

Green Brains & Ground Sloths: A Paleoecology-Based Exercise in Hypothesis Formation

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ABSTRACT

In organismic biology, the formation of ecological and evolutionary hypotheses on the basis of observable morphologies is a central element of research, and by extension of teaching and learning. Often it is necessary to take account of complex combinations of factors, some of which may be far from obvious. In the work described here, hypothesis formation and testing was exercised and studied in a learner-centered and object-based manner using an anachronistic, seemingly “nonsensical” plant, *Maclura pomifera* (Moraceae), in which the link between structure and function only becomes clear when considering past faunistic environments. The element of the unexpected and the allure of the large animals is thought to add to epistemic curiosity and student motivation to engage in the study of plants.

Key Words: Object-based learning; hypothesis formation; ecological anachronisms; megaherbivores; paleoecology; Osage-orange; *Maclura pomifera*.

○ Natural Curiosity & Natural Science: Explorative, Object-Based Inquiry Learning

Exploration and observation as steps toward hypothesis formation and testing are fundamental to research and thus to inquiry-based learning and teaching. In organismic biology, an authentic experience of the scientific method is thought to profit considerably from work on real-life problems involving real-life objects.

Object-based learning is an approach that is mostly used in teaching and learning in museums and is typically more focused on artifacts that students interact with in an explorative manner. As phrased by Hannan et al. (2013), “Facing students with an unknown object and asking

them to deduce what they can from its physical form, encourages just the sort of analysing and hypothesizing that are the life force of scholarly enquiry.” As Kador et al. (2017) note, “almost by default, [this] necessitates a research- and enquiry-based approach to learning.” Biology lab classes, which may be “object-based,” typically have to make use of model organisms, or parts thereof, and normally have to follow a clear protocol with often anticipated results. In this regard, Lückmann and Menzel (2014) also criticize work outside the lab: “Traditionally, outdoor excursions with botanical foci are organized as ‘ex-cathedra teaching’ experiences, which involve an expert introducing plants and learners listening.”

In the learning activity described here, the explorative mode of object-based learning is used in a biological context, drawing on the multiple facets a biological object can offer to learners. The aim is to exercise ecological and evolutionary systems thinking and to form ecological hypotheses based on the morphology of the object.

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The choice of the object for study is crucial to such an activity’s success. In particular, objects that have an aesthetic appeal and, at the same time, are unfamiliar and strange are expected to spark curiosity and invite exploration with multiple senses, thus “igniting an inquisitive mind-set and a drive to discover” (Kador et al., 2017).

In organismic biology, building hypotheses often involves the search for explanations of the ecological function or environmental factors to which a particular visible structure or observable behavior in an organism may be “best fitted.” To exercise this kind of thinking, students were confronted with a tree that shows an unusual morphological feature that is not readily explained

in the context of current ecological conditions but that makes sense when considering that in the past, a factor that is not obvious now may have played a role in the species’ evolution.

○ From Moth to Sloth: Interpreting Plant Morphologies in the Context of Plant–Animal Synecology

At times, an as-yet-unknown factor, such as an elusive pollinator or seed disperser, is implied by morphological adaptation in coevolved plants. A well-known, classic example is the flower of the Malagasy orchid (*Angraecum sesquipedale*), also known as the “comet orchid,” sporting an exceedingly long spur. “Good heavens what insect can suck it” a puzzled Darwin (1862) remarked, and he postulated that “in Madagascar there must be moths with probosces capable of extension to a length of between ten and eleven inches!” This description was found to fit Morgan’s sphinx moth (Sphingidae: *Xanthopan morgani*), whose Malagasy population received the subspecies epithet *praedicta* (Kritsky, 1991). In support of Darwin’s hypothesis, the visit of the unusually long-spurred flower by the moth with the unusually long proboscis was eventually documented (Wasserthal, 1997).

In an age of extinction, however, it is well conceivable that the animal “best fitted” to a given plant structure may never be found because it has vanished from the face of the earth. A considerable number of so-called anachronistic plants still show putative adaptations to ecological situations that are no longer current. This may include fruit that, for seed dispersal and germination, needs ingestion by a large herbivore that is no longer extant in the ecosystem in question. An illustrative, though disputed, case is the putative mutualism that may have once linked the Mauritian tree *Sideroxylon grandiflorum* (Sapotaceae) and the proverbially extinct columbiform *Raphus cucullatus*, the dodo (Temple, 1977). Janzen and Martin (1982) suggested that various Neotropical plants are adapted to dispersal by now extinct large frugivorous mammals. There has been extensive discussion of ecological anachronisms in the ecology literature (Janzen & Martin, 1982; Guimarães et al., 2008; Johnson, 2009; Gill, 2014). Popular natural history writing (Barlow, 2000, 2001; Bronaugh, 2010) has paid attention to some species native to temperate North America that may once have been dispersed by megaherbivores such as mammoths, mastodons, or ground sloths. A particularly striking example is *Maclura pomifera* (Raf.) C.K. Schneid., the Osage-orange.

○ “A Bumpy Green Object That Looks Like Neither Apple Nor Orange . . .”

The Osage-orange is a small, deciduous, dioecious tree of the family Moraceae, which includes mulberries, figs, breadfruit, and the colossal jackfruit. It grows to a medium-sized tree with a grayish to light brown bark that sometimes has an orange tinge. Its ovate leaves are a dark, shining green on the upper side and pale green on the underside. In the leaf axils there is a sharp single spine (Burton, 1990).

The nucleus of *M. pomifera*’s Holocene, pre-Columbian distribution was in southwest Oklahoma, southeast Arkansas, and northeast and central Texas (Turner, 2010, p. 48). It is hardy as far as USDA zone 5 and can be planted from southern Canada as far south as Florida. Given the wood’s usefulness for bow making (which is reflected in the name “bois d’arc” or “bodark”) it has expanded anthropogenically. Hundreds of thousands of miles of Osage-orange hedges were planted in the United States in the 19th century as windbreaks, for erosion control (Burton, 1990, p. 426;

Fergus, 2002, p. 252), and as impervious living fences that were “horse high, bull strong and pig tight” (Austin, 2004, p. 423). On an anecdotal note, the “hedgeapple,” as it is called locally, is said to have inspired the inventor of barbed wire (Austin, 2004, p. 423; Nachtigall, 2008, p. 18).

True to its taxonomic relationship to the genus *Morus*, its leaves were once used to feed silkworms (Kenrick, 1839). Today it is mainly used as an ornamental, with its “showpiece” being the baseball-sized, irregularly spherical, lime-chartreuse green fruit, a syncarp formed of many small drupes (Figure 1). The “bumpy green object that looks like neither apple nor orange” (Christian, 2009, p. 11) has a smooth, waxy-rubbery surface and a fibrous interior of stringy pulp and small, light brown seed. A characteristic feature shared with the fruit and leaves of many other Moraceae is the milk sap, for which it is sometimes called *Milchorange* (milk orange) in German. The sap, with an appropriate charm added, was applied in folk medicine to treat warts (Watts, 2007, p. 281).

The fruit is generally considered unpalatable. As phrased by Flint (1833, p. 47), “tempting as it is in aspect, it is the apple of Sodom to the taste,” though opinions vary (Barlow, 2002, p. 120ff.). Notwithstanding its questionable gustatory qualities, the fruit offers several rather pleasant stimuli, such as the haptic, tactile sensory impression of its pebbly surface. Also noteworthy is the olfactory sensation of its light aroma, reminiscent of citronella and orange peel. Paul Elmer More (1864–1937) wrote in a poem published in 1890 (p. 26): “Sweeter odor nor field nor forest offers / Than the scent of the osage orange ripening / In October. Forsooth the air is nectar. . . .” The scent is also said to ward off insects, and the fragrant green orb is sometimes sold in farmers markets as cockroach repellent, like an oversized natural mothball (Peterson et al., 2002).

As is evident in any ornamentally planted specimen, the fruit falls close to the mother tree’s stem, suggesting a dependence on zoochory for dispersal. Most native animals in the tree’s natural distribution do not eat the fruit. Those that do mostly destroy the seed by chewing,



Figure 1. A fruit of the Osage-orange (*Maclura pomifera*). Note the rodent bite in the center of the fruit in the foreground, showing that a seed has been eaten. A fallen leaf of the tree is seen on the fruit lowest in the pile in the front row and in the background.

This observation supports the hypothesis that a now extinct megaherbivore may have been the mutualist. It is at times eaten by horses (Turner, 2010, p. 48), but the seeds do not seem to survive the equine gut passage (Boone et al., 2015), making dispersal by native, pre-Columbian horses unlikely. No benefit of (though also no damage resulting from) passing through a proboscidean gut was shown in a feeding experiment carried out with the help of an Asian elephant (*Elephas maximus*) acting as a surrogate (Boone et al., 2015). The giant ground sloth (Megalonychidae: *Megalonyx jeffersonii*) has also been discussed as a possible mutualist (Bronaugh, 2010).

○ Tracking the Elusive Creature

The exercise described below was part of a dendrology module and a forestry and forest ecology module for university students in teacher's training (M.Ed.) in biology, agriculture, and horticulture. The location was the Berlin Botanical Garden's arboretum, which holds several specimens of the species.

To avoid the artificial context of post hoc methods such as interviews, which harbor a risk of reactivity (Cotton et al., 2010) and do not capture the authenticity of the first encounter with the object, the work was evaluated by observation, aided by field notes on students' contribution to the discussion.

When we approached the tree, I opened the exercise by offering a few details on the tree's distribution and past uses (see above), avoiding mention of aspects that might influence the students' own observations and perceptions. I initiated and supported discussion with a few guiding questions, as students on their own are unlikely to come to conclusions that are equivalent to results generated in long-term research (Hammer, 1997). The questions were intended to both trigger engagement with the object and induce hypothesis formation.

The first guiding question was "What does this remind you of?" Not surprisingly, mostly large, roundish fruits such as apple, orange, and even pomegranate were named. To students comparing it to an apple, I cited the common name "hedgeapple." To those likening it to an orange, I pointed out that (apart from the obvious reference in the name Osage-orange) an old synonym, *M. aurantiaca*, refers to this similarity in shape and that the fruit was sometimes fraudulently sold as a type of orange to unsuspecting customers (N.N., 1836). One student compared it to a strawberry, for its rugose textured surface. One student saw a resemblance to breadfruit and was told that the plant was, in accordance with the taxonomy, occasionally referred to as "breadfruit's cousin" (Thone, 1936). Several not-too-surprising non-botanical comparisons were brought up. A student who, in jest, compared the fruit to a "brain" for its furrowed surface was told that it is indeed sometimes called "monkey brains" (Weeks et al., 2010, p. 300). Students who likened it to horse droppings were quoted lines by poet Ernest Kroll (1914–1993), who saw "The Osage orange drop its hideous fruit/ Upon the cracking walk like a green / Excrement. . ." (Kroll, 1955, p. 57).

When asked to describe the fruit's scents, students mostly struggled for words that would fit and typically just referred to a "citrus-like" note or chose "green" and "fresh" as descriptions. All perceived it as a pleasant aroma.

To draw attention to the problem of dispersal, I pointed out that all the fruit were found within a rather short radius around the foot of the stem and asked the students how this plant might disperse in nature to avoid intraspecific competition between

seedlings and the parent tree. "Animals" was an obvious answer. One student offered "water," which is plausible as an alternative, though probably not very efficient, way of dispersal.

Finally, I asked the students which animal they thought might be a likely disperser, considering the size and firmness of the fruit. I pointed to the story of the *praedicta* moth as a case in which the morphology of a plant gave a clue to the morphology of an elusive animal. Suggestions included "deer," "roe deer," "cattle," "horses," "elephants," "elk," "moose," "large birds," "mice," "squirrels," "wolves," and "bears." One student jokingly offered "dinosaurs." To narrow the list down to potential dispersers, I asked the group to test the individual hypotheses using their knowledge of the respective animals and considering the morphology of the fruit. In this way, for example, the wolf hypothesis was dismissed because that animal is carnivorous. The rodent hypothesis was rejected because mice are likely to eat and thus destroy the seeds. The same reasoning excludes most birds, which are also likely to eat the seeds; moreover, the fruit lacks the bright colors of typical bird-eaten fruits. Many large birds that might be able to carry away the fruit, such as eagles or vultures, are carnivorous.

Studying the fruit, it appears that an ideal disperser would swallow it without too much chewing. This excludes further candidates. It is too big for deer to swallow. Native equids of the Americas are extinct, and Old World horses and donkeys – potential "surrogate species" – were brought across the Atlantic only in the early 16th century. In addition, the seeds do not survive the equine gut passage well (Boone et al., 2015). On the mention of dinosaurs, I commented that this hypothesis could not be rejected on the basis of animal anatomy, but solely in light of the timescales. As for the elephant, I agreed that the fruit had the shape and size of tropical "elephant fruits." Also, elephants have a rather inefficient digestion, and *Maclura* seeds were shown to survive passage through their gut. The sound of dropping Osage-oranges may also be thought of as similar to that of some large elephant fruits that cause a quite perceivable sound and thus, like a "talking drum," call in the disperser. However, it had to be noted that elephants were few and far between in the wild in the Americas.

Eventually a student, half in earnest, suggested "mammoth." Students were invited to search for a reason to reject this hypothesis. None was found. I further reminded them that there were a number of very large herbivorous and frugivorous animals in Pleistocene America. I added, in the words of Wood (2003, p. 228), that "the osage orange evolved in a world of club-tailed glyptodonts, shovel-tusked gomphotheres and imposing giant ground sloths who consumed it with gusto and propagated its seeds."

To understand present-day ecosystems in most parts of the world requires awareness of the fact that, as phrased by Alfred Russel Wallace (1876, p. 150), "we live in a zoologically impoverished world." On the question of why the tree was, with its disperser gone, not extinct now, I referred back to the much-reduced post-Pleistocene and pre-Columbian distribution and the more recent expansion due to human use. I also added that the time span of about 10,000 years since extinction of the putative megaherbivore mutualist was too short for evolutionary changes in a tree that can propagate vegetatively and whose lifetime can span a few hundred years. Also, I pointed out that changes in population structure and population genetics as a result of extinction of dispersing animals are understood to be an ongoing process (Guimarães et al., 2008) and mentioned that in the recent

example of a regional extirpation of the African elephant, shifts in plant community composition were shown (Beaune et al., 2013).

○ A Fruit “Good to Think”

Student behavior and engagement suggested that *M. pomifera* and its “story” were suitable to trigger substantial interest, evident not only in the students’ questions, but also in their taking pictures and picking up fruit from the ground, weighing it in their hands, smelling it repeatedly, trying to open the fruit, or dropping it on the ground to listen to the sound. One student wanted to know how the plant could be grown from seed. Others asked whether they could taste the fruit, indicating a strong curiosity. I discouraged them from doing so for general safety reasons, saying that this plant and its fruit were “chosen not because they are good to eat, but because they are good to think,” to paraphrase a dictum by Claude Lévi-Strauss (1963 [1962], p. 89). Some students immediately, when walking on, used their smartphones to check the “story” and to find more pictures of the tree. These observations are in accordance with results published by Strgar (2007), in whose work the fruit of *M. pomifera* triggered in pupils and students ages 9–23, at first sight, more interest than a choice of unusual plants and plant parts that included the carnivorous sundew (*Drosera aliciae*) and the sensitive plant (*Mimosa pudica*).

Striking features may be a key not only to a successful exploration and accessibility of content, but also to positive attitudes in students. Schussler and Olzak (2008) found that students recalled “atypical” carnivorous plants particularly well, making these species suitable to motivate students for plant work. Strgar (2007) found in work with plants that the element of surprise substantially raised the level of interest in learners. Surprise can be caused by plants that look unfamiliar or offer unusual multi-sensory experiences (Robischon, 2016), a story, or unexpected insights. Generally, “cognitive novelty” is believed to be an important factor influencing students’ experience of fieldwork (Cotton, 2009) and can be expected to both stir “epistemic curiosity” and reward that curiosity with the satisfying feeling of having learned something new.

Considering that interest in animals has been found to be greater than interest in plants (Lindemann-Matthies, 2005), botanical interest may be enhanced by an ecological connection to the animal world. This may be especially fruitful if a gigantic creature is part of the “story,” as large body size appears to add to animals’ appeal to people (Ward et al., 1998). Apparently, the allure of “giants” to some extent carries over to large plants too. Lückmann and Menzel (2014) found that teenagers knew trees better than herbs, suggesting a stronger interest in larger woody plants. Further, a link to large creatures of the deep past has frequently been pointed out as a factor that can create fascination and hold attention (Chang, 2000; Vujakovic, 2016 [2013], p. 214; Salmi et al., 2017). The paleoecological dimension in this work was clearly new to most students, who also appeared not to be used to linking information from other dimensions of knowledge to “school” or “college” biology. In any case, it appears to be fruitful for there to be a “story” to the plant, and even more so if some element of the story becomes tangle in the object. Finally, all these “factors of fascination” are brought together in plants with traits that are

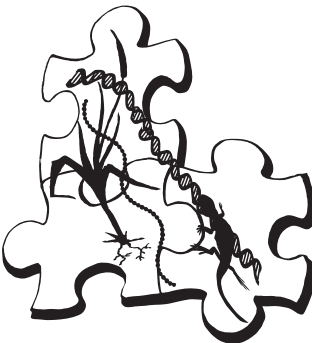
thought to be adaptations to the impact of extinct large animal species – an invitation to the learning adventure of making sense of the seemingly nonsensical.

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