6. Secondary Woodiness and Paedomorphosis

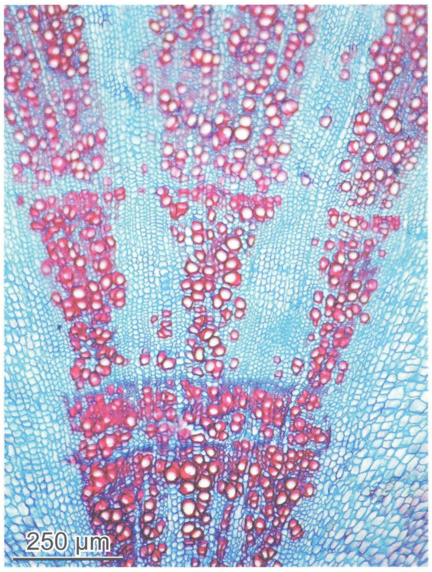
(Bruce Kirchoff, Michael Nobis & David Remington)

It has long been known that, in certain families where there is little secondary growth, some species produce a significant amount of secondary tissue (e.g. Asteraceae; Carlquist 1966). This suggests that species in these families have re-evolved secondary growth after its loss. Carlquist's identification of paedomorphosis in the secondary xylem is based on these types of observations (Carlquist 1962).

Paedomorphosis is a descriptive term used when there has been a change in the relative time of appearance of features between ancestral and descendant ontogenies (Raff and Wray 1989). A paedomorphic adult possesses characteristics that are only found in juvenile individuals of its ancestor. Despite how it is often portrayed in the literature, paedomorphosis is a result of some developmental or evolutionary process, not a causal or selective mechanism. A paedomorphic adult might be produced by any number of developmental and selective factors.

Since paedomorphosis is defined based on comparison with an ancestral ontogeny, and because it is uncommon to have direct access to ancestral ontogenies, inferred ancestral states are often used for comparison with the descendant ontogeny (see Maddison and Maddison 2011 for modern methods). Bailey's work on the major trends in xylem evolution in trees, and his formulation of the refugium hypothesis (the hypothesis that primitive features are retained in the primary xylem of dicotyledonous woods) form the basis for Carlquist's identification of paedomorphosis in the secondary xylem (Carlquist 1962). Carlquist noted that certain of the primitive features identified in trees by Bailey and his co-workers occur in the secondary xylem of plants with shrubby, suffrutescent, pachycaulous, or lianoid growth forms. These plants often occur in phylogenetically advanced families that would be expected to show advanced, not primitive, features. From these observations he developed the theory that the Bailean trends are not observed in these plants because their secondary xylem is paedomorphic. Although this formulation is problematic because it conflates result (paedomorphosis) with cause (perhaps a reduced need for structural support), it nevertheless codifies a number of observations on the secondary xylem of plants that had received little study up to that time.

Carlquist's (1962) initial list of paedomorphic characters included vessels that are angular in transectional outline; scalariform (**Fig. 6.4**) or pseudoscalariform (**Fig. 6.5**) lateral wall pitting on the vessel elements; wide, thin-walled fibers with a predominance of libriform fibers, or with parenchyma cells replacing fibers; either the absence of rays or delayed ray development[1] (**Fig. 6.1**); and, when present, rays very tall and wide and consisting of mostly upright (**Figs. 6.2** and **6.3**), or square cells. He also noted that tracheids are most often absent from paedomorphic woods. Finally, he emphasized that paedomorphic woods produce decreasing, or stable, vessel element lengths as the secondary xylem ages. This is in contrast to the pattern found in more typical woody species, where vessel element lengths first decrease, then increase to a stable plateau. More recent treatments of paedomorphosis have removed angular vessels, fibers (of any sort), and axial parenchyma from the list of paedomorphic features of the secondary xylem (Carlquist 2001, Lens et al. 2011, Carlquist 2009).[2]



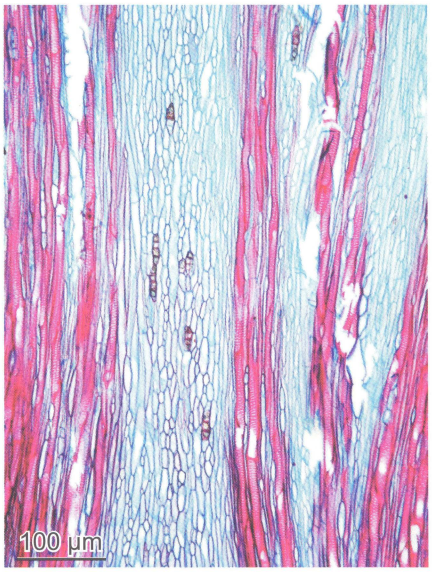


Fig. 6.1. Very large unlignified (blue) rays between radial strips of lignified (red) fibers and vessels. Note the origin of new rays in the second growth increment. This type of late origin of rays is typical of paedomorphic secondary growth. Cross section of a 20 cm-tall *Sanguisorba ancistroides*, Rosaceae, Andalusia, Mediterranean zone, Spain.

Fig. 6.2. Very large unlignified rays (blue) with mostly upright (axially elongated) cells, located between lignified strips of fibers and vessels (red). Rays with mainly or exclusively upright cells is one of the defining features of paedomorphic secondary growth. Tangential section of a 20 cm-tall *Sanguisorba ancistroides*, Rosaceae, Andalusia, Mediterranean zone, Spain.

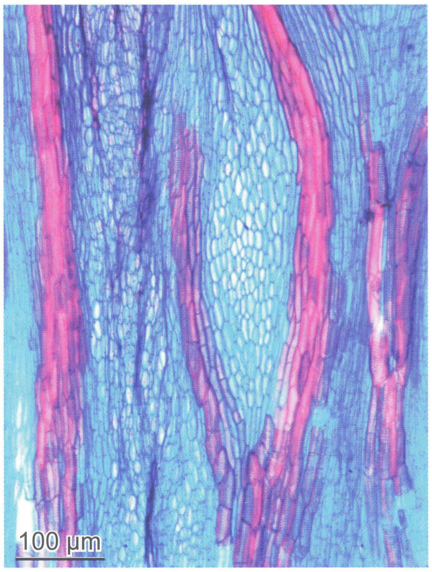


Fig. 6.3. Very large unlignified rays (blue) with upright (axially elongated) cells, between strips of lignified vessels (red). Tangential section of a 30 cm-tall *Pedicularis foliosa*, Orobanchaceae, subalpine zone, Alps, Switzerland.

Fig. 6.4. Scalariform (to opposite) intervessel pits on the lateral walls of vessels with simple perforation plates. Scalariform lateral wall pitting is one of the characteristics of paedomorphic secondary growth. *Campanula rhomboidalis*, Campanulaceae, mountain zone, Alps, Switzerland. Radial section of a 30 cm-tall plant.

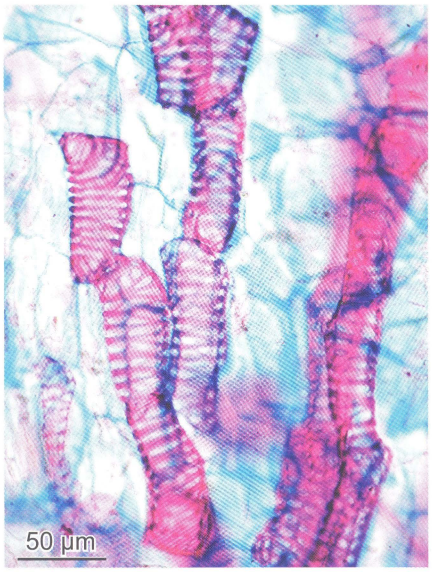


Fig. 6.5. Pseudoscalariform intervessel pits on the side walls of vessels. Pseudoscalariform lateral wall pitting differs from scalariform in that some of the pits are shorter than the side wall of the vessel. Radial section of a 15 cm-tall *Orobanche canescens*, Orobanchaceae, Mediterranean zone, Crete, Greece.

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[1] The use of raylessness as a paedomorphic character is a complex issue. See Dulin and Kirchoff (2010, pp. 477-478) for a fuller discussion.

[2] It is important to remember that determinations of paedomorphosis have traditionally been based on the primitive conditions established by the Baylean trends. The recent availability of molecular phylogenies coupled with high quality anatomical data sets (e.g. Lens et al. 2011) will allow the reconstruction of ancestral states within lineages. These reconstructions may lead to changes in which characters and character states are assessed as paedomorphic.

Because paedomorphic features can be expressed independently of each other (Carlquist 1962), the number of paedomorphic characteristics found in the secondary xylem has sometimes been used as a measure of the degree of paedomorphosis present in a taxon (Dulin and Kirchoff 2010). For instance, in the data presented in these volumes there are 161 species in 26 families that are completely rayless, but that lack sclariform or pseudoscalariform intervessel pits. Based on their raylessness, these species might be categorized as having a minimal amount of paedomorphosis. Of the 183 species of the Brassicaceae for which data is available, 157 have rays with solely upright cells or are rayless (i.e. have paedomorphic radial parenchyma), 26 have scalariform or pseudoscalariform intervessel pitting, and 23 have both paedomorphic radial parenchyma and scalariform or pseudoscalariform pitting. Of these 23, 3 are therophytes, 11 are hemicryptophytes, 7 are chamaephytes, and 2 are shrubs.

To further assess the occurrence of paedomorphosis in the data set, we used characters 20 (vessels with scalariform intervessel pits), 20.1 (vessels with pseudoscalariform to reticulate pits), 105 (rays with solely upright cells) & 117 (rayless) to define paedomorphosis in the following way: Paedomorphic secondary xylem = (20 OR 21) AND (105 OR 117). Using this definition, and removing the helophytes (5 species), hydrophytes (1 species) and succulents (1 species) as they do not have self-supporting stems, paedomorphic species occur in 9 families (**Tab. 6.1**), and in five growth forms (**Tab. 6.2**). A Chi–square test with simulated p-values (100,000 replicates) was used to assess the occurrence of paedomorphosis by family and growth form. Both the difference in the occurrence of paedomorphic taxa among families ($p << 0.001$) and growth forms ($p < 0.008$) is highly significant. Inspection of the data shows that paedomorphic secondary growth is more common in chamaephytes and hemicryptophytes than in other growth forms. These findings form the basis for the investigation of other paedomorphic features in these taxa, and for the study of their paedomorphic secondary xylem in a phylogenetic context.

As these preliminary analyses demonstrate, the existence of new data on plants traditionally considered herbaceous opens up new possibilities for the study of paedomorphosis. Investigating the association between raylessness and plant height (Chapter 3.5.2) demonstrates that raylessness is more common in smaller plants. This, in turn, strengthens the hypothesis that raylessness is associated with a reduced need for lateral transport. It remains to be determined whether this association represents loss of the developmental program for ray formation in smaller plants due to relaxed selection or, alternatively, whether ray formation is phenotypically plastic and activated through size-related developmental cues. Although clearer insights on the function of the characters associated with paedomorphic secondary growth will not remove the fact of paedomorphosis, they can cause paedomorphic characters and character states to be seen in a new light. Because plants with paedomorphic wood are often found on islands, the concept of paedomorphosis has been linked to insular woodiness, which is often viewed as a form of secondary woodiness, the loss and reappearance of woodiness within a lineage. Although the occurrence of paedomorphic characters has sometimes been used to suggest that a taxon is secondarily woody, a number of lines of evidence suggest that this is not an inevitable relationship (Dulin and Kirchoff 2010). First, the existence of insular woodiness is not incontrovertible evidence of secondary woodiness. In some cases, insular woodiness has been found to be plesiomorphic (relictual; Moore et al. 2002). Second, the occurrence of some paedomorphic characters has been shown to occur in taxa that are ancestrally woody (Dulin and Kirchoff 2010). Finally, insular woodiness cannot be equated with paedomorphosis. Plants with insular woodiness may or may not have paedomorphic secondary growth.

All of these lines of evidence suggest that paedomorphosis in the secondary plant body cannot be used as the sole basis for determining secondary woodiness. Since plants with paedomorphic characteristics may be either primarily or secondarily woody (Carlquist 1962), the evolutionary source of their woodiness must be determined through phylogenetic analysis. Whether woodiness is primary (relictual) or secondary should not be based solely on anatomical evidence.

Tab. 6.1. Occurence of paedomorphic characteristics by family (current data set only).

Familiy	N total	N paedomorphic
Asclepiadaceae	23	1
Asteraceae	399	1
Brassicaceae	160	23
Campanulaceae	30	9
Caryophyllaceae	138	2
Orobanchaceae	48	10
Primulaceae	28	1
Rosaceae	154	9
Urticaceae	5	1
Total	**985**	**57**

Tab. 6.2. Occurence of paedomorphic characteristics by growth form (current data set only).

Growth form	N total	N paedomorphic
Chamaephytes	52	8
Hemicryptophytes	538	41
Lianas	7	0
Shrubs	113	2
Trees	27	0
Therophytes	184	3
Woody chamaephytes	64	3
Total	**985**	**57**