



Morpho-anatomical diversity of the underground systems of *Arrojadoa* (Cactaceae), an endemic Brazilian genus

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Members of *Arrojadoa* exhibit a variety of underground structures that can originate from roots or stems. Although the development of underground structures of stem origin in *Arrojadoa* represents a unique trait among Cactaceae of eastern Brazil, no detailed reports on the morphological diversity of such structures are available. The present morpho-anatomical study of the underground systems of *Arrojadoa* has demonstrated that a single species can exhibit one or more structural types, such as single or branched stem tubers, short thick stems and/or long subterranean stems, thick and fleshy contractile roots and normal fibrous roots. Various morpho-anatomical structures relating to the underground storage systems in *Arrojadoa* spp. have also been observed, including thick contractile roots consisting mainly of secondary xylem formed by fibrous wood with wide-band tracheids (WBTs) and underground stems with a wide cortical region and WBTs-type wood. Based on the evidence presented, we suggest that such traits, together with the occurrence of contractile roots associated with underground stems, are important adaptive strategies for the survival of the plants during seasonal drought in areas of cerrado (savannah), campo rupestre (rocky uplands) and caatinga (dry thorny scrubland). © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, 173, 108–128.

ADDITIONAL KEYWORDS: contractile root – soboles – stem tuber – wide-band tracheids.

INTRODUCTION

Arrojadoa Britton & Rose (Cactaceae; subfamily Cactoideae; tribe Cereeae) is endemic to Brazil and is found in areas of cerrado (savannah), campo rupestre (rocky uplands) and caatinga (dry thorny scrubland). Although most representatives of Cereeae occur in eastern Brazil (Taylor & Zappi, 2004), most *Arrojadoa* spp. are restricted to just two states, Bahia (BA) and Minas Gerais (MG). *Arrojadoa rhodantha* (Gürke) Britton & Rose is an exception, however, as it also occurs in Pernambuco (PE) and Piauí (PI) (Taylor & Zappi, 2004).

The taxonomy of *Arrojadoa* is unresolved as different authors have proposed dissimilar classification

systems. In a synopsis of *Arrojadoa* subgenus *Albertbuiningia* P.J.Braun & Esteves, Braun & Esteves (2007) recognized the following taxa: *A. dinae* Buining & Brederoo, *A. dinae* subsp. *nana* (P.J.Braun & Esteves) P.J.Braun & Esteves, *A. beateae* P.J.Braun & Esteves, *A. multiflora* F.Ritter [although the last three mentioned are regarded by Anderson, (2001), Taylor & Zappi (2004) and Hunt (2006) as synonyms of *A. dinae* s.s.], *A. eriocaulis* Buining & Brederoo, *A. rosenbergeriana* (van Heek & Strecker) P.J.Braun, Esteves & van Heek, *A. albicoronata* (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves, *A. hofackeriana* (P.J.Braun & Esteves) P.J.Braun & Esteves [although the last three mentioned are regarded as synonyms of *A. dinae* subsp. *ericaulis* by Anderson, (2001) and Taylor & Zappi (2004) and as synonyms of *A. eriocaulis* by Hunt

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(2006)] and *A. albiflora* Buining & Brederoo [although Anderson, (2001), Taylor & Zappi (2004) and Hunt (2006) considered that this taxon is not a true species, but rather a naturally occurring hybrid between *A. dinae* and *A. rhodantha*]. Braun & Esteves (2001, 2003, 2007) also recognized *A. rhodantha*, *A. penicillata* (Gürke) Britton & Rose, *A. marylandae* Soares-Filho & Machado and *A. horstiana* P.J.Braun & Heimen as species, although the last mentioned is regarded by Anderson (2001), Taylor & Zappi (2004) and Hunt (2006) as a synonym of *A. rhodantha*.

In this context, Taylor & Zappi (2004) and Hunt (2006) reported that *A. dinae* subsp. *eriocaulis* (*A. eriocaulis sensu* Hunt) forms true tubers as underground structures, whereas *A. dinae* subsp. *dinae* (*A. dinae sensu* Hunt) has thickened underground stem structures that do not develop into true tubers. However, Braun & Esteves (2007) stated that both *A. dinae* and *A. eriocaulis* form true tubers and recognized the presence of tubers as one of the defining characters of subgenus *Albertbuiningia*. These authors also emphasized the substantial variability observed in the underground structures of taxa of this subgenus, but they did not report such differences in detail (Braun & Esteves, 2007).

Many authors have described morphological diversity in the root system in Cactaceae, including: (1) fibrous roots, which can be represented as a vertical component that is formed first and functions mainly as an anchorage, and/or a horizontal component, that develops as the plant grows and is responsible for most of the water and nutrient absorption; (2) con-

tractile roots, reported for only a few species of the family, and for which the mechanism of contraction has only been described for *Ariocarpus*; (3) tuberous roots, which may be thick, with thickening occurring in different parts of the root (Preston, 1900; Buxbaum, 1950; Garrett *et al.*, 2010). Besides the diversity of root structures, the family also has different types of underground stems (Braun & Esteves, 2007; Taylor & Zappi, 2004), especially in *Arrojadoa*, as mentioned above. However, the nature of these structures and their variations in *Arrojadoa* spp. has not been demonstrated.

Here we describe the morphology and anatomy of the underground system of 12 taxa of *Arrojadoa s.l.*, with the purpose of investigating the origin of such structures (e.g. stems or roots) and determining if storage reserve represented an adaptive strategy for these species against seasonal drought.

MATERIAL AND METHODS

For this study, we sampled 12 *Arrojadoa* taxa (see Table 1) according to the broader taxon circumscriptions of Braun & Esteves (2007). The use of this classification system is useful for ease of communication when comparing the subterranean structures found in the different taxa. *Arrojadoa bahiensis* (P.J.Braun & Esteves) N.P.Taylor & Eggli, considered a member of *Arrojadoa* by Anderson (2001) and Taylor & Zappi (2004), but placed in the genus *Pierrebraunia* Esteves by Hunt (2006) and Braun & Esteves (2007), was also included in the study. The species

Table 1. Taxa of *Arrojadoa* sampled and their corresponding collection sites in Brazil

Taxa	Collection sites	Voucher no.
<i>A. albicoronata</i> (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves	Grão Mogol, MG	Machado, M. 762
<i>A. albiflora</i> Buining & Brederoo	Jacaraci, BA	Machado, M. 754
<i>A. bahiensis</i> (P.J.Braun & Esteves) N.P.Taylor & Eggli	Mucugê, BA	Lemos, R 06
<i>A. dinae</i> Buining & Brederoo subsp. <i>dinae</i>	Montezuma, MG	Machado, M. 755
<i>A. dinae</i> subsp. <i>nana</i> (P.J.Braun & Esteves) P.J.Braun & Esteves	Cordeiros, BA	Machado, M. 790
<i>A. eriocaulis</i> Buining & Brederoo	Mato Verde, MG	Machado, M. 756
<i>A. hofackeriana</i> (P.J.Braun & Esteves) P.J.Braun & Esteves	Piatã, BA	Machado, M. 750
<i>A. marylandae</i> Soares-Filho & Machado, <i>A. multiflora</i> F.Ritter	Tanhaçú, BA	Machado, M. 28
<i>A. multiflora</i> F.Ritter	Caetité, BA	Machado, M. 751
<i>A. penicillata</i> (Gürke) Britton & Rose	Itaobim, MG	Lemos, R 07
	Seabra, BA	Machado, M. 773
<i>A. rhodantha</i> (Gürke) Britton & Rose	Abaíra, BA	Machado, M. 749
	Mato Verde, MG	Machado, M. 758
	Morro do Chapéu, BA	Machado, M. 803
<i>A. rosenbergeriana</i> (van Heek & Strecker) P.J.Braun, Esteves & van Heek	Santo Antônio do Retiro, MG	Lemos, R 08

Brazilian states of Bahia (BA) and Minas Gerais (MG).

A. beatae and *A. horstiana* were excluded from the investigation because specimens could not be found in the field.

In most cases, a single population of each taxon was visited, generally at the type locality, as many of the taxa are known only from the type locality or have a limited distribution range. *Arrojadoa penicillata* and *A. rhodantha* have wider distribution ranges and were sampled at two and three different localities, respectively. Each population visited was examined to identify possible morphological variations among individuals, the soil type (sand, loam, clay or rock), and the organization of the underground structures. Three adult specimens per taxon were collected, but when morphological variations were observed among individuals of a population, all of the different morphological types identified were sampled. Particular care was taken in uprooting specimens growing in rocky outcrops in order not to damage the underground structures. Voucher specimens were deposited at the herbarium of the Botanical Department of Universidade de São Paulo (USP) and at the herbarium of the Universidade Estadual de Feira de Santana (UEFS) (Table 1).

Anatomical studies were performed on samples from the apical, mid and basal regions of the underground structures observed during morphological analysis, which included fibrous roots, contractile roots and underground stems. All underground structures containing areoles were considered to be derived from the stem. Samples were fixed in formalin-acetic acid-ethanol 50% (FAA 50) (Johansen, 1940) for 48 h and subsequently stored in ethanol 70%. A portion of each sample was dehydrated in an ethanol/tertiary butyl alcohol series (50–100%) and subsequently embedded in paraffin (Ruzin, 1999). Transverse and longitudinal sections (10–20 µm) were prepared using a Reichert-Jung AutoCut 2040 microtome, and subsequently stained with 1% astra blue in ethanol 50% and 1% safranin in ethanol 50% [modified method of Kraus *et al.*, (1998)] and mounted permanently on slides with Canada balsam. Plant material was analysed with the aid of a Leica DMLB microscope and images recorded using a Leica IM50 scanning system.

RESULTS

MORPHOLOGY

Members of *Arrojadoa* were quite diverse regarding underground structures, with the following traits being observed: (1) single or branched stem tubers; (2) short thick stems and/or long underground stems; (3) thick and fleshy contractile roots; and (4) normal fibrous roots. All of the studied taxa had normal

fibrous roots, and these constituted the only underground structures observed in *A. albiflora*, *A. bahiensis*, *A. marylandae*, *A. penicillata* and *A. rhodantha* (Table 2). The remaining taxa exhibited unique combinations of underground structures in addition to fibrous roots. No variations in the types of underground structures were detected among individuals of a taxon, with the exception of *A. multiflora*, in which different individuals displayed underground structures with distinct morphologies.

ARROJADOA ALBICORONATA (FIG. 1A)

This taxon inhabits sandy-loam soils and can only be found at its type locality near Grão Mogol, MG. The underground structures observed in adult plants are more readily explained by considering the morphology of young plants that present a swollen and fleshy main underground stem (oval to round in shape) from which emerged a thick fleshy contractile main root and a thin above-ground stem (Fig. 1A). New swollen underground stems can develop from the thick main underground stem and these, in turn, are able to produce thick fleshy contractile roots, adventitious roots and aerial shoots. As the young plants grow, they form more (and increasingly thicker) underground tubers, which, in mature specimens, give rise to branched tubers with many thin aerial shoots.

ARROJADOA ALBIFLORA

Specimens of this taxon were collected from a population growing in shallow sandy soil among rocks near Jacaraci, BA. All of the individuals sampled possessed a short taproot and superficial, lateral fibrous roots.

ARROJADOA BAHIENSIS (FIG. 1B)

This rupicolous species was collected from a population growing in crevices in sandstone rocks located near Mucugê, BA (Fig. 1B). The plants exhibited a simple root system composed of a short taproot and a network of lateral fibrous roots.

ARROJADOA DINAE SUBSP. *DINAE* (FIG. 1C)

The studied population was found growing in rocky-loam soil close to Montezuma, MG. Young plants had a thick main underground stem with a thickened fleshy contractile root. The thick main stem was located along the root-stem seedling axis and probably arose from an expansion of the region around and above the hypocotyl. Additional thick, often short, underground stems formed from the thick main underground stem, and some of these displayed

Table 2. Main characteristics observed in the underground systems of the *Arrojadoa* species studied

Species	Underground structures	Type of wood in fibrous roots	Non-lignified parenchyma in fibrous roots	Formation of new rays in root	Lignification of xylem rays in root	Mucilaginous structures in underground stems	Origin of extra-xylem sclereids in underground stems	Type of wood in underground stems
<i>A. albicoronata</i>	Fibrous roots, contractile roots and branched tubers	Fibrous	Present	Present	Absent	Cells and cavities	Undetermined	Fibrous/non-fibrous
<i>A. albiglora</i>	Fibrous roots	Fibrous	Present	Present	Partial	–	–	–
<i>A. bahiensis</i>	Fibrous roots and common non-fibrous roots	Fibrous/WBTs/fibrous	Present	Absent	Absent	–	–	–
<i>A. dinae</i> subsp. <i>dinae</i>	Fibrous roots, contractile roots, simple tubers and plagiotropic stems	Fibrous	Present	Present	Partial	Cells and cavities	Pericycle	Non-fibrous
<i>A. dinae</i> subsp. <i>nana</i>	Fibrous roots and plagiotropic stems	Fibrous	Absent	Absent	Partial	Cells and cavities	–	Non-fibrous
<i>A. rosenbergiana</i>	Fibrous roots	Fibrous	Absent	Absent	Absent	Cells and cavities with the presence of epithelium	Pericycle	Fibrous
<i>A. eriocaulis</i>	Fibrous roots, contractile roots and simple tubers	Fibrous/WBTs	Present	Present	Absent	Cells and cavities with the presence of epithelium	Secondary phloem	WBTs/Fibrous
<i>A. hofackeriana</i>	Fibrous roots, contractile roots and branched tubers	Fibrous	Absent	Absent	Absent	Cells and cavities with the presence of epithelium	Pericycle	Fibrous
<i>A. marylandae</i>	Fibrous roots	Fibrous	Absent	Present	Almost entirely	–	–	–
<i>A. multiflora</i>	Fibrous roots, contractile roots short underground stem and plagiotropic stems	Fibrous/WBTs	Present	Present	Partial	Cells and cavities	Undetermined	Non-fibrous
<i>A. penicillata</i>	Fibrous roots	Fibrous	Present	Present	Partial	–	–	–
<i>A. rhodantha</i>	Fibrous roots	Fibrous	Absent	Present	Partial	–	–	–

WBTs, wide-band tracheids.

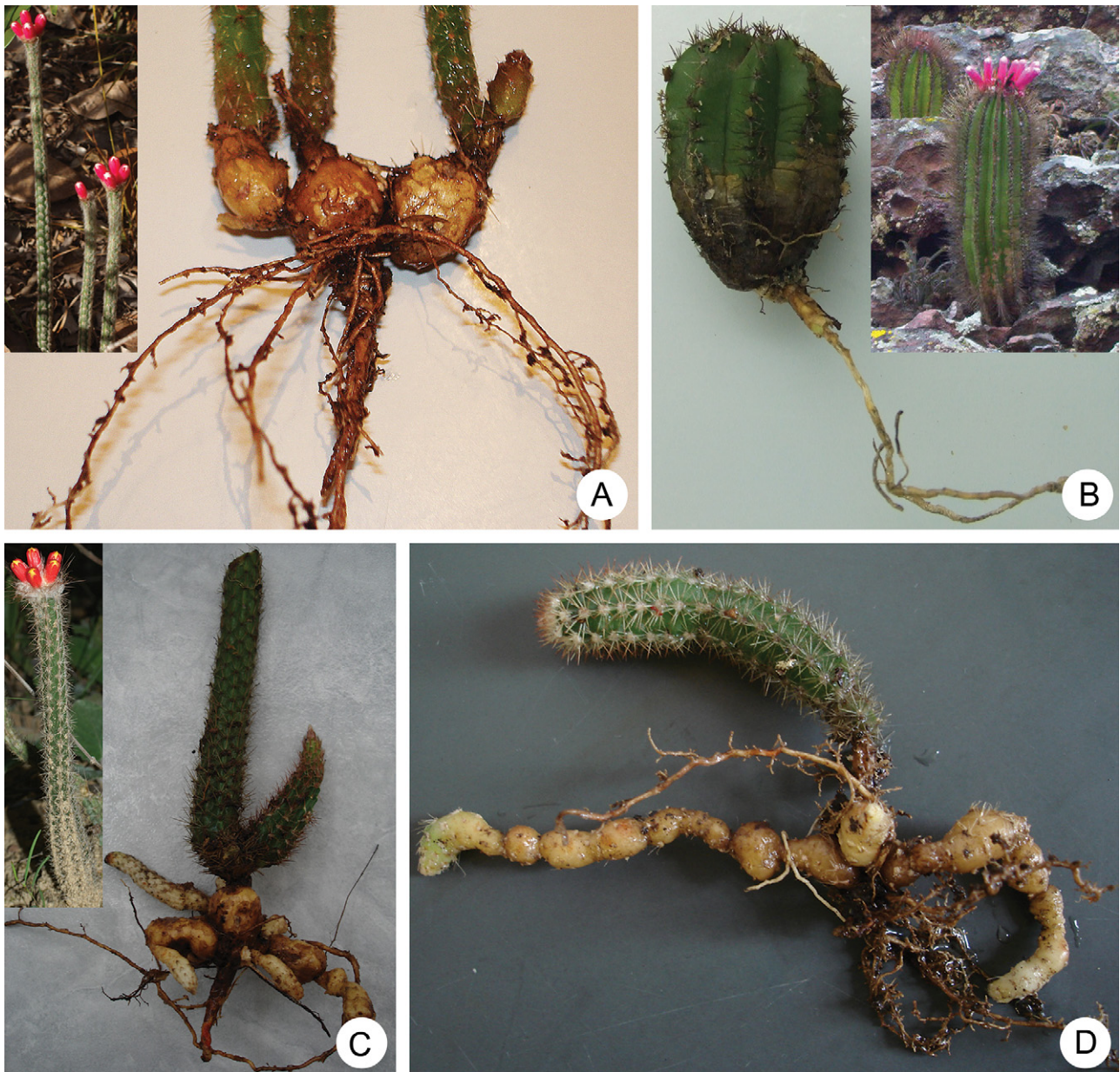


Figure 1. A, young specimen of *Arrojadoa albicoronata* (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves showing a thickened and succulent central tuber with a developing contractile main root and aerial segment and new lateral shoots. B, *A. bahiensis* (P.J.Braun & Esteves) N.P.Taylor & Eggli showing the main root and common lateral roots. C, young specimen of *A. dinae* Buining & Brederoo subsp. *dinae* showing a thickened central tuber, main contractile root, lateral roots and stem segments with plagiotropic growth (soboles). D, *A. dinae* subsp. *nana* (P.J.Braun & Esteves) P.J.Braun & Esteves showing soboles. Note the presence of spines in the areoles of the soboles.

plagiotropic growth, but did not elongate significantly (Fig. 1C). Normal fibrous roots were produced by the thickened fleshy contractile root and adventitious roots formed from the underground stems. Mature individuals exhibited vegetative propagation whereby the underground stems produced above-ground photosynthetic stems.

ARROJADOA DINAE SUBSP. *NANA* (FIG. 1D)

The population of this taxon was located in shallow rocky-loam soil in rock crevices near Cordeiros, BA. The plants possessed short to long, non-thickened underground stems that exhibited plagiotropic growth, branching and adventitious root formation

(Fig. 1D). The underground stems were able to emerge and become photosynthetic. Although only adventitious roots were present in the adult specimens sampled, it is assumed that normal fibrous roots occur in seedlings at least.

ARROJADOA ERIOCAULIS (FIG. 2A)

This taxon was found growing in sandy soil at its type locality near Mato Verde, MG, (Fig. 2A). In a young specimen, it was possible to observe thickening of the stem around and above the hypocotyl region, with the stem becoming constricted above and a taproot emerging below the thickened area. During further development, adventitious roots emerge from the thickened portion of the stem, whereas the taproot develops into a thick and fleshy contractile root that occasionally forms contractile lateral roots. In mature individuals, the thickened stem was distended, almost spherical and entirely subterranean (Fig. 2A), whereas the original above-ground stem had died back to the thick underground stem from which new aerial shoots had formed. The simple tuber can become quite large, with a diameter up to 20 cm or more. The fleshy contractile root also thickens considerably as the plant ages and lateral fibrous roots may be formed.

ARROJADOA HOFACKERIANA (FIG. 2B)

This taxon grows in sandy soils and can be found only at its type locality near Piatã, BA. The underground structures of the taxon appeared quite complex and displayed thick, fleshy, much enlarged underground stems from which new stems were produced in a manner similar to that found in *A. albicoronata*. However, in *A. hofackeriana*, the branched tubers were organized in a chain-like structure, with each tuber developing one or more thick and fleshy contractile roots; only one of the stem tubers had an above-ground stem (Fig. 2B).

ARROJADOA MARYLANAE (FIG. 2C)

This rupicolous taxon can be found only at its type locality near Sussuarana, Tanhaçú, BA, where it grows in gravel-filled crevices in rocky outcrops of white crystalline quartz. The species is the largest member of the genus and can attain a height of up to 3 m. The underground system consisted of a main non-thickened taproot and a network of fibrous lateral roots (Fig. 2C).

ARROJADOA MULTIFLORA (FIG. 2D–F)

The studied population inhabited an area of sandy soil at Caetité, BA. Among all of the taxa studied,

individuals of this species were unique in displaying discrete variations in their underground structures. Three distinctive morphologies were observed: (1) the presence of a contractile main root (forming lateral contractile roots) and normal fibrous roots only (Fig. 2D); (2) the presence of normal fibrous roots, short underground stems sprouting from the base of the above-ground photosynthetic stem and adventitious roots (occasionally contractile) formed on areoles (Fig. 2E); and (3) the presence of all features described in (2) together with long subterranean stems with plagiotropic growth from which adventitious roots and a new above-ground photosynthetic stem eventually emerged (Fig. 2F). Only one individual exhibiting morphological type (3) was discovered and this specimen had short thick underground stems at the base of the new above-ground stem that had been produced by the long underground stem.

ARROJADOA PENICILLATA (FIG. 3A)

This taxon grows on loam soil and two populations were sampled, one at Itaobim (MG) and one at Seabra (BA). The species possesses a main taproot that penetrates 15 to 20 cm into the soil, and lateral fibrous roots (Fig. 3A) that spread superficially for a distance of up to 1 m around the plant. No intra- or interpopulational variations were observed in the individuals collected.

ARROJADOA RHODANTHA (FIG. 3B)

This taxon grows in loamy soil and three populations were sampled from different areas of its range, northern Minas Gerais (Mato Verde), central Bahia (Abaíra) and northern Bahia (Morro do Chapéu). The root system of this species is quite similar to that of *A. penicillata* and is composed of a taproot and short lateral fibrous roots (Fig. 3B). In some cases, individuals had developed adventitious roots on fallen stems or stems touching the soil. No intra- or interpopulational variations were observed in the individuals collected.

ARROJADOA ROSENBERGERIANA (FIG. 3C)

This taxon was found growing on rocky-loam soil at its type locality near Santo Antônio do Retiro, MG, close to the site where *A. eriocaulis* was sampled. The underground structures of this species are quite similar to those of *A. dinae* subsp. *dinae*, comprising thick underground stems formed from a pre-existing subterranean stem, which can also develop into above-ground photosynthetic stems (Fig. 3C). The



Figure 2. A, *Arrojadoa eriocaulis* Buining & Brederoo showing a thickened tuber and main contractile root. B, *A. hofackeriana* (P.J.Braun & Esteves) P.J.Braun & Esteves showing successively organized tubers, each of which exhibits a thickened contractile root. C, *A. marylandae* Soares-Filho & Machado showing entangled common fibrous roots. D, *A. multiflora* F.Ritter showing an underground system comprising a contractile root and fibrous roots. E, *A. Multiflora* showing fibrous roots and short underground stem segments. F, *A. multiflora* showing an underground system consisting of soboles.



Figure 3. A, *Arrojadoa penicillata* (Gürke) Britton & Rose showing the main cortical root and superficial lateral roots. B, *A. rhodantha* (Gürke) Britton & Rose showing the main root penetrating the soil and lateral roots. C, *A. rosenbergiana* (van Heek & Strecker) P.J.Braun, Esteves & van Heek showing soboles producing aerial stem segments and adventitious roots that expand superficially.

lateral roots, which are mostly adventitious in origin, are shallow and spread horizontally.

ANATOMY

STRUCTURES OF ROOT ORIGIN (FIGS 4–7, TABLE 2)

All 12 species examined had fibrous (or common) roots, and *A. albicoronata*, *A. dinae* subsp. *dinae*, *A. eriocaulis*, *A. hofackeriana* and *A. multiflora* also had contractile roots.

In all species, and in all root types observed, the periderm originated from the pericycle (Fig. 4A), with the exception of *A. marylandae* (Fig. 4B), in which the periderm originated from the phloem. The pericycle of fibrous roots, when present, typically comprised one to four cell layers, but in *A. dinae* subsp. *dinae*, pericyclic sclereids were also observed (Fig. 4C). Roots had a collapsed primary phloem and a secondary

phloem with few conducting cells (Fig. 4C, D). The secondary xylem was formed by fibrous wood (Fig. 4A–C, F, G), although in *A. eriocaulis* (Figs 4H, 5A, B) and *A. multiflora* (Figs 4E, 5C) it was possible to observe a different type of wood presenting an initial fibrous phase followed by a second phase consisting of wide-band tracheids (WBTs) (see Carlquist, 2010 and references therein). The fibrous phase was not always observed in the contractile roots of *A. albicoronata*, *A. eriocaulis* and *A. hofackeriana*. In the fibrous roots of *A. bahiensis*, the cambium produced an initial fibrous phase followed by a phase with parenchyma matrix and WBTs and a third fibrous phase (Fig. 5D–F).

Roots that presented only a fibrous phase of secondary xylem displayed regions or bands of non-lignified parenchyma (Fig. 4G), as observed in *A. albicoronata*, *A. albiflora*, *A. bahiensis*, *A. dinae*

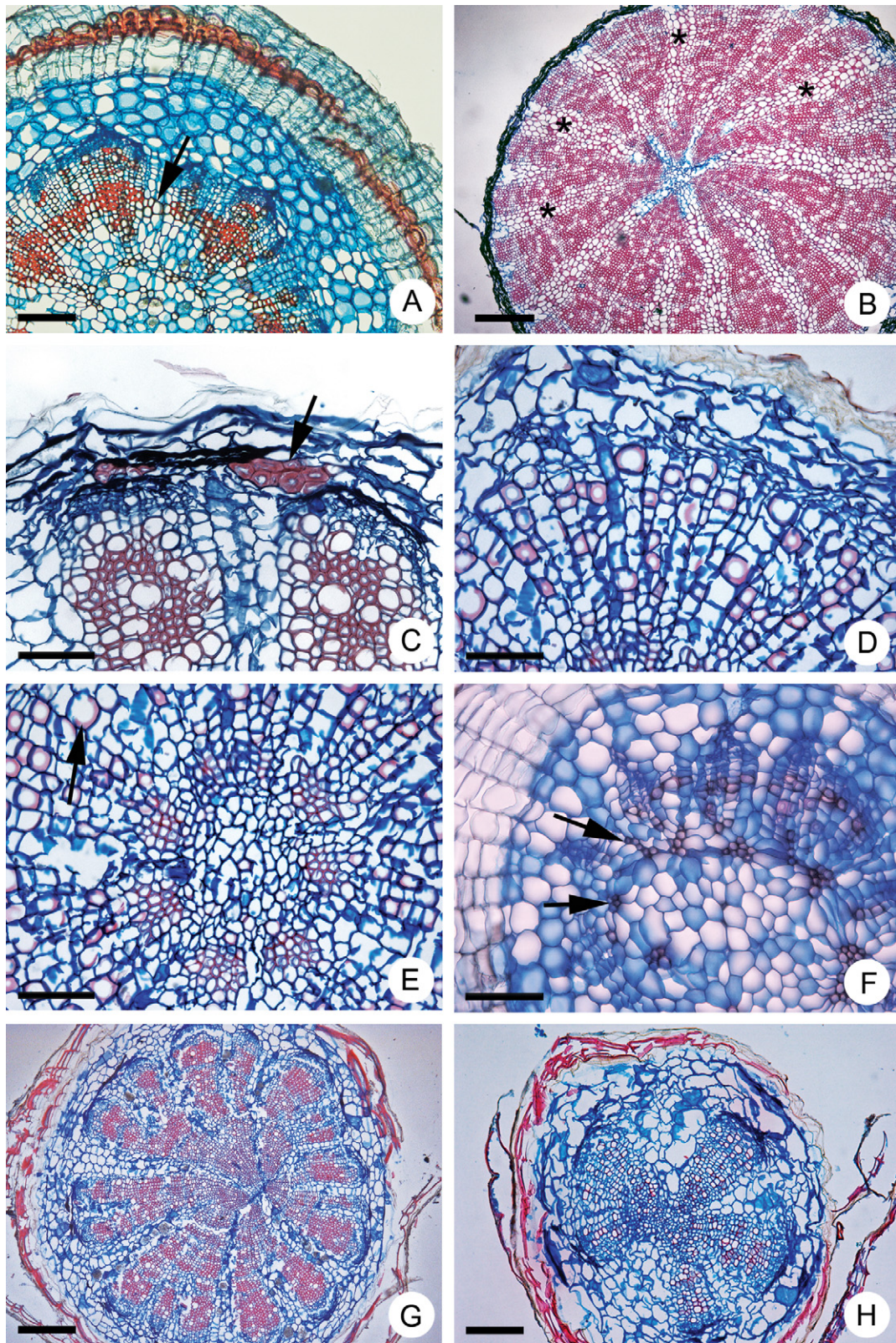


Figure 4. See caption on next page.

Figure 4. Cross sections of roots displaying: (A) *A. penicillata* (Gürke) Britton & Rose exhibiting periderm with alternating layers of lignified cells and other cells with walls containing suberin deposits. Note the beginning of the formation of fibrous wood and lignification of xylem rays (arrowed); (B) *A. marylandae* Soares-Filho & Machado displaying fibrous wood with the lignification of rays almost complete except for the central region. Note formation of new xylem rays (asterisked); (C) *A. dinae* Buining & Brederoo subsp. *dinae* showing sclereids in the outer phloem (arrowed); (D) *A. multiflora* F.Ritter showing WBTs-type wood; (E) *A. multiflora* showing dimorphic wood with fibrous initial phase followed by WBTs phase (arrowed); (F) *A. rosenbergeriana* (van Heek & Strecker) P.J.Braun, Esteves & van Heek showing extremities of protoxylem (arrowed) and the beginning of the formation of fibrous wood; (G) *A. albicoronata* (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves showing fibrous wood; (H) *A. eriocaulis* Buining & Brederoo showing the beginning of the lignification of the wood. Abbreviation: WBTs, wide-band tracheids. Scale bars, 150 µm (A, H); 300 µm (B, G); 100 µm (C–F).

subsp. *dinae*, *A. eriocaulis*, *A. multiflora* and *A. penicillata*, with the formation of new xylem rays (Fig. 4B, G, H), as exemplified by *A. albicoronata*, *A. albiflora*, *A. dinae* subsp. *dinae*, *A. eriocaulis*, *A. marylandae*, *A. multiflora*, *A. penicillata* and *A. rhodantha*.

The xylem rays of *A. marylandae* were almost completely lignified, except for the inner region (Figs 4B, 5G, H), whereas those of *A. albiflora*, *A. dinae* subsp. *dinae*, *A. dinae* subsp. *nana*, *A. multiflora*, *A. penicillata* and *A. rhodantha* were partially lignified (Fig. 4A).

The longitudinal sections of the three regions of contractile roots revealed the effects of contraction on the periderm and parenchyma cells outside the phloem (Fig. 6A–F). The periderm was completely collapsed in the proximal region (Fig. 6C) and displayed clearly delimited cells in the distal region (Fig. 6A). Moreover, it was possible to observe sharp wrinkling of the periderm in the areas of greatest contraction in the proximal region (Fig. 6C).

The parenchyma cells outside the phloem (Fig. 6A–F) and in the xylem rays (Fig. 6G–I) displayed the following attributes: (1) they were more elongated axially in the distal region of the contractile root (Fig. 6A, D, G); (2) they underwent axial contraction and tangential elongation in the middle region (Fig. 6B, E, H); and (3) in the proximal region, the radial cells exhibited the highest axial contraction and tangential increase, while the intercellular spaces were more visible (Fig. 6C, F, I). In the proximal region, the parenchyma cells outside the phloem were radially collapsed, forming rows of collapsed cells (Fig. 6C, F), while the parenchyma cells present in the rays were not collapsed (Fig. 6I). Along the longitudinal axis of the contractile region of the root, it was possible to observe areas of greater compression, including the peridermal layers, as described above (Fig. 6C, F). Tangential increase combined with axial contraction of the ray cells caused a slight deformation of the WBT lattice formed in the axial system, thereby ‘pushing’ this network laterally and compressing it longitudinally (Fig. 7A).

The tracheary element, consisting mainly of WBTs, also underwent compression (Fig. 7B, C) as was

evident from the smaller size of the WBTs of the proximal region in comparison with those of the distal region. Moreover, in the proximal region, the secondary wall bands were close together (Figs 6C, I, 7B, C) and the primary wall had undergone invagination (Fig. 7B, C).

Secondary growth continued even after the start of root contraction, and it was of interest to note the differences in contraction between the external and internal WBTs. Thus, the external WBTs (Fig. 7D) did not show the same signs of contraction as the internal WBTs (Fig. 7B–C) and the longitudinal section revealed a gradation in the proximity of the thickening bands. A further interesting characteristic was the sinuous appearance of the innermost cells of the xylem. In *A. hofackeriana*, which forms little or no fibre, it was possible to notice undulation of the first elements of the secondary xylem (Fig. 7E), whereas in species in which it was possible to identify a fibrous phase of the secondary xylem, the undulation occurred in the fibres (Fig. 7F, G).

STRUCTURES OF STEM ORIGIN (FIGS 8–10, TABLE 2)

The dermal tissues of the seven *Arrojadoa* taxa with underground stem structures, for example, *A. albicoronata*, *A. dinae* subsp. *dinae*, *A. dinae* subsp. *nana*, *A. eriocaulis*, *A. hofackeriana*, *A. multiflora* and *A. rosenbergeriana*, had a periderm (Fig. 8A–C) established immediately below the epidermis (Fig. 8A).

Areoles were detected on the tubers, soboles (diffuse underground stems that develop horizontally and generate aerial shoots; see DISCUSSION) and short underground stems of the studied taxa. The areole regions of the underground stems of these species typically produced only a few spines and trichomes, although the areole region of *A. eriocaulis* (Fig. 8C) was apparently more developed than in other species.

In all of the studied species, the cortical regions of the underground stems were extensive and had mucilaginous cells and cavities (Fig. 8; Table 2) and vascular bundles (Fig. 8G, H). The arrangement of the phloem and xylem in the vascular bundles varied and in some cases was ‘inverted’; for example, with the

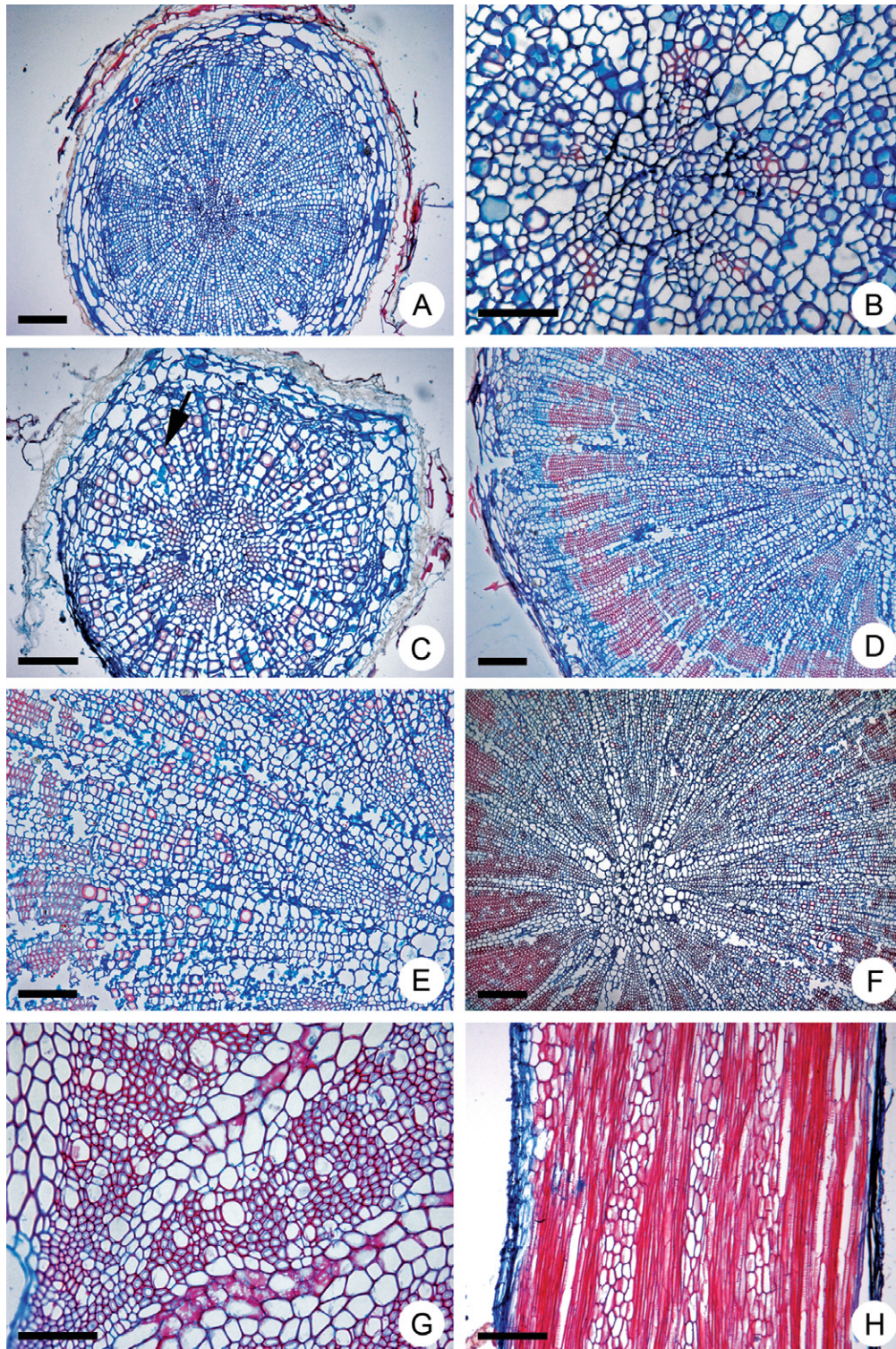


Figure 5. A–B, *Arrojadoa eriocaulis* Buining & Brederoo showing the initial phase of fibrous wood followed by the WBTs phase. C, *A. multiflora* F.Ritter showing a similar pattern to those of (A, B) [arrow indicates wide-band tracheids (WBT)]. D–F, *A. bahiensis* (P.J.Braun & Esteves) N.P.Taylor & Egli. showing trimorphic wood with fibrous initial phase followed by WBTs phase and fibrous external phase. G, *A. marylandae* Soares-Filho & Machado showing lignified radial cells (in cross section). H, *A. marylandae* showing lignified radial cells (in longitudinal section). Scale bars, 250 μm (A, D, F, H); 100 μm (B, G); 150 μm (C, E).

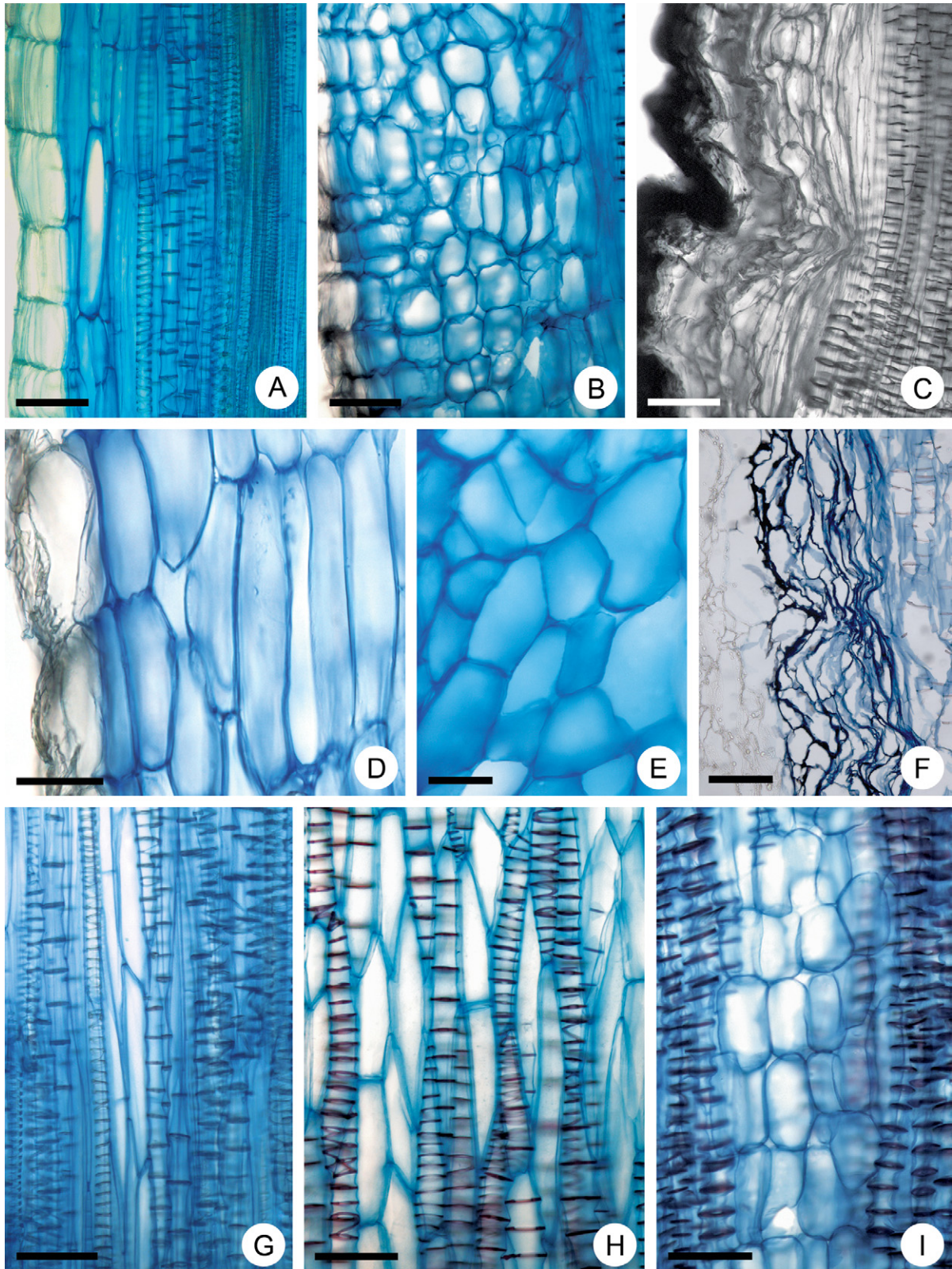


Figure 6. See caption on next page.

Figure 6. Longitudinal sections of contractile roots displaying: (A) distal region of the contractile root from *Arrojadoa multiflora* F.Ritter showing periderm and parenchyma cells outside the phloem elongated in the axial direction; (B) mid region of the contractile root from *A. multiflora* with periderm showing early signs of collapse, and parenchyma cells outside the phloem contracting axially and expanding in the radial direction; (C) proximal region of the contractile root from *A. multiflora* with collapsed periderm cells and layers of parenchyma cells outside the phloem collapsed in the radial direction; (D) distal region of the contractile root from *A. hofackeriana* (P.J.Braun & Esteves) P.J.Braun & Esteves with parenchyma cells outside the phloem elongated in the axial direction; (E) mid region of the contractile root from *A. hofackeriana* showing axial contraction and radial expansion of the parenchyma cells outside the phloem; (F) proximal region of the contractile root from *A. hofackeriana* with parenchyma cells outside the phloem collapsed in the radial direction; (G) distal region of the contractile root from *A. multiflora* showing ray parenchyma cells elongated in the axial direction; (H) mid region of the contractile root from *A. multiflora* showing axial contraction and tangential expansion of the ray parenchyma cells; (I) proximal region of the contractile root from *A. multiflora* showing considerable axial compression and tangential expansion. Note the large intercellular spaces. Scale bars, 100 µm (A, B, F–I); 200 µm (C); 50 µm (D–E).

xylem on the outside and the phloem on the inside. Additionally, in a well-developed tuber of *A. eriocaulis*, secondary growth could be observed in some of the vascular bundles of the cortical region (Fig. 8G).

The central vascular systems of the studied taxa exhibited remarkable differences (Figs 9, 10). *Arrojadoa dinae* subsp. *nana* (Fig. 9A) and *A. dinae* subsp. *dinae* (Fig. 9B) were quite similar in having little phloem (primary or secondary) and non-fibrous wood composed of vessel elements and parenchyma. It was also noticeable that the soboles of these two species had less pronounced secondary vascular growth than other species (Figs 9, 10). In *A. dinae* subsp. *dinae* (Fig. 9B), sclereids had formed externally to the phloem and vascular bundles were present in the medulla, features that were not observed in *A. dinae* subsp. *nana*.

The youngest, and therefore smallest, short underground stems of *A. multiflora* (Fig. 9C, D) had vascular systems similar to those of *A. dinae* subsp. *nana*. In more developed underground stems, however, the vascular cambium formed a non-fibrous wood with a parenchymal matrix and wide rays that showed no signs of lignification at the stages analysed (Fig. 9C). Medullary bundles were not observed in *A. multiflora* or *A. dinae* subsp. *nana*.

In the central vascular systems of *A. eriocaulis* tubers (Fig. 9E–G), the primary phloem was collapsed, whereas the secondary phloem was broad and had wide rays in the interfascicular region. Although a portion of the cells of the fascicular region of the phloem appeared collapsed, it was possible to observe the presence of phloem fibres in this area (Fig. 9F, G). The primary xylem was followed by polymorphic wood (Fig. 9E) comprising an initial WBT phase and a subsequent fibrous phase. The second phase of the wood contained non-lignified parenchyma layers (Fig. 9E–G). Xylem and phloem rays were large and contained druse-like crystals (Fig. 9F).

In *A. albicoronata* (Fig. 10A, B) and *A. multiflora*, it was not possible to determine if sclereids found in the

region external to the phloem had originated from cells of the primary phloem or of the pericycle since the outer phloem had collapsed. However, in *A. albicoronata*, the sclereids located in the interfascicular region were apparently of pericyclic origin (Fig. 10A). Furthermore, the wood of this species exhibited an initial fibrous phase followed by a non-fibrous phase (Fig. 10A).

Arrojadoa rosenbergeriana and *A. hofackeriana* were similar in that both exhibited sclereids in the region external to the primary phloem, which, in the case of *A. hofackeriana*, formed a continuous cylinder surrounding the central vascular system (Fig. 10C). Moreover, the wood of both species comprised a single fibrous phase with lignified rays (Fig. 10C, D), a characteristic that was not observed in the other species studied. Tubers of *A. hofackeriana* were, however, unique in exhibiting a transition region between stem and root.

DISCUSSION

The underground structures of members of *Arrojadoa* were diverse. Based on morphological analysis, they could be classified into five main types: (1) single or branched tubers; (2) short or long (soboles) underground stems; (3) thick and succulent contractile roots; (4) thick roots; and (5) fibrous roots.

The long underground stems were diffuse and displayed plagiotropic growth, spreading horizontally just below the soil surface. These stems produced adventitious roots at intervals and grew new, above-ground, photosynthetic stems, from which it would appear that their function is associated more with propagation and preventing the destruction of the above-ground stems than with reserve storage. Rizzini & Heringer (1966) used the name 'sobole' for diffuse underground stems that develop horizontally and generate aerial shoots. On this basis, it would seem appropriate to refer to the long underground stems in *Arrojadoa* as soboles. The term 'tuber' is

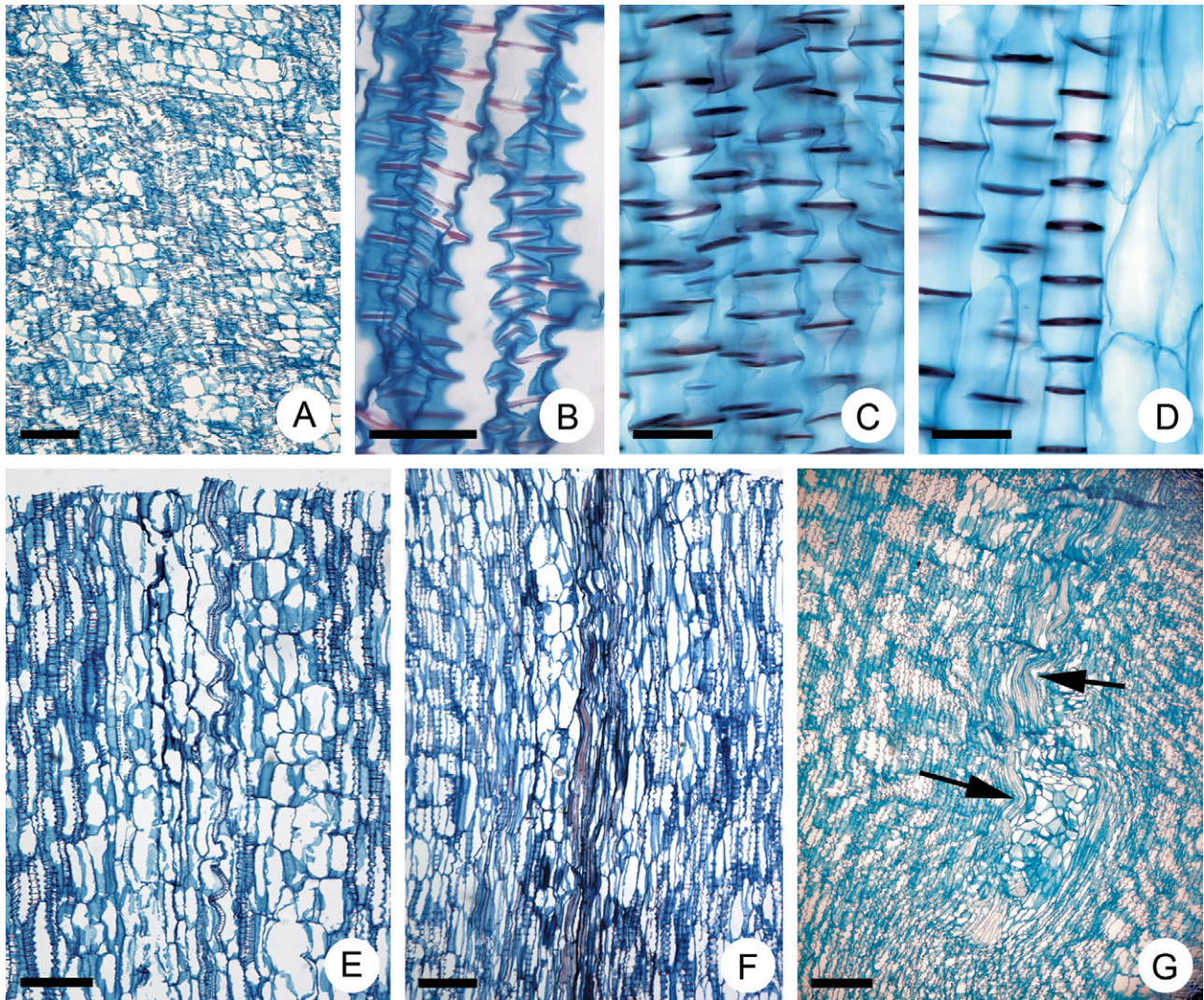


Figure 7. Longitudinal sections of contractile roots displaying: (A) proximal region of the contractile root from *Arrojadoa multiflora* F.Ritter showing deformation of the wide-band tracheids (WBTs) network in the axial system; (B) proximal region of the contractile root from *A. eriocaulis* Buining & Brederoo showing inner xylem. Note WBTs with rings of secondary wall and invagination of the primary wall resulting from contraction; (C) proximal region of the contractile root from *A. multiflora* exhibiting similar features to those described in (B); (D) proximal region of the contractile root from *A. multiflora* showing outer xylem. Note the wider spaces between the bands of the secondary wall of the WBTs compared with those observed in the inner xylem; (E) *A. hofackeriana* (P.J.Braun & Esteves) P.J.Braun & Esteves showing undulation of the first vessel elements in the secondary xylem; (F) undulation of fibres (arrowed) in *A. eriocaulis*; (G) undulation of the fibres (arrow) in *A. multiflora*. Scale bars, 150 μm (A); 50 μm (B–D); 250 μm (F–G).

typically applied to any swollen underground structure, irrespective of whether it is derived from root or stem tissue (Onwueme & Charles, 1994; Hickey & King, 2000; Bell & Bryan, 2008). In order to differentiate between the nature of the structures, the term ‘stem tuber’ is sometimes adopted to refer to the swollen structures derived from stem tissue and ‘root tuber’ for those derived from root tissue (Pate & Dixon, 1982; Onwueme & Charles, 1994; Hickey & King, 2000; Bell & Bryan, 2008). In this paper,

‘stem tuber’ has been applied only to the thick, fleshy, swollen underground stems that perform a storage function in some of the *Arrojadoa* taxa studied.

Preston (1900) described two components in the root system of Cactaceae: (1) a vertical component that is formed first and functions mainly in anchorage; and (2) a horizontal component that develops as the plant grows and is responsible for most of the water and nutrient absorption. In *Arrojadoa*, the ver-

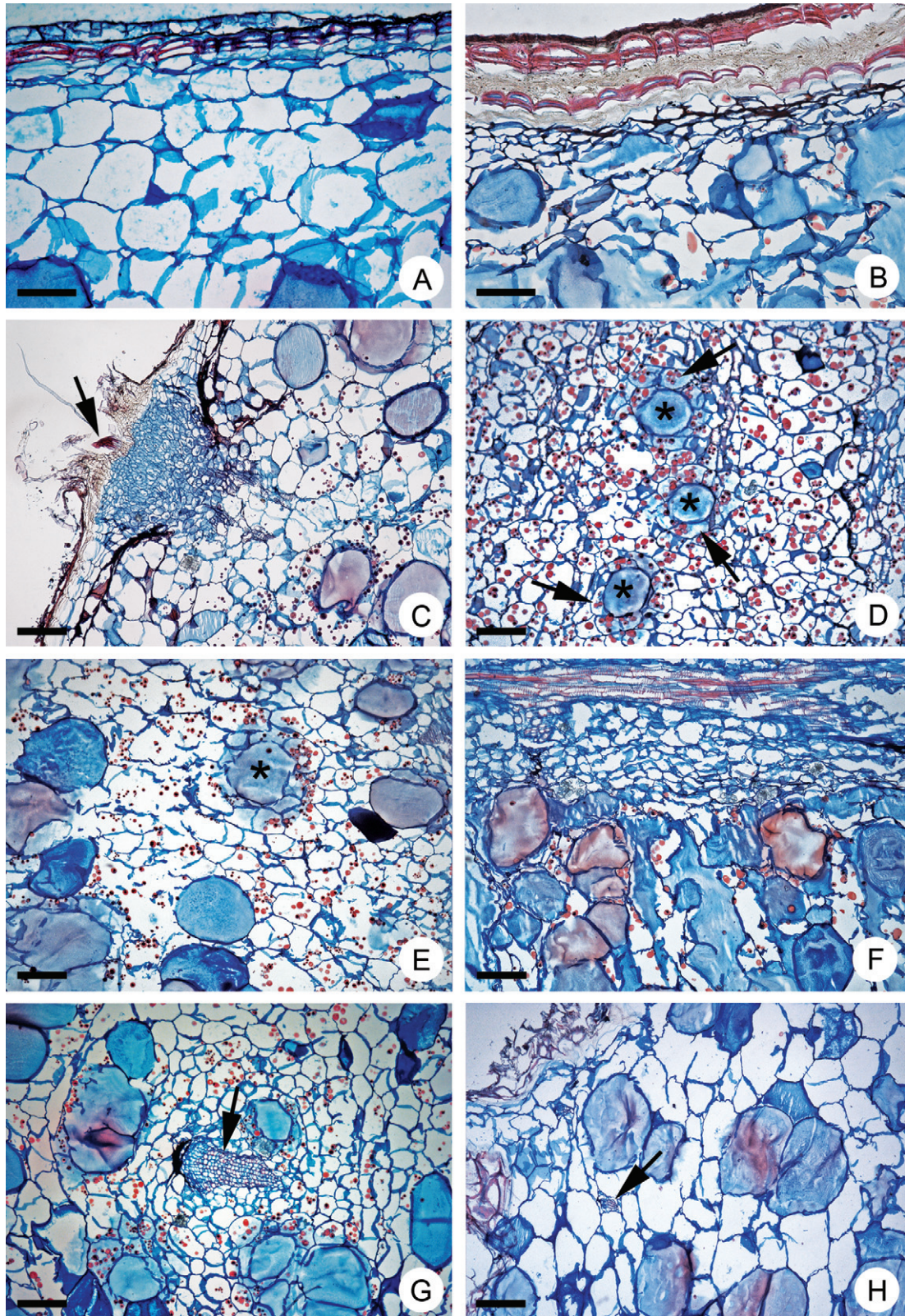


Figure 8. See caption on next page.

Figure 8. A, cross section of stem of *Arrojadoa dinae* Buining & Brederoo subsp. *dinae* showing the beginning of the formation of the periderm with the establishment of phellogen in the sub-epidermal region. B, longitudinal section of stem of *A. albicoronata* (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves showing the periderm with alternating layers of lignified cells and other cells with walls containing suberin deposits. C, cross section of stem of *A. eriocaulis* Buining & Brederoo stem showing the presence of areoles containing trichomes forming a multiserial base and a single spine with lignified tip (arrowed). D, longitudinal section of *A. eriocaulis* showing the cortical region with mucilaginous cavities (asterisked). The arrows indicate the cells of the epithelium cavity. E, cross section of stem of *A. eriocaulis* showing the cortical region with mucilaginous cavities (asterisked). F, longitudinal section of stem of *A. albicoronata* showing cavities produced by the lysis of secretory cells. G, cross section of stem of *A. eriocaulis* stem showing collateral bundles in the cortical region (arrowed) with secondary growth. H, cross section of stem of *A. rosenbergeriana* (van Heek & Strecker) P.J.Braun, Esteves & van Heek showing a minute cortical bundle (arrowed). Note the presence of mucilage secretory cells. Scale bars, 150 µm (A–B); 250 µm (C–H).

tical component, when present, may be in the form of fibrous or contractile roots.

In Cactaceae, contractile roots have been described for *Neomammillaria macdougalii* Britton & Rose (Hemenway & Breazeale, 1935), *Lophophora williamsii* (Lem. ex Salm-Dyck) J.M.Coult. (Terry & Mauseth, 2006), *Frailea castanea* Backeb. (Machado, 2007), *Leuchtenbergia principis* Hook. (Bobich & North, 2009) and *Ariocarpus fissuratus* (Engl.) K.Schum. (Garrett *et al.*, 2010). Contractile roots were observed in five *Arrojadoa* spp., and these species developed underground stems that generated aerial parts, thereby maintaining the bud below the surface.

Anatomical examination revealed a highly unusual mechanism of contraction in *Arrojadoa* that showed similarities to the ‘ring-collapsing’ type described in monocotyledons (Pütz & Froebe, 1995) and in some dicotyledons such as *Gymnarrhena micrantha* Desf. (Asteraceae; Zamski, Ucko & Koller, 1983). In the contractile roots of *Arrojadoa*, the innermost secondary xylem (produced prior to contraction) exhibited a greater contraction than the external xylem (formed during and after the contraction), thus demonstrating continuity of secondary growth after contraction as reported previously for *Ariocarpus fissuratus* (Garrett *et al.*, 2010).

As is the case for most contractile roots, those of *Arrojadoa* displayed radial and tangential extension in addition to axial reduction of the parenchyma cells. Generally, it is the parenchyma cells of the cortical region that are active during contraction (Smith, 1930; Wilson & Honey, 1966; Chen, 1969; Sterling, 1972; Reyneke & Schijff, 1974; Ruzin, 1979; Jernstedt, 1984; Pütz & Froebe, 1995; Pütz, 1999), although cells of the endodermis, pericycle and primary phloem are reportedly contractile-active in *G. micrantha* (Zamski *et al.*, 1983). In *Arrojadoa*, the cells that increase radially and tangentially and decrease axially are those that are external to the phloem and those of the xylem ray. Such modifications have been reported in Cactaceae only for the cells of the contractile root ray of *Ariocarpus fissura-*

tus (Garrett *et al.*, 2010), although it was not clear whether the alterations occurred in the parenchyma cells outside the phloem as presently described for *Arrojadoa* spp.

In *Arrojadoa*, the process of radial extension of parenchyma cells external to the phloem induces the collapse of the most external layers of parenchyma cells. Chen (1969) proposed two plausible explanations for the observed collapse; for example, the outer parenchyma cells are compressed by the inner parenchyma cells as they increase in radial diameter, or the outer parenchyma cells react differentially by loss of turgor and subsequently collapse. An alternative possibility is that these two mechanisms occur in combination, i.e. the increased pressure exerted by the expanding inner parenchyma cells induces loss of turgor in the outer parenchyma, signalling their collapse. The operation of such a mechanism would also prevent continuous pressure from rupturing the periderm, which Cutter (1986) described as a protective secondary tissue of roots and stems.

The overall process of contraction of the parenchyma cells in *Arrojadoa* causes the WBTs to contract, apparently in a passive manner, as the primary walls of these cells undergo invagination. One notable outcome of the contraction of WBTs is that the secondary wall bands are brought closer together. A similar pattern has been observed in *Narcissus pseudonarcissus* L. (Chen, 1969) where the longitudinal walls of the vessels, which are comparatively thinner and offer less resistance to longitudinal compression, seemed to bend between the secondary walls. In *Brodiaea lactea* S.Watson, c. 50% more secondary wall bands are present in contracted areas than in non-contracted regions, an observation that would be expected if the stele were being passively distorted (Smith, 1930). This finding suggests the occurrence of a purely mechanical process with no absorption of material from the vessel walls, a situation that is similar to that observed in the WBTs of *Arrojadoa*.

In an ecological context, the function most commonly attributed to contractile roots is anchorage of

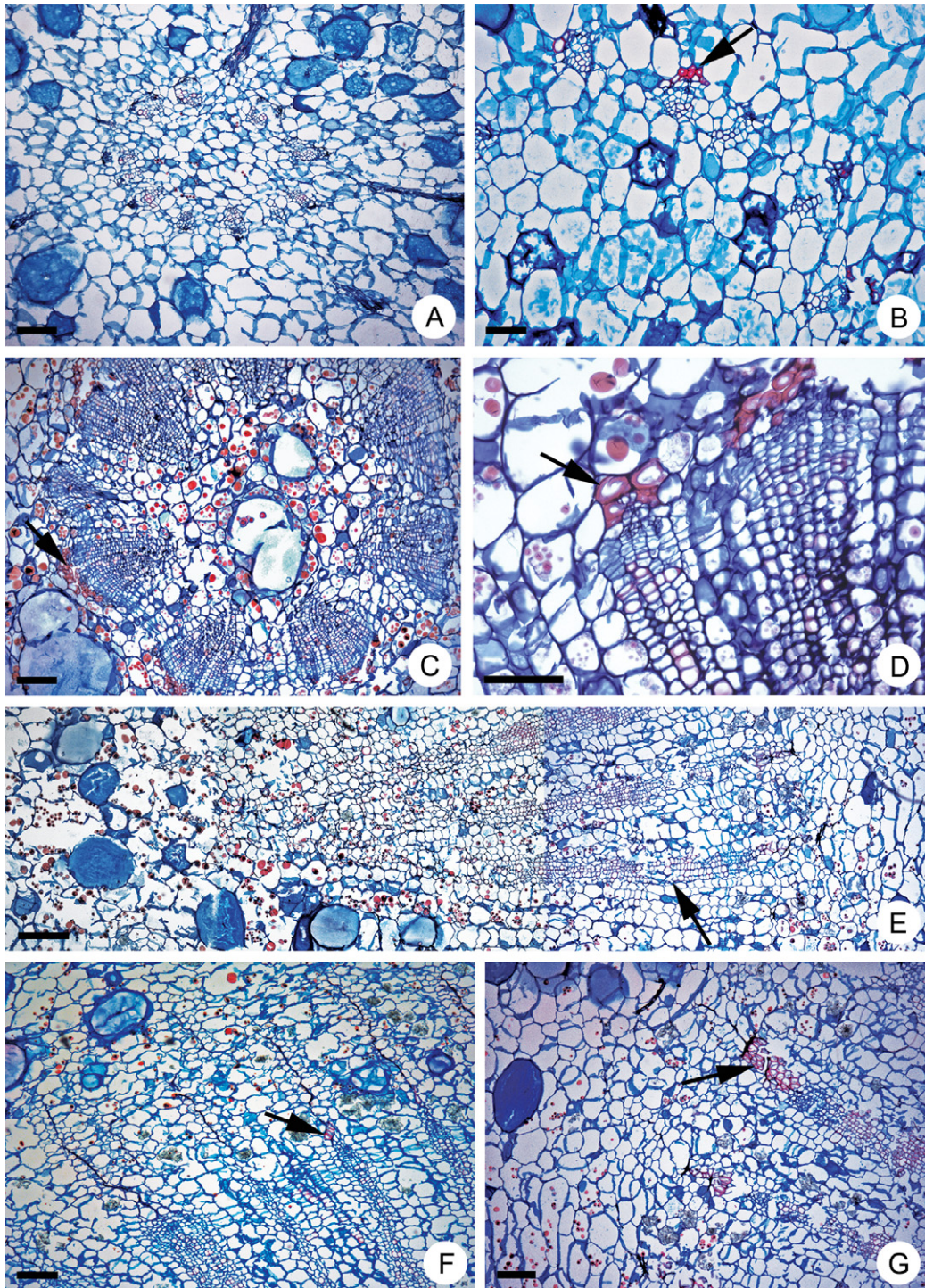


Figure 9. Cross sections of underground stems displaying the organization of the central vascular systems in: (A) *A. dinae* subsp. *nana* (P.J.Braun & Esteves) P.J.Braun & Esteves showing reduced cambium activity; (B) *A. dinae* Buining & Brederoo subsp. *dinae* showing reduced cambium activity and extra-xylem sclereids (arrowed); (C–D) *A. multiflora* F.Ritter showing greater cambium activity in the fascicular and interfascicular region than in (A–B). Note extra-xylem sclereids (arrowed); (E–G) *A. eriocaulis* Buining & Brederoo showing the initial phase of the wide-band tracheids (WBTs)-type wood followed by a fibrous phase with layers of non-lignified parenchyma [arrowed in (E)]; in (F–G), it is possible to identify the sclereids associated with the secondary phloem (arrowed). Scale bars, 200 μm (A, C, F, G); 100 μm (B, D); 300 μm (E).

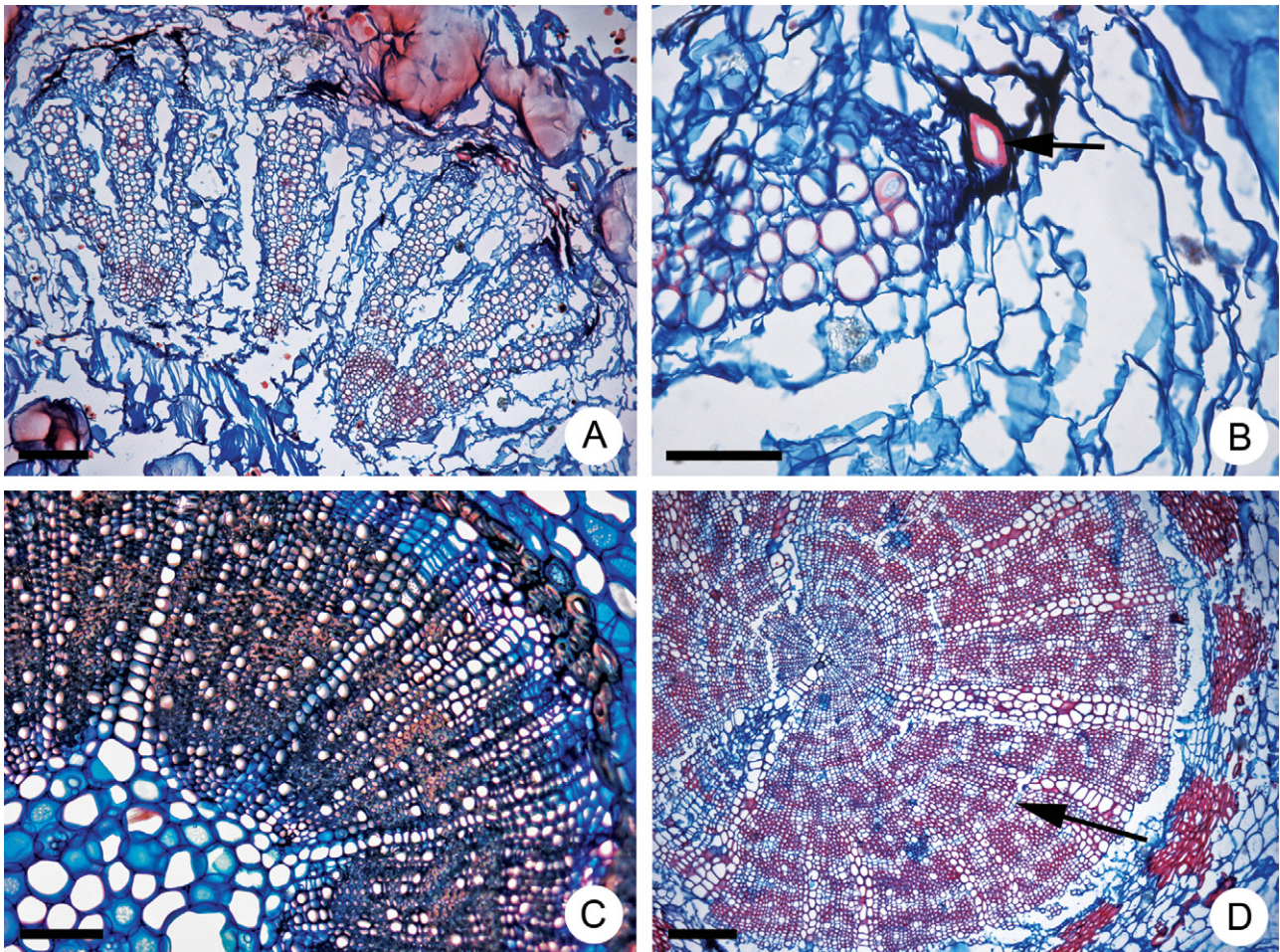


Figure 10. Cross sections of underground stems and transition root/stem zones displaying the organization of the secondary structure of the central vascular systems in: (A–B) underground stems of *A. albicoronata* (van Heek, R.J.Paul, Heimen, Hovens & W.Strecker) P.J.Braun & Esteves showing the initial phase of the fibrous wood followed by a parenchyma matrix phase. Note extra-xylem vascular sclereid in (B) (arrowed); (C) underground stems of *A. hofackeria* (P.J.Braun & Esteves) P.J.Braun & Esteves showing fibrous wood with lignification of xylem rays and the presence of layers and clusters of non-lignified parenchyma; (D) transition root/stem zone of *A. hofackeriana* showing fibrous wood with lignification of xylem rays and the presence of layers and clusters of non-lignified parenchyma (arrowed). Note that it is also possible to observe pericycle sclereids. Scale bars, 250 μm (A, D); 150 μm (C); 100 μm (B).

the plant in the soil (North, Brinton & Garrett, 2008). With regard to *Arrojadoa* spp. that grow in sandy or sandy-clay soil, the contractile capacity of the roots would help to re-anchor the plant during periods of ground motion provoked by the rearrangement of sand particles or the displacement of upper soil layers through the action of wind and rain. In addition to this important function, the thickened contractile roots of *Arrojadoa* may also serve as storage organs during seasonal drought.

Stone-Palmquist & Mauseth (2002) described four modifications of the xylem that may be related to the thickening of roots in Cactaceae: (1) the proliferation and increase in volume of parenchyma cells in the metaxylem and inner region of the secondary xylem;

(2) the presence of fibrous wood with abundant rays, which in some cases may be wider than the root axial system; (3) the presence of non-fibrous wood with a parenchymal matrix; and (iv) the presence of a non-fibrous wood with a WBT matrix. According to the classification of wood polymorphism in Cactaceae (Mauseth & Plemons, 1995), the fibrous roots of *Arrojadoa* can exhibit three types of wood: (1) monomorphic fibrous (found in all species); (2) dimorphic fibrous/WBTs (*A. eriocaulis* and *A. multiflora*); and (3) trimorphic fibrous/WBTs/fibrous (*A. bahiensis*). In the contractile roots of *Arrojadoa*, the wood was of two types, monomorphic WBTs and dimorphic fibrous/WBTs. Regarding the underground structures of stem origin, it was possible to verify the presence of

wood of the types: (1) dimorphic fibrous/WBT (*A. eriocaulis*); (2) fibrous/parenchyma (*A. albicoronata*); (3) monomorphic parenchyma (*A. dinae* subsp. *nana*, *A. dinae* subsp. *dinae* and *A. multiflora*); and (4) monomorphic fibrous (*A. rosenbergeriana* and *A. hofackeriana*).

Bands or small clusters of non-lignified parenchyma were observed in the fibrous roots (except in *A. marylandae*) and the fibrous phases of the underground stems of all *Arrojadoa* spp. studied. According to the International Association of Wood Anatomists (1989), non-lignified parenchyma generally occurs in the form of wide bands and is restricted to a few families of arboreal species, although the presence of this type of tissue has recently been demonstrated in other families. Melo-de-Pinna (2009) described the occurrence of layers, clusters or isolated cells of non-lignified parenchyma as a feature of the fibrous phase of the root and stem wood of members of Portulacaceae and Cactaceae, and Soffiatti & Angyalossy (2007) reported fibrous wood with bands and/or layers of non-lignified parenchyma in the aerial stems of some *Arrojadoa* spp.

The complete or partial absence of lignification in the xylem rays of roots was observed in all *Arrojadoa* spp. studied, with the single exception of *A. marylandae*, in which only the inner portion of the ray remained non-lignified. According to Milanez (1936), the delayed lignification observed in rays of *Rhipsalis regnellii* G.Lindb. is significant as, if the roots of this epiphytic species were entirely woody, the adaptation or fixation to the support plant would be difficult. Hence, late lignification of ray cells formed from cambium originating from the pericycle and non-lignified parenchyma cells are important traits that permit or facilitate fixation of plants to rocks, as in *A. bahiensis* and *A. albiflora*, or growth in clay-rocky soils, as in *A. dinae* subsp. *dinae* and *A. rosenbergeriana*.

Silva & Alves (1999) and Arruda *et al.*, (2005) considered that new rays result from alterations of the cambium that lead to an increase in the storage capacity of the roots. Based on the analysis of *Arrojadoa*, we propose that, along with new rays, the delayed lignification of ray cells and the non-lignified parenchyma also take part in the enhancement of the storage capacity of the roots as their main accumulation tissue is the xylem and not the cortical and medullary tissue as in the stem (Stone-Palmquist & Mauseth, 2002).

The underground stems of the *Arrojadoa* spp. studied here, exhibited three of the characteristics associated with the xylem of thickened roots in the Cactaceae, as described by Stone-Palmquist & Mauseth (2002): (1) fibrous wood with abundant rays that, in some cases, may be wider than the root axial

system; (2) non-fibrous wood with a parenchyma matrix; and (3) non-fibrous wood with a WBT matrix. However, the main tissue responsible for the thickening of the underground stems, particularly in respect to the broad tubers of *A. albicoronata*, *A. eriocaulis* and *A. hofackeriana*, is the fundamental tissue, especially the extensive cortex.

In *A. eriocaulis*, however, we identified a wide secondary phloem containing wide phloem rays in the interfascicular region, which contributed to the thickening of the stem and to the augmentation of the storage tissue of the tuber. The occurrence of this feature is rare in members of Cactaceae, which normally exhibit a thin band of phloem (Gibson & Nobel, 1986; Mauseth, Terrazas & Loza-Cornejo, 1998; Arruda *et al.*, 2005; Soffiatti & Angyalossy, 2007; Godofredo & Melo-de-Pinna, 2008; Arruda & Melo-de-Pinna, 2010; Lemos & Melo-de-Pinna, 2011).

Regarding non-xylem lignified cells, the sclereids originate from a parenchyma cell, whereas the fibres originate from a meristem cell (Esau, 1960; Fahn, 1990). The types of sclereids identified in the underground stems of *Arrojadoa* spp. were: (1) sclereids apparently originating from the pericycle (*A. dinae* subsp. *dinae*, *A. rosenbergeriana* and *A. hofackeriana*); (2) sclereids originating from the secondary phloem (*A. eriocaulis*); and (3) sclereids of uncertain origin, possibly from the pericycle or the phloem or both (*A. multiflora* and *A. albicoronata*). According to Melo-de-Pinna *et al.* (2007), fibres of Cactaceae and Portulacaceae may originate from the phloem, pericycle or both, although pericycle fibres are the most frequent. Following a study of epiphytic species of Cactaceae at different developmental stages, Lemos & Melo-de-Pinna (2011) reported the generation of pericycle fibres and sclereids in the pericycle region between the extremities of the phloem, which formed a ring of lignified cells surrounding the vascular region. Furthermore, Soffiatti & Angyalossy (2007) described the occurrence of sclereids in the pericycle region of the aerial stem of four *Arrojadoa* spp., similar to the findings reported here for the underground stem of *A. dinae* subsp. *dinae*, *A. rosenbergeriana* and *A. hofackeriana*.

In the present study, we have identified different morpho-anatomical features associated with underground storage in *Arrojadoa*, including thickened contractile roots, formed by secondary xylem and WBTs, and underground stems comprising a broad cortical region and WBT wood. We suggest that such structures represent adaptive strategies that are essential for the survival of the plants during seasonal drought in areas of savannah, rocky uplands and dry thorny scrubland; the contractile roots associated with subterranean stems, when present in an environment with large soil movement and severe droughts,

increase the parenchyma tissue, providing greater storage of water and keeping the buds below ground with successive contractions of the root.

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