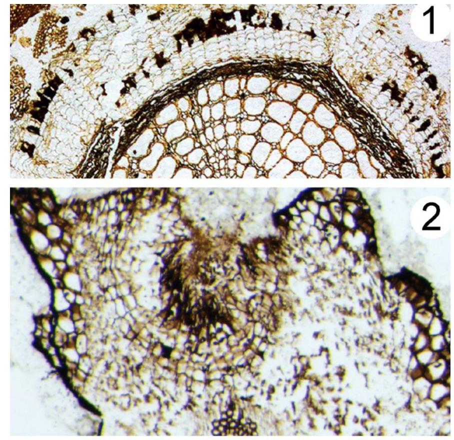
Origins of secondary growth: the periderm perspective



1. Canonical periderm in Pennsylvanian *Sphenophyllum*. 2. Wound periderm in new Early Devonian plant (NMNH-Smithsonian)

The idea. The fossil record holds keys to major evolutionary questions, but it has been sparsely queried to address the evolution of plant development. I plan to explore the evolution of plant secondary growth by studying its fossil record from a perspective never taken before: that of the periderm. Periderm production shares structural features with woody secondary growth and is a canonical ontogenetic feature of seed plants, but can also act as a systemic wound response.

My goals are to: (1) study the earliest fossil occurrences of periderm to understand their development based on anatomy and to document the relative timing of appearance of periderm-type vs woody growth; (2) review occurrences of periderm as a canonical process and as a wound response across the taxonomic breadth of living plants; (3) review published data on the regulation of periderm development to identify potential shared mechanisms with woody secondary growth.

By integrating data from the fossil record with information from living plant anatomy and developmental regulation, I will be able to address: whether woody growth and periderm growth both diverged from a basic shared regulatory program or if, alternatively, they evolved from one another; and, related to the latter, whether periderm growth evolved initially as a wound response mechanism that was subsequently co-opted in canonical developmental patterns, or vice-versa.

Background. Secondary growth proceeds from lateral meristems that produce new layers of tissue bidirectionally, in two forms [1]. One type, vascular secondary growth (woody growth), produces conducting tissues: secondary xylem (wood) and secondary phloem. The other type, periderm-type growth, occurs: as a canonical process that forms protective outer tissues (phelloderm and cork) or as a self-repair growth response sealing wound areas. In both cases, the consistent orientation of cell divisions produces a characteristic pattern of radial cell files recognizable deep in the fossil record. The similarity in development and structure between tissues of woody growth and periderm suggests shared developmental mechanisms and evolutionary origins, but these aspects have not been explored to date.

The fossil record of secondary growth goes as far back as the Early Devonian for woody growth [2], which is documented in most lineages recognized in the Middle Devonian [3]. This deep fossil record suggests that woody growth may have evolved only once [4,5]. By contrast, the fossil record of periderm is much sparser. Only one occurrence (wound periderm), coeval with the oldest woody growth, has been reported from the Early Devonian [6], but the 40 million-year gap to the next oldest evidence (Mississippian canonical periderm) makes it difficult to draw evolutionary parallels with woody growth.

Periderm-type growth is a canonical developmental feature in living seed plants [1] also known in extinct groups of lycophytes, ferns, sphenopsids, and progymnosperms [7]. As sessile organisms, plants can only rely on wound responses to address challenges in their environment, safeguarding water and nutrients and keeping out pathogens. Wound responses include callus formation and periderm production. The most effective is the periderm, where new cell layers are produced in organized fashion to seal wounds [8, 9]. A survey of wound periderm occurrences among living plants outside seed plants has never been undertaken; in the fossil record, it is known only from one Early Devonian occurrence [6].

Developmental regulation of periderm growth is only known from angiosperms, where the vascular cambium is a developmental switch that triggers periderm formation [10]. Multiple genes involved in periderm regulation have been identified [11], but their functions and interactions are poorly characterized. Nevertheless, comparisons between periderm and woody growth reveal shared regulatory components, as well as specific regulatory aspects in each [12].

Research plan. 1) Periderm growth creates patterns recognizable in fossil anatomy (fig), allowing studies of periderm within the fossil record. Through such investigations, I will build a comparative

framework for periderm anatomy in fossil and living plants. I will also characterize the oldest wound periderms in National Museum of Natural History - Smithsonian specimens I have been studying (fig); I will visit Cornell University and Universite Liege (Belgium) collections rich in specimens relevant to my study. Visiting Dr. Decombeix's lab (Universite Montpellier, France) will stimulate collaboration with an expert on secondary growth. From these, I expect to identify trends in periderm anatomy and development across lineages and reconstruct their evolutionary history in a phylogenetic context.
2) I will conduct a thorough review of the literature on canonical and wound periderm to circumscribe the extent to which they have been documented among living plants and identify gaps in this knowledge. To fill the gaps, I will perform wounding experiments (already initiated) in different lineages (e.g., wound periderm production has not been tested in most seed-free plants) using histological techniques. The experiments will expand the body of data on the taxonomic extent of wound response periderm.
3) I will conduct an in depth review of the literature on molecular regulation of periderm development. This is a growing field of study, so over the next few years data will allow for drawing parallels between woody growth vs periderm regulation to identify potential shared mechanisms and construct hypotheses on the sequence of evolution of these two types of secondary growth. Visiting a lab that focuses on secondary growth and periderm regulation, e.g., Dr. Ragni's lab at the University of Rome (Italy), would allow for synergistic exchanges to integrate fossil anatomy and molecular biology.

Intellectual merit and expected outcomes. Periderm evolution has never been addressed in a perspective that integrates living plants, the fossil record, developmental anatomy and regulation. Taking such an approach, my project will yield as direct outcomes: (1) a database of fossil periderm occurrences worldwide including anatomical observations and developmental inferences; (2) descriptions of the oldest periderm occurrences known to date; (3) a database of published periderm occurrences across living plant diversity; (4) new experimental data on wound periderm in multiple extant lineages; (5) an updated synthesis of data on developmental regulation of periderm. These will generate data for publications providing a measure of my project's success. The trends I identify by integrating these data will allow me to draw a timeline of periderm evolution paralleling that of woody growth evolution, and to map the phylogenetic distribution of periderm as a canonical ontogenetic feature and as a wound response. My results will also demonstrate the importance of fossils in understanding the evolution of development by integrating anatomy and developmental regulation, and will add value to specimens in an important national museum collection.

Broader Impacts. Working at Humboldt State University I will be in an excellent position to make a positive impact because: (1) the region is home to the highest concentration of Native American communities in California, (2) located in a remote rural area, HSU is the only science hub for several large counties, (3) and Hispanic-Serving Institution, and (4) hosts a high percentage of first generation college students. During my graduate career, I plan to teach botany labs and work alongside our INRSEP (Indian Natural Resources, Science & Engineering) Program. These positions will allow me to connect with undergraduate students, especially those belonging to underrepresented groups, that are interested in a wide range of STEM topics. My biggest priority is to mentor a few undergraduates and involve them in my project, which has the potential for students with any kind of scientific background or interests to experience research in a collaborative environment. This is because my project is relevant to several major topics in science: paleontology, plant anatomy, taxonomy, evolutionary biology, etc. Throughout this process, I want to emphasize the importance of effective and inclusive scientific communication to those that I mentor. I see this as an opportunity to practice for my future career as a researcher and professor, and hope that I can promote a continuous cycle of research and mentoring others.

[1] Esau K 1965 *Plant anatomy*. Wiley. [2] Strullu-Derrien C et al. 2014 *Bot J Linn Soc* 17:423-437. [3] Pfeiler K, Tomescu A 2021 *Pap Palaeontol* 7:1081-1095. [4] Hoffman L, Tomescu A 2013 *Am J Bot* 100:754-763. [5] Tomescu A, Groover A 2019 *New Phyt* 222:1719–1735. [9] Banks H 1981 *Palaeobotanist* 28:20-25. [7] Decombeix A, Galtier J 2021 *Int J Plant Sci* 182:430-444. [8] Holden H 1912 *Ann Bot* 26:777-793. [9] Lulai E et al. 2016 *Plant Signal Behav* 11:12-17. [10] Xiao et al. 2020 *Curr Biol* 30:4384-4398. [11] Singh et al. 2021 *Potato Res* 64:131-146. [12] Campilho et al. 2020 *Curr Opin Plant Biol* 53:10-14.