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The modern and fossil record of farming behavior

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Abstract.—Farming is a behavior in which an organism promotes the growth and reproduction of other organisms in or on a substrate as a food source. A number of trace fossils have been suggested to record the occurrence of farming behavior. These include the deep-sea graphoglyptid trace fossils, proposed to be microbial farms on the seafloor, and terrestrial fossil social insect nests thought to represent fungicultural behavior. The presumed farming behavior of graphoglyptids is the basis of the ethological category agrichnia. Four criteria have been proposed as diagnostic of farming behavior, and these can be applied to both observed modern and proposed trace fossil examples of farming behavior. The evidence for farming behavior in the social insect trace record is strong but is much weaker in the case of graphoglyptids. The use of agrichnia as an ethological category should be limited to well-supported cases.

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Introduction

Although intensive agriculture is characteristic of humans, a number of species of animals have also been described as engaging in farming. The most familiar of these are the leaf-cutter ants (Mueller and Gerardo 2002), which grow and harvest fungal gardens. Similar behavior (fungiculture) occurs among termites and beetles (Mueller et al. 2005).

Drawing a comparison to terrestrial fungiculture (“mushroom gardens”), Seilacher (1977) suggested that some graphoglyptids, complex burrows often found in turbidites, represented analogous farming systems where unknown animals cultivated microbes within deep-sea floor sediments. Seilacher (1977) initially considered most graphoglyptids to be traps for migrating microorganisms, as suggested for *Paraonis* burrows by Röder (1971; cf. Lehane and Ekdale 2013b), and further speculated that tunnel systems with multiple outlets could be further developed into farms. In particular, he proposed that the hexagonal network of *Paleodictyon* efficiently covered an area and allowed for water flow through the structure, capturing nutrients and allowing the farming of bacteria (Rona et al. 2009). Ekdale et al. (1984) named the trace fossil ethological category “agrichnia” to include such inferred farming structures.

Over time, the use of agrichnia as an ethological category has become virtually inseparable from “graphoglyptids” (Fuchs 1895), a morphological group of deep-sea trace fossils (Uchman 2003; Uchman and Wetzel 2012; Vallon et al. 2016). Uchman and Wetzel (2012) defined agrichnia as burrow systems “produced for the trapping or farming of microbes or other very small organisms”; they are characterized as being “shallow, mostly delicate, regularly patterned; and “most are termed ‘graphoglyptids.’” Uchman (2003) recognized 27 ichnogenera and 67 ichnospecies as graphoglyptids, of which the best-known examples are *Paleodictyon*, *Cosmorhaphe*, *Belorhaphe*, *Helminthorhaphe*, and *Spirorhaphe*. The list of ichnotaxa that have fallen under agrichnia has been variously revised and modified (Vallon et al. 2016), but has generally included many, if not all, graphoglyptids, plus occasionally a few other ichnotaxa for which farming behavior has been proposed (e.g., *Zoophycos*; Löwemark 2015). In contrast, Miller (2014) laid out criteria for defining graphoglyptids that do not require a farming interpretation; for example, complex geometry, usually occurring in oligotrophic settings, and preserved as casts on the soles of turbidite beds.

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Other papers have suggested that farming and trapping can be better distinguished. Lehane and Ekdale (2013b) separated putative trapping traces as a distinct ethological category "irretichnia," a distinction accepted by Vallon et al. (2016), and demonstrated that *Paraonis* did not engage in trapping. Miller (2014) proposed such a trapping mechanism for *Paleodictyon*.

Here, we will discuss what defines "farming" as a behavior and describe proposed criteria for its recognition. In this context, we will review instances of farming behavior in modern marine and terrestrial organisms. Following this, we will then describe and assess suggested cases of farming in the trace fossil record, including graphoglyptids, and will make suggestions on the continued use of the term "agrichnia."

Definition of and Identifying Criteria for Farming

We define agriculture or farming as the active generation in or on a substrate of a useful food crop from less nourishing precursor materials over time. For example, human farming broadly comprises the transformation of inedible soil mineral and organic matter into edible plants. Similarly, leaf-cutter ant farming transforms inedible leaves within their burrows into edible fungus. Farming can be considered a form of symbiosis, whereby one organism breeds and promotes the growth of another for its use as a food source (Mueller 2002; Aanen 2006). Farming also is associated with territoriality, as the farmer protects an area where food generation takes place. Because farming is an active behavior and thus has a metabolic cost, it will only be used when the energetic value of the harvested food exceeds this cost.

Farming can be distinguished from trapping, storing, or caching of already edible items, which does not involve a transformation of the materials to make them comestible (Lehane and Ekdale 2013b). Additionally, although endosymbiotic relationships also involve the generation of food for host organisms, we exclude these cases from agricultural behavior, because they do not involve active propagation and harvesting of a food source on an external substrate.

Mueller et al. (2005), in their review of insect agriculture, proposed four criteria to characterize agriculture in the animal kingdom: *habitual planting*, or seeding the desired crop on new substrates; *cultivation*, actively maintaining conditions to promote the crop's growth and well-being; *harvesting* the crop for consumption; and obligate or near-obligate *nutritional dependency* on the crop, so that lack of crop threatens the survival or reproductive success of the farmer. Based on these criteria, these authors considered fungiculture in social insects, as well as human farming, to represent the most clear-cut examples of this behavior. Other cases, because they only partially filled the criteria, were deemed "proto-agricultural."

Schultz et al. (2005) focused on fungiculture and considered agricultural behavior on a spectrum between low- and high-level cultivation strategies. Low-level strategies involve only simple modifications of the ecosystem to promote the spread and growth of the crop to be consumed. Some forms of ecosystem engineering may grade into low-level cultivation. Many organisms promote positive feedbacks directly or indirectly benefiting their food organisms (such as herbivores' fertilization of plants), that are akin to cultivation, but without deliberate planting or a high degree of dependency on the results of the cultivation behavior. These effects are often diffuse across an area, rather than territorially bounded, as in a farmer–crop mutual relationship. Higher-level strategies involve much more complexity and effort across the various stages of farming, including cultural transmission of the crop, fertilization, defense and protection, or harvesting (Schultz et al. 2005). In many cases, as for insect-farmed fungi (Mueller et al. 2005) and damselfish-farmed algae (Hata and Kato 2006), coevolution between crop and farmer has advanced to the point that farmed cultivars are genetically distinct from their free-living relatives.

Agriculture in Extant Organisms

The concepts of Mueller et al. (2005) and Schultz et al. (2005) can be used to assess proposed examples of farming in extant organisms (Table 1). There are many reported cases of agricultural behavior in extant animals, especially among insects. Fungiculture evolved once among attine ants (tribe Attini, which includes the leaf-cutters) and the macrotermitine termites and seven times in ambrosia beetles (Mueller et al. 1998, 2005; Farrell et al. 2001; Aanen et al. 2002; Mueller and Gerardo 2002). All these insect groups construct characteristic chambers or tunnels to contain the fungus, which is grown on fecal matter or plant debris within their nests, in the case of ants and termites, or on the tunnel walls of woody substrates, in the case of beetles. The fungal crops may be a carefully maintained monoculture (Aanen 2006) or a mix of cultivars. These can be passed along not only from one generation to the next, but in some situations can be shared among different farming species (Aanen et al. 2002; Mueller and Gerardo 2002). These insects use great care in cultivation, including controlling their crops' weedy competitors, parasites, and pathogens chemically or through maintenance of other symbionts (Fernández-Marín et al. 2009). Such farming insects are generally social to some extent, often having multiple related individuals working together with some division of labor to increase efficiency. These examples meet all the criteria of Mueller et al. (2005) and represent the high-level strategies of Schultz et al. (2005)

Other examples of agricultural behavior described across various taxa have been noted (Table 1). Some meet Mueller et al.'s (2005) criteria and can be considered high-level strategies, but most are either missing or have less developed forms of the criteria and can be considered lower-level cultivation strategies.

A social bee described by Menezes et al. (2015) cultivates fungus in its brood cells on semiliquid food regurgitated by workers. The fungus is eaten by larvae and is required for their survival. The fungus is transmitted over generations through inoculated building materials recycled for new cells or transported to new nests. Unlike the termites and ants, however, the worker bees do not tend the fungal crop after deposition of the precursor.

Larval feeding was also described by Toki et al. (2012), who discussed nonsocial lizard beetles that cultivate yeast for their larvae in dead bamboo culms. They considered this case to fit the criteria of Mueller et al. (2005) of farming. Although they considered their study species to demonstrate relatively high-level cultivation, they suggested that overall, nonsocial taxa tend to have lower-level or more "primitive" farming than social taxa.

Similarly, Rohfritsch (2008) discussed gall midges that inoculate host plants with a fungus, thought to help gall formation, that also provides food for the larvae living inside the gall. A leaf-rolling weevil that inoculates rolls of leaf material (its larvae's food source) with symbiotic fungal spores was portrayed by Kobayashi et al. (2008), who considered that although the fungus helps improve the quality of the food, perhaps with antimicrobial properties, it itself is not the food source.

Many suggested examples of agricultural behavior have been documented among marine organisms, although none meet all of the criteria for farming or demonstrate higher-level cultivation. The grazing salt marsh snail *Littoraria irrorata* engages in a form of proto-farming or low-level facultative cultivation by wounding salt marsh grass with its radula and feeding on the resulting fungal growth that develops (Silliman and Newell 2003). The snails concentrate their fecal pellets, rich in nitrogen and undigested fungal hyphae, onto wounds to stimulate more fungal growth. Silliman and Newell (2003) suggested that fungal farming may be common but overlooked, as it may be easy to promote fungal growth on wounded, dead, or decaying plant material.

Damselfish also engage in farming of algae, by actively maintaining certain desirable species to be harvested, weeding out other unpalatable species inside their territory, and defending their crop from intruding grazers (Lassuy 1980; Hata and Kato 2002, 2003, 2006). Hata and Kato (2006) considered damselfish algal farming to be the second recorded example, after humans, of a consumer growing plants rather than fungi in an obligate cultivation symbiosis and the first case known in a marine setting. However, it appears the fish

TABLE 1. Proposed examples of modern organisms that farm, their crops, and their fit toward the four criteria of Mueller et al. 2005 (see text for details).

Farmer	Crop	Farming criteria				Reference
		Habitual planting	Cultivation	Harvesting	Nutritional dependency	
Attine ants	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Macrotermitine termites	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Ambrosia beetles	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Social bee	Fungi	Yes	Yes	Yes	Yes	Menezes et al. 2015
Lizard beetles	Fungi	Yes	Suggested	Yes	Yes	Toki et al. 2012
Gall midges	Fungi	Yes	No	Yes	Yes	Rohfritsch 2008
Weevils	Fungi	Yes	No	No	No	Kobayashi et al. 2008
Marsh snails	Fungi	No	Yes	Yes	No	Silliman and Newell 2003
Damselfish	Algae	No	Yes	Yes	Yes	Hata and Kato 2006
Limpets	Algae	No	Yes	Yes	No	Stimson 1973; McQuaid and Froneman 1993; Plagányi and Branch 2000
Ragworms	Cordgrass	Yes	No	Yes	No	Zhu et al. 2016
Lugworms	Microbes	No	Yes	Yes	No	Hylleberg 1975; Reichardt 1988; Ashforth et al. 2011
Nereid polychaetes	Algae	Yes	No	Suggested	No	Woodin 1977
Callianassid shrimp	Bacteria	Yes	Yes	Not demonstrated	Not demonstrated	Ott et al. 1976; Bromley 1996
Cryptochirid crabs	Algae	Not demonstrated	Proposed	Yes	Not demonstrated	Carricart-Ganivet et al. 2004
Slime molds	Bacteria	Yes	No	Yes	No	Brock et al. 2011, 2017
Nematodes	Bacteria	Yes	No	Yes	No	Thutupalli et al. 2017
Fungi	Bacteria	Yes	Yes	Yes	Not tested	Pion et al. 2013

do not engage in habitual planting, as the algae can spread and grow unaided.

Algal gardening is also used to describe the situation wherein territorial grazing limpets promote increased regeneration and growth of the algae they feed on. They provide added nutrients from excretion, as well as protection of the algae from competitors and other grazers (Stimson 1973; McQuaid and Froneman 1993; Plagányi and Branch 2000). There does not appear to be habitual planting or nutritional dependency.

The omnivorous ragworm *Hediste diversicolor* opportunistically engages in collecting, burying, and sprouting cordgrass seeds in its burrows (Zhu et al. 2016). As husked seeds are generally not edible to it, in contrast to the sprouts, such "gardening" behavior provides a form of supplementary nutrition on top of the more abundant, but often less nutritious, marine detritus in the worm's habitat. Zhu et al. (2016) suggested that burying and sprouting seeds for food might be present in other seed-caching animals, such as rodents that also consume seedlings or seed-caching ants (Silva et al. 2007).

Lugworms in the sandy littoral zone have been described as performing "gardening" of microbes for food (Hylleberg 1975; Reichardt 1988; Ashforth et al. 2011). Bacterial growth is stimulated by irrigation and oxygenation within their J-shaped living burrows, as well as by the worm's waste products. The microbial growth produced by the lugworm's gardening provides a food source supplemental to nutrients obtained by deposit feeding or suspension feeding (Hylleberg 1975; Riisgard and Banta 1998). However, the lugworm does not appear to deliberately emplace this food source.

Woodin (1977) discussed nereid polychaetes attaching drift algae to their tubes and allowing the algae to grow. They considered it to be algal gardening in that it provides food, as well as other benefits such as oxygenation, shade, and cooling. However, a large degree of harvesting and nutritional dependency was not shown.

Callianassid burrowing shrimp (*Upogebia*, *Callianassa*) have been proposed to garden microbes from decaying plant matter carried and incorporated into the burrow walls (Ott et al. 1976; Bromley 1996). Ott et al. (1976) suggested that *Upogebia pusilla* was culturing bacteria for food in decaying leaf matter in the irrigated, oxygenated burrow walls. That these cultured microbes provide an important food source was not conclusively demonstrated, only suggested.

Cryptochirid crabs (gall crabs) are associated with corals and can modify their growth by forming "galls" or "pits" on some of them. Organic materials are deposited in the pit, supporting the growth of filamentous algae, which are then fed on by the crabs (Carricart-Ganivet et al. 2004). Similar algae are found in the gut contents of the crabs, though the degree of cultivation, planting, and dependency on it as food was not specified. These crab-induced pits on coral are also found in the fossil record (Klompmaker et al. 2016) and can be assumed to have similarly supported algal growth and harvesting.

Bromley (1996) suggested additional cases in which various detritus-feeding and suspension-feeding invertebrates promote microbial growth nearby or in their burrows, through fertilization with fecal pellets or organic matter packed in burrow walls and lining and/or irrigation and oxygenation. He considered these cases to be possible gardening if the resulting microbial growth can be a resource consumed by the animal. Examples given include the echiurid worm *Echiurus echiurus*, the deep-sea bivalve *Abra longicallus*, and the terebellid polychaete *Amphitrite ornate.* However, because no habitual planting or significant harvesting or nutritional dependency have been demonstrated, many of these ideas remain speculative. Wheatcroft (1991), in his review of Bromley (1990), considered the idea of gardening in these cases to be unsupported, saying that no energetic importance for the burrow residents from microbial growth has been reliably demonstrated.

Farming also occurs in simpler organisms. The social amoeba, or slime mold, *Dictyostelium discoideum* farms bacteria (Brock et al. 2011, 2017). Rather than consuming all bacteria in an area, some are saved and incorporated into the slime mold's fruiting bodies, to be dispersed to seed new ground. These farmers even carry defensive symbionts to protect their bacterial crops from non-farmers who would exploit their resource (Brock et al. 2013). The nematode worm *Caenorhabditis elegans* was likewise found by Thutupalli et al. (2017) to engage in farming of *Escherichia coli* bacteria, distributing the bacteria either on its skin or through the digestive tract to new places where it can grow.

Both nematodes and slime molds illustrate the cost/benefit aspects of faming; in both groups, individuals that farm coexist with other individuals of the same species that do not. The advantage of farming is dependent on the situation. For slime molds, Brock et al. (2011) found that farming individuals have an advantage relative to non-farmers only on sites where no bacteria already exist. Likewise, for the nematode, Thutupalli et al. (2017) showed that in some situations, non-farmers freeload off the food spread by farmers and thus are at an advantage. Interestingly, Thutupalli et al. (2017) described how *C. elegans* can disperse *Dictyostelium discoideum* and use it too as a food source, raising the intriguing possibility of a situation in which an organism farms an organism that itself is a farmer.

Fungi may farm bacteria too. Pion et al. (2013) described the fungus *Morchella crassipes* farming the soil bacterium *Pseudomonas putida* by dispersing it through the fungal network, nourishing it through exudates, and harvesting it. The researchers were not able to test for nutritional dependency.

Agriculture in the Fossil Record

Recognizing Agriculture in the Fossil Record.— The four criteria of Mueller et al. (2005) suggest an approach to assessing the presence of farming behavior in the fossil record. First, habitual planting might be inferred by co-occurrence of the animal, the animal's traces, and the symbiotic crop. For example, fungal hyphae among putative fossil leaf-cutter ant nests have been found in situ (Genise et al. 2013). Obligate symbioses can lead to some crops being absent in free-living form and only found in association (Mueller et al. 2005). However, showing that an animal planted, rather than utilized a preexisting food source may be difficult. Crops must be distinguishable from organic matter that was not planted and ended up inside a trace for other reasons. Crop carrying can result in fossilizable morphological adaptations; for example, mycangia (pouches used to carry fungal associates) are known from a variety of farming insects, such as ants, ambrosia beetles, and weevils, though more study is needed to distinguish which carried fungi as crops (Toki et al. 2012). Planting as an action may also leave bioglyphs, but this may be difficult to distinguish from other activities involved in burrowing or general feeding.

Second, cultivation might be shown by the presence of high inferred crop productivity near traces, though these could result from animals seeking out high-productivity areas for food sources without having farmed them. Resources added to the crop, such as fecal pellets or plant debris, may preserve in traces, but must be distinguished from burrow lining and wall material that is used for construction only. For example, the trace fossil *Ophiomorpha* is attributed to thalassinidean shrimp that pack their fecal pellets into their burrows to construct knobby walls (Frey et al. 1978), which may result in microbial growth (Bromley 1996). However, this has not yet been shown to be deliberate fertilization. A chemically different microenvironment needed for the crop can exist (e.g., aerating a burrow to create an oxic environment for bacteria), though non-farming activities can also change chemistry. Protecting and maintaining the garden from competitors like "weeds" or other grazers trying to eat the crop might also involve an actively mobile animal staying in and around the farm to tend and guard it in a way that may leave distinctive traces. Neoichnological research could potentially test whether weeding, pruning, and guarding crops can leave different traces on the substrate than non-farming behaviors.

Third, the act of harvesting the crop might leave traces, perhaps bioglyphs as the farmer collects and consumes the crop on a substrate. But this should be distinguished from consumption of stored or cached food that was not grown there.

Finally, nutritional dependency is a criterion unlikely to be directly testable with fossils. It can be shown in the modern record with gut contents or experiment and observation that the farmer starves or is unable to thrive without the crop in question. Highly derived modifications or specializations in body fossils can suggest a high reliance on farming as a life mode.

There are some obvious difficulties in applying these criteria to fossils, mostly imposed by taphonomy. Most of the crops used by extant farming organisms are not heavily mineralized and are thus low in preservational potential. However, there are some fossil examples, for example, fungal hyphae, which can be biomineralized (Genise et al. 2010, 2013). Biomarkers also could possibly demonstrate their presence. A farming structure might in many cases preserve more easily than the crop. A major consideration is the medium or substrate on which the agricultural crop itself grows or a structure, like a tunnel or chamber, that houses the farm. In many cases, the substrate is organic with poor preservation potential, such as the wood where ambrosia beetles grow their fungi. Structures composed of or made in sediment, such as the chambers of fungus-growing ants and termites, have higher potential. These include the nests and structures found and studied by Laza (1982), Genise et al. (2010, 2013), Roberts et al. (2016), and Duringer et al. (2006, 2007).

In many cases, modern analogues could be used to infer farming and provide a potential constraint for other examples. If lugworms garden microbes in their burrows (e.g., Hylleberg 1975; Reichardt 1988; Ashforth et al. 2011) or cryptochirid crabs farm algae in pits on coral (Carricart-Ganivet et al. 2004), then trace fossils attributed to them might also represent this behavior. Phylogenetic bracketing of clades known to farm might be useful here. The ages of phylogenetic lineages known to farm, as well as their biogeography, can help constrain the times and places that farming lineages existed in (e.g., the amber fossil record of leafcutter ants; Baroni Urbani 1980).

Trace Fossils Proposed as Examples of Agriculture.—As is the case with modern organisms, the best fossil evidence for farming is associated with social insects. Interestingly, these traces have never been explicitly assigned to the ethological category agrichnia.

Laza (1982) described the ichnospecies *Attaichnus kuenzelii* in the Miocene as a leafcutter ant nest; this was also the first described record of insect fungiculture. These fossil nests were later reexamined in more detail by Genise et al. (2013). These authors reaffirmed that the nests belonged to fungus growers, in particular, *Acromyrmex* or *Trachymyrmex* ants. The presence of fungal hyphae was confirmed by SEM imaging.

Ancient termite nests in the Miocene and Pliocene of the Chad Basin were discussed by Duringer et al. (2006, 2007). They attributed three of their described ichnospecies to the fungus-growing macrotermitine termites. One of their ichnospecies, *Microfavichnus alveolatus*, a trace that is alveolar-like in structure and contains small pellets, was interpreted as a fungus comb (the honeycomb-like structure where the fungi grow) and its associated mylospheres. Mylospheres are the termites' ball-like fecal pellets used to construct the comb and are newly added to the comb as older parts of the comb are eaten.

Rhizolith balls containing tube and tunnel structures have been found in the Cretaceous of Argentina (Genise et al. 2010). Genise et al. (2010) hypothesize that these rhizolith balls may represent an early stage in fungiculture in social insects; they were first building nests and chambers around roots to take advantage of root-associated mycorrhizal fungi; these later became a farmed crop.

We have examined the literature on graphoglyptids in an attempt to determine whether any of the criteria suggested by Mueller et al. (2005) have been met or whether there is any direct evidence to support the interpretation of farming behavior. Most graphoglyptid genera have not been discussed individually with regard to evidence of farming, but were assigned an agricultural function by morphological association with *Paleodictyon* and related "complex" graphoglyptids discussed in Seilacher (1977). Assignment of graphoglyptids to agrichnia by later authors for the most part ultimately derive from this source.

Proposed evidence for the criterion of cultivation by Seilacher centers on network morphology, where increased surface area and multiple outlets allowed ventilation, promoting microbial growth. An argument for nutritional dependency has also been tied to habitat, with farming suggested to increase food supply in the resource-poor deep sea (Seilacher 1977, 2007). No description of habitual planting is discussed nor is the manner in which the tracemaker harvested the crop. Debates over assignments of agrichnial behavior to these traces, where the tracemaker is unknown and heavily disputed, have tended to be theoretical and interpretive (Honeycutt and Plotnick 2005; Seilacher 2007; Lehane and Ekdale 2013a; Miller 2014) rather than observational. Lehane and Ekdale (2013a) used the dissimilarity in fractal dimension of graphoglyptids compared with other trace fossils assigned to mining and grazing to argue for an agrichnial interpretation. They also considered that the ability of bacteria to break down the cellulose component of deep-sea debris, relative to the inability of most animals to do so, makes bacteria-cultivating activity likely. Direct evidence of farming in the only extant form studied, *Paleodictyon nodosum*, has so far have remained elusive (Ekdale 1980; Rona et al. 2009). Seilacher's (1977) original argument, that the geometry of *Paleodictyon* efficiently covered an area and enhanced ventilation, are also consistent with other interpretations, such as osmotrophy or brooding. Although farming behavior is frequently assumed or suggested for other graphoglyptids, we have found no compelling evidence to support this interpretation. Bioglyphs, which might indicate cultivation or harvesting, are unlikely to preserve, given that graphoglyptids are typically preserved at the base of turbidite sands in hyporelief (Buatois and Mángano 2011).

Aside from graphoglyptids, the benthic ichnogenus *Zoophycos* has also been proposed to represent microbial farming, alongside other explanations such as food caching, based on evidence of microbial growth (Löwemark 2015). However, Löwemark also notes that there is not yet evidence that such a resource was being actively harvested and depended on.

Discussion

Modern examples that best fit Mueller et al.'s (2005) criteria for agriculture unambiguously are terrestrial, with a few shallow-marine examples that fit only some of the criteria. The lack of demonstrable examples of farming in deep-water environments might be an artifact of sampling, given the lack of accessibility. Alternatively, oceanic habitats may be less suited for agricultural activities. Hata and Kato (2006), in their discussion of damselfish algal farms, suggest that habitual planting might be less necessary in marine settings where crop propagules can easily disperse through water to colonize new substrates. Similarly, Grosberg et al. (2012) also mention that animal-mediated dispersal of gametes or propagules, such as pollen or seeds, are well known in the terrestrial realm but uncommon in the sea. This may also be true of the propagules of farmed crops, and thus farming might be less developed as a lifestyle in water.

The "mushroom garden"-graphoglyptid analogy (Seilacher 1977) inspired the erection of agrichnia as a category (Ekdale et al. 1984). We see, however, no convincing evidence that graphoglyptids are the product of farming. In comparison, fossil nests assigned to leaf-cutter ants are well constrained by morphology and comparisons to similar modern nests (Genise et al. 2013). Inference of agricultural behavior needs to be informed by neoichnology and behavioral biology (Plotnick 2012; Vallon et al. 2016), and the preservation potential of verified examples of modern animal farming should be studied.

It is better to restrict agrichnia to well-supported cases; for example, the fossil fungus-growing termite nests as described in Duringer et al. (2006, 2007) and Roberts et al. (2016), fossil leaf-cutter ant nests (Laza 1982; Genise et al. 2013). and possibly the rhizolith balls of Genise et al. (2010). Demonstration of farming in graphoglyptids will depend on additional evidence, possibly through additional deep-sea submersible studies of modern examples (Ekdale 1980; Rona et al. 2009)

Terrestrial social insects and their traces provide the best examples and evidence for farming in the fossil record, showing strong evidence for farming on land by the Cenozoic, if not the late Mesozoic. And certainly, by the Holocene, they are joined by the human farmers who have dramatically changed the landscapes of the biosphere on Earth.

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