indicate absence of trait, whereas black branches denote presence of the trait.

- CONRAN, J. G. 2008. Aestivation organ structure in *Drosera* subgen. *Ergaleium* (Droseraceae): corms or tubers; roots or shoots? *Austral. J. Bot.* **56**: 144–152.
- DE WILDE, W. J. J. O. 1968. A key to the species of *Adenia* section *Ophiocaulon* (Passifloraceae) mainly based on vegetative characters, with the description of two new taxa. *Acta Bot. Neerl.* **17**: 126–136.
- . 1971a. A monograph of the genus *Adenia* Forsk. (Passifloraceae). Mededelingen Landbouwhogeschool, Wageningen, The Netherlands. 281 p.
- . 1971b. The systematic position of the tribe Paropsieae, in particular the genus *Ancistrothursus*, and a key to the genera of Passifloraceae. *Blumea* **14**: 99–104.
- . 1974. The genera of tribe Passiflorea (Passifloraceae), with special reference to flower morphology. *Blumea* **22**: 227–250.
- ESAU, K. 1977. Anatomy of seed plants, 2nd ed. John Wiley & Sons, New York, USA.
- FELGER, R. AND J. HENRICKSON. 1997. Convergent adaptive morphology of a Sonoran desert cactus (*Peniocereus striatus*) and an African spurge (*Euphorbia cryptospinosa*). *Haseltonia* **5**: 77–85.
- FRANCESCHI, V. R. AND P. A. NAKATA. 2005. Calcium oxalate in plants: formation and function. *Annual Rev. Pl. Biol.* **56**: 41–71.
- FROST, F. H. 1930a. Specialization in secondary xylem of dicotyledons. I. Origin of vessel. *Bot. Gaz.* **89**: 67–94.
- . 1930b. Specialization in secondary xylem of dicotyledons. II. Evolution of end wall of vessel segment. *Bot. Gaz.* **90**: 198–212.
- . 1931. Specialization in secondary xylem of dicotyledons. III. Specialization of lateral wall of vessel segment. *Bot. Gaz.* **91**: 88–96.
- GASPERI-CAMPANI, A., L. BARBIERI, L. LORENZONI, L. MONTANARO, S. SPERTI, E. BONETTI, AND F. STIRPE. 1978. Modeccin, the toxin of *Adenia digitata*: purification, toxicity, and inhibition of protein synthesis in vitro. *Biochem. J.* **174**: 491–496.
- HARMS, H. 1893. Über die Verwertung des anatomischen Baues für die Umgrenzung und Einteilung der Passifloraceae. *Bot. Jahrb. Syst.* **15**: 548–633.
- . 1925. Passifloraceae, pp. 470–507. In A. Engler and K. Prantl [eds.], Die natürlichen Pflanzenfamilien, 2nd ed., vol. 21. Duncker & Humblot, Berlin, Germany.
- HEARN, D. J. 2004. Growth form evolution in *Adenia* (Passifloraceae) and a model of the evolution of succulence. Ph.D. dissertation. University of Arizona, Tucson, USA.
- . 2006. *Adenia* (Passifloraceae) and its adaptive radiation: phylogeny and growth form diversification. *Syst. Bot.* **31**: 805–821.
- . 2007. Novelties in *Adenia* (Passifloraceae): Four new species, a new combination, a vegetative key, and diagnostic characters for known Madagascan species. *Brittonia* **59**: 308–327.
- HEISKA, S., O.-P. TIKKANEN, M. ROUSI, AND R. JULKUNEN-TITTO. 2007. Bark salicylates and condensed tannins reduce vole browsing amongst cultivated dark-leaved willows (*Salix myrsinifolia*). *Chemoecol.* **17**: 245–253.
- IAWA COMMITTEE ON NOMENCLATURE. 1964. Multilingual glossary of terms used in wood anatomy. International Association of Wood Anatomists, Zürich, Switzerland.
- JANSE VAN VUUREN, D. R. 1970. 'n morfologiese studie van die stingels van die houtagtige verteenwoordigers van die genus *Adenia* Forsk. in Suid-Afrika. Ph.D. dissertation, University of Pretoria, South Africa.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within dry season in Central America. *Evolution* **21**: 620–637.
- JUMELLE, H. 1907. Quelques plantes nouvelles ou peu connues du nord-ouest de Madagascar. *Annales du musée colonial de Marseille* **5**: 338–342.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* **96**: 547–557.
- . 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. *Bull. Torrey Bot. Club* **64**: 177–187.
- KUKACHKA, B. F. 1977. Sectioning refractory woods for anatomical studies. USDA For. Serv. Res. Note FPL 0236. 9 p.
- MADDISON, W. P. AND D. R. MADDISON. 2007. Mesquite: a modular system for evolutionary analysis, vers. 2.01. <http://lmesquiteproject.org> (Dec 2007).
- MAUSETH, J. D. 1993. Water-storing and cavitation-preventing adaptations in wood of cacti. *Ann. Bot. (Oxford)* **72**: 81–89.
- . 1995. Collapsible water-storage cells in cacti. *Bull. Torrey Bot. Club* **122**: 145–151.
- . 2000. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. *Amer. J. Bot.* **88**: 1107–1115.
- . 2004. The structure of photosynthetic succulent stems in plants other than cacti. *Int. J. Pl. Sci.* **165**: 1–9.
- . 2006. Structure-function relationships in highly modified shoots of Cactaceae. *Ann. Bot. (Oxford)* **98**: 901–926.
- AND B. J. PLEMONS-RODRIGUEZ. 1998. Evolution of extreme xeromorphic characters in wood: a study of nine evolutionary lines in Cactaceae. *Amer. J. Bot.* **85**: 209–218.
- AND M. SAJEVA. 1992. Cortical bundles in the persistent, photosynthetic stems of cacti. *Ann. Bot. (Oxford)* **70**: 317–324.
- AND M. E. STONE-PALMQUIST. 2001. Root wood differs strongly from shoot wood within individual plants of many Cactaceae. *Int. J. Pl. Sci.* **162**: 767–776.
- METCALFE, C. R. AND L. CHALK. 1983. Anatomy of the dicotyledons, 2nd edition, vol. II: wood structure and conclusion of the general introduction. Clarendon Press, Oxford, UK. 276 p.
- OBATON, M. 1960. Les lianes ligneuses a structure anormale des forêts denses d'Afrique Occidentale. *Ann. Sci. Nat. Bot., sér. 12* **1**: 1–220.
- OLSON, M. E. 2003. Stem and leaf anatomy of the arborescent Cucurbitaceae *Dendrosicyos socotrana* with comments on the evolution of pachycauls from lianas. *Pl. Syst. Evol.* **239**: 199–214.
- AND S. CARLQUIST. 2001. Stem and root anatomical correlations with life form diversity, ecology, and systematics in *Moringa* (Moringaceae). *Bot. J. Linn. Soc.* **135**: 315–348.
- RONQUIST, F. AND J. P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- ROWLEY, G. D. 1987. Caudiciform & pachycaul succulents. Strawberry Press, Mill Valley, California, USA. 282 p.
- RUZIN, S. E. 1999. Plant microtechnique and microscopy. Oxford University Press, New York, USA. 322 p.
- SALISBURY, F. B. AND C. W. ROSS. 1991. Chapter 5: the ascent of sap, pp. 93–115. In F. B. Salisbury and C. W. Ross [eds.], Plant physiology, 4th ed. Brooks/Cole Publishing Co., Florence, Kentucky, USA.
- SCHWINNING, S. 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.* **89**: 464–480.
- SIMPSON, G. G. 1944. Tempo and mode in evolution. Columbia University Press, New York, USA.
- STEINMANN, V. W. 2001. The evolution of succulence in the new world species of *Euphorbia* (Euphorbiaceae). Ph.D. dissertation, Claremont Graduate University, Claremont, California, USA.
- STERN, W. L. AND G. K. BRIZICKY. 1958. The woods and flora of the Florida Keys. Passifloraceae. *Trop. Woods* **109**: 45–53.
- TYREE, M. T. AND J. S. SPERRY. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Rev. Pl. Physiol. Mol. Biol.* **40**: 19–38.
- WOODWORTH, R. H. 1934. Perforated fiber-tracheids in the passion flowers. *Science* **80**: 449–450.
- . 1935. Fibriform vessel members in the Passifloraceae. *Trop. Woods* **41**: 8–16.
- YESSON, C. AND A. CULHAM. 2006. Phylotoclimatic modeling: combining phylogenetic and bioclimatic modeling. *Syst. Biol.* **55**: 785–802.
- ZIMMERMANN, M. H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Germany. 250 p.