



# The evolutionary and ecological significance of phylloclade formation: A morpho-anatomical approach

Veit M. Dörken<sup>1</sup>, Philip G. Ladd<sup>2</sup> and Robert F. Parsons<sup>3</sup>

## Abstract

Instead of leaves, in a few species the main photosynthetic organ is a flattened structure that can be a modified branch (e.g. *Ruscus*, *Jacksonia*) or a fused combination of branch and leaf tissue (e.g. *Phyllocladus*) called a phylloclade. The phylloclades of *Phyllocladus* lack xeromorphic features in their wet habitat. They are broad under the low light conditions as are those of *Ruscus* which can occur in forest understories. However *Ruscus* is also common in dry habitats and shows numerous xeromorphic features. In *Jacksonia* extensive sclerenchyma and thick cuticle protect the phylloclades from desiccation damage in xeric seasonal conditions. Despite former contrary definitions of phylloclades we advocate they be defined as pseudo-petiolate organs determinate in growth which arise from axillary buds in the axil of reduced leaves and resemble a leaf.

## Addresses

<sup>1</sup> Department of Biology, University of Konstanz, M 613, Universitätsstr. 10, 78457 Konstanz, Germany

<sup>2</sup> Environment and Conservation Science, Murdoch University, Murdoch, WA 6150, Australia

<sup>3</sup> Department of Environment and Genetics, La Trobe University, Melbourne, VIC 3086, Australia

Corresponding author: Dörken, Veit M. ([veit.doerken@uni-konstanz.de](mailto:veit.doerken@uni-konstanz.de))

Current Opinion in Plant Biology 2024, 79:102545

This review comes from a themed issue on **Growth and development 2024**

Edited by **Madelaine Bartlett** and **Annis Richardson**

For complete overview of the section, please refer the article collection - [Growth and development 2024](#)

Available online 5 May 2024

<https://doi.org/10.1016/j.pbi.2024.102545>

1369-5266/© 2024 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).

## Keywords

Leaf reduction, Drought, Shade, Photosynthesis, Light harvesting, Environment, Climate change.

## Key message

This is the first detailed comparison of the two extremes of phylloclade formation in vascular plants; a monocot and dicot with purely cauline structures formed by a single lateral short shoot and a gymnosperm with a complex fusion product of entire leafy lateral short shoots.

## Introduction

In the majority of cormophytes photosynthesis is carried out by green leaves. Leaves are one of the most variable vegetative structures of plants and they always reflect the conditions in which a taxon evolved and occurs. They not only differ in size and shape, but also in their anatomical structure and life span. Leaves of taxa growing on moist, fertile soils are usually markedly larger than those of taxa growing on dry or infertile soils [1] where small leaf size often reduces the loss of water e.g. in microphyllous xerophytes.

Such true leaf reduction can be so strong that the foliage is entirely reduced and photosynthesis is finally exclusively transferred to green shoot axes. These may be green, flattened, or acicular leaf-like structures, called phylloclades or cladodes. There has been considerable discussion on the origin of phylloclades (see references in the study by Cooney-Sovetts et al. [2]). The terms phylloclade and cladode have been used interchangeably but often have completely contradictory specific definitions [3–5] We propose that the root of the terms be acknowledged in that phylloclades are leaf-like (phyllo)-clades (clados – Greek for a young shoot or branch) that are not obviously segmented and have determinate growth. Cladodes do not have the connotation of leaf-like, they are just a modified shoot but can be somewhat flattened. We use the definitions from the study by Chappill et al. [6] – “phylloclades ... are

determinate flattened branchlets with a tapered pseudo-petiole that are articulated to the main stem or branch” while cladodes “are flattened branchlets that are indeterminate and without a tapered pseudo-petiole.” Phylloclades are not restricted to a distinct systematic group, and can be found in different unrelated taxa, angiosperms e.g. Asparagaceae, Fabaceae, Euphorbiaceae [2,7–9] but more rarely in gymnosperms (*Phyllocladus*) as well [10,11].

Phylloclades found in different taxa do not form in exactly the same way. Here we compare three types from woody taxa – *Ruscus* (Asparagales), *Jacksonia* (Fabales) and *Phyllocladus* (Gymnospermae), with a special emphasis on phylloclade anatomy and morphology.

Phylloclades in *Ruscus* resemble a single entire leaf with an entire margin, while in *Jacksonia* they are a single elongate sclerophyll leaf-like organ with distant acute marginal projections. Those of *Phyllocladus* can be entire and resemble a single leaf or be distantly and dichotomously arranged on long shoots reminiscent of a pinnate compound leaf with numerous lateral small leaflets. The large non-pinnate phylloclades of *Jacksonia* are in some ways intermediate between those of *Ruscus* and *Phyllocladus*.

Phylloclade formation in all three taxa will be discussed in the light of their ecological strategy and evolution. It will focus on the topic of how environmental conditions affect plant structures, so that species can survive under new climates and be competitive with other plant species in their plant communities.

## Results

### ***Ruscus aculeatus*: Asparagaceae; Eurasia, North Africa**

*R. aculeatus* is an “evergreen” rhizomatous shrub up to 0.5–0.8 (–1 m). The shoot system has a long shoot/short shoot differentiation (Figure 1a). Long shoots usually grow for only a year and new aerial long shoots are developed from the subterranean rhizomes [8,12].

The orthotropic long shoots are dark green and roundish with numerous strongly developed longitudinal ridges. The shoot cortex between the epidermis and the large inner pith consists of numerous small, chlorophyllous cells (Figure 2a). The central pith consists of larger cells, with slightly thicker lignified walls than in the cortex. As is typical for monocots, the vascular bundles are irregularly arranged in the centre of the long shoot axis (Figure 2a). Each vascular bundle strand is surrounded by a distinct sclerenchymatic sheath of thick-walled, lignified cells. Long shoot leaves are strongly reduced to white or brownish, dry membranous scales, which are non-photosynthetic (Figure 1c). The long shoots are of limited growth because their apex is terminated by a

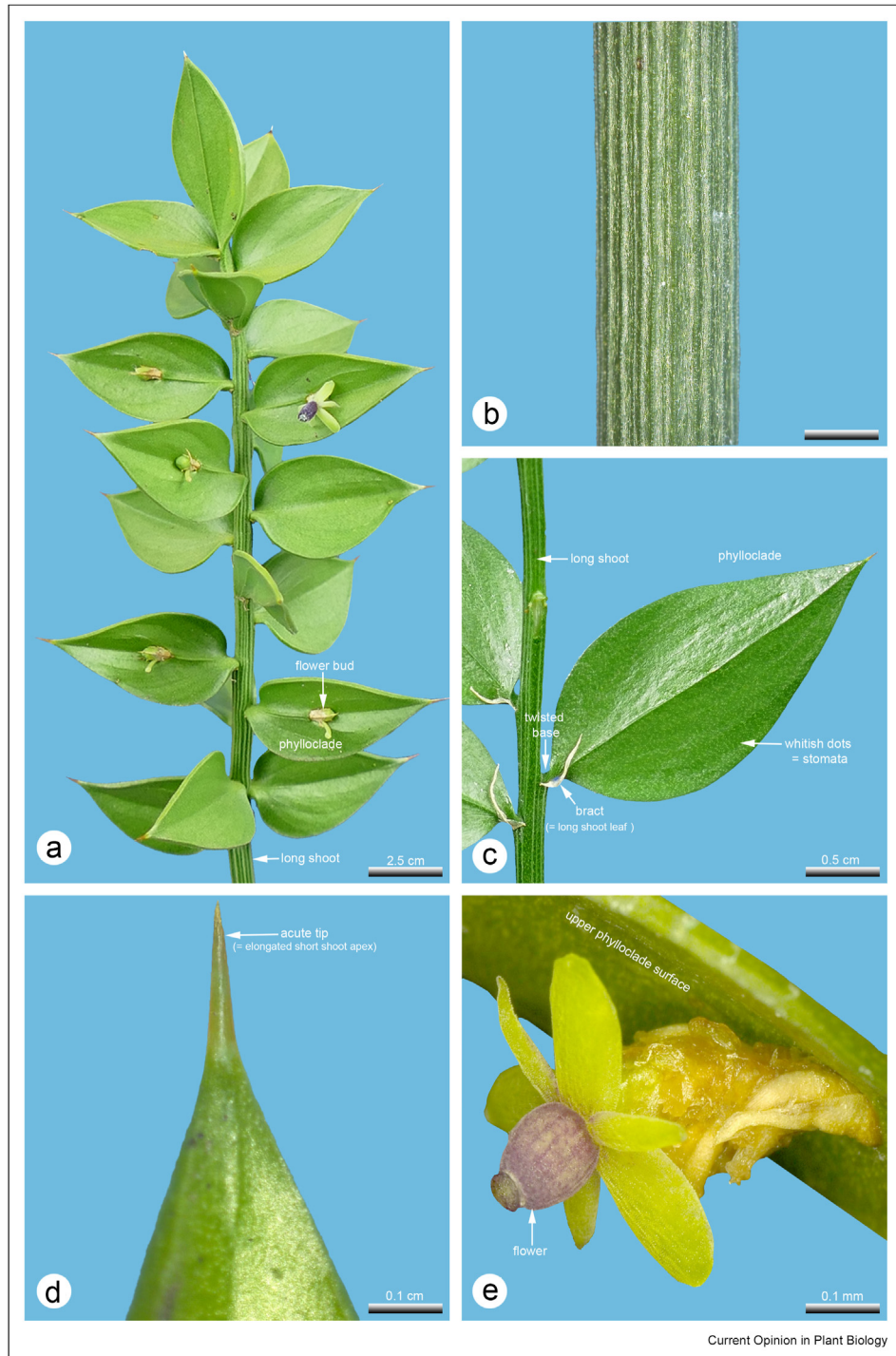
phylloclade (Figure 1a) (a detailed ontogenetic study of phylloclade formation is available in the study by Hirsch et al. [8]).

Short shoots are modified flattened, leaf-like structures (=phylloclades) inserted in the axil of a scaly long shoot leaf (Figure 1c). The foliar shape of the phylloclade results from meristematic activities occurring along the margins of the elongated shoot apex [8]. The phylloclades are a flattened stem and the shoot apex becomes determinate and forms an acute and elongated tip (Figure 1c); Their margin is entire and unlobed. Their base is usually strongly twisted, so that in sun-exposed individuals the surface turns to a vertical position and midday solar radiation hits only the margin. Anatomically the phylloclade resembles an isobilateral leaf (=aequifacial leaf) (Figure 2i). Despite the helical insertion of the phylloclades, in shaded individuals the foliar parts of the phylloclades are orientated more or less distichously so that there is a light exposed and a shaded surface of each phylloclade. There is no difference between the structure of both surfaces. On fertile phylloclades the flowers are developed in the centre on the adaxial phylloclade surface in the axil of scaly brownish, dry, membranous bracts (Figure 1a). There are numerous stomata of approximately the same density on the ad- and abaxial surface of the phylloclade. They are arranged in an irregular pattern (Figure 2r) but tend to be elongated in the direction of the long axis of the phylloclade and are slightly sunken in the epidermis. Phylloclade parenchyma lacks a differentiation into palisade- and spongy-parenchyma (Figure 2i). In the centre of the phylloclade a continuous water storage tissue layer (=hydrenchyma) is developed. It consists of 2 or 3 layers of large, thin-walled cells, with large vacuoles (Figure 2i). The vascular bundles have a planar arrangement, are located in the hydrenchyma (Figure 2i) and lack a cambium between the xylem and the phloem. Xylem is always located towards the centre of the phylloclade and phloem towards the epidermis of the phylloclade. Each bundle strand is surrounded by a distinct sclerenchymatic vascular bundle sheath consisting of numerous thick-walled, strongly lignified cells. The central vascular bundle strand is thicker and forms a kind of midrib. It has the largest sclerenchymatic vascular bundle sheath, helping to stabilize the phylloclade (Figure 2i). The vascular bundle strands terminate blindly in distal parts of the phylloclade, without fusing to each other (=open vasculature).

### ***Phyllocladus*: Podocarpaceae s.l.; Australasia, New Guinea, Borneo, the Philippines**

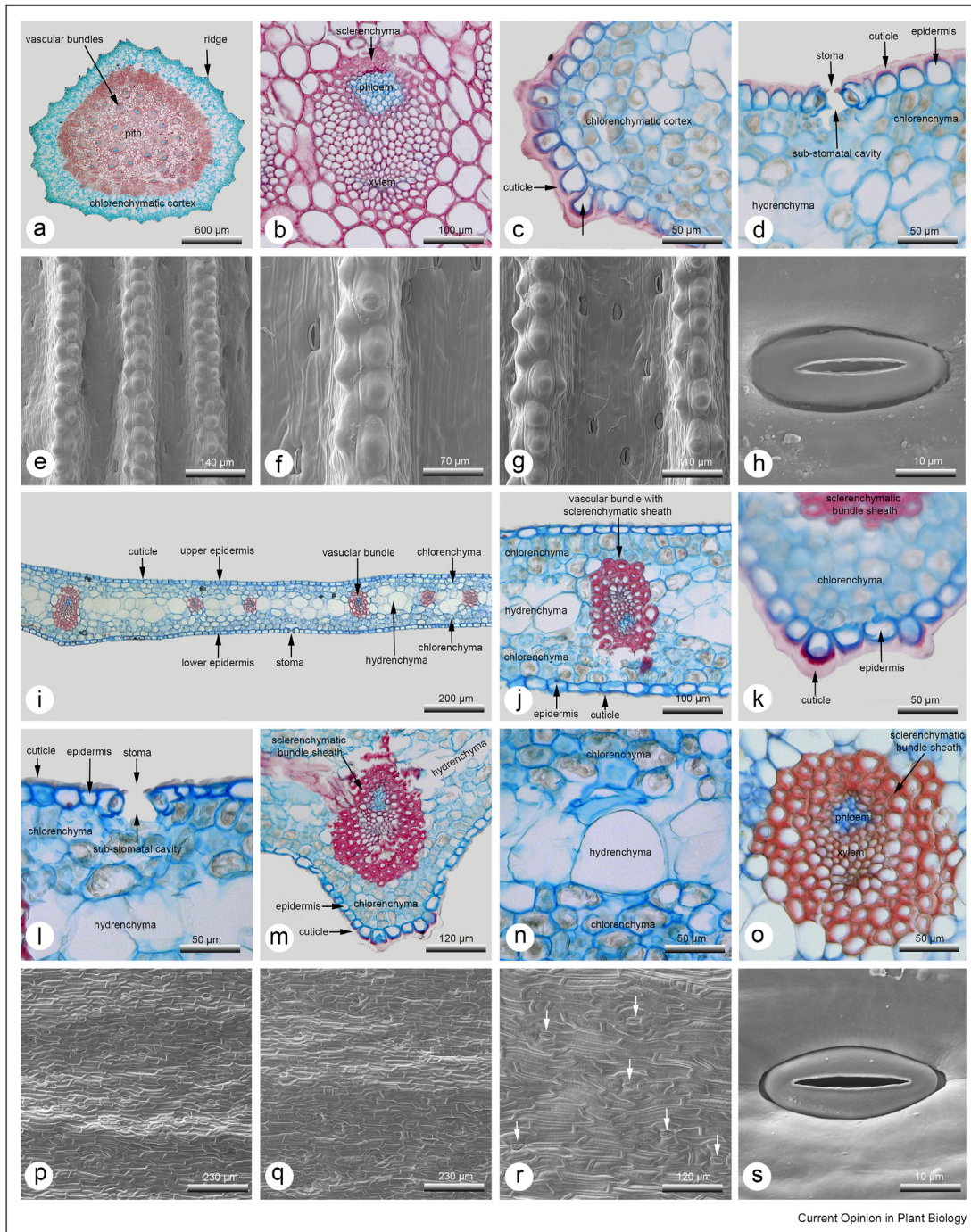
*Phyllocladus* species are evergreen shrubs or trees with a distinct long shoot/short shoot differentiation and strongly modified foliage. In seedlings long shoot leaves represent true needle leaves showing the typical structure of a coniferous needle leaf but few develop. Short

Figure 1



*Ruscus aculeatus*, morphology of long shoots and phylloclades; (a) Orthotropic long shoot of a sun exposed individual; phylloclades helically arranged; (b) Long shoot axis green with numerous longitudinal ridges; (c) Insertion of a phylloclade in the axil of a strongly reduced long shoot leaf; phylloclade with a petiole-like, strongly twisted base; (d) Elongated, acute tip of the phylloclade; (e) Fertile phylloclade; due to the twisted phylloclade base, the flower carrying adaxial surface turns downwards.

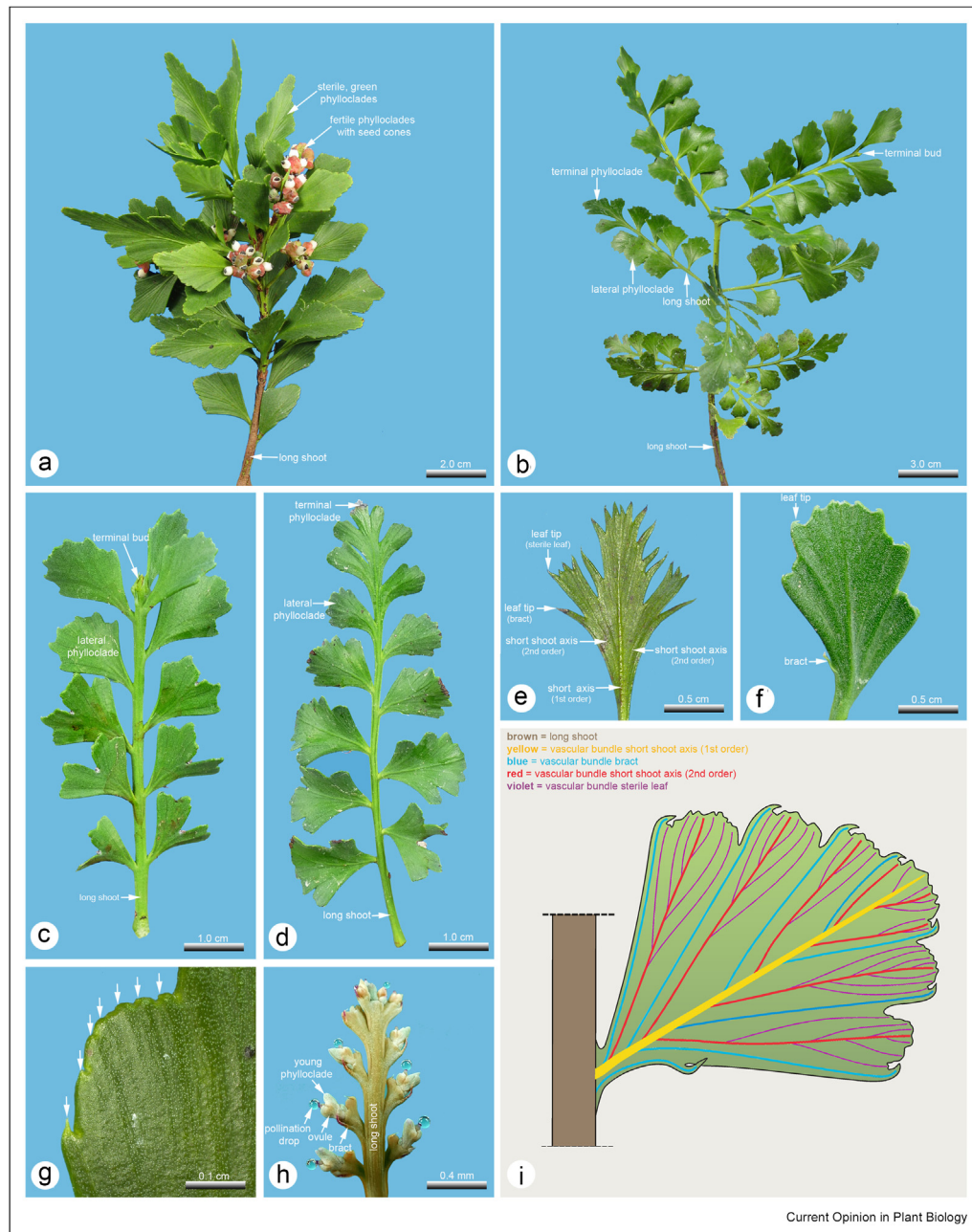
Figure 2



Current Opinion in Plant Biology

*Ruscus aculeatus*, anatomy and micromorphology of long shoots and phylloclades; (a-h) Long shoot; (a) Cross section of a long shoot; (b) Detail of a vascular bundle; (c) Outer parts of the shoot axis with a chlorenchymatic cortex; epidermis covered with a dense cuticle; (d) Stomata slightly sunken in the epidermis; (e) Shoot surface; (f) Detail of a ridge; (g) Stomatal arrangement; (h) Single stoma; (i-p) Phylloclade; (i) Cross section of a phylloclade showing the aequifacial structure and the planar arrangement of the vascular bundles; (j) Lateral vascular bundle located in the hydrenchyma; (k) Outer parts of the phylloclade; epidermis covered with a dense cuticle; (l) Stomata slightly sunken in the epidermis; (m) The central vascular bundle strand forms a kind of “midrib” on the abaxial side of the phylloclade; bundle with a distinct sclerenchymatic sheath; (n) Inner tissue layers, with a central hydrenchyma and chlorenchyma towards the outer surfaces; (o) Detail of a lateral vascular bundle with a distinct sclerenchymatic sheath; (p) Adaxial phylloclade surface; (q) Abaxial phylloclade surface; (r) Abaxial stomatal arrangement (each stoma marked with an arrow); (s) Single stoma.

Figure 3



*Phyllocladus*, morphology of long shoots and phylloclades; (a, e, i) *P. aspleniifolius*; (b, c, d, f, g, h) *P. trichomanoides*; (a) Orthotropic shoot system with numerous sterile, vegetative and some fertile phylloclades; (b) orthotropic shoot system, the lateral long shoots are plagiotropic, each with numerous phylloclades; (c) long shoot with a terminal vegetative bud; (d) long shoot with a terminal phylloclade; (e) phylloclade of a young individual; the short shoot axes and the inserted leaves are only partly fused in basal parts; (f) phylloclade of a mature individual; the short shoot axes and the inserted leaves are entirely fused; the leaf tips are only visible as small incurved teeth at the margin; (g) detail of f; leaf tips marked with arrows (h) fertile phylloclades at pollination time; the development of the reproductive structure precedes the formation of the phylloclades; (i) schematic drawing of a *P. aspleniifolius* phylloclade illustrating the vascular system in a mature phylloclade.

shoots are highly modified to form phylloclades (Figure 3e, f) that are subtended by a minute bract. The first phylloclades occur in the earliest developmental stages of the seedlings and there are no transitional forms leading from leafy lateral short shoots to phylloclades.

The detailed characteristics of the foliage have been described in detail by Dörken *et al.* [13] so are abbreviated in the following. The phylloclades are fusion products of shoot axes and the inserted foliage. Usually, they are a fusion of an entire lateral short shoot system, with a

central leafy short shoot axis of the first order carrying several leafy short shoots of the second, in rare cases also of the third order and the inserted short shoot foliage (Figure 3l). The only remnants of the original components are the apices that are visible as small incurved teeth, leading to the appearance of a denticulate leaf margin (Figure 3l).

On *P. trichomanoides*, phylloclades occur singly or on two types of long shoots: 1.) strongly growing long shoots with unlimited growth and a terminal vegetative bud and distantly inserted lateral phylloclades (Figure 3a); 2.) weakly growing long shoots limited in growth without a vegetative terminal bud, but with a terminal leaf-like phylloclade instead; lateral phylloclades are distantly inserted so that the entire long shoot is reminiscent of a pinnate leaf (Figure 3b). In *P. aspleniifolius* pinnate long shoots do not occur and the single phylloclades are reminiscent of a single leaf (Figure 3f).

The stomatal distribution is strongly correlated to the light exposure of the phylloclades - those well exposed to light are more or less “hypostomatic” with the majority of stomata developed on the adaxial surface; while shaded phylloclades tend to be “amphistomatic.” Stomatal distribution is either irregular over the entire surface or in longitudinal rows and each is surrounded by a distinct raised Florin ring (Figure 4l). The epidermis is covered with a dense cuticle (Figure 4f). In light exposed phylloclades a palisade parenchyma-like tissue is developed towards the light (Figure 4f). In the cortex there are clusters of large, slightly lignified cells, which are similar to the “water storage cells” of the long shoots (Figure 4f). In the middle of the phylloclade the vascular bundles have a planar arrangement. There are two types, 1.) concentric bundle strands, with inner xylem and outer phloem, without an adjoining resin duct (Figure 4g); 2.) collateral bundle strands with an adjoining resin duct (Figure 4h). There are few transfusion tracheids located at the horizontal margins of the collateral vascular bundles.

#### ***Jacksonia floribunda*: Fabaceae; SW Western Australia**

Seedlings and some very young resprout shoots have true leaves that are broadly ovate, hairy and about 1 cm wide. After 2–4 nodes the leaves reduce to about 3 mm wide eventually becoming brown bracts subtending phylloclades, that are then the only photosynthetic organs produced (Figure 5a). Most phylloclades tend to be upright (Figure 5a) while plagiotropic ones are only found on drooping shoots. Phylloclades are up to 16 cm long and 1 cm wide, stiff, glabrous or hairy, with mucronate points that alternate on each side along the scalloped edge of the phylloclade (Figure 5b). There is a main mid vein and secondary veins that usually extend to just above the edge mucros, being the main veins of the fused

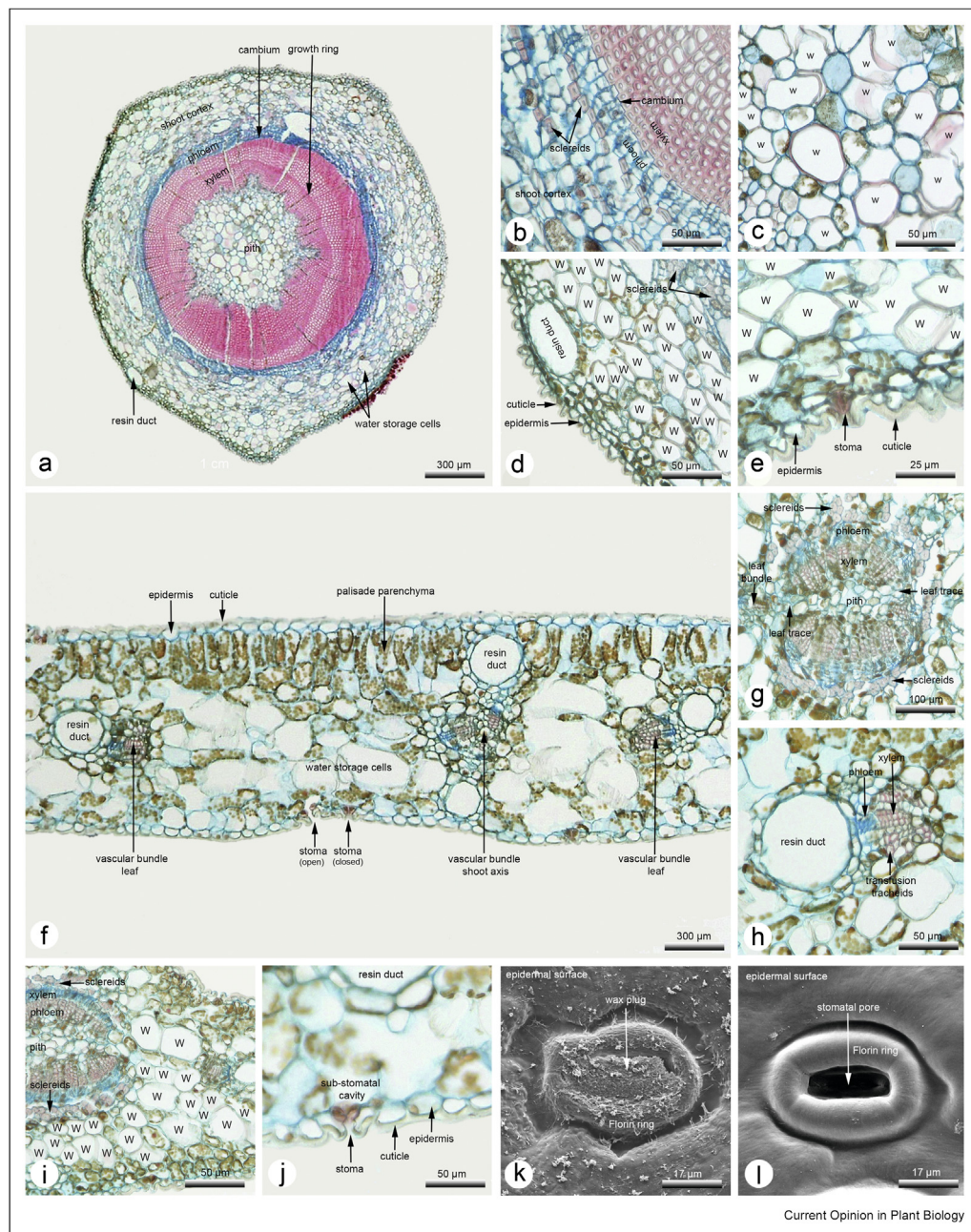
branchlets (Figure 5b). In between the main veins there is a clear reticulate network of finer veins (Figure 5b). The phylloclades are highly scleromorphic and have an isobilateral structure. Palisade parenchyma occurs under both surfaces as islands delimited by sclerenchyma bundles (Figure 5c). Vascular bundles lie in the pith tissue and in all cases alternate in orientation across the phylloclade with the phloem always facing the epidermis and surmounted by a sclerenchyma bundle. There is no spongy mesophyll. Stomata only occur above the palisade parenchyma islands between the sclerenchyma ridges and there is no difference in the stomatal density between the ad- and abaxial surface. The epidermal cells on both surfaces are similar in size and shape. They are thick walled and covered by a dense cuticle.

#### **Discussion**

The taxa we investigated are not closely related and they emphasise there are a number of ways to construct a phylloclade. In *Ruscus* they represent a single flattened, exclusively cauline short shoot (Figs. 1, 2) and in its close relatives similar structures are produced but with some morphological variation in size and shape [2,9,14]. In *Phyllocladus* the phylloclade is a fusion of an entire lateral short shoot system, consisting of shoot and leaf tissue (Figure 3i). In *P. trichomanoides* the phylloclades on most shoots have a pinnate leaf-like arrangement (Figure 3d). The phylloclades arise from the shoot in an approximately helical fashion but become oriented into one plane so they appear distichous and pinnule-like. In *P. aspleniifolius* phylloclades are borne as single entities and not arranged in apparently compound structures (Figure 3a). In the Podocarpaceae leaves vary from scales to broad planar forms but the most common are relatively narrowly elliptical with a single midrib. Only in *Phyllocladus* is there fusion of shoots, bracts and leaves to produce a broad leaf-like organ and intermediate stages of phylloclade development can be recognized as the young plant matures. *Jacksonia* is somewhat intermediate between *Ruscus* and *Phyllocladus* with leaves produced by juvenile plants and the phylloclade a product of ontogenetically fused branchlets where only veins and mucronate tips along the phylloclade margin indicate the number of branchlets involved.

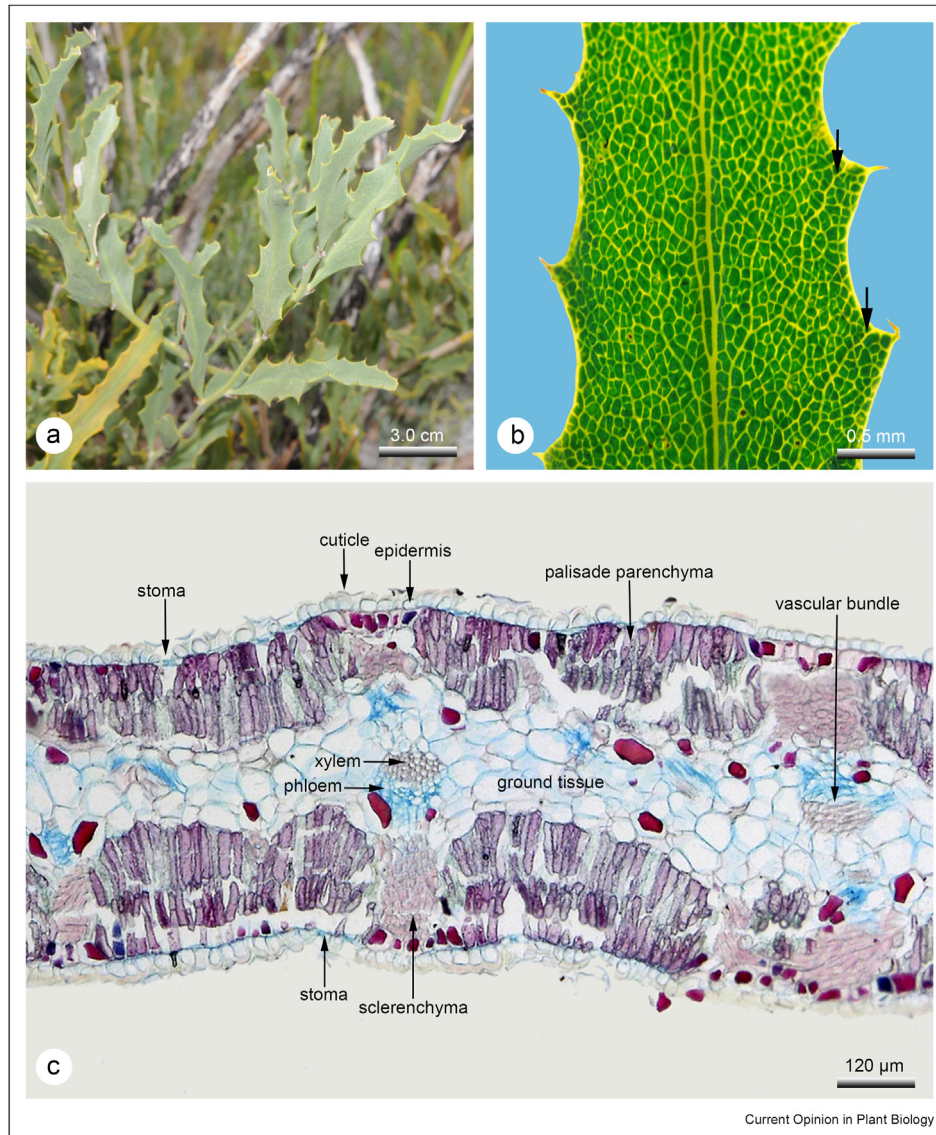
The evolutionary pressures leading to phylloclade evolution in *Phyllocladus* are very different from those of the other taxa studied, with much higher rainfall usually producing much denser vegetation and leading Hill and Scriven [15] and Dörken et al. [13] to suggest that the broad *Phyllocladus* phylloclade developed as an adaptation to low light levels in wet forest understories. *Phyllocladus* and its closest relatives, *Lepidothamnus*, *Lagarostrobos* and *Prumnopitys* [16] have very small leaves, so in an evolutionary sense there was no genetic predisposition to forming larger leaves and the innovation of phylloclades is a novel adaptation to low light

Figure 4



*Phyllocladus*, anatomy and micromorphology of long shoots and phylloclades; (a–k) *P. trichomanoides*; (l) *P. asplenifolius*; (a–d) long shoot; (f–l) Phylloclade; (a) Cross section of a long shoot; (b) transitional zones of xylem to phloem and phloem to outer shoot cortex; there is a cambium between xylem and phloem; (c) cortical tissue with clusters of water storage cells (W); (d) outer cortical tissue with resin ducts and clusters of water storage cells; (e) stomata slightly sunken in the epidermis; epidermis covered with a dense cuticle; (f) cross section showing the bifacial structure and two types of vascular bundles, collateral and concentric ones; (g) detail of a concentric vascular bundle; (h) detail of a collateral vascular bundle, which is always adjoined by a resin duct; (i) cluster of water storage cells; (j–l) stomata; (j) stomata slightly sunken in the epidermis; (k) stoma with a distinct Florin ring; the epi-stomatal cavity filled with a dense wax plug (SEM-image); (l) cleaned stoma; for a better overview the epi-stomatal wax plug was removed with chloroform (SEM-image).

Figure 5



*Jacksonia floribunda*, morphology and anatomy of phylloclades (a) Branch with numerous leaf-like phylloclades; the phylloclades are in a more or less upright position; image taken in the field, south western Australia (b) Phylloclades have a distinct reticulate venation and numerous mucros inserted at the margin; secondary veins usually extend to just above the edge mucros (arrows) (c) Cross section of a phylloclade showing an isobilateral structure with palisade parenchyma towards both surfaces; the phylloclades are highly scleromorphic with numerous sclerenchymatic cell clusters between the palisade parenchyma clusters.

conditions. As well, the somewhat coriaceous phylloclades of *P. aspleniifolius*, the retention of dense vascular bundles and the raised Florin ring around the stomata are also likely a preadaptation to assist the plant's success on drier open sites. As there are undisputed fossil *Phyllocladus* from early Oligocene sediments (compare the overview in the study by Dörken et al. [13]), this broad photosynthetic organ developed early in Podocarpaceae prehistory.

*Jacksonia* habitat is similar to some extent to where *Ruscus* grows in areas with at least an arid summer climate when water availability would be low but *Ruscus* also occurs in heavy shade in forests where the broad phylloclade may have evolved as an adaptation to low light; movements into more arid sites may have been facilitated due to preadaptation of the broad coriaceous phylloclade to xeric conditions [17]. On open sites the twisting of the phylloclade to be parallel with the stem also decreases the



heat interception during the hottest part of the day. In addition, a dense cuticle covering both surfaces of the phylloclade, a high number of densely arranged stomata on both sides with an epi-stomatal cavity filled with a thick wax plug and large, thick-walled epidermal cells are xerophytic adaptations. Finally, the pointed acute tip of the phylloclade (Figure 1c), which represents the elongated and sclerified shoot apex [8] seems to fulfill two major tasks: 1.) protection against herbivores and 2.) condensation point for water e.g. dew, which is important in dry habitats [18].

On the basis of a morphologically based cladogram [19] *Jacksonia* was placed as sister to *Leptosema* and both genera have leaves reduced to non-photosynthetic scales. However, *Leptosema* has either winged or terete stems and not phylloclades. Nevertheless there is similarity in the complete absence of normal leaves. Further, phylogenetic analysis of the tribe (Mirbelieae) to which both genera belong based on plastid DNA [20] was less specific about sister group relationships and several genera were part of a polytomy with *Leptosema* and *Jacksonia* but all others had normal leaves. There is no phylogeny of *Jacksonia* so no clear indication of what might be ancestors that could provide clues to how phylloclades have evolved. Juvenile foliage of *Jacksonia* tends to be mesomorphic but after growth of several nodes, cladodes or phylloclades replace leaves depending on the species and likely evolved as a response to seasonal water deficit. The foliage of most species consists of cladodes and only a minority have phylloclades. A hypothesis could be that cladodes are ancestral in the group and scleromorphic phylloclades have evolved to increase photosynthetic surface while still retaining xeromorphic features. The phylloclade is an emergent property of the fusion and subsequent planation of branchlets (*sensu* evo-devo) [21]. In the pseudo-petiole the vascular system is cylindrical with internal xylem and external phloem, as found in a classical stem. Within the phylloclade the disposition of the collateral bundles can be understood as derived from bundles diverging from the concentric pseudo-petiole vascular ring as the phylloclade expands in two dimensions and these then further branch to produce the reticulate venation. Due to the lateral broadening of the phylloclade, vascular bundles diverge from the vascular cylinder of the pseudo-petiole and tend to alternate in orientation so that alternate ones in what seems to be an “abaxial” position appear to be inverted. This is the result of how the phylloclade forms and highlights one of the differences between a true leaf and a phylloclade (Dörken, Ladd, Parsons unpublished data).

The phylloclade is a structural and ontogenetic entity. There has been considerable argument about the definition and it turns on the requirement that a leaf cannot

be subtended by a leaf but a shoot is produced from a stem in the axil of a leaf. Cooney-Sovetts and Sattler [2] discussed the question extensively and concluded that the phylloclades of *Ruscus* have characteristics of leaves and caulomes (stems). At first glance, especially fertile *Ruscus* phylloclades resemble a simple leaf carrying a flower that is recaulescently shifted to the adaxial leaf surface in the sense of epiphyllly. Such epiphyllous structures are not rare among today’s angiosperms and can be found in numerous distantly related taxa [22]. However, phylloclades and fertile leaves carrying an epiphyllous structure can be easily distinguished by the strict axillary position of phylloclades. Fertile leaves however, are not axillary structures as is typical for a leaf, which is well illustrated in [22 Figure 1 on page 190]. Leaves are always developed as lateral structures on the shoot apex. This ontogeny excludes, *a priori*, an axillary position of leaves.

The position of *Ruscus* flowers appears to be axillary on the phylloclade but it could be hypothesized that the flower is actually terminal with the distal part of the phylloclade the extension of a subtending bract and not a shoot apex. However in the closely related *Semele* the location of the inflorescences is instructive. They are often on the margins of the broad phylloclades [23] emphasizing that several shoots have fused to form the phylloclade as is seen in some *Jacksonia* species [6]. Unlike *Ruscus*, *S. menezesii* phylloclades are often bifurcate [23] which could be interpreted as two leaf or shoot apices. However, the more parsimonious explanation is that the *Ruscus* phylloclade apex is a shoot apex as are the two of *S. menezesii* - anatomical examinations have not been published but could help clarify the interpretation.

The genetics of phylloclade formation is poorly studied so at present morphological and anatomical studies about the phylloclade ontogeny remain the best evidence for their origin. However, Hirayama *et al.* [9] examined two genetic markers in *R. aculeatus* associated with shoot meristems and lateral organs and concluded that the phylloclade in this species is “not homologous to either the shoot or leaf.” Despite the range of views we suggest the term phylloclade be used for photosynthetic organs that have a pseudo-petiole, determinate growth and look like a leaf. Further genetic analysis of species with phylloclades of different structure would help shed light on the evolution of these unusual organs.

### Author contributions

Writing— preparation of the original draft: VMD, revision and editing: VMD, RP, PL. Conceptualization and planning the project: VMD, RP, PL. Data analysis: VMD, RP, PL. Investigation and enquiry: VMD. Methods—sectioning and photography: VMD. Material—collecting VMD, PL.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgments

We thank the Botanic Gardens Düsseldorf and Konstanz (Germany) and the Palmgarten Frankfurt a. M. (Germany) for providing research material and Dr. Michael Laumann and Dr. Paavo Bergmann (Electron Microscopy Center, University of Konstanz, Germany) for technical support (paraffin technique and SEM). We are grateful for the helpful comments of the two anonymous reviewers, which improved the manuscript.

## References

Papers of particular interest, published within the period of review, have been highlighted as:

\* of special interest

\*\* of outstanding interest

- Cunningham SA, Summerhayes B, Westoby M: **Evolutionary divergence in leaf structure and chemistry, comparing rainfall and soil nutrient gradients.** *Ecology* 1999, **69**:569–588, [https://doi.org/10.1890/0012-9615\(1999\)069\[0569:EDILSA\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0569:EDILSA]2.0.CO;2).
- Cooney-Sovetts C, Sattler R: **Phylloclade development in the Asparagaceae: an example of homoeosis.** *Bot J Linn Soc* 1987, **94**:327–371, <https://doi.org/10.1111/j.1095-8339.1986.tb01053.x>.
- Harris JG, Harris MW: *Plant identification terminology: an illustrated glossary.* Spring Lake Publishing; 1994.
- Hickey M, King C: *The Cambridge illustrated glossary of botanical terms.* Cambridge University Press; 2000.
- Bentje H: *The Kew plant glossary: an illustrated dictionary of plant terms.* Kew Publishing; 2010.
- Chappill JA, Wilkins CF, Crisp MD: **Taxonomic revision of *Jacksonia* (Leguminosae: Mirbelieae).** *Aust Syst Bot* 2007, **20**:473–623, <https://doi.org/10.1071/SB06047>.
- Keng H: **The phylloclade of *Phyllocladus* and its possible bearing on the branch systems of Progymnosperms.** *Ann Bot* 1974, **38**:757–764, <https://doi.org/10.1093/oxfordjournals.aob.a084864>.
- Hirsch AM: **A developmental study of the phylloclades of *Ruscus aculeatus* L.** *Bot J Linn Soc* 1977, **74**:355–365, <https://doi.org/10.1111/j.1095-8339.1977.tb01187.x>.
- Hirayama Y, Yamada T, Oya Y, Ito M, Kato M, Imaichi R: **Expression patterns of class I KNOX and YABBY genes in *Ruscus aculeatus* (Asparagaceae) with implications for phylloclade homology.** *Dev Gene Evol* 2007, **217**:363–372, <https://doi.org/10.1007/s00427-007-0149-0>.
- Robertson A: **Some points in the morphology of *Phyllocladus alpinus* Hook.** *Ann Bot* 1906, **20**:259–265.
- Tomlinson PB, Takaso T, Rattenbury JA: **Cone and ovule ontogeny in *Phyllocladus* (Podocarpaceae).** *Bot J Linn Soc* 1989, **99**:209–221, <https://doi.org/10.1111/j.1095-8339.1989.tb00400.x>.
- Dörken VM, Jagel A: ***Ruscus aculeatus* – Stechender Mäusedorn, Stechmyrte (Asparagaceae) – vielseitige Nutzpflanze mit ungewöhnlicher Morphologie.** *Jahrb Bochumer Bot Ver* 2022, **213**:241–253.  
A detailed morpho-anatomical study which focuses on the structure of long shoots and phylloclades, and also on the reproduction biology and ecology of *Ruscus aculeatus*.
- Dörken VM, Hill RS, Jordan GJ, Parsons RF: **Evolutionary and ecological significance of photosynthetic organs in *Phyllocladus* (Podocarpaceae).** *Bot J Linn Soc* 2021, **196**:343–363, <https://doi.org/10.1093/botlinnean/boaa106>.  
This paper provides a very clear and detailed description of the structure of *Phyllocladus* phylloclades and an assessment of the geological evolution of the organs.
- Nakayama H, Yamaguchi T, Tsukaya H: **Acquisition and diversification of cladodes: leaf-like organs in the genus *Asparagus*.** *Plant Cell* 2012, **24**:929–940, <https://doi.org/10.1105/tpc.111.092924>.
- Hill RS, Scriven LJ: **The fossil record of conifers in Australia.** In *Flora of Australia, Volume 48. Ferns, gymnosperms and allied groups.* Edited by Orchard AE; 1998:527–537.
- Andruchow-Columbo A, Escapa ICH, Aagesen L, Matsunaga KKS: *In search of lost time: tracing the fossil diversity of Podocarpaceae through the ages.* *Bot J Linn Soc*; 2023, <https://doi.org/10.1093/botlinnean/boad027> (published online first).
- Pivovarov A, Sharifi R, Scoffoni C, Sack L, Rundel P: **Making the best of the worst times: traits underlying combined shade and drought tolerance of *Ruscus aculeatus* and *Ruscus microglossum* (Asparagaceae).** *Funct Plant Biol* 2014, **41**:11–24, <https://doi.org/10.1071/FP13047>.
- Düll R, Düll I: *Taschenlexikon der Mittelmeerflora.* Quelle & Meyer; 2007.
- Crisp MD: **Revision of *Leptosema* (Fabaceae: Mirbelieae).** *Aust Syst Bot* 1999, **12**:1–54, <https://doi.org/10.1071/SB97031>.
- Barrett RL, Clugston JAR, Cook LG, Crisp MD, Jobson PC, Lepschi BJ, Renner MAM, Weston PH: **Understanding diversity and systematics in Australian Fabaceae tribe Mirbelieae.** *Diversity* 2021, **13**:391, <https://doi.org/10.3390/d13080391>.
- Petrone-Mendoza E, Vergara-Silva F, Olsen ME: **Plant morpho evo-devo.** *Trends Plant Sci* 2023, **28**:1257–1276, <https://doi.org/10.1016/j.tplants.2023.06.007>.  
An insightful article on the relevance of morphological studies as a way to understand how characteristics develop in plants and how some attributes are not solely related to genetics.
- Dickinson TA: **Epiphyllly in angiosperms.** *Bot Rev* 1978, **44**:181–232, <https://doi.org/10.1007/BF02919079>.
- Carvalho MÂAPD, Wilcock CC, Santos TMMD, Lucas ICV, Ganança JFT, Franco E, Thangadurai D, Rao DM, Sousa NF: **A review of the genus *Semele* (Ruscaceae) systematics in Madeira.** *Bot J Linn Soc* 2004, **146**:483–497, <https://doi.org/10.1111/j.1095-8339.2004.00351.x>.