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Reconstructing the Botanical Past: Art and Paleobotany

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ABSTRACT

Paleoart is an important tool for paleobotanists when reconstructing fossil plants and ancient ecosystems, and communicating with diverse audiences. Plants are fundamental components of terrestrial ecosystems. Thus, accurately depicting ancient plants in art is crucial for communicating comprehensive knowledge about ancient life. Here, we briefly review the history of paleobotanical art, discuss the challenges when accurately depicting plants in paleoreconstructions, and highlight recent works that reconcile isolated plant organs into scientifically accurate whole-plant and landscape-level reconstructions. Historically, paleoart has included plants as background elements in art featuring charismatic vertebrates, resulting in poorly depicted plants and ecosystems. Plant blindness—the phenomenon in which humans are more inclined to detect and appreciate fauna than flora—is a persistent problem for science communicators, botanists, and paleobotanists. Although plant blindness is rampant in 20th-century paleoart, modern paleoart that accurately incorporates and focuses on ancient plants can increase plant visibility in portrayals of the geologic past.

KEYWORDS

art, fossils, paleoart, paleobotany, plant awareness disparity, plant blindness, plant fossils, scientific reconstructions

Art is an important tool for scientists to engage with both scientific and general audiences (Lesen et al., 2016). Paleontological art—or paleoart—has been used to reconstruct extinct organisms and environments for almost 200 years and has influenced many of our assumptions about the past (Davidson, 2008; Stroud, 2008; Witton et al., 2014; Clary et al., 2022b; Manucci and Romano, 2022). Paleoart can also be useful to better understand and advance paleontological paradigms—most famously, the extensive updated paleoart that accompanied the Dinosaur Renaissance of the late 20th century (McDermott, 2020). Paleoart includes drawings and paintings, museum reconstructions and sculptures, as well as documentaries, movies, and even video games; here, we will mostly reference drawings and paintings, the most common form of paleoart.

Plants are fundamental for ecosystems and society, supporting biodiversity, terrestrial biomass, ecosystem structure, and as critical food and oxygen sources for humans and other organisms. Unfortunately, general audiences, policymakers, and other scientists are more likely to recognize and appreciate animals compared to plants. This disparity, termed *plant blindness* (also known as *plant awareness disparity* in recent years) has been attributed to reduced funding for plant-related projects compared to animal-focused research, as well as a global decrease in plant-centered education, conservation, and recognition (Wandersee and Schussler, 1999; Drea, 2011; Balding and Williams, 2016; Jose et al., 2019; Margulies et al., 2019; Parsley, 2020; Brownlee et al., 2021; Stagg and Dillon, 2022; Stroud et al., 2022; Walton et al., 2023).

Paleontology is widely thought of as a "gateway science" to other fields in science, technology, engineering, and mathematics (STEM), and as a way to teach broader audiences larger scientific concepts such as evolution, mass extinctions, climate change, and biodiversity (Moran et al., 2015). Often, these education and outreach initiatives include, or center on, paleoart (Burns et al., 2003; Clary et al., 2022a; Lipps et al., 2022). Additionally, plant fossils show how environments have responded to climate change, and knowledge of fossil history can be used as a rationale for the direct conservation of plants and ecosystems (e.g., the UNESCO World Heritage Gondwana Rainforests of Australia; Young and McDonald, 1987; Burnham, 2001; Wilson et al., 2011; Ivory et al., 2016; Lézine et al., 2019; Kooyman et al., 2020). Accurately representing fossil plants in paleoart is fundamental for conveying information about life in the past.

Paleoart has tended to focus on animals, with plants seen as a backdrop or scene-setting, rather than as "central characters" (however, see Benca et al., 2014; Sanders, 2014; Beans, 2022; Benca, 2022). Here, we discuss how plants have been depicted in paleoreconstructions over time within the context of plant blindness. We also consider the challenges facing plant paleoart and present promising trends for the future.

BRIEF HISTORY OF PLANT PALEOART

Duria antiquior ("A More Ancient Dorset"), painted by Sir Henry Thomas De la Beche in 1830 (Figure 1A), is widely considered the first example of a new genre of art: the reconstruction of life in the past based on scientific evidence (Rudwick, 1992, 2014; Lescaze, 2017). Although largely a marine scene, this first paleoreconstruction included palms and other less easily identifiable vegetation on background landmasses. In the lithograph versions, produced from De la Beche's work by George Scharf, fern-like and cycad-looking plants are also recognizable (Rudwick, 1992; Sharpe, 2022; Sharpe and Clary, 2022).

The circulation of lithographic prints of *Duria antiquior* began the proliferation of paleoreconstructions as a means of conveying information about life in the deep past to broad, non-scientific audiences from the 1830s onwards (Clary et al., 2022a), and these illustrations frequently incorporated detailed plant reconstructions (Vujaković, 2019; Manucci and Romano, 2022). Christian Hohe's final lithograph for Georg August Goldfuss' *Petrefacta Germaniae*, produced in 1844, is an exquisitely detailed scene from the Coal Measures with a key detailing the plant taxa, demonstrating that Goldfuss expected his audience to be as interested in them as in animal fossils (Rudwick, 1992).

The importance and ubiquity of coal in people's everyday lives (Yuval-Naeh, 2019), combined with popular interest in ferns and their allies (Whittingham, 2012), meant that paleoart focusing on Carboniferous plants was widespread in the latter half of the 19th century (Figure 1B). For instance, Carboniferous plants featured in Franz Unger's *Die Urwelt in ihren verschiedenen Bildungsperioden* ("The Primeval World in Various Developmental Periods") published in 1851, with artwork by Josef Kuwasseg, which inspired Edouard Riou's illustrations for Louis Figuier's *La terre avant le deluge* ("The Earth Before the Flood") in 1863 (Rudwick, 1992; Davidson, 2015; Vujaković, 2019; Collins, 2022).

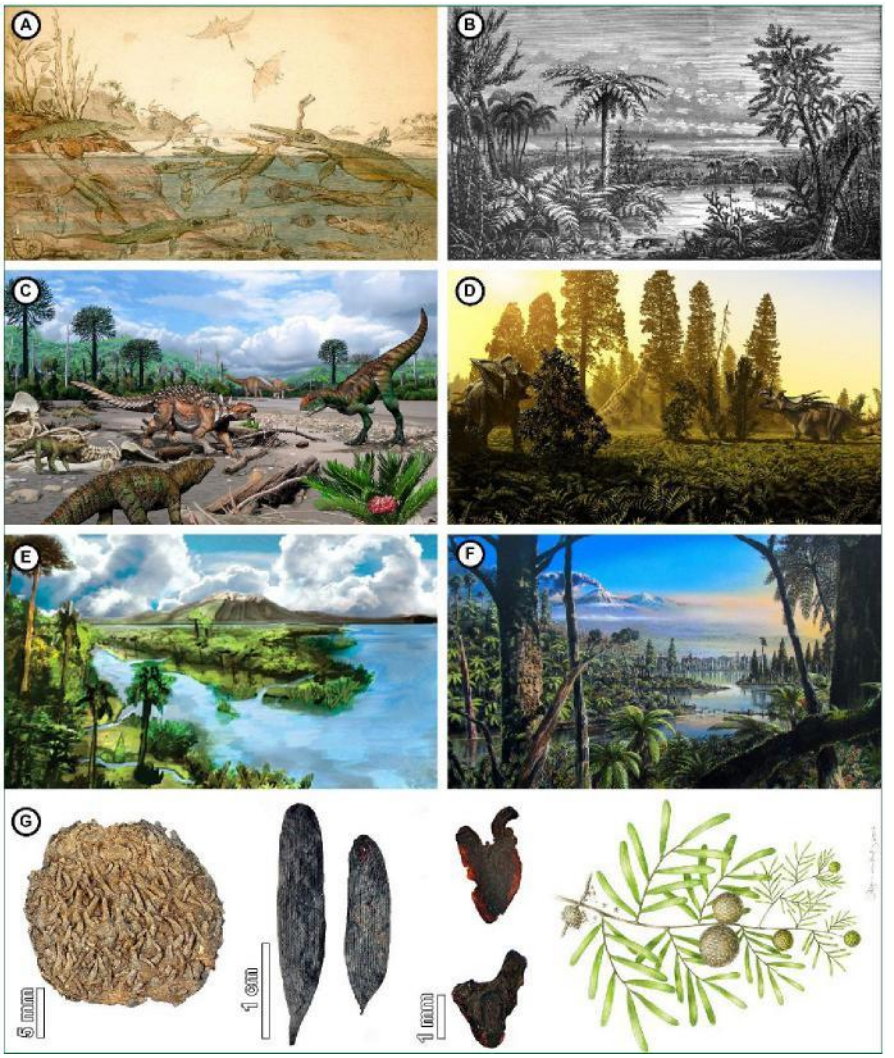

Figure 1. *Representative examples of plant paleoart throughout history and modern plant-centered paleoart. (A) Henry De la Beche's* Duria antiquior. *Note palms on the middle-right and some less easily identi~able vegetation on the middle-left. (B) Lycophyte, sphenophyte, and pteridosperm taxa from the Carboniferous of the United States depicted in Underwood (1896; artist unknown), in turn based on Dana (1874). (C) Dinosaur-centered reconstruction of the Late Cretaceous of Argentina, with some minor plant elements in the back (*Araucaria*) and front right (*Zamuneria*) (artist: Jorge Antonio González, modified from Paulina-Carabajal et al., 2021). (D) Dinosaur-centered reconstruction of the Late Cretaceous of Canada, with more prominent plant elements covering the ground (ferns), background (conifers), and with which the dinosaurs are interacting (angiosperms) (artist: Julius T. Csotonyi, modified from Mallon and Anderson, 2013). (E) Paleoenvironmental reconstruction of the Late Cretaceous of Argentina based on pollen data, which provides a more regional signature. Plants depicted include ferns, palms, and conifers (artist: F. Guillén, modi~ed from Barreda et al., 2012). (F) Paleoenvironmen-tal reconstruction of the mid-Cretaceous of West Antarctica based on pollen, geochemical, sedimentological, and organic biomarker data, providing a more accurate depiction of the landscape. Plants depicted included* Cyathea *(Cyatheaceae), Podocarpaceae, and Araucariaceae (artist: James McKay, modi~ed from Klages et al., 2020). (G) Fossil material and reconstruction of the Early Cretaceous conifer* Krassilovia mongolica *and the associated leaf morphotaxon* Podozamites harrisii. *From left to right: Articulated seed cones, leaves, winged seeds; and reconstruction of a branch of* K. mongolica *reconciling all of the fossil elements including alternately arranged* P. harrisii *leafy shoots (artist: Pollyanna von Knorring, modi~ed from Herrera et al., 2020).*

All images used here are either Public Domain or have full CC-BY 4.0 rights (https://creativecommons.org/licenses/by/4.0/). (A) Duria Antiquior *[https://commons.wikimedia.org/wiki/File:Duria_Antiquior.jpg] by Henry De la Beche, 1830. Public Domain (B) Carboniferous Pteridophyta [https://commons.wikimedia.org/wiki/File:Our_Native_Ferns_-_Carboniferous_Pteridophyta.jpg#filelinks] by Lucien Marcus Underwood, 1896. Public Domain. (C) © 2021 Paulina-Carabajal et al., CC-BY-4.0 (Paulina-Carabajal et al., 2021). (D) © 2013 Mallon, Anderson, CC-BY-4.0 (Mallon and Anderson, 2013). (E) © 2012 Barreda et al, CC-BY-4.0 (Barreda et al., 2012). (F) © 2020 Klages et al., CC-BY-4.0 [https://www.nature.com/articles/s41586-020-2148-5/~gures/3] (Klages et al., 2020) (G) © 2020 Herrera et al, CC-BY-4.0 (Herrera et al., 2020).*

The "Classic era of paleoart" began in the 1890s in the United States with the hugely influential work of Charles R. Knight (Milner, 2012; Witton, 2018). Knight was famously commissioned to create paintings and murals for some of the largest natural history museums in the United States (including the American Museum of Natural History and the Field Museum). Often collaborating extensively with vertebrate paleontologists, Knight's murals centered on the charismatic extinct vertebrates at the forefront of paleontological discovery with naturalistic, but often homogenous, vegetation (Vujaković, 2019). However, Knight conducted detailed research on the Gilboa forests of New York and communicated with paleobotanist Winifred Goldring to maximize the paleobotanical accuracy of his plant-centered mural *Devonian Forest* (on display at the Field Museum; VanAller Hernick, 2003). Meanwhile, in Europe, Czech painter Zdeněk Burian painted lavish reconstructions including flora from Devonian to Quaternary times (Lavas, 2016; Witton, 2018).

Unfortunately, the paleoart of the mid-late 20th century pushed plants into the background. Dinosaurs and other charismatic vertebrates were the centerpieces of most paleoart from this time, and plants were rarely given much consideration. Monkey puzzle trees (*Araucaria*), cycads (Cycadales), *Williamsonia* (Bennettitales), palms (Arecaceae), and tree ferns (e.g., Cyatheales)—a very small fraction of the known fossil floral diversity—made up the majority of paleoartistic reconstructions of Mesozoic vegetation. The majority of known Mesozoic seed plants were rarely featured in dinosaur habitats and museum reconstructions of the time (Philippe et al., 2009; Sanisidro and Barrón, 2016; Herrera et al., 2020). Dinosaurs were often reconstructed standing on dry, lifeless earth with a handful of nondescript monkey puzzle trees in the distance, a plant-blind art style coined by Kirk Johnson as "monkey puzzles and parking lots" (Johnson and Troll, 2007; Figure 1C).

The rise of the Internet and digital art at the end of the 20th century enabled a paleoart community to develop and thrive online (Witton, 2018). Although tetrapod-centered approaches continued to dominate paleoart at the start of the 21st century (Figure 1D), some artists deliberately flipped this orthodoxy, such as Robert Nicholls in his reconstruction of the early Cretaceous Antarctic Peninsula (McKie, 2011), and influential practitioners such as Witton (2018) have advocated for far greater consideration of plants by paleoartists (Figure 1E–G).

CHALLENGES TO PLANT PALEOART AND THE POTENTIAL FOR SPECULATION

The fundamental challenge in paleobotany and plant paleoart is creating whole-organism reconstructions (Martine et al., 2019) given the fragmentary nature of the plant fossil record (Spicer and Thomas, 1986). The shedding and differential preservation of various plant organs—including leaves, wood, cones, flowers, spores or pollen, as well as fruits and seeds—throughout the plant life cycle result in a multitude of disarticulated fossils produced by the same plant (Dilcher, 1974; Kvaček, 2008; Wilf, 2008a; Manchester et al., 2014; Cleal et al., 2021), and whole-plant preservation is exceedingly rare (e.g., Boucher et al., 2003; Zamaloa et al., 2006). Additionally, these isolated fossil organs are often named as separate species (or even genera), which can be confusing for non-experts and paleoartists. For example, a single Carboniferous lycopsid tree could be the source of at least six separate fossil species if found in isolation (Spicer and Thomas, 1986). Similarly, the use of morphotaxa—species or genera representing a certain morphology rather than a biological unit—can be confusing for paleoartists (Figure 1G). For example, the wood genus *Araucarioxylon* and the leaf genus *Brachyphyllum* were produced by multiple conifer groups (Philippe et al., 2009; Philippe, 2011) but are often reconstructed as *Araucaria*, fueling their overuse in paleoart.

Although leaves are the most abundant plant macrofossils, leaf morphology can be highly variable and plastic, even on leaves of the same plant; most paleobotanists today use caution when taxonomically identifying isolated fossil leaves (Dilcher, 1974; Doyle, 2007; Wilf, 2008a; Spagnuolo et al., 2022). During the 19th and 20th centuries, numerous angiosperm leaves from the Cretaceous and Cenozoic were inaccurately assigned to extant genera and families, largely due to superficial similarities. This has led many paleoartists, especially during the 20th century, to include genera that were likely not present (such as *Quercus*, *Populus*, *Acer*, and *Salix*) in late Cretaceous and early Paleogene landscape reconstructions. Although reproductive organs—such as fruits, seeds, flowers, and cones—are the basis for most modern fossil plant taxonomy and identification, they are often more delicate and produced at much lower abundances than leaves (Gastaldo, 1992; Cleal et al., 2021).

When reconstructing ancient ecosystems, paleoartists must also consider the scale at which they are working. Compressed leaves have been shown to mostly represent a snapshot of local vegetation, with low levels of non-local influences (Burnham, 1994, 1997; Wing and DiMichele, 1995; Cleal et al., 2021). Conversely, pollen and spore data can represent regional vegetation from many habitats within a larger region (Behrensmeyer et al., 2000; Birks et al., 2016). When combined, these data can be used to accurately depict local (e.g., beside a pond) to regional (basin-level) vegetation (Figure 1E and F; Opluštil et al., 2014; Costamagna et al., 2018; Barreda et al., 2020; Wilf et al., 2022). When depicting ancient landscapes, paleoartists should also consult with scientists from other geological disciplines (e.g., sedimentologists) to understand the paleo-topography of the region and how that would influence the distribution of past vegetation.

While paleobotany deals with fragmentary evidence, illustrations often require a well-developed organismal concept, often based on comparative morphology or nearest living relative approaches (Witmer, 1995; Witton, 2018; Martine et al., 2019). The nature of the plant fossil record and the difficulties associated with reconstructing whole plants (Bateman and Hilton, 2009) imply a certain degree of speculation regarding the reconstruction of most plant fossils. Although the practice of representing "known unknowns" has become an important part of vertebrate paleoart (Conway et al., 2013; Nieuwland, 2020), paleoartists seem to be more cautious with plant reconstructions.

The reason for such caution could be a lack of accessibility to botanical and paleobotanical knowledge, as well as limited input from scientists. Since the late 19th century, paleoart has been driven by commissions, most often by vertebrate paleontologists, not paleobotanists. Scientists must provide artists with more paleobotanical information when possible; however, this can be a challenge because plants and animals require different environmental settings to fossilize and often are not found in the same rocks (Behrensmeyer et al., 2000). Navigating the jargon-rich botanical and paleobotanical literature can be incredibly difficult for non-experts, especially given the decrease in botanical education in general curricula over time (Drea, 2011; Stroud et al., 2022). Although botanical illustration is a well-established field with a rich history spanning centuries (Ben-Ari, 1999; Swann and Pye, 2019; Bienvenue and Chare, 2022), paleoartists rarely come from a formal background in botanical illustration (Sutton, 2019; Dart and Coiro, 2022; von Knorring and Coiro, 2022) and instead have more varied professional stories (Orr, 2019). The expansion of paleoart-focused education in traditional botanical illustration curricula might provide a way forward to better integrate these two fields.

THE FUTURE IS BRIGHT FOR PLANT PALEOART

Over the last 20 years, scientists have made massive advancements in understanding plant evolution and ancient ecosystems due to the

advent of molecular data, mass digitization of natural history collections, and new imaging and statistical methods (Donoghue and Doyle, 2000; Bebber et al., 2010; *Amborella* Genome Project, 2013; Page et al., 2015; Coiro et al., 2019; Leebens-Mack et al., 2019; Bakker et al., 2020; Hedrick et al., 2020; Romero et al., 2020; Johnson et al., 2023). Plant paleoart has also made significant strides in accurately reconstructing ancient plants and paleo-landscapes (see art in Phillips and DiMichele, 1992; DiMichele et al., 2007; Benca et al., 2014; Hetherington et al., 2016; McElwain et al., 2021; Beans, 2022; Benca, 2022). Fossil discoveries worldwide have yielded additional fossil plants with connected organs, allowing for more accurate whole-plant artistic reconstructions (art in Sun et al., 1998, 2002; Hermsen et al., 2009; Zhang et al., 2010; Opluštil et al., 2014; Gomez et al., 2015; Bodnar and Escapa, 2016; Rothwell et al., 2022). Extinct plant lineages, which often lack whole-organismal concepts, are being reconstructed and properly included in landscapes (Philippe et al., 2009; Barreda et al., 2012; Wang et al., 2012a; Herrera et al., 2020). Cretaceous charcoalified flowers, and their incredibly detailed artistic reconstructions by Pollyanna von Knorring and others, have provided an unexpected window into early angiosperm evolution (Crepet et al., 2004; Schönenberger, 2005; Crepet, 2008; Takahashi et al., 2008; Friis et al., 2011). Fossil Lagerstätten, amber deposits, and insect damage found on fossil plants have been shown to document plant-insect interactions, including pollination, herbivory and palynivory, insect mining and galling, and insect-plant mimicry (Wilf and Labandeira, 1999; Wilf, 2008b; see art in Wang et al., 2012b, 2014; Bao et al., 2019; Correia et al., 2020; Cariglino et al., 2021; Tihelka et al., 2021; Xiao et al., 2021; Prevec et al., 2022).

Plants are emerging from the background of ancient ecosystems in modern paleoart. The *Ancient Colorado* and *Ancient Denvers* murals and related museum reconstructions accurately reconstruct the history of the Denver Basin based on decades of detailed stratigraphic, paleontological, and paleobotanical research and collaboration with artists and sculptors (commissioned by Kirk Johnson and the Denver Museum of Nature and Science, and brought to life by artists Jan Vriesen, Donna Braginetz, and Gary Staab; Johnson and Raynolds, 2006; Johnson and Stucky, 2006). These murals reconstruct ancient environments from specific fossil localities, instead of broad summaries of entire time periods that tend to depict plants and animals in the same reconstruction that did not actually coexist (common in 20th-century paleoart). Some of the exceptional plant-centered artwork of Smithsonian scientific illustrator Mary Parish includes the floristic turnover of the Carboniferous Rainforest Collapse and the vegetation of the latest Cretaceous (Montañez, 2016; Sutton, 2019). The murals of Jay Matternes expertly recreated the ecosystems of North America throughout the Cenozoic, detailing the diversification of modern mammal lineages and the rise of grasslands (Carrano and Johnson, 2019). By assembling detailed geochemical, stratigraphic, and palynological data, Klages et al. (2020) together with artist James McKay illustrated the once-diverse late Cretaceous polar forests of Antarctica (Figure 1F). Even traditional vertebrate-centered paleoart is often more conscious of the plant constituents than similar art 20 years ago (Figure 1D). In recent documentaries, video games (e.g., *Saurian*, Urvogel Games), and comic books, the vegetation is carefully considered to reflect the fossil record of the time period and region (Ehret, 2019; Parker, 2021; Clements et al., 2022; Wings et al., 2023).

Among the resources available for plant paleoartists, the Extinct Plant Paleoart Database (Jud, 2020) collects examples of published paleoart in an accessible and continuously updated format. The database currently includes 177 references to plant paleoart, as well as a separate list of plant paleoartists. Although the issue of paywalls associated with scientific journals still hinders full accessibility to paleoartists, this represents an important first step to increase visibility of available resources. We hope that these recent scientific and artistic advancements encourage paleobotanists to continue collaborating with artists in their research and engagement to reduce

plant blindness and inspire future generations of paleobiologists to study extinct plants and animals.

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