

Reiterative growth in the complex adaptive architecture of the Paleozoic (Pennsylvanian) filicalean fern *Kaplanopteris clavata*

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Abstract. Reiteration is a widespread component of plant growth whose evolutionary importance in ferns is not recognized widely. We introduce and discuss the growth architecture of *Kaplanopteris clavata*, a fossil filicalean fern from the Pennsylvanian (ca. 305 million years old), focusing on types of reiteration exhibited by this species and on the adaptive and phylogenetic significance of reiteration for ferns in general. *Kaplanopteris clavata* combines two types of reiterative growth where growth modules are borne on fronds: (1) entire fronds derived from primary pinnae, and (2) epiphyllous plantlets. This combination of reiterative pathways, unique among fossil and living ferns, allowed *K. clavata* to explore ecospace through an opportunistic combination of scrambling, climbing and epiphytic growth. *Kaplanopteris clavata* underscores the organographic importance of fronds (as opposed to stems) in the adaptive architecture of ferns, emphasizing functional convergences between the different Baupläne of ferns and angiosperms. This unique combination of reiterative pathways is interpreted as a derived condition illustrating the structural and developmental complexity achieved by some

filicaleans during the first major evolutionary radiation of leptosporangiate ferns.

Keywords: architecture; ferns; Filicales; fossil; *Kaplanopteris*; morphology; Pennsylvanian; reiteration

Plants and animals have very different ways of interacting with the environment. Whereas animals typically exhibit rapid neurological responses that involve movement, plants respond to stimuli and maximize fitness through differential patterns of growth. As a result, plants have evolved developmental pathways controlling a diverse range of growth patterns that allow them to effectively forage for resources in the environment and to resume growth following damage. In some cases growth responses can be so effective that they have led some authors to equate different aspects of plant growth with intelligence (Trewavas 2005). One particularly important

Fig. 1–5. *Kaplanopteris clavata*, anatomy of reiteration. **1, 5** epiphyllous stems; **2–4** latent croziers (arrested fronds). **1** Transverse sections of frond rachis and stem diverging from it, distal to divergence; stipe trace is diverging from the cauline trace and stem bears adventitious roots; arrowhead indicates adventitious root. OUPH 16818. Scale bar = 1 mm. **2** Latent crozier with four orders of branching; rachis intersects plane of section five times; selected primary pinnae and secondary pinnae (arrows) with pinnules are indicated. OUPH 16841. Scale bar = 0.5 mm. **3** Attachment of latent crozier to frond rachis in position of primary pinna; primary pinna trace (seen in grazing longitudinal section) intersects plane of section at several places; at one end (bottom of figure) it rejoins the rachis trace (sectioned obliquely), and at the other (top of figure) it supplies the crozier stipe. OUPH 16850. Scale bar = 1 mm. **4** Latent crozier diverging from frond rachis in position of primary pinna. OUPH 16860. Scale bar = 1 mm. **5** Stem diverging from rachis; stem intersects plane of section three times (sections are progressively more distal to the right) and bears two frond stipes and adventitious roots (arrowheads). OUPH 16817. Scale bar = 1 mm. **1–3** published with permission from the University of Chicago Press *Abbreviations:* *cr* latent crozier (arrested frond); *pp* primary pinna (trace); *ra* frond rachis; *rh* stem; *ro* root; *s* frond stipe

aspect of plant growth that confers adaptive advantage is the process of reiteration – the capacity to repeat the same growth module in the plant body (Hallé 1999). Reiteration shapes the architecture of most plants and has been studied extensively in seed plants (Hallé et al. 1978, Tomlinson 1983). By contrast, reiteration has received comparatively little attention in ferns, where its importance for the life history patterns has yet to be fully assessed.

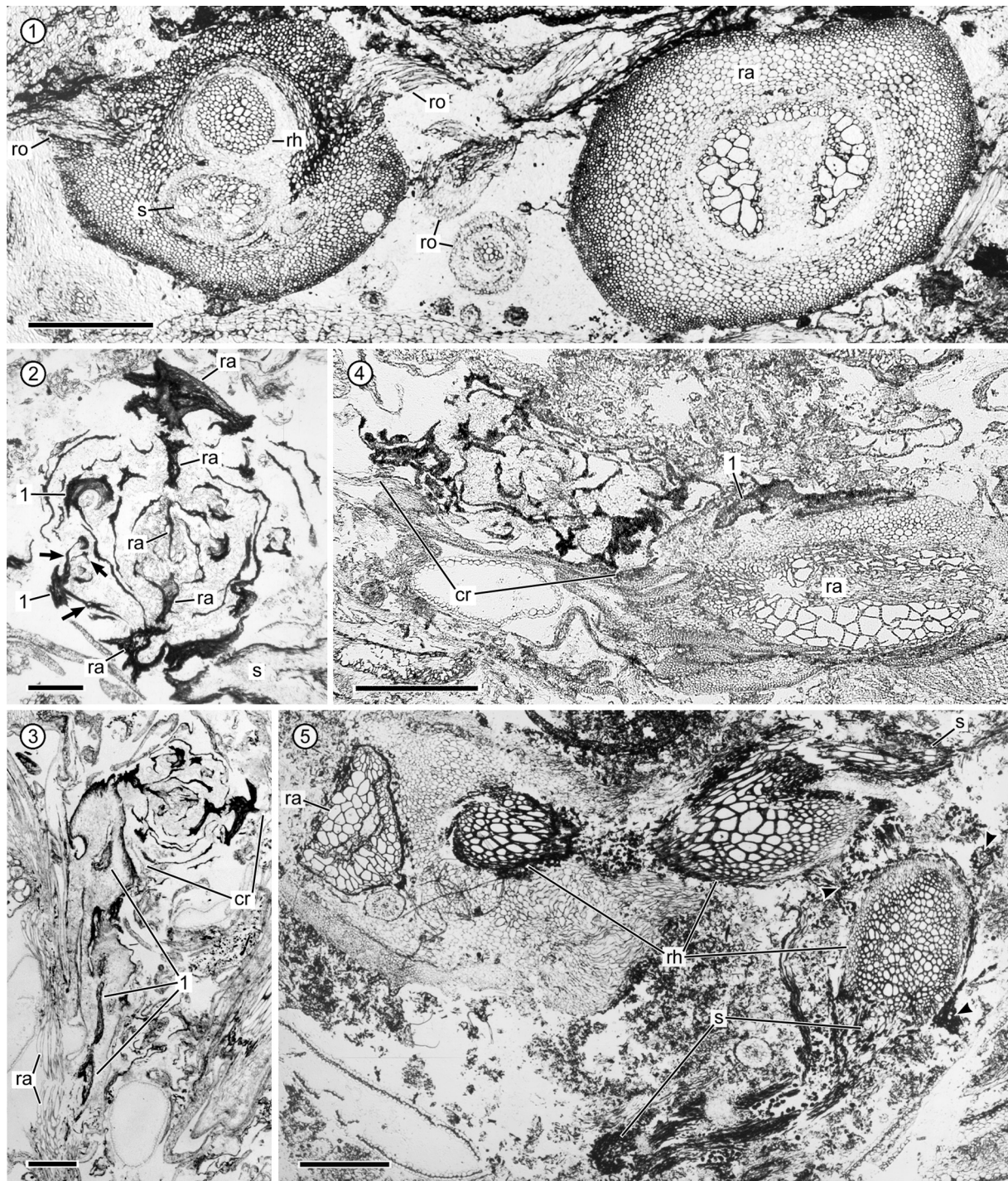
This article builds on the reconstruction of the fossil filicalean fern *Kaplanopteris clavata* (Graham) Tomescu, Rothwell and Trivett provided by us elsewhere (Tomescu et al. 2006). Since the anatomy of *K. clavata* has been documented in detail by Tomescu et al. (2006), here we focus on a previously unexplored aspect of this species, the growth architecture. *Kaplanopteris clavata* exhibits a unique combination of reiterative growth patterns heretofore unknown for fossil or living ferns. In the results section we summarize those aspects of the anatomy and morphology of the species, described previously by us and others (Delevoryas and Morgan 1954, Trivett and Rothwell 1988, Tomescu et al. 2006), which characterize two distinct forms of reiteration. We then introduce and evaluate the architecture that they engender in terms of adaptive potential for growth and fitness. We also emphasize the major role that frond architecture plays in the success of ferns as a whole, and that in turn supports hypotheses of constructional convergence between ferns and flowering plants.

Materials and methods

The fossil filicalean fern *Kaplanopteris clavata* has been reconstructed as a whole plant based on a complete set of interconnected vegetative and fertile organs that are anatomically preserved in Late Pennsylvanian (late Kasimovian \approx mid-Stephanian) coal balls from North America (Graham 1935; Delevoryas and Morgan 1954; Phillips 1974, 1980; Smoot 1985; Rothwell 1987; Trivett and Rothwell 1988; Tomescu et al. 2006). The fossil material is preserved in several coal balls that contain numerous vegetative and fertile frond segments, and has been prepared using the cellulose acetate peel technique (Joy et al. 1956). Foliar organs of *K. clavata* share a diagnostic horseshoe-shaped rachis trace configuration (Fig. 1) that originally was described as the morphospecies *Anachoropteris clavata* Graham (Graham 1935), and that has provided confirming data for the whole-plant reconstruction (Tomescu et al. 2006). Material is deposited in the Ohio University Paleobotanical Herbarium (OUPH) and the Paleobotanical Collections at the University of Connecticut. For a detailed account of the materials, methods, and underlying paradigms used in the reconstruction of *K. clavata*, see Tomescu et al. (2006).

Results

Kaplanopteris clavata is a filicalean fern with marked organographic dominance of the fronds. It is characterized by short, inconspicuous stems (Delevoryas and Morgan 1954, Tomescu et al. 2006) (Figs. 1, 5, 6) and large fronds of indeterminate growth (Trivett and Rothwell



1988, Tomescu et al. 2006). Reiteration (as defined in the following section) is a distinguishing component of the growth architecture of this species which develops two types of reiterative units, both of which are produced on the fronds.

The first consists of croziers borne on otherwise mature fronds (Trivett and Rothwell 1988). Reevaluation of the Trivett and Rothwell (1988) material by Tomescu et al. (2006) has revealed that each crozier (Fig. 2) is attached to a frond

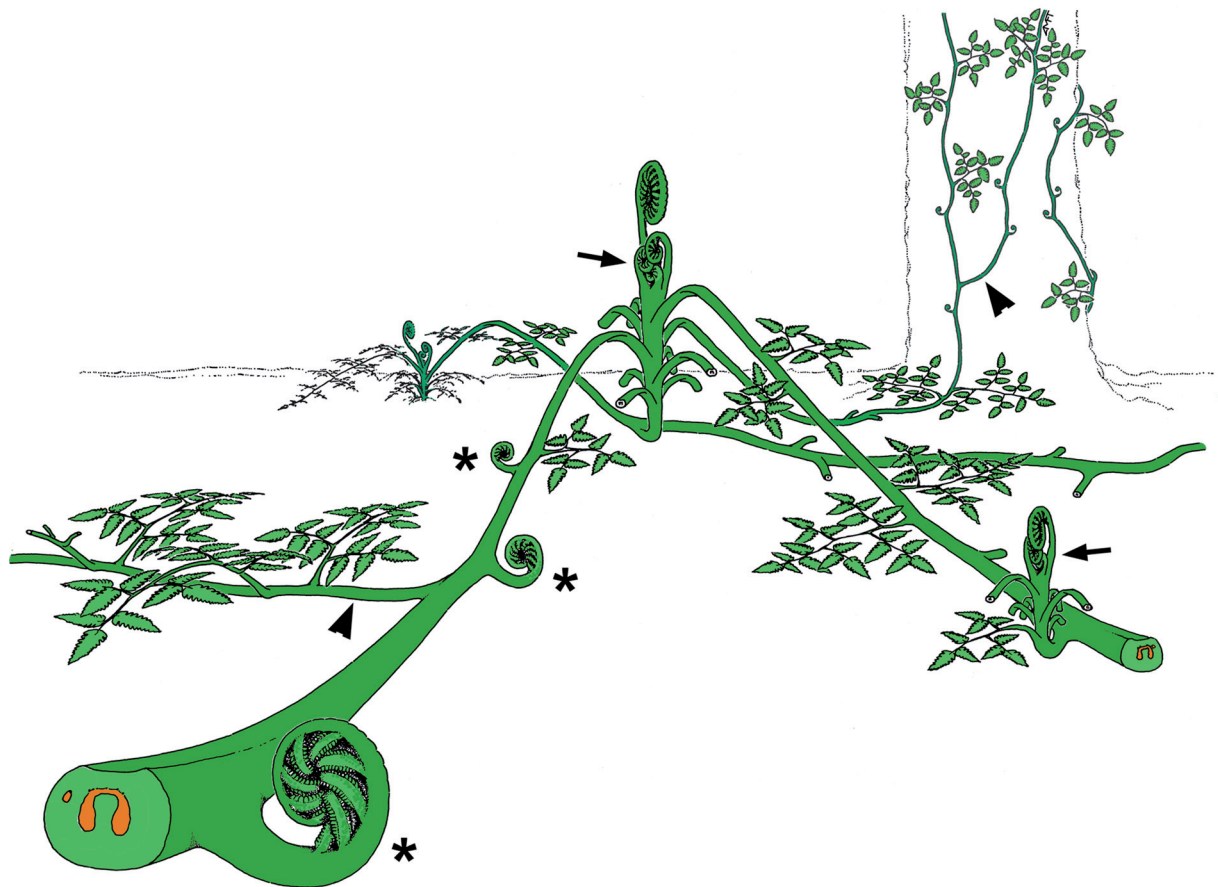


Fig. 6. Reconstruction of *Kaplanopteris clavata* illustrating growth architecture and the two types of reiterative units. The reconstruction emphasizes the potential of the plant to grow as a scrambler, as well as a climber (as shown on a small tree-fern trunk in the background). Short orthotropic stems produced fronds with indeterminate growth and scrambling or climbing habit; frond rachises bore latent croziers of arrested epiphyllous fronds (asterisks; also shown on climbing rachises in background) in position of primary pinnae and epiphyllous stems (arrows); reiterative fronds (arrowheads) developed from latent croziers. Most fronds have been cut off to keep the image uncluttered. The reconstruction is speculative in that it does not illustrate any particular order of development of latent croziers (reiterative fronds) on subtending fronds, and in that it illustrates all possible growth habits on a single plant

rachis in the position of a primary pinna (Figs. 3, 4, 6). The croziers incorporate the whole complexity of mature fronds of the species (i.e. four orders of branching), rather than that of primary pinnae (i.e. three orders of branching; Fig. 2) that they replace. Based on the combination of the croziers 1) being preserved as immature structures on otherwise fully differentiated fronds, 2) having the developmental potential to produce mature fronds, and 3) being equivalent in complexity to entire fronds, they clearly represent

reiterative growth modules (Trivett and Rothwell 1988) in the form of arrested fronds.

Kaplanopteris clavata frond rachises also produce epiphyllous plantlets (Delevoryas and Morgan 1954, Tomescu et al. 2006). Attached laterally on rachises (as in *Botryopteris ramosa*; Holmes 1984, 1989), these plantlets are not associated with primary pinnae (as is the case in *Botryopteris hirsuta* where shoots originate in the “axils” or on the base of pinnae; Holmes 1984, 1989). Rather, they replace the primary

pinnae. *Kaplanopteris clavata* plantlets have stems with a terete protostele that diverges laterally from the rachis trace. The stems bear both helically arranged fronds and adventitious roots (Figs. 1, 5, 6). Helical phyllotaxis, short internodes, and the radial divergence of roots reveal that the epiphyllous stems form erect, orthotropic shoots (Delevoryas and Morgan 1954, Tomescu et al. 2006). These epiphyllous plantlets display the potential to repeat the complete architectural model of the plant. Therefore, they represent a second type of reiterative unit.

Discussion

Reiteration in plants – ferns vs. seed plants. Reiteration is defined as the repetition of the same architectural unit within an organism (Hallé 1999), or the reappearance of the juvenile form on a mature structure (Gay 1993). Both definitions derive from the work of Oldeman (1974). In plants, reiteration occurs both above and below the ground (Hallé 1999), but architectural studies have concentrated almost exclusively on the above-ground parts. Reiteration of roots has been the subject of very few studies (see Atger and Edelin 1994), and remains poorly documented.

Reiterative growth has been documented extensively and analyzed carefully in seed plants, particularly in relation to arborescent growth (e.g. Oldeman 1974, Hallé et al. 1978, Hallé 1999), but aside from isolated examples (Trivett and Rothwell 1988, Héban-Mauri and Gay 1993, Rothwell 1995) the significance of reiteration has not been explored in ferns. In seed plants, reiteration results from a relatively rigid and canalized developmental program based primarily on stem branching (usually from axillary buds), but the reiterative growth of ferns results from several alternative developmental pathways with morphologically distinct outcomes.

In ferns, reiteration occurs both on stems (*cauline reiteration*, see below) and on fronds (*foliar reiteration*), and involves two distinct categories of reiterative units. These are either fronds or whole plants, and they represent two distinct hierarchical levels of complexity within the plant. Cauline reiteration, defined as the

production of reiterative units on stems, produces shoots that develop into whole plants and that repeat the architectural model for the species [e.g. *Lomagramma guianensis* (Aublet) Ching; Gay 1993]. Foliar reiteration occurs on the leaves, where it results in the production of two different reiterative units. These are either epiphyllous plantlets with potential to develop into whole plants (numerous examples in Troop and Mickel 1968, Kaplan and Groff 1995, Héban-Mauri 1990), or complete fronds that develop from latent croziers borne directly on fronds (e.g. some Gleicheniaceae and *Lygodium*; Holtum 1957, Mueller 1983).

In the fossil record, the potential for reiteration in ferns has been documented from the most ancient Paleozoic radiation of Filicales, where several extinct species of *Botryopteris*, *Tubicaulis*, *Anachoropteris* and *Psalixochlaena* are known to exhibit epiphyllous plantlets (e.g. Long 1943; Phillips 1974; Galtier and Holmes 1982; Holmes 1984, 1989; Rothwell and Good 2000). One relatively modern dennstaedtioid fern from Cenozoic sediments of Oregon also produced epiphyllous plantlets (Arnold and Daugherty 1964). *Kaplanopteris clavata* displays the only known fossil evidence for latent epiphyllous frond croziers (Trivett and Rothwell 1988). Moreover, the growth architecture of *K. clavata* (Fig. 6) is unique by combining two types of reiteration. No other extant or extinct fern species is known to produce growth modules with the potential to reiterate both fronds and whole plants.

Reiteration in the growth architecture, ecology and life history of *Kaplanopteris clavata*. As a form of wound response following damage to the apical meristem (i.e. traumatic branching and reiteration; Hallé 1999, 2001), reiteration maximizes the vitality of individual organisms by allowing for renewed growth from centers other than the shoot apical meristem. Fern growth is widely viewed as arising almost exclusively from apical meristems, and the potential vulnerability ensuing from it traditionally has been thought to restrict life history potential (Page 2002), especially when compared with the tremendous reiterative potential conferred on seed plants by

axillary meristems (Rothwell 1995). However, the numerous instances and varied pathways of reiteration documented in ferns constitute an important body of evidence demonstrating that this view needs to be reconsidered in light of those pteridophytic organisms that are highly resilient and better equipped for exploitation of resources (e.g. Tiffney and Niklas 1985, Rothwell 1996) than is commonly recognized.

This is particularly true of *K. clavata*, an extinct plant that displays all of the structural features that characterize highly opportunistic growth, as well as the ability to explore physical space by means of fronds with indeterminate growth. If this interpretation of life history pattern is correct, then the fronds of *K. clavata* acted as vectors of clonal propagation. Fronds of this species would have produced epiphyllous stems that rooted where the rachises touched a suitable rooting medium, and would have explored for supports to climb (Fig. 6), much like the creeper rachises of the Paleozoic fossil *Botryopteris tridentata* (Felix) Scott (Rothwell and Good 2000) or the twining fronds of living *Lygodium* (Mueller 1983, Kaplan and Groff 1995). *Kaplanopteris* was probably also a facultative epiphyte, as is suggested by the frequent co-occurrence of *K. clavata* organs with pecopterid pinnules and scolecopterid synangia (Rothwell 1996), indicating that some of the epiphyllous stems could have produced epiphytic ramets rooted on climbing supports, such as the trunk of the tree-fern *Psaronius* (Rößler 2000). This highly opportunistic life history pattern that potentially includes scrambling, climbing, epiphytism, indeterminate growth, and clonal propagation, was ideally suited to efficiently exploit ecospace in the extensive wetland habitats of the Carboniferous equatorial tropics (Greb et al. 2006).

Phylogenetic significance of reiteration in *Kaplanopteris clavata*. Bierhorst (1971, 1974), echoing earlier views of Zimmermann, Bower, and Eames, has interpreted developmental plasticity in ferns to be an expression of a lower level of organ differentiation as compared to seed plants. While this may be true for trimerophyte grade ancestors of ferns, Kaplan (1977) has made a strong case for a level of stem-

leaf differentiation in ferns that is equivalent to that of seed plants. Therefore, although the broad reiterative potential of *K. clavata* fronds could be viewed as a plesiomorphic trait reflecting a high level of developmental plasticity, it is more likely that the complex reiterative architecture of *Kaplanopteris* represents a derived mode of growth. This view is concordant with several other traits of *K. clavata* that are considered to be derived among living filicaleans, including soral sporangia, indusiate sori, gradate soral maturation, small sporangial capsules with only 64–128 spores, and long, uniseriate sporangial stalks (Rothwell 1987, Tomescu et al. 2006).

The fossil record of leptosporangiate ferns reveals that the clade underwent the first of three major evolutionary radiations in the Carboniferous, resulting in the origin and diversification of several now-extinct families (Rothwell 1987). Phylogenetic analyses support this hypothesis and show *K. clavata* (i.e. “*Anachoropteris clavata* plant” in Rothwell 1999) nested with other extinct filicaleans in a clade that corresponds to the major Paleozoic radiation. However, in the results of Rothwell (1999) the Paleozoic clade forms a polytomy with a clade consisting of Hydropteridales + “derived” living Filicales, so it is possible that at least some of the individual characters that are considered to be derived among living filicales had evolved independently during the first radiation of now-extinct leptosporangiate ferns (also suggested by Galtier and Phillips 1996).

This first major radiation of filicaleans is considered to have produced nearly all the basic body plans ever to evolve among ferns, and to have engendered a diversity of anatomy and growth architectures greater than that seen in ferns after the Paleozoic (DiMichele and Phillips 2002). *Kaplanopteris clavata* is a pointed illustration of this ancient diversity, and shows that during their first major radiation filicaleans had already explored considerable expanses of the available morphospace. Evolution of developmental pathways that translated into traits allowing for efficient exploration of ecospace certainly contributed to the structural and taxonomic diversity of filicaleans in the Carboniferous. As an example, the climbing habit, a trait that

characterizes several Paleozoic filicaleans (Rothwell 1996, Rößler 2000, DiMichele and Phillips 2002), is also considered to be a key innovation contributing to diversification among flowering plants (Gianoli 2004).

Construction and organization in ferns and angiosperms – the significance of reiteration. In a benchmark paper for understanding the functional morphology of plants, Kaplan and Groff (1995) emphasized widely encompassing convergences between ferns and angiosperms involving *construction* (function). These convergences attenuate marked differences in the *organization* (Bauplan) of the plant body between the two major groups. In contrast to angiosperms, where the stem is the dominant morphological and functional element in the *organization* of the plant body, the fern plant body is dominated by leaves. Nevertheless, these contrasting organizational plans and organographies fulfill closely analogous *functional* roles in the construction of the plants (Kaplan and Groff 1995). Viewed in this context, reiteration is an attribute that adds a new facet to the convergence of functional construction in flowering plants and ferns. This convergence is expressed both in terms of the organs that support the reiterative units, as well as in the nature of the reiterative units themselves. Whereas in angiosperms reiterative units are almost exclusively borne on, and represented by, stems, in ferns they are produced on, and consist of, both leaves and stems.

Kaplanopteris clavata is an exceptional example of both functional convergence with flowering plants and of the frond dominance in fern organography. With very few exceptions (e.g. Mueller 1983), the developmental potential of reiterative growth in ferns remains undocumented and therefore underappreciated, and its adaptive and evolutionary significance have yet to be explored. By adding a new dimension to the wide spectrum of developmental pathways expressed by fern fronds, *K. clavata* emphasizes the importance of studies that explore the molecular and genetic underpinnings of fern growth architecture, a terra incognita of plant development. The architecture of *K. clavata* also

reinforces the importance of the frond, as an organ, in the adaptive success of the fern plant body, and illustrates the broad constructional versatility that has contributed to the species richness of living leptosporangiate ferns (i.e. Filicales + Hydropteridales) being second only to that of the flowering plants (Rothwell 1996).

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