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Fossil Focus: Using Plant Fossils to Understand Past Climates and Environments

by Leyla J. Seyfullah^{*1}

Introduction:

Fossils provide us with our only direct record of prehistoric life. Studying them can help us to reconstruct the anatomy, behaviour and evolution of long-extinct organisms. Perhaps less obviously, fossils are also among the most important sources of information for scientists attempting to learn about past (palaeo) climates and environments — a major focus of research in Earth and environmental sciences, motivated in part by concerns over future climate change. Fossil plants (Fig. 1), in particular, can be useful for decoding past climate signals. Most plants are terrestrial (meaning that they live on land). They are generally incapable of moving around, and so are totally dependent on the atmosphere and the soil or rock (substrate) on which they grow. Certain species are restricted to specific climatic conditions (such as temperatures and humidities), whereas others can alter their form, structure or features according to the environment in which they live. This means that plants can be used as [proxies](#) for the terrestrial conditions that prevailed when they were alive: data from fossil plants can be compared with records based on marine organisms and chemical isotopes to reconstruct past climates. Several methods have been developed that help us to interpret the climate signals stored in the plant fossil record; the most important of these are outlined below.

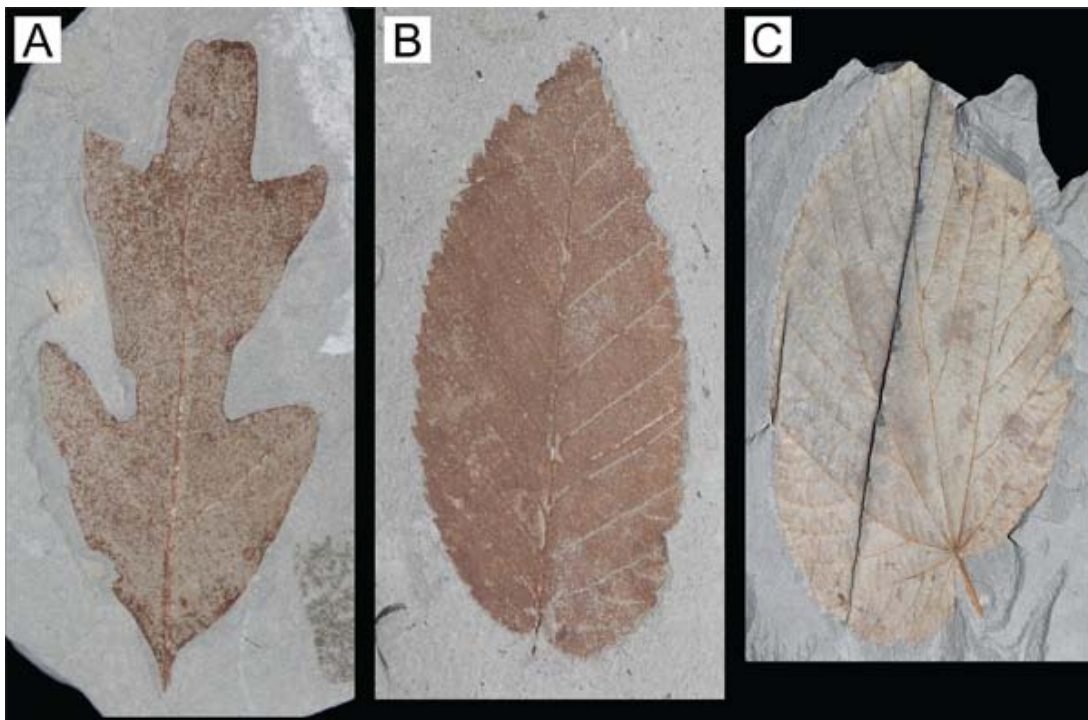


FIGURE 1 — FOSSIL PLANTS FROM THE PLIOCENE OF GERMANY. (A) OAK LEAF. (B) BIRCH LEAF. (C) LIME TREE LEAF. CREDIT: L. SEYFULLAH.

Nearest living relative:

One way to use plants to learn about palaeoclimates is to identify the nearest living relative of a fossil (Fig. 2) and document its environmental tolerance, its relationship with the environment (its [autecology](#)) and which other species live in the same area. These are used to extrapolate conditions for the extinct species. A recent example of this kind of work examined fossils of *Nyssa* (tupelo) and *Taxodium* (swamp cypress) from the [Miocene](#) (5 million to 23 million years ago) of the Rhine area of Germany. The modern living relatives of these fossils are no longer found in Europe, but in the warm, humid swamps of Mississippi. We can infer that the climate of Germany during the Miocene was much wetter and hotter than it is today. It should be noted, however, that this approach depends on the accurate identification of the nearest living relative of a fossil, which can be problematic for some extinct lineages. In addition, the more species used, the better: inferring past climates on the basis of multiple species is expected to yield more accurate results than doing so from just one.

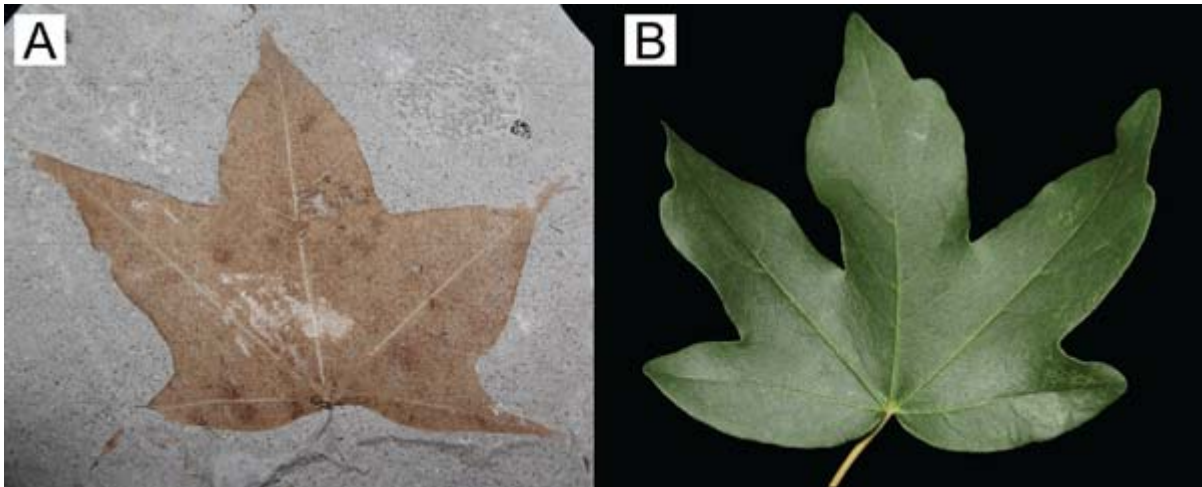


FIGURE 2 — (A) FOSSIL MAPLE TREE LEAF FROM THE PLIOCENE OF GERMANY AND (B) ITS NEAREST LIVING RELATIVE. CREDIT: L. SEYFULLAH.

Plant adaptations:

Like all organisms, plants have been forced to adapt to their surroundings in order to survive, and these adaptations may be recorded in their fossilized remains. Careful interpretation of fossils therefore provides clues as to the environment in which these plants once lived. Adaptations reflect how the plant deals with temperature, light and the availability of water and nutrients. Together, all these factors control how a plant grows. For interpreting climate signals, there are two parts of the plant that are especially useful: leaves and wood.

Uses of leaves 1: Climate–leaf analysis multivariate program (CLAMP)

CLAMP is a statistical technique for decoding climatic signals from the [physiognomy](#) (overall appearance) of leaves from woody [dicotyledonous](#) plants. It is based on the pioneering work of US palaeontologist [Jack Wolfe](#) (1936–2005), who studied the physiognomic features of leaves from modern flowering plants and correlated them with climate for different communities across the globe. Leaf size is related to water loss: in hot, dry regions, plants have either no leaves or very small ones, whereas in wetter places, such as rainforests, leaves can get very large. Wolfe showed that, in general, the shape of the leaf margin, or edge (Fig. 3), varies with mean annual temperature. The higher the proportion of plants with smooth ('entire') margins, the higher the temperature of the environment; leaves with toothed edges by contrast, tend to dominate in cooler climates. Wolfe went on to compare many combinations of leaf characters in different extant plant communities;

this formed part of a detailed [multivariate](#) statistical analysis, in which numerous characters with multiple states were analysed collectively to obtain a picture of climate. Finally, this approach was applied to fossil leaf floras and the results were used to infer palaeoclimate.

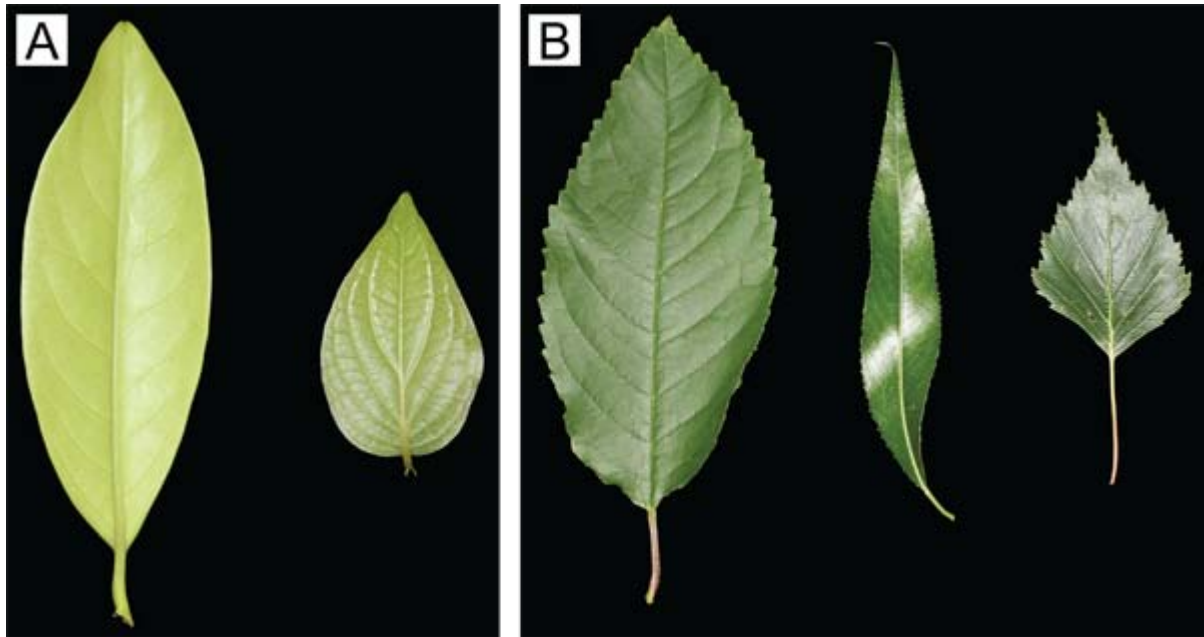


FIGURE 3 — (A) LEAVES OF MODERN PLANTS WITH SMOOTH ('ENTIRE') MARGINS. (B) LEAVES OF MODERN PLANTS WITH TOOTHED MARGINS. CREDIT: L. SEYFULLAH.

CLAMP is a very useful tool for researchers trying to identify palaeoenvironmental signals in fossil leaf assemblages. This approach has been successfully used on a number of occasions, with some recent examples including work on the [Cretaceous](#) floras (145 million to 65 million years old) from the high Arctic, and the Miocene flora of Yunnan, China. Unfortunately, CLAMP has several limitations that hamper its effectiveness, most notably that the analyst must score features on a leaf subjectively. It also has difficulty with some types of climate or vegetation, such as rainforests.

Uses of leaves 2: Leaf-margin analysis

A simpler method is leaf-margin analysis, which makes use of the observed relationship between the shape of the leaf margin (entire versus toothed) and the climate to estimate palaeotemperatures from fossil leaf floras. It is easier to use than CLAMP, since only one character is measured, but provides only limited information. [Temperate](#) floras contain the highest proportion of leaves with toothed margins, and this proportion decreases with increasing temperature. The underlying causes of this link between leaf margins and temperature are not well understood. Nevertheless, it has been shown that physiological activity at leaf margins is greatest early in the growing season, and that toothed margins are more active with respect to [photosynthesis](#) and [transpiration](#) — both of which are vital for growth — than are untoothed, entire margins. Thus, toothed margins apparently help plants in temperate regions to maximize their growth and productivity at the start of the growing season. Leaf-margin analysis has been used on numerous fossil floras (Fig. 4) across both the Northern and Southern hemispheres, from Central European [Cenozoic](#) floras (65 million years old and younger), to those from the Late Cretaceous and [Paleocene](#) (100 million to 56 million years old) of New Zealand. However, the method can only give an estimate of mean annual temperature, and so does not reveal the complete climate story of a plant.

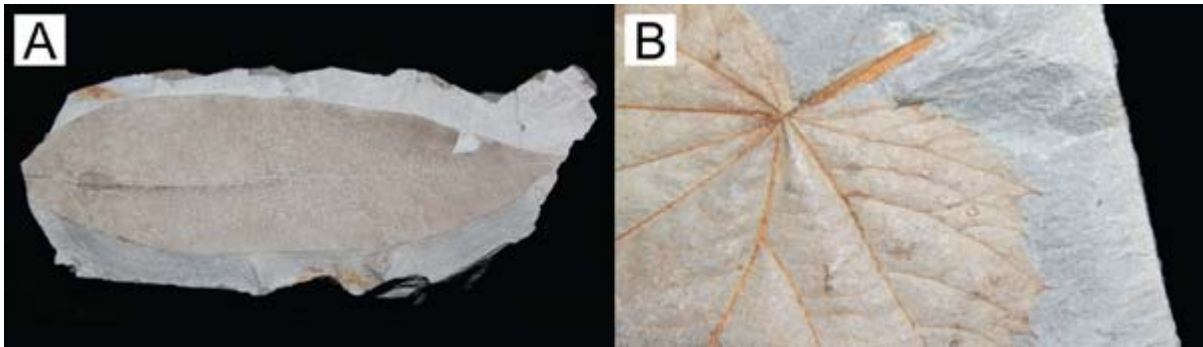


FIGURE 4 — (A) FOSSIL LEAF WITH SMOOTH MARGIN. (B) FOSSIL LEAF WITH TOOTHED MARGIN. BOTH FROM THE PLIOCENE OF GERMANY. CREDIT: L. SEYFULLAH.

Uses of leaves 3: Leaf cuticle and stomatal density

The cuticle is the waxy surface layer on leaves that protects them from dust, [pathogens](#), mechanical injury and some of the ultraviolet radiation in sunlight. It is also important for regulating temperature and water loss. It is not a solid barrier: to live and grow, plants need efficient gas exchange, which is controlled by the [stomata](#) (pores) in the leaves (Fig. 5). The thickness of the cuticle itself is an indicator of how much water stress the plant experiences: the more abundant water is in the environment, the less need the plant has to prevent water escaping, and the thinner the cuticle. So plants with thin cuticles live in areas where water is freely available; these plants include the filmy ferns (Hymenophyllaceae), which are commonly found near waterfalls and are constantly wetted by spray. Plants with thick cuticles, such as cacti and succulents, experience more water stress, and may display other features that reduce water loss, such as sunken stomata and [papillae](#).

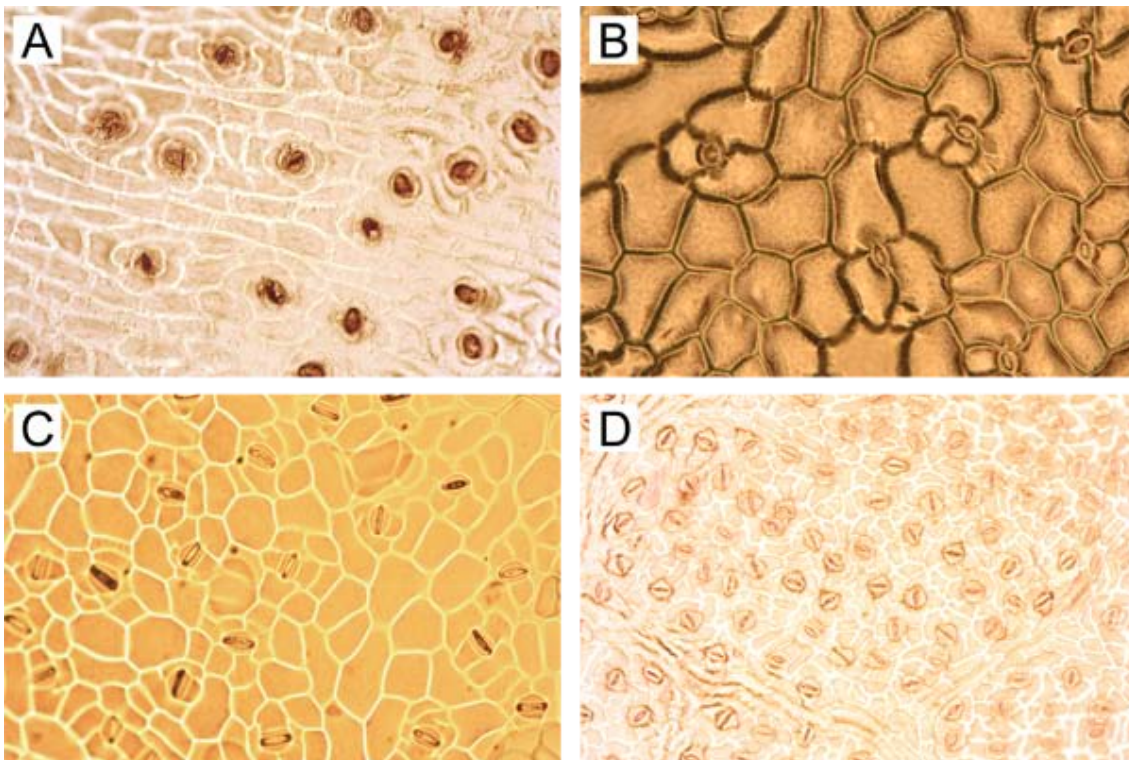


FIGURE 5 — STOMATA OF MODERN PLANTS. (A) WOLLEMI PINE. (B) NASTURTIUM. (C) BAOBAB. (D) BAY LEAF. CREDIT: L. SEYFULLAH.

There have been numerous experiments on modern plants testing how the density — number per unit area of the leaf — and function of the stomata change with different environmental factors, such as water stress or increased carbon dioxide levels. Overall, this work shows that some living angiosperms (flowering plants) and conifers subjected to high carbon dioxide concentrations have low stomatal densities, whereas plants in very windy conditions have high stomatal densities, but the stomata are very small. Assuming that fossil plants also show this correlation, the relationship between the number of stomata and the number of [epidermal](#) cells (the stomatal index) can be a useful palaeoclimate proxy.

Uses of wood

Wood is a useful indicator of environmental changes throughout the lifespan of a tree. It consists of cells formed on a regular basis, which record the environment at the time of their development and maturation. The sizes and shapes of cells in the wood can provide a good indication of climate, including the frequency of frost. The cells grow outwards in a radial pattern; in the early growth season, larger thin-walled cells (early wood) develop, and these are followed by smaller thicker-walled cells (late wood) (Fig. 6). This alternating pattern formed by the rings of early and the late wood is the principle behind [dendrochronology](#) (dating using tree rings). In tree-ring analysis, there are several components that might give us a good indication of climate. First, the presence of growth rings, which can be indicative of where in the world the tree grew; absence of growth rings is common, although not universal, in humid equatorial climates. False rings are tree ring anomalies that form when the tree experiences stressful conditions (usually a dry spell), interrupting normal cell growth during the growing season, and can indicate frost or defoliation. Finally, the ratio between the amount of dense late wood, formed late in the growing season, and less-dense early wood may provide information about levels of summer rainfall. The interpretation of these features is difficult in fossil material, but if used cautiously, it can provide a fair indication of past climate, as shown by recent work on the trunks of *Xenoxylon* from the [Mesozoic Era](#) (251 million to 65 million years ago) of Asia.

Summary:

There are several key ways in which fossil plants can contribute evidence that will help us to reconstruct past environments and climates. For the most robust models of palaeoclimate, evidence from many sources, not just plants, should be considered. Moreover, although the methods outlined above are potentially informative, they can be used with a high level of confidence only for Cenozoic fossils (65 million years old or younger). The study of older plant fossils can offer broad indications of environment and some climatic signals, but interpreting these in extinct groups, especially those that are very different from extant plants, remains contentious.

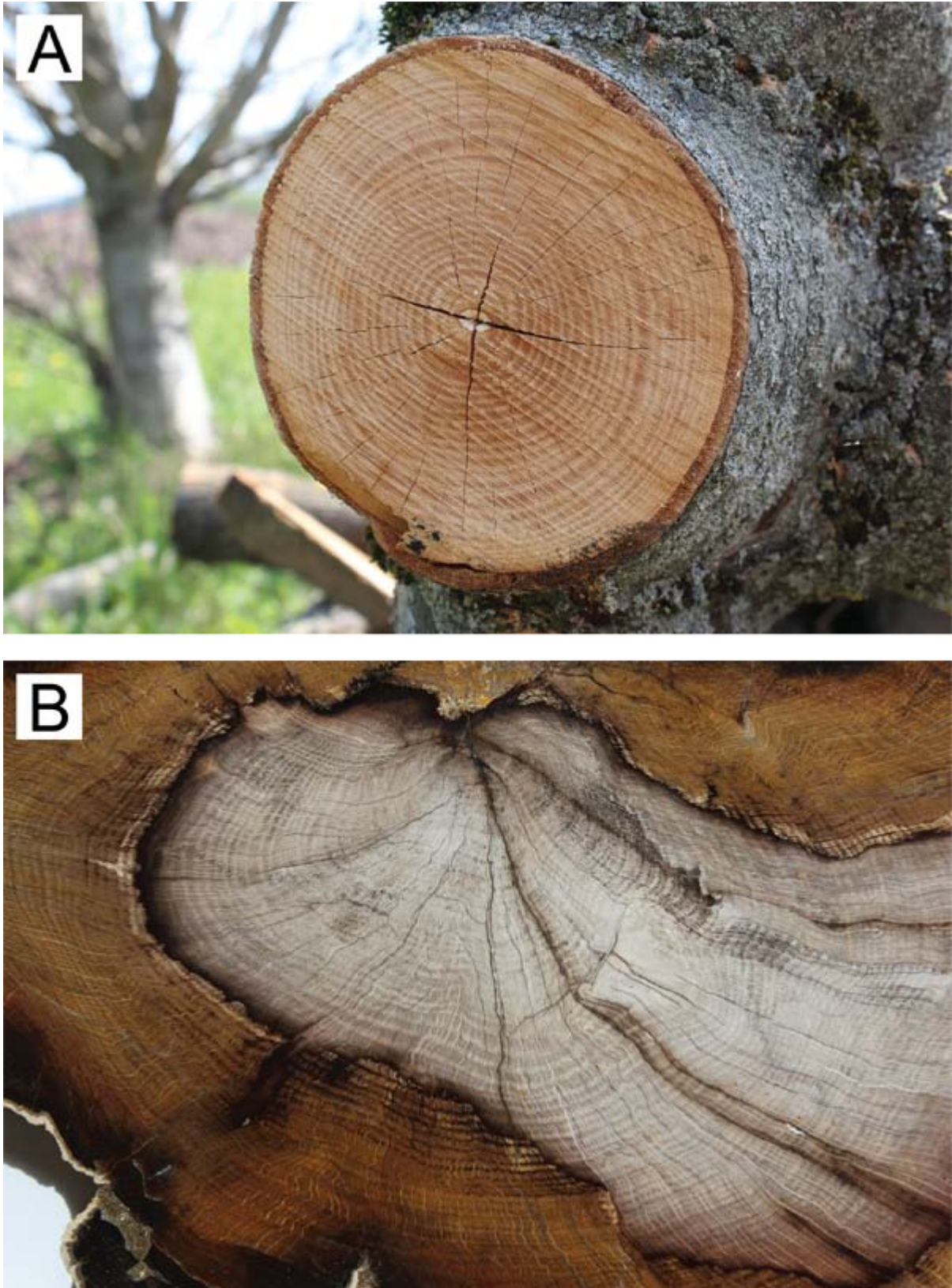


FIGURE 6 — TREE RINGS IN (A) MODERN AND (B) FOSSIL WOOD (FROM THE EOCENE OF USA). CREDIT: L. SEYFULLAH.

Suggestions for further reading:

CLAMP online. <http://clamp.ibcas.ac.cn/Clampset2.html> — *A website explaining the CLAMP method.*

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