Dragons have been a common thematic focus in art and literature since ancient times (Table 1). Exegeses of dragons, or at least of the origin of the lore that is their essence, have been posed by a number of theorists (see the table in the online supplements) [1–16]. Variations between western and eastern descriptions of dragons’ heads may be culturally understood: Western dragons’ heads often resemble common, nondescript reptiles’, although some appear as hybrid animals (e.g. the French Tarasque). Eastern dragons’ heads are a combination of several animals: head of a camel or horse, horns of a stag, eyes of a rabbit or demon, ears of a bull, the neck of a snake. The diversity of conjecture may suggest the origins to be a semantic game with no definitive answer. Are myths and legends born from a single inspiration or from a multiplicity of perspectives? Or is it a combination of these that brings them to life?

Scientific explanations have been used to bring light to the origins of many folktales. The werewolf myth is thought to derive from the genetic hair disorder hypertrichosis [17,18]. Mermaid myths may have emerged from encounters with people suffering from sirenomelia, which causes fused limbs—usually legs [19]. Even the unicorn may be scientifically explained as a mutation producing single antlers or horns on mammals. Is it then plausible that a plant fossil occurring worldwide, covered in beautiful scale patterns, may be an inspiration for dragons?

Humans have always needed to understand the world around them in order to survive. This understanding begins with basic observation. What killed; what helped sustain and heal; what connected people to God? Similar to Aristotelian ideals, these were likely the first natural science categories. Plants provided food, medicine or mind-altering experiences, given knowledge of their properties. Aristotle used observational methods in his taxonomic hierarchy, placing plants at the bottom of his Ladder of Life [20]. As botanical knowledge grew, classification became more elaborate and scientifically accurate. Plants were broken down into trees, shrubs and herbs. Today we categorize species based on evolutionary adaptations in genetics, metabolism, development and ecological habitats. The evolution of categorization reveals the progression of cultural/societal needs.

As this understanding evolved, so did our comprehension of extinct life. Fossils of marine animals were noted as early as the sixth century, but scientific identification did not occur until the eighteenth century. In the interim, people collected and classified findings, trying to comprehend how these strata were formed. Geology was born. Scholars began to appreciate how Earth’s landscapes changed over millions of years. Yet most sixteenth-century naturalists did not acknowledge that fossils were the remains of living organisms [21], because, for example, complete plant specimens were rarely found. Therefore, a paleobotanist would name a stem one genus, a root another and leaves yet another. It is only after parts were found together that they were referred to by the first genus assigned. Still, the individual parts are often referred to by their original designation. But how do we arrive at dragons from these seemingly disparate parts?
<table>
<thead>
<tr>
<th>Time Period</th>
<th>In Art or Literature</th>
<th>Origin of Mythos</th>
</tr>
</thead>
<tbody>
<tr>
<td>c. 5000 BCE</td>
<td>Mushshu/Dragon likeness of Marduk/Tiamat on the Ishtar Gate, Babylon, Mesopotamia</td>
<td>Sumerian mythology</td>
</tr>
<tr>
<td>c. 2600 BCE</td>
<td>Lung or long, serpentine dragon with scales, lizard legs, eagle talons</td>
<td>Chinese mythology</td>
</tr>
<tr>
<td>c. 1000 BCE</td>
<td>Feathered serpents</td>
<td>Mesoamerican mythology: Quetzalcoatl</td>
</tr>
<tr>
<td>c. 470 BCE</td>
<td>Apollo and Python, black-figure lekythos, Greek vase, Musée du Louvre</td>
<td>Greek mythology: serpent Python</td>
</tr>
<tr>
<td>c. 400 BCE</td>
<td>The Hesperides in the Garden, Attic red-figure hydria, British Museum, London</td>
<td>Greek mythology: Ladon, dragon guarding apples of Hesperides</td>
</tr>
<tr>
<td>c. 400 BCE</td>
<td>The Colchian Dragon Disgorging Jadon, Athenian red-figure kylix, Gregorian Etruscan Museum, Vatican Museums</td>
<td>Greek mythology: the dragon and the golden fleece</td>
</tr>
<tr>
<td>c. 200 BCE</td>
<td>Perseus and Andromeda, Roman mosaic, Bardo Museum, Tunis, Tunisia</td>
<td>Greek mythology: sea serpent Ketos</td>
</tr>
<tr>
<td>c. 50</td>
<td>Pliny the Elder, Natural History</td>
<td>Roman literature: Indian and Ethiopian cave dragons</td>
</tr>
<tr>
<td>c. 900</td>
<td>Historia Brittonum (literature)</td>
<td>Welsh mythology: the red dragon</td>
</tr>
<tr>
<td>c. 1000</td>
<td>Beowulf (literature)</td>
<td>Anglo-Saxon mythology: dragon killed by hero</td>
</tr>
<tr>
<td>c. 1100</td>
<td>Nibelungenlied (literature)</td>
<td>Germanic mythology: Fafnir</td>
</tr>
<tr>
<td>c. 1200</td>
<td>The Mabinogion (literature)</td>
<td>Welsh mythology: red and white dragons fighting</td>
</tr>
<tr>
<td>c. 1200</td>
<td>The Eddas (literature)</td>
<td>Norse mythology: serpent Jormungandr</td>
</tr>
<tr>
<td>c. 1200</td>
<td>Various bestiaries (literature)</td>
<td>European mythology: dragons and dragon-like animals</td>
</tr>
<tr>
<td>c. 1280</td>
<td>Volsunga Saga (literature)</td>
<td>Norse mythology: Scandinavian dwarf prince turned into a dragon slain by Siegfried</td>
</tr>
<tr>
<td>1489–1605</td>
<td>1489, Bernt Notke, St. George and the Dragon, sculpture, Church of St. Nicholas, Stockholm 1506, Raphael, St. George and the Dragon, painting, National Gallery of Art, Washington, DC 1555, Jacopo Tintoretto, St. George and the Dragon, painting, The National Gallery, London 1559, Titian, St. Margaret and the Dragon, painting, Museo del Prado, Madrid 1588, van Haarlem, Two Followers of Cadmus Devoured by a Dragon, painting, National Gallery, London 1605, Peter Paul Rubens, St. George and the Dragon, painting, Museo del Prado, Madrid</td>
<td>European Christian mythology: St. George, St. Margaret, La Tarasque, La Vibria</td>
</tr>
<tr>
<td>1590–1596</td>
<td>Edmund Spenser’s Faerie Queene (literature)</td>
<td>English Christian mythology</td>
</tr>
</tbody>
</table>
Lepidodendron, a common Carboniferous Period (approximately 300 million years ago) plant fossil, stood 100 feet tall and was approximately 8–12 feet wide (Fig. 1a); the scale pattern, the result of leaves falling off throughout the plant's growth, gives the fossil a reptilian appearance (Figs 1b, 2). The root structure of this plant, Stigmaria, is a five-pronged structure that sits partially exposed above ground (Fig. 3a). When a Lepidodendron trunk is still attached to that root structure, it takes little imagination to envision a leg with a foot/claw. Branch scars (Ulodendron when found as solitary fossils) resemble a reptile's eye, complete with eyelid (Fig. 3b). Other Carboniferous plants in this stratum, such as tree-ferns and ferns, possessed fronds whose fossils may be misidentified as feathers (Fig. 3c). It is common for modern humans, especially laypeople, to examine fossils and misidentify them; ancient humans may have looked at what we now know to be Carboniferous plant fossils and seen what we would consider the fantastic: a dragon.

Many dragon origin theories have been put forth (see the online supplemental table). Dinosaurs may provide the inspiration for the size attributed to dragons, but discovering complete organisms in fossil form is an improbable occurrence and makes a direct dinosaur–dragon connection unlikely.
PERCEPTION: CHASING THE DRAGON

Our research idea originated in a West Virginia rock quarry, where we "saw" a dragon in the rock face. What appeared as the body, legs and eye of a dragon embedded in the black and gray Carboniferous shale were actually Lepidodendron fossils (Figs. 1b, 2). On the basis of this initial field observation, we chose to test human perceptions of the pattern exhibited by the fossils (Roanoke College Institutional Review Board, IRB approval #15ED013).

Participants, all adults with at least some college education, were shown Lepidodendron casts (Fig. 1b); of these, three groups were given an open-ended writing prompt on paper: "You are walking along a cliffside when you trip over this object. It appears to be _______." Participants were asked not to confer until all had completed the task, which involved handling the fossil cast and completing the response within a 10-minute period. Responses (n=115) were approximately 25–50 words. Answers do not match the number of participants, as many responses included more than one of the coded words.

After we analyzed the responses for repeated words or phrases (Table 2), 9 code categories emerged: scales, volcanic/lava/ash, serpent/snake, reptile, dragon, fire, char, fish and other. These are listed in Table 2 in hierarchical order by number of responses and are undergirded by dragon folklore and critical literature that includes descriptions of creatures that are called worms, serpents, snakes and dragons. Analysis of responses assumes similar connotations for these terms and supports our plant fossil–folklore hypothesis. In addition, the perceptual connection to volcanic rock, ash, charring, scales, reptiles—and ultimately dragons—supports the contention that humans in an earlier era were likely to have reacted like our modern participants, who had the advantage (and bias) of knowing that fossils exist and that dragons are mythical. Participants not only often "saw" a beast but were willing to create a story around this idea, though the prompt did not require it. A sample response:

The scales were too long for any fish I knew, or even any kind of snake. . . . Dragons only existed in fairy tales. But I knew it must have been for it's the only creature with scales that large.

The plant fossil–folklore investigation began in earnest after we realized that others perceived dragon-like qualities in these specific fossils. The following questions guided our research: (1) In what specific regions of the world do Carboniferous plant fossils exist, and how do they correlate with dragon folklore? (2) How do dragon folklore elements (e.g. appearance, environment, behavior) correlate with such fossils? (3) How do these fossils help us understand why a variety of cultures worldwide created myths and legends about a similar creature?

UNCOVERING THE FOSSILS:
LOCATING DRAGON PARTS

During the Carboniferous Period, Pangaea was the major landmass on Earth. Plants were numerous in equatorial swamps and in prime locations to fossilize. Lycopods (Lepidodendron and relatives), tree ferns, ferns, Calamites and progynnosperms dominated the landscape (Fig. 1a). Today, shale, sandstone and, particularly, coal seams from these areas are full of the fossil remains of these physically elaborate plants. However, what was once an equatorial location is now found at different longitudes and latitudes, Pangaea having broken apart and become our current continents. Furthermore, fossilization varies in different locations, and not every location has a complete set of plants represented during those ancient times.

To identify fossil locations, we searched primary scientific literature for Carboniferous plant genera (e.g. Lepidodendron, Sigillaria, Stigmaria, Ulodendron and Lepidophilos) up to 2016. All these species exhibit the unique reptilian scale, chain mail or eyelike forms we saw in the West Virginia quarry face. We noted the exact locations of fossil acquisitions as reported in the literature in a chart; only sources mentioning primary fossil discovery were used. Note that plants do not grow in a single location but may represent large groves of fossils. The final data include 217 fossil locations worldwide. Fossil sites

<table>
<thead>
<tr>
<th>Code Term</th>
<th>Instances</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scales</td>
<td>47</td>
</tr>
<tr>
<td>Volcanic/lava/ash</td>
<td>45</td>
</tr>
<tr>
<td>Serpent/snake</td>
<td>44</td>
</tr>
<tr>
<td>Reptile</td>
<td>41</td>
</tr>
<tr>
<td>Dragon</td>
<td>37</td>
</tr>
<tr>
<td>Fire</td>
<td>21</td>
</tr>
<tr>
<td>Char</td>
<td>17</td>
</tr>
<tr>
<td>Other (obsidian, tar, cave rock, cliff rock, chain mail)</td>
<td>15</td>
</tr>
<tr>
<td>Fish</td>
<td>5</td>
</tr>
</tbody>
</table>

Prompt response narrative codes from 115 participants. Many participants listed multiple terms.
are distributed over the British Isles, North America and Asia but also exist in Europe, Scandinavia and Australia.

The documentation of Carboniferous-Period plant fossil locations is incomplete, even though it is possible to predict where coal should be located due to proximity of a given area during Pangaea’s existence. Countries do not always disclose the location of Carboniferous fossils because they may be tightly linked to proprietary coal rights. Some countries guard natural resource locations from public knowledge to protect against security threats or business competition.

**Building a Dragon: Finding the Stories**

Our examination of dragon folklore began with establishing criteria for what constituted a dragon tale. Keyword searches for “dragon,” “folklore,” “myth,” “legend” and “tales” led to both folktales and literary or critical analyses of the folklore. We limited the search to English translations because these were most accessible to the research team. The search for dragon stories led to tales of worms [25], serpents [26], taniwaha [27], loong [28], the Rainbow Serpent [29] and uktena and tlamuwa [30]. Given our focus on story origin points, we searched for multiple iterations to divine earliest appearances. For example, the telling of St. George’s dispatch of a dragon was popular in medieval Britain but appears to have originated hundreds of years earlier in the Middle East.

These searches, refined by country or region and initial geographical location, allowed data points to be logged in chart form, using the following documentation categories: (1) folktale name; (2) location (as specific as possible); (3) date of origin (if known); and (4) brief tale synopsis. In this literature, we noted several similarities in physical descriptions or artistic representations: triangular scales, clawed feet, serpentine shape and large size. We also considered the purpose or function of the beast within a particular culture, e.g. creation, treasure-guarding, human sacrifice, community scourge or beneficent gift-giver. After accounting for variants, we pinpointed 76 folktales across the world, particularly in the British Isles, North America, Asia and the Middle East.

**INTERWOVEN BOUNDARIES: FINDING CONNECTIONS THROUGH MAPPING**

In order to compare the plant fossil and dragon folklore data, we constructed maps using MapBox Studio [31]. When we had only approximate locations of plant fossils, we used Google Earth to gain coordinates so more centralized locations could be accurately plotted (Fig. 4). Often the locations of tale origins could be pinpointed to castles, rivers or prominent landmarks. Where tales were less localized and often more ancient, the geographic locations were drawn from as many sources as possible and then estimated, e.g. “Set, the red serpent from Egypt” [32] (Fig. 5). If a tale was known to have traveled, we did not duplicate tale points.

We overlaid the fossil and folklore world maps (Fig. 6), revealing similar global patterns. Many fossil and folklore points coincided exactly. Although correlated points appear throughout the world, given the proliferation of sites in the U.K., we chose that location as a case study to highlight ongoing research findings. United Kingdom points appear in Fig. 7 as larger maps; the corresponding references appear in Appendix A in the online supplements.

**DISCUSSION: CLOSING THE LOOP**

Even though most fossils in many strata are difficult to find, one stratum is fossil-rich: the Carboniferous layer. Carboniferous plant fossils, especially *Lepidodendron*, form the major part of the coal seams found in all dragon folklore locations. English tales (see online Appendix A for references)—such as of the Lambton, Sockburn and Pollard worms in Durham; the Handale, Wharncliffe and Filey dragons in Yorkshire; and the Mosten and Wormelowe dragons in Cheshire—correspond to Carboniferous fossil beds located within a few miles’ radius, near the sites of ancient (and modern) coal
mines, castles, quarries or water sources that are easily accessible, making plausible the supposition that humans had opportunity to encounter the fossils.

In a 1658 bestiary, Edward Topsell alludes to humans encountering animal fossils near limestone and marble mines that may have birthed the story of the Greek dragon of Chios [33]. In 1889, geologist Charles Gould noted a possible origin of dragons in Victorian fossilists’ findings of early Iguanodon [34]. Modern theorists Justin Delair and William Sarjeant [35] concur with Gould, while Paul Newman [36] chronicles several theories, one of which is a connection to animal fossils. Mayor [37] refers to ancient historians’ accounts of the Chios scenario as she describes human encounters with animal fossils engendering dragon lore.

Looking deeper into a few tales reveals their relationships to the plant fossils’ appearance as well as their locations. According to lore, John Lambton yanks the Lambton worm from the Wear River on the end of a fishing line and flings it into a well, where it reaches enormous size [38]. Years later, pieces of the worm are hacked off in an effort to kill it, but it regenerates these parts and lives on. Lambton’s worm grows so large that it can wrap itself around a hill seven times, a feat that causes a (still-visible) circular indentation around Worm Hill, located near a documented fossil site. Eventually, Lambton hacks the worm to pieces, which float down the Wear before the worm is finally torn completely apart, having impaled itself on Lambton’s armor. Note that Lambton’s estate sits at the site of lead, coal and limestone mines that have operated for centuries. Interestingly, up until the seventeenth century, coal was believed to be a living thing with “special seeds for its reproduction and growth under the ground” [39]. Could the pieces of the Lambton worm that washed down the Wear River have been the coal-black, scaly fossils of *Lepidodendron*?

The Sockburn Worm lived just a few miles from where Lambton dispatched his. The Sockburn area was an important location as far back as eighth-century Anglo-Saxon rule and was a key religious site throughout the medieval period [40]. The legend of the worm appears in text in the seventeenth century, but the tale is believed to be much older, as the medieval Conyers falchion sword figures as the weapon used on the beast. The Sockburn Worm was a black dragon whose poisonous breath killed all who came near. When Conyers slays it, the worm’s head rolls down from its black lair like a boulder. The allusion to the color of the dragon’s lair and his rock-like head are consistent with the plant fossil-folklore hypothesis. Also, in mines, carbon dioxide and carbon monoxide are silent killers; likewise methane can arise, hissing from rock fissures or suddenly exploding [41]. “The Mosten Dragon,” a tale from the west of England, lends a concrete physical description of the dragon’s hide: “Its body like a serpent low, And scaled o’er as with mail” [42]. The chain mail detail coincides with the appearance of Sigillaria (Fig. 8). Geat (Scandinavian) warrior Beowulf, fatally encountering “the fire-dragon . . . the breath of the monster/ [bursting] from the rock . . . raise[s] his hand and stri[kes] hard/at the enameled scales,” killing the beast [43]. In North America, James Mooney describes the Uktena, said to live in
the passes of the Smokey Mountains, as "a great snake, as large around as a tree trunk . . . scales glittering like sparks of fire" [44]. Mooney relates that a man preserved a scale from the monster and "burned the Uktena scale to a coal" [45].

Examining the world map overlay (Fig. 6), it appears that many dragons may originate from the plant fossils; locations where fossils and folklore do not correspond may have used indigenous reptiles for inspiration. The discrepancy may reflect language barriers inherent in folklore study; however, it could also be that dragon myths evolved at least twice in human history. For example, in South America and New Zealand, respectively the Rainbow Serpent and Taniwha may be more reptile-based, as the plant fossils lie much deeper or are not found there [46]. Therefore, our current hypothesis may evolve to include "sister-dragon species." While the U.K. provides a strong case study for the plant fossil–folklore hypothesis, plotting the plant fossil (n=217) and folklore (n=76) data points on a world map provided the perspective necessary to see a global trend. Precedent for generalizing similar data was set by Mayor, who uses relatively few data points (45 total) on maps of the Aegean and Mediterranean worlds to represent contentions related to animal fossil bones and giants [47].

A plant fossil–folklore connection does not negate other dragon origin hypotheses. There is a wide cross-section of theories ranging from dragons as living reptiles, metaphorical representatives and the rational explanation for fossilized bones encountered by early humans (see the table in the online supplements). Folklorist Hilda Ellis Davidson contends that dragon lore may have a common environmental factor. Her idea of a synergy between natural world and art remains timely:

Archaeology here serves to illuminate the poetry and literature puts new meaning into the archaeology, and while there are many unsolved problems, it is, I believe, by such piecing together of scattered evidence from different sources that we may hope to draw nearer to an understanding of the thoughts and beliefs of a vanished age [48].

Plant fossils may be the catalyst for the outward characteristics of the dragon and therefore impact the lore. In some scientific circles, studying fantastical beasts may be considered frivolous and illogical. One may contend that the magnificent dragon should not have such a plausible, seemingly mundane, genesis. But the dragon's magic is not diminished by the plant fossil–folklore hypothesis. Making this connection requires seeing around and beyond the awareness of one discipline to embrace the symbiosis of seemingly disparate fields of knowledge.

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8 E. Ingersoll, Dragons and Dragon Lore (New York: Payson & Clark, 1928) p. 6.


33 T. Topsell [3].

34 S. Gould [4].

35 J. Delair and W. Sarjeant [22].


37 J. Delair and W. Sarjeant [22].

38 J. Crawhall, *History of the Lambton worm . . . to which is annexed, a prose account of the same . . . also, The laidley worm of Spindleston Head by Duncan Frasier, the Cheviot bard* (Newcastle, U.K.: W. and T. Fordyce, 1821–1896).


46 Molnar and Pole [7].

47 J. Delair and W. Sarjeant [22].

48 L. Egerton [26].

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**DOROTHYBELLE POLI** is an evolutionary plant physiologist who received her PhD from the University of Maryland (2005). She is also a research associate with the Virginia Museum of Natural History. She studies plant axis evolution.

**LISA STONEMAN** is a social scientist specializing in pedagogy and curriculum design. She received her PhD from Virginia Polytechnic Institute and State University. Years ago, she designed folklore courses that continue to allow her to blend her research with her avocation.

Together Poli and Stoneman codirect the Dragon Research Collaborative, an evolving body of interdisciplinary scholars.