

the extensive population of apoptotic cells that are produced during this process. This raises several looming questions concerning the breadth vs. depth of immune cell roles: to what extent does immunological function demonstrate pleiotropy with other traits like development, and to what extent do these traits antagonize, or depend upon, each other? There is extensive overlap in the genetic and cellular architecture that controls development and immunity [12], but the dynamics of any potential antagonism or temporal dependence are still largely unresolved. How do these kinds of memory responses contribute to functional heterogeneity within populations of immune cells and over the life of an organism? Innate immune memory may play a key role in the connection between early life exposure to microbes [13] and patterns of disease susceptibility in individuals. These questions could be united under the banner of hysteresis within a multi-dimensional manifold of all organismal life history traits.

We suggest that phenotypic plasticity [14] be considered a form of memory; plasticity manifests as a shift in phenotype in response to environmental stimuli, allowing an organism to adjust to the particular difficulties of its present situation. This approach would bring into immunological research the rich conceptual frameworks that have been developed by ecologists to explore phenotypic plasticity, and would give paradigm-shifting teeth to recent studies that have reported innate immune memory in taxa as diverse as beetles, flies, and mice.

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Development: Paleobotany at the High Table of Evo–Devo

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A Carboniferous root apex reiterates the importance of the fossil record and classic developmental plant anatomy for modern evo–devo perspectives on plant diversity and evolution.

We humans have determinate growth: we stop growing at maturity. In contrast, plants have indeterminate growth that can reach tremendous sizes and durations (Figure 1). This is possible because of meristems maintained throughout a plant’s lifespan, where continued cell division increases length and girth. When plant cells divide, daughter cells remain in place, stuck to each other and neighboring cells by their cell walls. Consequently, cell positioning in a meristem records the sequence of past cell divisions (Figure 1). In meristems located at root tips — root apical

meristems — such cell division patterns differentiate major lineages and can be used to identify the type of plant that produced a root. A new study by Hetherington *et al.* [1] in this issue of *Current Biology* now reports the oldest fossil of an actively growing root meristem from Carboniferous rocks (ca. 320 million years old) and uses cell patterning to identify it as a gymnospermous root (Figure 2) with unique organization.

Plant roots have a sparse fossil record [2–4] and anatomically preserved meristems, with their delicate dividing cells, are rare [1]. Nevertheless,





Figure 1. Outcomes of plant meristematic growth.

Continued meristematic growth can lead to plant heights exceeding 100 m in coast redwoods (*Sequoia sempervirens*) (A) and can extend over more than 5,000 years in bristlecone pines (*Pinus longaeva*) (B). Because plant cells are immobile and connected to each other through their cell walls, the relative positions of cells in a meristem can be used to reconstruct the sequence of cell divisions, like in this horsetail (*Equisetum*) root apex (C); scale bar = 50 μm .

plant structures as delicate as sperm, cell nuclei or pollination drops can be fossilized [5–7]. Such exceptional preservation is due to permineralization — mineral precipitation around plants buried in sediment. During the Carboniferous, the present-day temperate latitudes of Europe and North America straddled the tropics, hosting extensive coal-generating wetlands. Adjacent the coal seams, permineralization formed nodules known as ‘coal balls’ that contain anatomically

preserved plants. It is in one such ‘coal ball flora’ that Hetherington *et al.* found the new root.

Although tiny (<2 mm across), this fossil carries remarkable implications. The first is that the type of root meristem structure present in living gymnosperms was conserved for over 300 million years. Gymnosperms, including the oldest seed plants of the Devonian (ca. 370 million years old), had undergone a first evolutionary radiation by Carboniferous time and are abundant in coal ball floras.

The finding of a Carboniferous root with gymnospermous anatomy may, then, not seem earth-shattering. However, this singular fossil provides the only direct evidence for the presence of this type of meristem structure at that time, as well as a minimum age for it. These are excellent reminders that the fossil record opens windows onto the past that provide the only opportunities for independent tests of hypotheses drawn from studies of extant biotas [8–10]. Furthermore, it is reassuring that the resolving power of the theoretical framework assembled by anatomists to distinguish living plant lineages — in this case gymnosperms — does not fade over 300 million years of plant evolutionary history.

In their closing lines, Hetherington *et al.* imply that extant anatomical diversity represents only a subset of all the diversity that ever existed. That the fossil record hides tracts of biodiversity (and anatomical novelty) that cannot be sampled by studying only extant floras is commonplace to those of us studying the fossil record [11,12]. The thrill of discoveries and the conviction that they enrich our understanding of evolution is what keeps us digging deeper. It is refreshing, therefore, to see ‘neobotanists’ working in the same system and reaching the same conclusion.

Carboniferous coal ball floras, studied intensely through the 1980s, are among the most completely explored fossil floras. This new discovery from a coal ball flora reminds us that even thoroughly studied fossil assemblages hide additional information and that renewed focus, coming from new perspectives and approaches, can uncover novelty where we thought nothing was left to find. This study also emphasizes the value of natural history collections, not only as specimen repositories, but also as sources of new discoveries: the fossil root was found on a slide kept in the Oxford University Herbaria since at least 80 years ago.

In another nod to the classic tradition and achievements of comparative anatomy, Hetherington *et al.* apply concepts developed a century ago to demonstrate that, beyond its gymnospermous structure, the fossil root exhibits unique cellular organization. In the 1910s Swiss botanist Otto Schüeppe

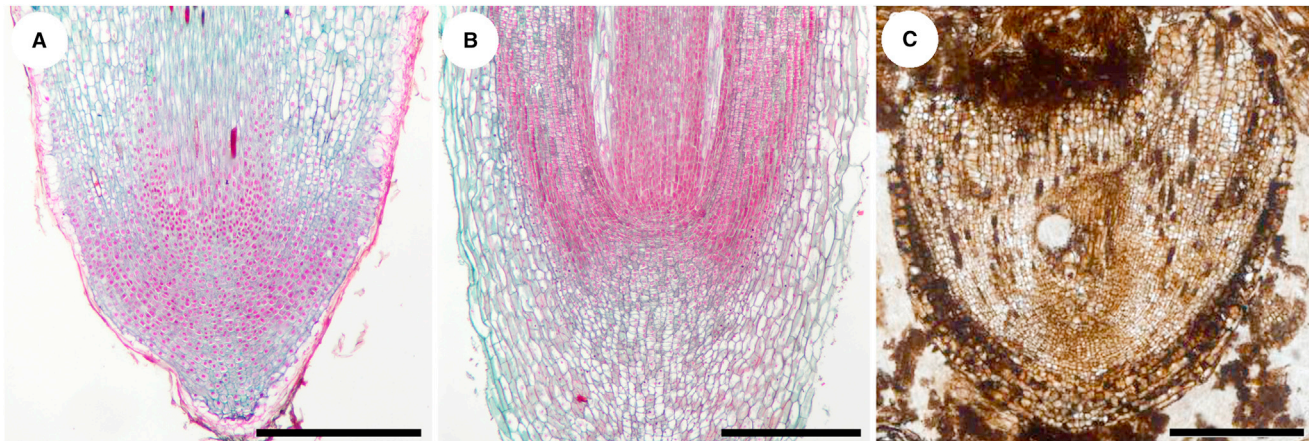


Figure 2. Gymnosperm root apical meristems compared.

Depicted are three different gymnosperm root apical meristems: (A) cycad, (B) *Gnetum*, (C) Carboniferous root described by Hetherington *et al.* [1]; scale bars = 500 μ m.

showed that cellular patterning can be used to distinguish in root apical meristems two domains of clonally related cells: the body (Körper) and the cap (Kappe). He later showed that the positioning of the two domains differs between vascular plant groups and designated several types. Using this yardstick, Hetherington *et al.* demonstrate that the new root is different in organization from all types previously described. This reconfirmation of the relevance of the Körper–Kappe concept leads into the section richest in implications (coincidentally also the section that many would consider the most pedestrian): the taxonomic treatment.

Having demonstrated that the new root has unique cellular organization, Hetherington *et al.* erect a new genus for it. In a bold move, they use its Körper–Kappe organization as the main diagnostic feature. I dare taxonomists to find even a single genus defined (in the diagnosis, no less!) by the Körper–Kappe organization of its root. This is unheard of, yet, as an approach to taxonomy it is common in paleobotany.

Taxonomy is, for practical reasons, thrifty about characters used to distinguish taxa: the fewer and easier to observe, the better. However, plant fossils often preserve few (if any) of the features used in taxonomic treatments of extant members of their group. Paleobotanists, thus, cannot be picky — they look for alternative features of the fossils that, although not used in the standard taxonomy of extant plants,

are still diagnostic. It is not rare to see comparative surveys documenting arcane characters of living plants, conducted by paleobotanists to justify the taxonomic placement of fossils [12]. Back to roots — does all this mean that taxonomists will now rush to redo classifications based on Körper–Kappe characters? Certainly not, but by emphasizing root development as a source of additional taxonomic characters, this study opens new horizons for discoveries relevant to systematics and evolution.

Equally important, Hetherington *et al.* assess Körper–Kappe root organization in a phylogenetic context, including the new fossil root. The major patterns of plant phylogeny remain unresolved [10,13]. For a while it looked like gene sequences would provide all the answers but, when confronted with 400 million years of evolutionary history, molecular phylogenies run into a major taxon sampling issue: fossil taxa, lacking gene sequence data, are excluded [10,14]. However, extant biodiversity represents only a small fraction of all biodiversity that spans the entire history of life [11]. To think that we can uncover phylogenetic events from several hundred million years ago by sampling exclusively the extant flora would be foolhardy. Conversely, inclusion of fossils in phylogenetic studies involves recourse to morphology and anatomy, which provide much narrower sets of characters than gene sequences [10,14]. This gap between genes and morphology is

bridged by anatomical and morphological features that represent signatures for developmental processes and molecular mechanisms [15]. Such ‘fingerprints’, which can be observed in both living and extinct plants, have been used by paleobotanists to integrate fossils and extant plants in an evo–devo perspective [15,16]. Hetherington *et al.* now provide, in the form of Körper–Kappe organization, another useful fingerprint and added example of combining hard data from living and extinct plants into an evo–devo outlook.

If science is a system of testable explanations for the world around us, the tiny Carboniferous root described by Hetherington *et al.* has several lessons to teach about its workings. First, the fossil record is an important repository of past biodiversity that is otherwise unknowable, hides novel characters, and provides unique opportunities for independent tests of hypotheses based on living biotas. Far from being fully documented, the fossil record necessitates continued exploration. Natural history collections, too, hide many surprises. They host part of the fossil record that has made its way within easy reach of our labs. As such, these collections are invaluable and need to be further studied and preserved.

Second, comparative developmental anatomy provides powerful tools for exploring plant relationships and evolution, using both the modern flora and the fossil record. The insights of this

classic discipline should be integrated in modern curricula, so we don't have to reinvent the wheel, and actively expanded upon. Third, against this background, basic descriptive observations from comparative surveys of extant and extinct biotas can provide fresh, novel insights into the evolution of plant form. We would be ill-advised to not perpetuate (and by that I mean, continue funding) such endeavors.

In praising Swedish paleontologist E.A. Stensjö's detailed reconstruction of cranial anatomy in *Cephalaspis*, S.J. Gould [17] sang an incisive paean to the contribution of observational data in the big picture of science. The enormous body of information produced by paleontologists over two centuries is a testament to this. Recognizing these contributions, John Maynard Smith was famously welcoming of paleontology at the 'high table' of evolutionary biology [18,19]. At the time, the focus was on integrating paleontological data with the tenets of 'Modern Synthesis', in a macroevolutionary outlook. Evolutionary developmental biology was still seeking a distinct identity among modern approaches to evolution. However, once evo-devo staked its territory, it didn't take long for paleontology to be regarded as an equal contributor to evolutionary questions — although this may be a matter of perspective and some may beg to differ.

Nevertheless, it is hardly a matter of perspective that, on the botanical side, paleobotanists have been working singlehandedly to integrate the fossil record into the evo-devo perspective [15]. It is, therefore, both gratifying and exhilarating to see established plant molecular biologists not only emphasizing the importance of the fossil record, but querying it in search of answers. What a nice way to spell the welcome of paleobotany at the high table of *plant* evo-devo from across what could be an epistemological divide!

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Innate Immunity: ER Stress Recruits NOD1 and NOD2 for Delivery of Inflammation

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NOD1 and NOD2, two members of the intracellular NOD-like receptor family, sense bacterial peptidoglycan-derived fragments and induce pro-inflammatory responses. Recent work provides evidence for a role for NOD1/NOD2 signaling in mediating ER-stress-induced inflammatory responses via a peptidoglycan-independent mechanism.

The innate immune sensors nucleotide-binding oligomerization domain 1 (NOD1) and NOD2 are the founding members of the intracellular NOD-like receptor family

[1,2]. By sensing conserved motifs in bacterial peptidoglycan (PGN), these receptors promote host defenses against bacteria through the induction of