

1 **Convergent Evolution of Agriculture in Bilaterian Animals: An Adaptive Landscape Perspective**

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In all cases of two very distinct species furnished with apparently the same anomalous organ, it should be observed that, although the general appearance and function of the organ may be the same, yet some fundamental difference can generally be detected. I am inclined to believe that in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection, working for the good of each being and taking advantage of analogous variations, has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor.

—Charles Darwin, *On the Origin of Species* (1859, 193–194)

In 1859 Darwin faced the dilemma of dealing with the problem of convergence in biological evolution—that is, of accounting for morphological traits and instinctive behaviors that were “almost identically the same in animals so remote in the scale of nature, that we cannot account for their similarity by inheritance from a common parent, and must therefore believe that they have been acquired by independent acts of natural selection” (Darwin 1859, 235–236). In an attempt to explain to his readers how natural selection might produce convergent biological evolution, Darwin (1859, 193–194) called upon the human analogy that “two men have sometimes independently hit on the very same invention”—a phenomenon he was very well aware of as the theory of natural selection itself had been independently formulated by both Darwin and Wallace, just as the logic of the calculus had been independently formulated by both Newton and Leibniz, and so on throughout human history.

Lycett (2011, 157) has pointed out that in 1859, when Darwin used the analogy of two men independently creating the very same invention, he was de facto giving an “example of convergence within the realm of human technology.” The analysis of convergent evolution in a very specific form of human technology—the creation of similar stone tools in different human cultures—was the subject of the 33rd Altenberg Workshop in Theoretical Biology at the Konrad Lorenz Institute for Evolution and Cognition Research (O’Brien, Buchanan, and Eren 2018).

The 38th Altenberg Workshop in Theoretical Biology at the KLI continues that research focus by examining the convergent evolution of agriculture—except this time the focus is not only on the convergent evolution of agricultural techniques in different human cultures, but also on the convergent evolution of agricultural techniques in different clades of animals that are not human. Agriculture has evolved, independently and convergently, in

nine phylogenetic lineages of bilaterian animals: actinopterygian vertebrates, sarcopterygian vertebrates, polychaete annelids, patellogastropod molluscs, neogastropod molluscs, littorinoid molluscs, polyneopteran insects, hymenopteran insects, and coleopteran insects (table 1.1). The analysis of that agricultural convergence from an adaptive landscape perspective is the subject of this chapter.

Table 1.1
Phylogeny of the convergent evolution of agriculture in bilaterian animals

Metazoa
– Ctenophora
– †Archaeocyatha
– Porifera
– Parahoxozoa
– – Placozoa
– – Eumetazoa
– – – Cnidaria
– – – BILATERIA (agriculturalist lineages 1–9)
– – – – Unnamed clade
– – – – – Xenoturbellida
– – – – – Acoelomorpha
– – – – – Nemertodermatida
– – – – – Acoela
– – – – – Nephrozoa
– – – – – DEUTEROSTOMIA (agriculturalist lineages 1–2)
– – – – – Ambulacraria
– – – – – Echinodermata
– – – – – Hemichordata
– – – – – CHORDATA
– – – – – Vertebrata
– – – – – Gnathostomata
– – – – – Osteichthyes
– – – – – ACTINOPTERYGII (agriculturalist lineage 1)
– – – – – Neopterygii
– – – – – Teleostei
– – – – – Euteleostei
– – – – – Eurypterygii
– – – – – Ctenosquamata
– – – – – Acanthomorpha
– – – – – Acanthopterygii
– – – – – Percomorpha
– – – – – Ovalentaria
– – – – – Pomacentridae
– – – – – Pomacentrinae (<i>Stegastes nigricans</i>) lineage 1
– – – – – SARCOPTERYGII (agriculturalist lineage 2)
– – – – – Tetrapodomorpha
– – – – – Tetrapoda
– – – – – Reptiliomorpha

Table 1.1
(continued)

----- Amniota
 ----- Synapsida
 ----- Therapsida
 ----- Cynodontia
 ----- Mammalia
 ----- Theria
 ----- Eutheria
 ----- Boreoeutheria
 ----- Euarchontoglires
 ----- Primates
 ----- Anthropoidea
 ----- Catarrhini
 ----- Hominoidea
 ----- Hominidae
 ----- Homininae
 ----- Hominini (*Homo sapiens*) **lineage 2**
 ----- PROTOSTOMIA (agriculturalist lineages 3–9)
 ----- SPIRALIA (agriculturalist lineages 3–6)
 ----- Platyrochozoa
 ----- Lophotrochozoa
 ----- ANNELIDA (agriculturalist lineage 3)
 ----- Polychaeta
 ----- Aciculata
 ----- Phyllodocida
 ----- Nereididae (*Platynereis dumerilii*) **lineage 3**
 ----- MOLLUSCA (agriculturalist lineages 4–6)
 ----- Eumollusca
 ----- Ganglioneura
 ----- Visceroconcha
 ----- Gastropoda
 ----- Patellogastropoda
 ----- Patelloidea
 ----- Scutellastridae (*Scutellastra longicosta*) **lineage 4**
 ----- Caenogastropoda
 ----- Hypso gastropoda
 ----- Neogastropoda
 ----- Buccinoidea
 ----- Nassariidae (*Bullia digitalis*) **lineage 5**
 ----- Littorinimorpha
 ----- Littorinoidea
 ----- Littorinidae (*Littoraria irrorata*) **lineage 6**
 ----- ECDYSOZOA (agriculturalist lineages 7–9)
 ----- Panarthropoda
 ----- Arthropoda
 ----- Euarthropoda

(continued)

Table 1.1
(continued)

-----	Mandibulata
-----	Pancrustacea
-----	Hexapoda
-----	Insecta
-----	POLYNEOPTERA
-----	Isoptera
-----	Termitidae
-----	Macrotermitinae (<i>Odontotermes formosanus</i>) lineage 7
-----	HOLOMETABOLA
-----	HYMENOPTERA
-----	Formicidae
-----	Myrmicinae
-----	Attini
-----	Attina
-----	Neoattina (<i>Atta texana</i>) lineage 8
-----	COLEOPTERA
-----	Curculionidae
-----	Scolytinae
-----	Xyleborini
-----	<i>Ambrosiodmus/Ambrosiophilus</i> clade
-----	(<i>Ambrosiophilus atratus</i>) lineage 9

Sources: Phylogeny modified from Nielsen (2012), Near et al. (2013), Bourguignon et al. (2014), Misof et al. (2014), Struck et al. (2014), Benton (2015), Li et al. (2015), and Branstetter et al. (2017).

Note: Major clades containing agriculturalist animals are given in capital letters. Extinct taxa are marked with a dagger “†.”

The Phenomenon of Convergent Evolution in Agricultural Behaviors

A list of the farming species and their agricultural crops is given in table 1.2. Five of the farming lineages cultivate plants, and four cultivate fungi. Of the plant crops, four lineages farm marine algae, and one lineage farms land plants. Of the fungal crops, three lineages farm land fungi, and one lineage farms marine fungi.

A list of 12 agricultural traits is here used to create a comparative measure of the agricultural complexity found in the nine independent lineages of agriculturalist animals, modified from the list of agricultural traits found in insects and humans compiled by Mueller et al. (2005). These traits are: (A) preparing the substrate for growing crops, (B) planting the crops, (C) usage of naturally occurring organic fertilizers for the crops, (D) usage of artificially produced chemical fertilizers for the crops, (E) protecting the crops from raiders, (F) weeding invasive species out of the crops, (G) using chemicals for pest control of parasites or diseases in the crops, (H) using living microbes for pest control of parasites or diseases in the crops, (I) development of a one-way symbiosis between the farming species and its crop (either the crop is obligately dependent on the farmer, or the farmer is obligately dependent on the crop), (J) development of a two-way mutualism between the farming species and its crop (both farmer and crop are obligately dependent

Table 1.2
Convergent agricultural lineages, their farming animals, and their crops

Lineage	Farmer	Crop
1	Damselfish (<i>Stegastes nigricans</i>)	Photosynthetic marine red alga (<i>Polysiphonia</i> sp. 1)
2	Human primate (<i>Homo sapiens</i>)	Photosynthetic terrestrial plants (numerous species)
3	Polychaete annelid worm (<i>Platynereis dumerilii</i>)	Photosynthetic marine algae (several species)
4	Limpet snail (<i>Scutellastra longicosta</i>)	Photosynthetic marine brown alga (<i>Ralfsia verrucosa</i>)
5	Whelk snail (<i>Bullia digitalis</i>)	Photosynthetic marine green alga (<i>Eugomontia sacculata</i>)
6	Periwinkle snail (<i>Littoraria irrorata</i>)	Saprophytic intertidal fungi (species of <i>Phaerosphaeria</i> and <i>Mycosphaerella</i>)
7	Macrotermite termite (<i>Odontotermes formosanus</i>)	Saprophytic terrestrial fungi (species of <i>Termitomyces</i>)
8	Leaf-cutter ant (<i>Atta texana</i>)	Saprophytic terrestrial fungus (<i>Leucoagaricus gonglyophorus</i>)
9	Ambrosia beetle (<i>Ambrosiophilus atratus</i>)	Saprophytic terrestrial fungus (<i>Flavodon ambrosius</i>)

on one another), (K) the usage of artificial selection to improve the crops, and (L) the usage of genetic engineering to improve the crops.

The distribution of these 12 agricultural traits across the nine lineages of agriculturalist animals is given in table 1.3. The metric of “agricultural complexity” is here defined as the number of agricultural traits found in a given lineage of agriculturalist animals. The agricultural-complexity level achieved by each of the nine agriculturalist lineages is given in the “sum of convergent agricultural behaviors” row at the bottom of table 1.3. In this summation a two-way obligate mutualism between the farmer and the crop (trait J) is counted as being the sum of two one-way obligate symbioses (trait I); that is, trait I (Y) + trait I (Y) = trait J (2Y).

Two of the agriculturalist lineages are found in the clade of the deuterostomes—the damselfishes and humans (table 1.1). Humans have complex agricultures that can exhibit nine of the 12 agricultural traits chosen here to measure differential agricultural complexity (table 1.3). In contrast to some other agriculturalist animals, humans and their crops have a generally facultative relationship with one another rather than an obligate one, and humans do not use (as yet) microbial pest-control methods (table 1.3; see also the discussion in Mueller et al. 2005). Human agriculture is itself convergent, in that several populations of humans made the transition from hunter-gatherers to agriculturalists independently of each other around the world about 10,000 years ago (Gupta 2004; chapter 10, this volume). Of the other agriculturalist animals only the clades of the ambrosia beetles and damselfishes have exhibited numerous independent convergences in agricultural evolution: 11 independent lineages of ambrosia beetles have arisen in the past 50 million years (Jordal and Cognato 2012; Li et al. 2015; chapter 7, this volume), and, in the damselfishes, “multiple independent transitions to algaculture have occurred” (Aanen 2010, 3).

Table 1.3
Convergent evolution of specific agricultural traits in nine lineages of bilaterian animals

Behavior	Phylogenetic lineage								
	1	2	3	4	5	6	7	8	9
A. Substrate preparation for crops	Y	Y	Y	Y	Y	Y	Y	Y	Y
B. Planting the crops	n	Y	Y	n	n	Y	Y	Y	Y
C. Fertilizing the crops: organics	n	Y	Y	Y	n	Y	Y	Y	n
D. Fertilizing the crops: chemicals	n	Y	n	n	n	n	n	n	n
E. Protecting the crops from raiders	Y	Y	n	Y	Y	n	Y	Y	Y
F. Weeding invasive species out of crops	Y	Y	n	Y	Y	n	Y	Y	Y
G. Pest control: chemicals	n	Y	n	n	n	n	n	Y	n
H. Pest control: microbes	n	n	n	n	n	n	n	Y	Y
I. Symbiosis: one-way obligate	n	n	n	Y	n	Y	n	n	n
J. Mutualism: two-way obligate	2Y	n	n	n	n	n	2Y	2Y	2Y
K. Artificial selection to improve crops	n	Y	n	n	n	n	Y	Y	n
L. Genetic engineering to improve crops	n	Y	n	n	n	n	n	n	n
Sum of convergent agricultural behaviors	5	9	3	5	3	4	8	10	7

Notes: Y = yes, present; n = no, absent. Phylogenetic lineages: 1 = damselfish, 2 = human primate, 3 = polychaete annelid worm, 4 = limpet snail, 5 = whelk snail, 6 = periwinkle snail, 7 = macrotermitine termite, 8 = leaf-cutter ant, 9 = ambrosia beetle.

In contrast to humans, the damselfishes have simpler agricultures that exhibit only five of the 12 agricultural traits (table 1.3). Hata and Kato (2006, 159) have observed that species of the damselfishes maintain “dense stands of filamentous algae as algal farms.” In particular, the “territorial damselfish, *Stegastes nigricans*, maintains algal farms by excluding invading herbivores and weeding unpalatable algae from its territories” (Hata and Umezawa 2011, 809); it also carefully grazes its crops to stimulate the algae to remain in the rapid-growth, early-succession phase (Hato, Watanabe, and Kato 2010; Aanen 2010). Hata and Kato (2006) have further noted that the mutualism between the damselfish *Stegastes nigricans* and the red alga *Polysiphonia* sp. 1 is “the first record of an obligate plant-herbivore cultivation mutualism in a marine ecosystem” (see also Hata and Kato 2004; Hata, Watanabe, and Kato 2010; Hata and Umezawa 2011). Aanen (2010, 1, 3) proposed that this “fascinating agricultural mutualism” was started by the damselfish’s “weeding or consumption of all the algae in a territory, and that the fast-growing algae remained, and started to specialize on this new niche. With their behavior, the fish shows some parallels with cattle, which by grazing create and improve their own niche—grassland. The difference is that the fish seem to remove unpalatable algae without consuming these, and that they are territorial.”

Hata, Watanabe, and Kato (2010, 2), however, have noted that “this fish neither sows nor transplants the algae.” Further, *Stegastes nigricans* has not been observed to fertilize its crops or to use any type of pest control against crop parasites or diseases, and the damselfish does not use artificial selection or genetic engineering to improve its crops, unlike humans.

The other seven agriculturalist animals are all protostomes. Four of the agriculturalist lineages are found in the clade of the spiralian protostomes and all are marine—the poly-

chaete annelid worms, the limpet snails, the whelk snails, and the periwinkle snails (table 1.1). Of these, the limpet snails have the most complex agricultures, consisting of five of the 12 agricultural traits; thus, this gastropod mollusc has an agricultural complexity rivaling that of an actinopterygian chordate (tables 1.1 and 1.3). Species of the scutellastrid limpets cultivate *Ralfsia verrucosa* algae in two types of gardens: periphery gardens (*Scutellastra cochlear*, *S. flexuosa*, *S. mexicana*, and others) and patch gardens (*Scutellastra longicosta*, *S. laticosta*, *S. chapmani*, and others; Lindberg 2007). Periphery-gardening limpets cultivate algae in a zone around the periphery of a permanent home base, in the center of which the snail resides. These limpets prepare their periphery substrates by rasping the coral surface, “and the alga within the garden area is restricted to the interstices of the rasped surface” (Lindberg 2007, 222). The more mobile patch-gardening limpets cultivate algae in larger patches over which the snails graze.

Both types of gardening limpets fertilize their gardens, but in a different manner: by the release of nitrogenous excretions (ammonium and urea in their urine and feces) in the periphery gardeners, and by the spreading of nutrient-rich mucus in mucus trails from their feet by the patch gardeners (Lindberg 2007). Field measurements have shown that the periphery-gardening species *Scutellastra cochlear* fertilizes its crop with “nitrogenous excretions released along the shell edge” (Lindberg 2007, 229). Plagányi and Branch (2000, 113) have demonstrated that the amount of ammonium (NH₄) excreted by *Scutellastra cochlear* on its gardens “supplied approximately 30% of the algal garden’s daily nitrogen growth requirements” and that these limpets “enhance the productivity of their algal gardens through the regeneration of limiting nutrients.”

The patch-gardening snail *Scutellastra longicosta* has been demonstrated to weed its gardens—it “removes algal species other than *Ralfsia* from its territory”—and its weeding activity is “important in preventing the competitive exclusion of *Ralfsia* by foliose algae,” particularly the sea lettuce *Ulva* (McQuaid and Froneman 1993, 132). The scutellastrid limpets also defend their crops from raiding herbivores, as *Scutellastra longicosta* was observed to have “actively excluded vagrant grazers, preventing overgrazing” of the crop (McQuaid and Froneman 1993, 128). Likewise, “by keeping the site free of other grazers, *Patella* [= *Scutellastra*] *longicosta* ensures the survival of *Ralfsia* plants” (McQuaid and Froneman 1993, 132).

In their study of the “mutualism between the territorial intertidal limpet *Patella* [= *Scutellastra*] *longicosta* and crustose alga *Ralfsia verrucosa*,” McQuaid and Froneman (1993, 128) noted that “adult *Patella* [= *Scutellastra*] are found exclusively in association with *Ralfsia*, on which they feed, while *Ralfsia* occurs primarily, but not exclusively, in *Patella* [= *Scutellastra*] territories.” That is, the farmer species is obligately dependent on its particular crop but the crop species, although benefiting from the activities of the farmer species, is not obligately dependent upon it (table 1.3).

As with the agriculturalist damselfishes, the agriculturalist limpets have not been observed to plant their algal crops or to use any type of pest control against crop parasites or diseases, and they are not known to use artificial selection or genetic engineering to improve their crops. Although they do use natural, organic fertilizers, they do not use chemical ones as the agriculturalist humans do.

The remaining three agriculturalist spiralian-protostome lineages (table 1.1) all have even simpler agricultures, consisting of only three or four of the 12 agricultural traits (table 1.3).

The nereidid polychaete annelid *Platynereis dumerilii* uses its own self-grown mucus-tube habitat as the substratum for its algal garden, according to Levinton (1982, 284), who has noted that some species of nereidids “attach pieces of sea lettuce (*Ulva*) to their tubes and maintain algal gardens.” Gambi et al. (2000) have further described the gardening of filamentous algae by the nereidid *Platynereis dumerilii* on leaves of the Mediterranean seagrass *Posidonia oceanica*, whereby the worms feed on erect filaments of algae, particularly the large macroalgae *Cystoseria*. They have noted that the worms “live inside semi-permanent mucous tubes, that are generally attached to macroalgal thalli. . . . *P. dumerilii* generally feeds close to the tube entrance, to which worms attach small pieces of algae” (Gambi et al. 2000, 190). At the tube entrance, these pieces of algae are also in close proximity to the nitrogenous urine and feces of the polychaete and thus may be fertilized, even if inadvertently.

Woodin (1977) has argued that the gardening behavior of *Platynereis dumerilii* is an adaptation to reduce the risk of predation. Gambi et al. (2000, 199) agree with this hypothesis, noting that “*P. dumerilii* feeding requires the partial or total exit of the worm from the tube” and that during such “searching for food, the worms are more vulnerable to potential predators.” Maintaining a garden of crop algae on the worm’s tube itself, near its opening, is clearly advantageous to the worm.

The nassariid whelk snail *Bullia digitalis* also has an agricultural technique that uses only three of the 12 agricultural traits, but they are not the same three traits as those used by the polychaete worms (table 1.3). Like *Platynereis dumerilii*, *Bullia digitalis* uses its own, self-grown calcareous-shell habitat as the substratum for its algal garden. Da Silva and Brown (1984, 64) have noted that the snail “frequently has an algal growth on the upper surface of its shell and especially on the last whorl,” and that “only a single species of alga is present and that in all cases it appears to have been cropped almost down to the shell.” Harris et al. (1986) further note that the garden consists of chlorophyte algae that bore into the shell material of the snail, that the snail periodically grazes on filamentous strands of the algae that protrude from its shell, and that the most commonly seen alga appears to be *Eugomontia sacculata*.

Unlike *Platynereis dumerilii*, *Bullia digitalis* has not been observed to plant the alga on its shell, but the presence of “only a single species of alga” (Da Silva and Brown 1984, 64) argues for weeding behavior by the snail to prevent other algal species from overgrowing its crop, and obviously the snail does not allow other species to graze its shell, thus defending its crop. Because the snail is mobile in high-energy sandy beaches (Harris et al. 1986), it is unlikely that it fertilizes its crop with nitrogenous excretions as the agriculturalist limpets do, since these excretions would be quickly washed away rather than being absorbed by the alga. The snail appears to use its algal garden as a supplementary source of food to augment its normal scavenging mode of feeding.

Last, the littorinid periwinkle snail *Littoraria irrorata* also has a simpler agricultural technique consisting of only four agricultural traits (table 1.3), but of overwhelming interest is that this periwinkle snail farms saprophytic fungi rather than photosynthetic algae (table 1.2). Thus, in its crop choice this agriculturalist marine species is convergent with the land-dwelling insect agriculturalists, all of which cultivate fungi instead of plants (table 1.2). As summarized by Silliman and Newell (2003, 15643), field observations confirm a “farming mutualism between *Littoraria* and intertidal fungi. Snails graze live grass primarily not to feed but to prepare substrate for fungal growth and consume invasive fungi. . . .

These results provide a case of fungal farming in the marine environment and outside the class Insecta.”

Littoraria irrorata prepares the substrate for its garden by actively producing longitudinal wounds with its radula on the leaves of the salt marsh cordgrass *Spartina alterniflora*; these wounds are then colonized by species of the ascomycete fungi *Phaerosphaeria* and *Mycosphaerella* (Silliman and Newell 2003; Sieg et al. 2013). Silliman and Newell (2003, 15643) have argued that “(i) *Littoraria* promote fungal growth on live *Spartina* plants through their grazing activities and direct application of fecal pellets and that this growth promotion has a positive effect on snail growth; and (ii) fungi benefit from snail wound-grazing by gaining access to nutritious and relatively defenseless inner plant tissues and by receiving supplements (potentially nutrients and/or propagules) from snail feces.” Further, Sieg et al. (2013, 122) have observed that *Littoraria irrorata* snails “consume fungal hyphae during garden maintenance”; they have also been seen engaging in “selectively depositing hyphae-laden feces within wounded plant tissues to facilitate fungal establishment and growth” and actively engaging in the “establishment of new fungal cultures on plants by defecating in wounded plant tissues” (Sieg et al. 2013, 128).

Silliman and Newell (2003, 15647) have further argued that *Littoraria irrorata* “snails can grow only on fungus-colonized *Spartina* or pure mycelium and not on sterile leaves or ones colonized by bacteria. These growth-study results indicate that *Littoraria* obligately employs fungus-promoting feeding strategies . . . and consumption of facilitated invasive fungi.” Thus, the farmer is obligately dependent upon the presence of the fungal crop, but the fungal crop, although benefiting from the activities of the farmer species, is not obligately dependent upon it (table 1.3). Sieg et al. (2013, 122) have further noted that this “snail-fungal mutualism increases exposure of the foundation species *Spartina alterniflora* to infection, whereas fungal farming on other local marsh plants is rarely observed. . . . We propose that the weak chemical defenses produced by *S. alterniflora* make it a preferred plant for fungal farming, whereas less abundant species that invest in potential chemical defenses against grazers and fungi are not as frequently colonized, consumed, or subjected to fungal farming by *L. irrorata*.”

The last three of the agriculturalist lineages are found in the clade of the ecdysozoan protostomes and all are land dwellers—the macrotermite termites, the leaf-cutter ants, and the *Ambrosiodmus/Ambrosiophilus*-clade ambrosia beetles (table 1.1). All three ecdysozoan agriculturalist animals farm fungi rather than plants, and all three have a two-way obligate relationship between the farming animals and their crops (tables 1.2 and 1.3).

The macrotermite termites have an agricultural technique that uses eight of the 12 agricultural traits and is almost as complex as human agriculture (table 1.3). Unlike the human-plant facultative agricultural mutualism, the relationship between the macrotermite termites and their crops, species of *Termitomyces* fungi, is one of obligate mutualism: “termites depend on the fungi for food, and the fungi depend on the termites for growth and protection” (Aanen 2006, 209; see also Aanen et al. 2002; Mueller et al. 2005; Aanen and Eggleton 2017; chapter 6, this volume). Also unlike humans, the termites are not known to use any type of pest control against crop parasites or diseases (Mueller et al. 2005).

In addition to substrate preparation, crop planting, crop fertilization with organics, and protection and weeding of crops (Mueller et al. 2005), Aanen (2006, 209) also observed that “the termites ‘artificially’ select for high nodule production” to improve their *Termitomyces*

crops and that “genetic screening of *Termitomyces* strain diversity happens in at least some of the genera either directly through active selection of symbionts or indirectly through inter-strain competition for comb space.”

The leaf-cutter ants have an agricultural technique that uses ten of the 12 agricultural traits—an agriculture that is more complex than human agriculture in this analysis (table 1.3). Like humans, the ants use “chemical herbicides to combat pests,” but, unlike humans (as yet), the ants also use “disease-suppressant microbes for biological pest control” (Mueller et al. 2005, 565; chapter 11, this volume), in particular an “antibiotic produced by the *Pseudonocardia* bacterial symbiont” that is used against fungal parasites (Schultz and Brady 2008). Also unlike the human-plant agricultural mutualism, the mutualism between the leaf-cutter ants and their fungal crops is obligate: all attine ants obligately depend on the cultivation of fungus gardens for food, and, whereas the fungal cultivars of the non-leaf-cutting “lower” attine ants are facultative symbionts, ants in the leaf-cutter genera *Atta* and *Acromyrmex* cultivate “higher attine” fungi (principally *Leucoagaricus gongylophorus*) that are incapable of living separately from their ant farmers (Schultz and Brady 2008; Branstetter et al. 2017; chapters 8 and 14, this volume).

Like termites, ants practice artificial selection through the selection of variant fungal symbionts (Mueller et al. 2005). Thus leaf-cutter ants are known to utilize all of the agricultural techniques used by humans in this analysis except two: the usage of artificially produced chemical fertilizers and genetic engineering to improve their crops. However, it is possible that the ants may even use genetic engineering—through the introduction of viruses and horizontal-gene transfer into their crops—but this remains to be proved (T. R. Schultz, personal communication, 2014).

Last, of the 11, independently evolved, fungus-farming lineages of ambrosia beetles, the *Ambrosiodmus/Ambrosiophilus*-clade ambrosia beetles utilize the most complex agricultural techniques (Jordal and Cognato 2012; Li et al. 2015). Their agricultures use seven of the 12 agricultural traits (table 1.3), although the ten other convergent agriculturalist lineages of ambrosia beetles may use fewer than these seven traits and have simpler agricultures (Farrell et al. 2001; Mueller et al. 2005). Like the fungus-farming termites and ants, the *Ambrosiodmus/Ambrosiophilus*-clade ambrosia beetles are obligate mutualists with their fungal crop species *Flavodon ambrosius* (Li et al. 2015; Kasson et al. 2016; Simmons et al. 2016).

The *Ambrosiodmus/Ambrosiophilus*-clade ambrosia beetles possess the general agricultural traits of substrate preparation, crop planting, crop protection, and crop weeding (Mueller et al. 2005; Li et al. 2015; Kasson et al. 2016). Like the ants, they use microbes for biological pest control (U. G. Mueller, personal communication, 2014), but they are not known to fertilize their crops (table 1.3). They also are not known to practice artificial selection to improve their crops, but some are known to practice another type of crop choice: “Several Asian species within the genus *Ambrosiophilus* engage in another interspecific interaction—fungus stealing (mycocelestism; Hulcr and Cognato 2010). Instead of making their galleries in uninhabited wood, these parasitic *Ambrosiophilus* species search for galleries established by the much larger ambrosia beetles in the genus *Beaverium* and excavate their galleries immediately next to the existing tunnels. The fungus established by *Beaverium* spp. therefore immediately grows in the gallery of *Ambrosiophilus* spp.” (Kasson et al. 2016, 94).

Potential Causes of Convergent Agricultural Evolution

Why does convergent biological evolution occur? Convergence arises because the possible evolutionary pathways available to life are not endless, but *limited* (McGhee 2011, 2015). If the number of possible evolutionary pathways were infinite, then each species on Earth would be morphologically different from every other species, and each species would have its own unique ecological role or niche. Such an Earth does not exist. Instead, repeated evolutionary convergences on similar morphologies, niches, molecules, and even mental states is the norm for life on Earth (McGhee 2011).

Evolutionary limits are the product of functional constraints, developmental constraints, and the two processes acting in concert. Functional constraints are imposed by the laws of physics, chemistry, and geometry and are *extrinsic* to the organisms affected by those constraints (McGhee 2007). Convergence results from the fact that there are limited numbers of ways to solve a functional problem within the boundaries imposed by these extrinsic constraints. In contrast to functional constraints, developmental constraints are *intrinsic* and are imposed by the biology and phylogeny of specific organisms (McGhee 2007). First, the developmental pathways that are available to specific organisms are limited by what has been variously called “phylogenetic legacy,” “phylogenetic inertia,” or “phylogenetic constraint” (see discussion in McGhee 2007). Second, even given a certain phylogenetically available repertoire of traits, the processes of developmental bias, such as the “repeated, differential re-use of developmental modules, which enables novel phenotypes to arise by developmental rearrangements of ancestral elements, as in the parallel evolution of animal eyes” (Laland et al. 2015, 3), may make the development of some of those traits more probable than others. Third, “phenotypic variation can be channeled and directed towards functional types by the process of development”; this phenomenon is known as “facilitated variation” and can “sometimes elicit substantial, non-random, well-integrated and apparently adaptive innovations in the phenotype” (Laland et al. 2015, 3).

Is convergent agricultural evolution the product of functional constraints, developmental constraints, or both? The functional constraint hypothesis proposes that there exists a limited number of ways to successfully cultivate crops and that convergent agricultural techniques must necessarily result because independent lineages of animals have a limited number of farming options to discover. The developmental constraint hypothesis proposes that there exists a limited repertoire of shared agricultural behaviors that are inherited within a phylogenetic lineage and that convergent agricultural techniques must necessarily result because members of those phylogenetic lineages of animals have a limited repertoire of behavioral options to utilize in farming.

A phylogenetic classification of the nine lineages of agriculturalist bilaterian animals is given in table 1.1. As discussed in the previous section of the chapter, agriculture has evolved independently in both the clades of the deuterostome and protostome bilaterians. The molecular analyses of Dos Reis et al. (2015) indicate that the deuterostome-protostome split occurred by 578 million years ago (Mya) in the Ediacaran period of the Neoproterozoic (Gradstein et al. 2012), and possibly as early as 653 Ma in the older Cryogenian period. Thus, if developmental constraint is responsible for the convergent evolution of agriculture in the nine agriculturalist lineages of animals, then those constraints would have had to be present in animals that existed before the deuterostome-protostome divergence in animal

evolution. Metazoan nervous systems evolved independently and convergently in the ctenophores and eumetazoans before the deuterostome-protostome divergence (table 1.1; Dunn et al. 2008; Ryan et al. 2013; Hejnol 2014; Moroz et al. 2014; see discussion in McGhee 2019). The eumetazoan nervous system is surely a prerequisite for the later evolution of agricultural behaviors in the bilaterian animals, but possession of that nervous system does not constrain these animals to any particular behavior in terms of farming crops. Rather, convergence in agricultural behaviors appears to be the result of functional constraint.

The ecdysozoan macrotermite termites, leaf-cutter ants, and ambrosia beetles do not farm fungi because their ecdysozoan-style development constrains them to that crop; instead they farm fungi because fungi do not require light in order to grow—thus fungi can be cultivated in dark tunnels within wood and underground in soil. Deuterostomes are not developmentally constrained to farm plants—plants are also farmed by annelids and gastropods (table 1.2), animals with protostome developmental systems (table 1.1). Animals in these different clades simply farm plants because light is available in the habitats in which they live, and plants require light in order to grow. Damselfishes, annelid worms, and gastropods have no manipulative appendages, yet this developmental constraint does not prevent them from farming.

Convergence in the agricultural methods used by animals for the farming of plants and fungi (table 1.3) appears to be the result of similar functional constraints imposed by these two very different types of crop organisms. Although plants require light and fungi do not, both crop types grow better when their growth substratum is prepared for them, when they are fertilized, when they are weeded, and when they are protected from raiders and parasites. The hypothesis of the primacy of functional constraint in the convergent evolution of agriculture will be explored in more detail in the next section of this chapter.

Adaptive Landscapes: A Spatial Approach to Evolutionary Analysis

The concept of the adaptive landscape was first proposed by Wright (1932) and has become a “standard imagination prosthesis for evolutionary theorists. It has proven its worth in literally thousands of applications, including many outside evolutionary theory” (Dennett 1996: 190; see discussion in McGhee 2007). It is usually portrayed as a three-dimensional grid surface, where the two dimensions of the x - y plane are morphological or ecological traits and the vertical z -dimension is the degree of adaptation of permutations of those traits (figure 1.1). Regions in the landscape where trait permutations have a high degree of adaptation are called *adaptive peaks*, and regions of trait permutations with low degrees of adaptation are called *adaptive valleys*. The geometric arrangement of the adaptive peaks within the landscape thus represents, in a spatial fashion, the different possible ways of life available to organisms. The spatial distribution of the adaptive valleys and plains represents trait permutations that range from nonfunctional to lethal in nature. The adaptive landscape can also be portrayed as a two-dimensional contour map, where the third dimension of the degree of adaptation is given by the contour values within the map (figure 1.1).

A basic rule of modeling evolution in an adaptive landscape is that natural selection will operate to move a population up the slope of an adaptive peak, from lower degrees of adaptation to higher degrees of adaptation. Thus, using the adaptive landscape concept,

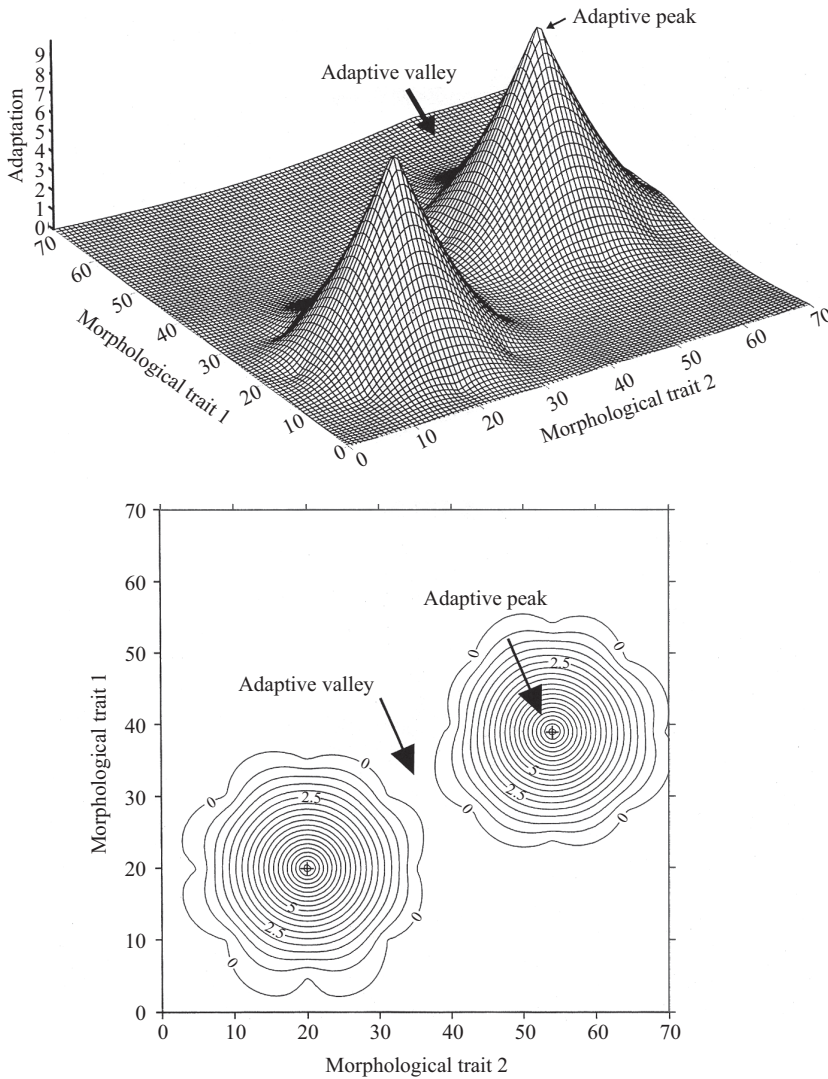


Figure 1.1

A hypothetical adaptive landscape, portrayed as a three-dimensional grid at the top of the figure and a two-dimensional contour map at the bottom. Topographic highs represent adaptive morphologies that function well in natural environments (and therefore are selected for), while topographic lows represent nonadaptive morphologies that function poorly in natural environments (and therefore are selected against). From McGhee (2007).

evolution via the process of natural selection can be spatially visualized as a journey across adaptive hills and valleys, mountains and ravines (McGhee 2007).

The actual utilization of the adaptive landscape concept in the analysis of evolution requires a metric for measuring the different degrees of adaptation of different morphological traits. One commonly used metric is *efficiency*—for example, the filtration efficiencies of different colony geometries in the analysis of evolution in the filter-feeding bryozoans, or the swimming efficiencies of different shell forms in the analysis of evolution in swimming ammonoid cephalopods (McGhee 2007, 2015).

In the analysis of the convergent evolution of agriculture an obvious analog would be a metric of agricultural efficiency, perhaps some measure of the cost to the farmer in producing a crop in contrast to the profit the farmer receives on selling the crop. I am not an anthropologist or economist, but it seems to me that measures of agricultural efficiency would be difficult to obtain even for different human agricultures and nearly impossible to obtain from nonhuman agricultures. Thus, for the current analysis I am using the metric of agricultural complexity (table 1.3) as a proxy for the degree of adaptation of different animal agricultural systems. The assumption here is that the more complex agricultural systems are more highly adapted to the efficient cultivation of crops, and that the less complex agricultural systems are less so.

Figure 1.2 gives a contour map of the agricultural complexities of the nine phylogenetic lineages of agriculturalist animals with respect to the two crop types farmed by these animals, plants or fungi. Two main landscape peaks are apparent, with similar peak heights and slopes. The plant-crop landscape has a maximum agricultural-complexity peak of 9, with human agriculture at the top of the peak and damselfish and polychaete agricultures on the lower slopes of the peak (figure 1.2). A second and smaller plant-crop peak on the slope from the main plant-crop peak has limpet agriculture at the top, with a peak complexity of 5, and whelk agriculture lower on the slope of the overall peak.

The fungus-crop peak has a maximum agricultural-complexity peak of 10, with leaf-cutter ant agriculture at the top of the peak and termite, beetle, and periwinkle agricultures located on progressively lower positions on the slope of the peak. At first glance at the top of the fungus-crop peak it would appear that the ecdysozoan protostomes, the insects, are the exclusive cultivators of fungus crops and that the deuterostome and spiralian protostome animals are all cultivators of plant crops. This is not true, however, as located farther down from the top of the fungus-crop peak, at complexity level 4, the periwinkle agriculturalists also cultivate fungi, and they are snails, spiralian protostomes, not insects (figure 1.2).

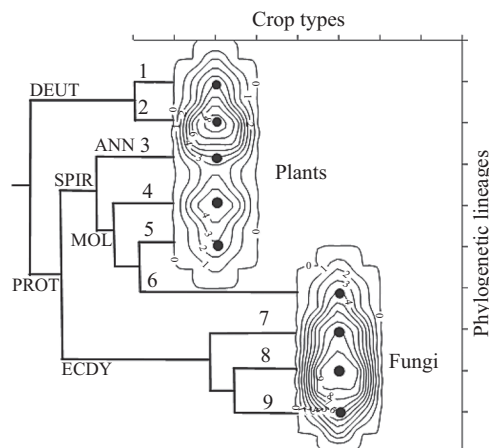


Figure 1.2

Contour map of the distribution of agricultural-complexity levels found in the nine agriculturalist animal lineages that cultivate either plants or fungi. The phylogenetic relationship of the nine lineages is given in the cladogram at the left of the figure; where DEUT = deuterostomes, PROT = protostomes, SPIR = spiralian, ECDY = ecdysozoans, ANN = annelids, and MOL = molluscs. The identities of the phylogenetic lineages are: 1 = damselfish, 2 = human primate, 3 = polychaete annelid worm, 4 = limpet snail, 5 = whelk snail, 6 = periwinkle snail, 7 = macrotermite termite, 8 = leaf-cutter ant, and 9 = ambrosia beetle.

The two main peaks present in figure 1.2 are solely the result of the two crop types farmed by agriculturalist animals, plants or fungi. The height of the peaks, and their slopes, are very similar, just as the range of agricultural complexities exhibited by plant farmers and fungus farmers are similar (table 1.3). This similarity supports the hypothesis that there exists a single adaptive peak, a best way to conduct agriculture, that applies both to the farming of plants and the farming of fungi.

In contrast to figure 1.2, figure 1.3 gives a contour map of the agricultural complexities of the nine agriculturalist lineages with respect to the two habitat types in which the farms of these animals are located, marine or land. Two main landscape peaks are apparent, but they have noticeably different peak heights and slopes. The overall marine-habitat landscape has a maximum peak height of 5 but possesses two peaks of that height, one with damselfish agriculture at the top and one with limpet agriculture at the top. On the slopes of this second peak, the periwinkle, whelk, and polychaete agricultures are progressively located on lower levels.

The land-habitat peak has a maximum agricultural complexity of 10 and is occupied by the ants, with human, termite, and beetle agriculturalists progressively located lower on the slopes of the land-habitat peak. Note the large “phylogenetic gap” between the deuterostome human agriculturalists and ecdysozoan-protostome insect agriculturalists (figure 1.3). All of the intervening spiralian-protostome agriculturalists are marine farmers, as are the deuterostome damselfishes. In addition to the height of the land-habitat peak, which is twice that of the marine farmers, note the steepness of the slope. This is due to the fact that all of the farmers on land have agricultures of high complexity, ranging from a maximum of level 10 to a minimum of level 7, below which the slope sharply drops off to the base of the land-habitat peak (figure 1.3).

In contrast to figure 1.2, figure 1.3 could support the hypothesis that two agricultural adaptive peaks exist—a land-agriculture peak and a marine-agricultural peak—where the

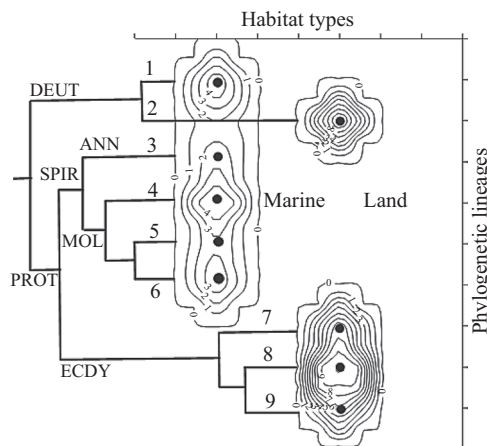


Figure 1.3

Contour map of the distribution of agricultural-complexity levels found in the nine agriculturalist animal lineages that farm either in marine habitats or on land. The phylogenetic relationship of the nine lineages is given in the cladogram at the left of the figure; where DEUT=deuterostomes, PROT=protostomes, SPIN=spirilians, ECDY=ecdysozoans, ANN=annelids, and MOL=molluscs. The identities of the phylogenetic lineages are: 1 = damselfish, 2 = human primate, 3 = polychaete annelid worm, 4 = limpet snail, 5 = whelk snail, 6 = periwinkle snail, 7 = macrotermite termite, 8 = leaf-cutter ant, and 9 = ambrosia beetle.

height of the land-agricultural peak is twice that of the marine-agricultural peak (figure 1.4). This two-peak hypothesis would imply that animals that live on land are capable of better agricultural efficiencies and higher degrees of adaptation than marine animals (figure 1.5), or that land-dwelling animals must develop more efficient agricultures in order to survive whereas marine agriculturalists can survive with simpler agricultural techniques.

In a summary contrasting fungal farming by land-dwelling and marine animals, Silliman and Newell (2003, 15646–15647) have argued that “evolutionary biologists have recently suggested that fungus-growing animals, like human agriculturalists (Diamond 1999), use a range of cultivation strategies, varying from ‘low-’ to ‘high-level food production’ (Schultz et al. 2005). . . . In terrestrial ecosystems, instances of high-level fungal cultivation have been extensively documented,” but examples “of low-level fungal production have not been experimentally demonstrated (Schultz et al. 2005), although evolution of this strategy could be common, given its relative engineering simplicity.” The agricultural behaviors of substrate preparation, weeding, fertilizing, and defense of the crop from other herbivores have been independently evolved in marine animal clades, though not all of these traits may be present in a given single lineage (table 1.3). Silliman and Newell (2003, 15647) argue that “if there is an important message to be learned from *Littoraria*’s distinct lower-level fungal production strategy, it may be that evolutionary success of fungal farmers may not depend on intricate pest management and inoculation techniques as long as cultivated fungi naturally occur and are successful even without farmer’s care (i.e., fungi are effective dispersers and have strong pathogen and competitor resistance).” That is, it may be that marine farms do not need to be as complex as agriculture on dry land. Other traits that marine agricultural systems have

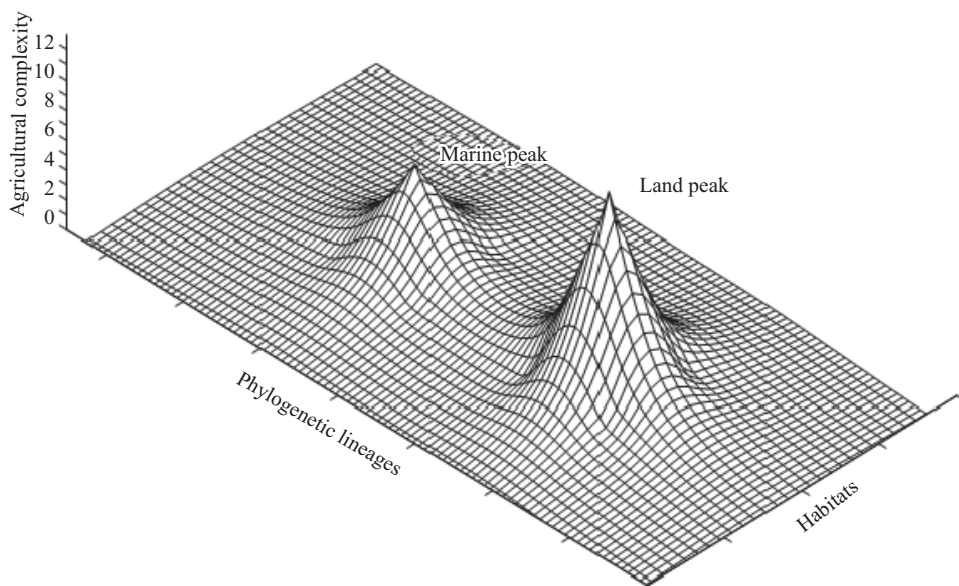


Figure 1.4

Three-dimensional grid representation of the two adaptive peak hypothesis, where a marine agriculture adaptive peak exists with a maximum agricultural-complexity peak (level 6) that is half the magnitude of that of a land agricultural adaptive peak (level 12).

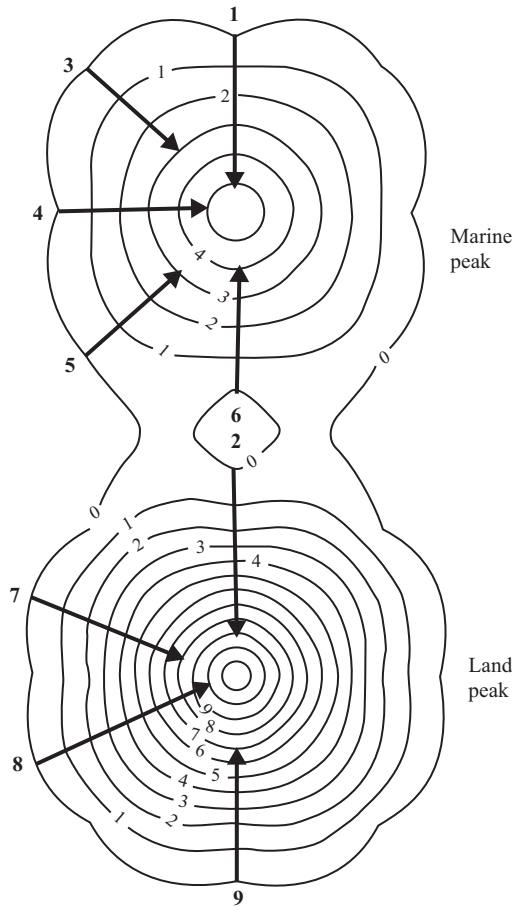


Figure 1.5

The evolution of five agriculturalist animal lineages on a hypothesized marine adaptive peak (top of figure) and the evolution of four agriculturalist animal lineages on a hypothesized land adaptive peak (bottom of figure). Vectors illustrate the maximum agricultural-complexity levels achieved by each lineage on the respective adaptive peak. The identities of the phylogenetic lineages are: 1 = damselfish, 2 = human primate, 3 = polychaete annelid worm, 4 = limpet snail, 5 = whelk snail, 6 = periwinkle snail, 7 = macrotermite termite, 8 = leaf-cutter ant, and 9 = ambrosia beetle.

in common are the sizes of both the farms and the farmer populations. Marine farms are small in areal extent compared to the huge farms of ants, termites, and some human agricultures. The population sizes of marine farming species are small in contrast to the huge population sizes of ant, termite, and human farming species.

Nevertheless, from the perspective of theoretical morphology, the demonstrable convergent evolution of even simple agricultural behaviors in clades of animals in radically different environmental conditions—in the oceans and on dry land—can be argued as evidence that there is a limited number of ways to successfully cultivate crops, and that convergent behavior must necessarily result because independent lineages of animals have a limited number of farming options to discover—whether in the oceans or on dry land.

Thus the alternative to the two-adaptive-peak agricultural hypothesis (figures 1.4 and 1.5) is the single-adaptive-peak hypothesis (figure 1.6). In figure 1.6 the hypothesis is that

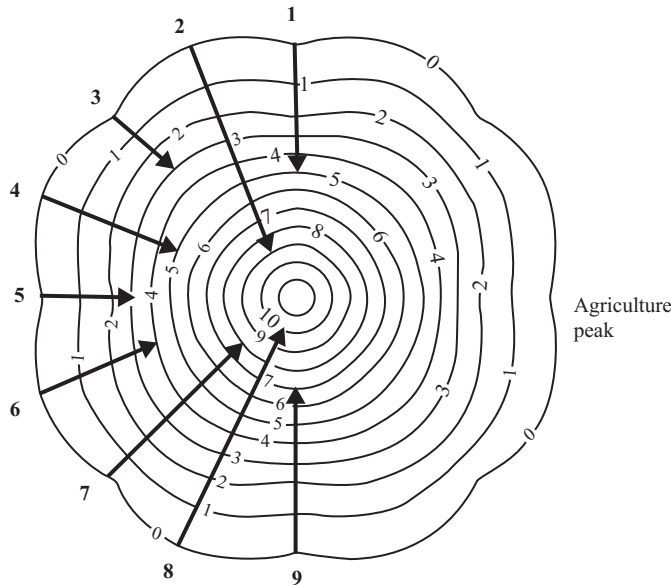


Figure 1.6

The evolution of nine agriculturalist animal lineages on a hypothesized single adaptive peak of agriculture, representing a limited number of ways to successfully cultivate crops that are found in both marine and land habitats. Vectors illustrate the maximum agricultural-complexity levels achieved by each lineage on the single adaptive peak. The identities of the phylogenetic lineages are: 1 = damselfish, 2 = human primate, 3 = polychaete annelid worm, 4 = limpet snail, 5 = whelk snail, 6 = periwinkle snail, 7 = macrotermite termite, 8 = leaf-cutter ant, and 9 = ambrosia beetle.

there exists a limited number of ways to do agriculture and that these constitute the complexity levels of a single adaptive peak—regardless of whether the crop type is plants or fungi, and whether the habitat is marine or terrestrial. Independent agricultural-animal clades differ in the number of those limited ways that they have discovered or have been able to master. Even the agricultural-animal clades that have managed to reach the higher levels of the adaptive peaks—ants, humans, and termites—initially started out at lower levels of the peak in the evolution of their agricultural systems (Schultz et al. 2005; Schultz and Brady 2008; Branstetter et al. 2017; Gupta 2004; Lieberman 2018; Aanen and Eggleton 2017; chapter 14, this volume).

Types of Agricultural Convergence

There exist three pathways to convergent evolution that can be formalized by using a unified terminology of convergence (McGhee et al. 2018; see discussion in McGhee 2019, 21–31). In that terminology the *phenomenon* of convergent evolution is a *set*, and the *types* of convergent evolution are *subsets* of that phenomenon. In this unified terminology the *phenomenon* of convergence is the *suffix* of the term, and the *type* of convergent evolution is the *prefix* of the term. The unified convergence terminology is outlined in table 1.4. The set of the convergence phenomenon contains all of the same or very similar traits that have evolved independently in different lineages of organisms. This set contains three subsets that specify

Table 1.4
The types of convergent evolution

SET:

CONVERGENT EVOLUTION: The evolution of the same or very similar traits independently in different lineages of organisms.

SUBSETS:

1. Allo-convergent evolution: The independent evolution of the same or very similar new trait from different precursor traits in different lineages.
2. Iso-convergent evolution: The independent evolution of the same or very similar new trait from the same precursor trait in different lineages.
3. Retro-convergent evolution: The independent re-evolution of the same or very similar trait to an ancestral trait in different lineages.

SUBSETS:

- 3a. Retro-alloconvergent evolution: The independent re-evolution of the same or very similar trait to an ancestral trait from different precursor traits in different lineages.
- 3b. Retro-isoconvergent evolution: The independent re-evolution of the same or very similar trait to an ancestral trait from the same precursor trait in different lineages.

Sources: McGhee et al. (2018), McGhee (2019).

the three pathways by which evolution may produce convergence: allo-convergent evolution, iso-convergent evolution, and retro-convergent evolution (table 1.4).

Allo-convergent evolution is the independent evolution of the same or very similar new trait from *different precursor traits* in different lineages (the prefix “allo” means “different”). Iso-convergent evolution is the independent evolution of the same or very similar new trait from the *same precursor trait* in different lineages (the prefix “iso” means “same”). Retro-convergent evolution is the independent *re-evolution* of the same or very similar trait to an ancestral trait in different lineages (the prefix “retro” means “reverse”).

The general subset of retro-convergent evolution contains two specific subsets that further differentiate the type of retro-convergence that may occur: retro-alloconvergent evolution and retro-isoconvergent evolution (table 1.4). Retro-alloconvergent evolution is the independent *re-evolution* of the same or very similar trait to an ancestral trait from *different precursor traits* in different lineages. Retro-isoconvergent evolution is the independent *re-evolution* of the same or very similar trait to an ancestral trait from the *same precursor trait* in different lineages.

The convergent evolution of agricultural traits by the nine lineages of bilaterian animals (tables 1.1 and 1.3) is a mixture of both allo-convergence and iso-convergence. Allo-convergence is evidenced by the evolution of the same agricultural behaviors from three different precursor feeding types: hunter-gatherers, herbivorous grazers, and scavengers (table 1.5). The fact that animals independently evolved the same agricultural behaviors (table 1.3) while starting from three different ancestral modes of feeding (table 1.5) can be argued as evidence that there exists a limited number of ways to successfully cultivate crops regardless of the ancestral feeding behaviors of the agriculturalist lineages, and as evidence that a single adaptive peak for agriculture exists (figure 1.6).

Iso-convergence is evidenced by the independent evolution of the same agricultural behaviors (table 1.3) by three different lineages of ancestral hunter-gatherers in parallel—the

Table 1.5
Pre-agricultural feeding methods in nine lineages of agriculturalist bilaterian animals

Farmer	Clade	Predominant pre-agricultural feeding method within clade
1	Damselfishes	hunter-gatherers (carnivorous-herbivorous)
2	Humans	hunter-gatherers (carnivorous-herbivorous)
3	Polychaetes	scavengers (omnivorous)
4	Limpets	grazers (herbivorous)
5	Whelks	scavengers (carrion-feeders)
6	Periwinkles	scavengers (herbivorous)
7	Termites	grazers (herbivorous)
8	Ants	hunter-gatherers (carnivorous-herbivorous)
9	Beetles	grazers (herbivorous)

Sources: 1=Aanen (2010), Hata and Umezawa (2011); 2=Gupta (2004), Lieberman (2018); 3=Gambi et al. (2000); 4=Lindberg (2007); 5=Da Silva and Brown (1984), Harris et al. (1986); 6=Sieg et al. (2013); 7=Aanen (2010), Aanen and Eggleton (2017), D. Aanen (personal communication 2018); 8=Mueller et al. (2001), Branstetter et al. (2017); 9=Farrell et al. (2001), Jordal and Cognato (2012), Li et al. (2015), J. Hulcr (personal communication 2018).

damselfishes, humans, and ants (table 1.5). Likewise, the same agricultural behaviors were iso-convergently evolved by three different lineages of herbivorous grazers in parallel—the limpets, termites, and ambrosia beetles—and three different lineages of scavengers in parallel—the polychaete worms, whelks, and periwinkles (table 1.5).

Moreover, *within* some of these iso-convergent bilaterian lineages the iso-convergent evolution of agricultural behaviors has independently occurred *repeatedly*—a phenomenon known as *iterative evolution* (Bayer and McGhee 1984; see discussion in McGhee 2007). Thus Aanen (2010, 3) notes that within the damselfish lineage “multiple independent transitions to algaculture have occurred” from ancestral fishes that fed on both animals and plants (Kato and Umezawa 2011). Likewise, multiple groups of humans independently transitioned to agriculture from ancestral hunter-gatherers about 10,000 years ago (Gupta 2004; Lieberman 2018; chapter 10, this volume), and 11 independent lineages of ambrosia beetles iteratively evolved agriculture in the past 50 million years (Jordal and Cognato 2012; Li et al. 2015; chapter 7, this volume). In contrast, the convergent evolution of agricultural behaviors has occurred only once in the lineages of the *Platynereis* polychaete worms (Gambi et al. 2000), scutellastrid limpets (Lindberg 2007), *Bullia* nassariid whelks (Da Silva and Brown 1984; Harris et al. 1986), *Littoraria* periwinkles (Silliman and Newell 2003; Sieg et al. 2013), macrotermitine termites (Mueller et al. 2005; Bourguignon et al. 2014; chapter 6, this volume), and attine ants (Mueller et al. 2005; Branstetter et al. 2017; chapters 8 and 14, this volume). However, it should be noted that Silliman and Newell (2003, 15647) have posed the question “Is fungal farming common but overlooked?” in marine environments and have argued that “given the relative engineering simplicity of low-level fungal production, the benefits of having predictable food supply . . . [suggest that] fungal farming on live, senescing, and/or dead plants may be more geographically and phylogenetically widespread than presently envisioned, especially in systems where fungal spores are abundant, grazers can manipulate fungus-growing media, and fungus is a major diet component of consumers.”

Last, retro-convergence has also occurred in the history of the evolution of agriculture, where an agriculturalist species reverts back to a prior ancestral mode of feeding that is nonagricultural. Thus *Homo sapiens*, a species that has iteratively evolved agriculture in the past, also has populations that have abandoned agriculture and gone back to being hunter-gatherers (Oota et al. 2005). However, they are not primarily hunter-gatherers in the sense that their hunter-gatherer mode of feeding is secondary, a retro-convergence on an ancestral mode of feeding (table 1.5).

Some of the agriculturalist ambrosia beetles “have lost their capacity to culture their own fungal gardens and depend on mycocolecty, or fungus theft” (Hulcr and Cognato 2010, 3). This phenomenon does not meet the strict definition of retro-convergence (table 1.4) because a feeding mode involving fungal-theft scavenging is not the ancestral feeding mode of the agriculturalist ambrosia beetles, which was grazing on dead phloem tissues in plants by ancestral bark beetles (Farrell et al. 2001; J. Hulcr, personal communication, 2018). Farrell et al. (2001, p. 2011) further state that the ambrosia beetle’s agricultural “habits have evolved repeatedly and are unreversed.” Still, this phenomenon represents another interesting example of the loss of agriculture in an agriculturalist lineage.

Conclusions

Agriculture has evolved independently and convergently in nine phylogenetic lineages of bilaterian animals: actinopterygian vertebrates, sarcopterygian vertebrates, polychaete annelids, patellogastropod molluscs, neogastropod molluscs, littorinoid molluscs, polyneopteran insects, hymenopteran insects, and coleopteran insects. Using a measure of agricultural complexity, it can be demonstrated that the most complex agricultural systems exist in terrestrial animals and that lower-complexity agricultural systems exist in marine animals, regardless of whether the farmed crops are plants or fungi. Convergence in the agricultural methods used by animals for the farming of plants and fungi appears to be the result of similar functional constraints imposed by these two very different types of crop organisms, and not by developmental constraints within the clades of the agriculturalist animals. Allo-convergence in the evolution of agriculture is evidenced by the independent appearance of the same agricultural behaviors in the nine lineages of bilaterian animals while starting from three different, nonagricultural, ancestral types of feeders—hunter-gatherers, herbivorous grazers, and scavengers. Once acquired, agricultural behaviors have rarely been lost.

From an adaptive landscape perspective, there appears to exist a limited number of ways to do agriculture that constitute the levels of a single adaptive peak—regardless of whether the crop type is plants or fungi and whether the habitat is marine or terrestrial. Independent agricultural-animal clades differ in the number of those limited ways that they have discovered or been able to master.

Acknowledgments

I thank the organizers, Peter Peregrine, Ted Schultz, and Rick Gawne, for inviting me to the Altenberg Workshop on the convergent evolution of agriculture, and I thank the Konrad

Lorenz Institute for Evolution and Cognition Research for its present and past support of my research on the phenomenon of convergent evolution.

References

- Aanen, D. K. 2006. "As You Reap, So Shall You Sow: Coupling of Harvesting and Inoculating Stabilizes the Mutualism between Termites and Fungi." *Biological Letters* 2:209–212.
- Aanen, D. K. 2010. "As You Weed, So Shall You Reap: On the Origin of Algalculture in Damsel fish." *BMC Biology* 2010 8:81. <http://www.biomedcentral.com/1741-7007/8/81>.
- Aanen, D. K., and P. Eggleton. 2017. "Symbiogenesis: Beyond the Endosymbiosis Theory?" *Journal of Theoretical Biology* 434:99–103.
- Aanen, D., P. Eggleton, C. Rouland-Lefèvre, T. Guldborg-Frøsvlev, S. Rosendahl, et al. 2002. "The Evolution of Fungus-32 Growing Termites and Their Mutualistic Fungal Symbionts." *Proceedings of the National Academy of Sciences* 99:14887–14892.
- Bayer, U., and G. R. McGhee. 1984. "Iterative Evolution of Middle Jurassic Ammonite Faunas." *Lethaia* 17:1–16.
- Benton, M. J. 2015. *Vertebrate Palaeontology*, 4th ed. Chichester, UK: Wiley-Blackwell.
- Bourguignon, T., N. Lo, S. L. Cameron, J. Šobotnik, Y. Hayashi, et al. 2014. "The Evolutionary History of Termites as Inferred from 66 Mitochondrial Genomes." *Molecular Biology and Evolution* 32:406–421.
- Branstetter, M. G., A. Ješovnik, J. Sosa-Calvo, M. W. Lloyd, B. C. Faircloth, et al. 2017. "Dry Habitats Were Crucibles of Domestication in the Evolution of Agriculture in Ants." *Proceedings of the Royal Society*, B284:20170095. <http://dx.doi.org/10.1098/rspb.2017.0095>.
- Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection; or the Preservation of Favoured Races in the Struggle for Life*. London: Murray.
- Da Silva, F. M., and A. C. Brown. 1984. "The Gardens of the Sandy-Beach Whelk *Bullia digitalis* (Dillwyn)." *Journal of Molluscan Studies* 50:64–65.
- Dennett, D. C. 1996. *Darwin's Dangerous Idea*. New York: Simon and Schuster.
- Diamond, J. 1999. *Guns, Germs, and Steel*. New York: Norton.
- Dos Reis, M., Y. Thawornwattana, K. Angelis, M. J. Telford, P. C. J. Donoghue, et al. 2015. "Uncertainty in the Timing of Origin of Animals and the Limits of Precision in Molecular Timescales." *Current Biology* 25:2939–2950.
- Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, K., W. E. Browne, et al. 2008. "Broad Phylogenetic Sampling Improves Resolution of the Animal Tree of Life." *Nature* 452:745–749.
- Farrell, B. D., A. S. Sequeira, B. C. O'Meara, B. B. Normark, J. H. Chung, and B. H. Jordal. 2001. "The Evolution of Agriculture in Beetles (Curculionidae: Scolytinae and Platypodinae)." *Evolution* 55:2011–2027.
- Gambi, M. C., V. Zupo, M. C. Buia, and L. Mazella. 2000. "Feeding Ecology of *Platynereis dumerilii* (Audouin & Milne-Edwards) in the Seagrass *Posidonia oceanica* System: The Role of the Epiphytic Flora (Polychaeta, Nereididae)." *Ophelia* 53:189–202.
- Gradstein, F. M., J. G. Ogg, M. Schmitz, and G. Ogg. 2012. *The Geologic Time Scale 2012*. Amsterdam, The Netherlands: Elsevier B. V.
- Gupta, A. K. 2004. "Origin of Agriculture and Domestication of Plants and Animals Linked to Early Holocene Climate Amelioration." *Current Science* 87:54–59.
- Harris, S. A., F. M. da Silva, J. J. Bolton, and A. C. Brown. 1986. "Algal Gardens and Herbivory in a Scavenging Sandy-Beach Nassariid Whelk." *Malacologia* 27: 299–305.
- Hata, K., and M. Kato. 2004. "Monoculture and Mixed-Species Algal Farms on a Coral Reef Are Maintained through Intensive and Extensive Management by Damsel fish." *Journal of Experimental Marine Biology and Ecology* 313:285–296.
- Hata, K., and M. Kato. 2006. "A Novel Obligate Cultivation Mutualism between Damsel fish and *Polysiphonia* Algae." *Biological Letters* 2:593–596.
- Hata, K., and Y. Umezawa. 2011. "Food Habits of the Farmer Damsel fish *Stegastes nigricans* Inferred by Stomach Content, Stable Isotope, and Fatty Acid Composition Analyses." *Ecological Research* 26:809–818.
- Hata, K., K. Watanabe, and M. Kato. 2010. "Geographic Variation in the Damsel fish–Red Alga Cultivation Mutualism in the Indo-West Pacific." *BMC Evolutionary Biology* 10:185. <http://www.biomedcentral.com/1471-2148/10/185>.

- Hejnal, A. 2014. "Excitation over Jelly Nerves." *Nature* 510:38–39.
- Hulcr, J., and A. I. Cognato. 2010. "Repeated Evolution of Crop Theft in Fungus-Farming Ambrosia Beetles." *Evolution* 64:3205–3212.
- Jordal, B. H., and A. I. Cognato. 2012. "Molecular Phylogeny of Bark and Ambrosia Beetles Reveals Multiple Origins of Fungus Farming during Periods of Global Warming." *BMC Evolutionary Biology* 12:133. <http://www.biomedcentral.com/1471-2148/12/133>.
- Kasson, M. T., K. L. Wickert, C. M. Stauder, A. M. Macias, M. C. Berger, et al. 2016. "Mutualism with Aggressive Wood-Degrading *Flavon ambrosius* (Polyporales) Facilitates Niche Expansion and Communal Social Structure in *Ambrosiophilus* Ambrosia Beetles." *Fungal Ecology* 23:86–96.
- Laland, K. N., T. Uller, M. W. Feldman, K. Sterelny, G. B. Müller, et al. 2015. "The Extended Evolutionary Synthesis: Its Structure, Assumptions and Predictions." *Proceedings of the Royal Society B* 282:20151019. <https://doi.org/10.1098/rspb.2015.1019>.
- Levinton, J. S. 1982. *Marine Ecology*. Englewood Cliffs, NJ: Prentice-Hall.
- Li, Y., D. R. Simmons, C. C. Bateman, D. P. G. Short, M. T. Kasson, et al. 2015. "New Fungus-Insect Symbiosis: Culturing, Molecular, and Histological Methods Determine Saprophytic Polyporales Mutualists of *Ambrosiodinus* Ambrosia Beetles." *PLoS ONE* 10(9): e0137689. <https://doi.org/10.1371/journal.pone.0137689>.
- Lindberg, D. R. 2007. "Reproduction, Ecology and Evolution of the Indo-Pacific Limpet *Scutellastra flexuosa*." *Bulletin of Marine Science* 81:219–234.
- Lieberman, D. E. 2018. "Being a Carnivorous Hominin in the Lower Paleolithic: A Biological Perspective on Convergence and Stasis." In *Convergent Evolution in Stone-Tool Technology*, edited by M. J. O'Brien, B. Buchanan, and M. I. Eren, 91–105. Cambridge, MA: MIT Press.
- Lycett, S. J. 2011. "'Most Beautiful and Most Wonderful': Those Endless Stone Tool Forms." *Journal of Evolutionary Psychology* (Budapest) 9:143–171.
- McGhee, G. R. 2007. *The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces*. Cambridge: Cambridge University Press.
- McGhee, G. R. 2011. *Convergent Evolution: Limited Forms Most Beautiful*. Cambridge, MA: MIT Press.
- McGhee, G. R. 2015. "Limits in the Evolution of Biological Form: A Theoretical Morphologic Perspective." *Interface Focus* 5:1–6. <https://doi.org/10.1098/rsfs.2015.0034>.
- McGhee, G. R. 2019. *Convergent Evolution on Earth: Lessons for the Search for Extraterrestrial Life*. Cambridge, MA: MIT Press.
- McGhee, G. R., I. Hue, J. Dardaillon, and P. Pontarotti. 2018. "A Proposed Terminology of Convergent Evolution." In *Origin and Evolution of Biodiversity*, edited by P. Pontarotti, 331–340. Berlin: Springer International Publishing AG.
- McQuaid, C. D., and P. W. Froneman. 1993. "Mutualism between the Territorial Intertidal Limpet *Patella longicosta* and the Crustose Alga *Ralfsia verrucosa*." *Oecologia* 96:128–133.
- Misof, B., S. Liu, K. Meusemann, R. S. Peters, A. Donath, C. Mayer, et al. 2014. "Phylogenomics Resolves the Timing and Pattern of Insect Evolution." *Science* 346:763–767.
- Moroz, L. L., K. M. Kocot, M. R. Citarella, S. Dosung, T. P. Norekian, et al. 2014. "The Ctenophore Genome and the Evolutionary Origins of Neural Systems." *Nature* 510:109–114.
- Mueller, U. G., N. M. Gerardo, D. K. Aanen, D. L. Six, and T. R. Schultz. 2005. "The Evolution of Agriculture in Insects." *Annual Review of Ecology, Evolution and Systematics*. 36:563–595.
- Mueller, U. G., T. R. Schultz, C. R. Currie, R. M. M. Adams, and D. Malloch. 2001. "The Origin of the Attine Ant-Fungus Mutualism." *Quarterly Review of Biology* 76:169–197.
- Near, T. J., A. Dornburg, R. I. Eytan, B. P. Keck, W. L. Smith, et al. 2013. "Phylogeny and Tempo of Diversification in the Superradiation of Spiny-Rayed Fishes." *Proceedings of the National Academy of Sciences* 110:12738–12743.
- Nielsen, C. 2012. *Animal Evolution: Interrelationships of the Living Phyla*. Oxford: Oxford University Press.
- O'Brien, M. J., B. Buchanan, and M. I. Eren, eds. 2018. *Convergent Evolution in Stone-Tool Technology*. Cambridge, MA: MIT Press.
- Oota, H., B. Pakendorf, G. Weiss, A. von Haeseler, S. Pookajorn, et al. 2005. "Recent Origin and Cultural Reversion of a Hunter-Gatherer Group." *PLoS Biology* 3(3): e71. [doi:10.1371/journal.pbio.0030071](https://doi.org/10.1371/journal.pbio.0030071).
- Plagányi, E. E., and G. M. Branch. 2000. "Does the Limpet *Patella cochlear* Fertilize Its Own Algal Garden?" *Marine Ecology Progress Series* 194:113–122.
- Ryan, J. R., K. Pang, C. E. Schnitzler, A.-D. Nguyen, R. T. Moreland, et al. 2013. "The Genome of the Ctenophore *Mnemiopsis leidyi* and Its Implications for Cell Type Evolution." *Science* 342:1242592. [doi:10.1126/science.1242592](https://doi.org/10.1126/science.1242592).

- Schultz, T. R., and S. G. Brady. 2008. "Major Evolutionary Transitions in Ant Agriculture." *Proceedings of the National Academy of Sciences* 105:5435–5440.
- Schultz, T. R., U. G. Mueller, C. R. Currie, and S. A. Rehner. 2005. "Reciprocal Illumination: A Comparison of Agriculture in Humans and Ants." In *Ecological and Evolutionary Advances in Insect-Fungal Associations*, edited by F. Vega and B. Meredith, 149–190. Oxford: Oxford University Press.
- Sieg, R. D., K. Wolfe, D. Willey, V. Ortiz-Santiago, and J. Kubanek. 2013. "Chemical Defenses against Herbivores and Fungi Limit Establishment of Fungal Farms on Salt Marsh Angiosperms." *Journal of Experimental Marine Biology and Ecology* 446:122–130.
- Silliman, B. R., and S. Y. Newell. 2003. "Fungal Farming in a Snail." *Proceedings of the National Academy of Sciences* 100:15643–15648.
- Simmons, D. R., Y. Li, C. C. Bateman, and J. Hulcr. 2016. "*Flavodon ambrosius* sp. nov., a Basidiomycetous Mycosymbiont of *Ambrosiodmus* Ambrosia Beetles." *Mycotaxon* 131:277–285.
- Struck, T. H., A. R. Wey-Fabrizius, A. Golombek, L. Herig, A. Weigert, et al. 2014. "Platyzoan Paraphyly Based on Phylogenomic Data Supports a Noncoelomate Ancestry of Spiralia." *Molecular Biology and Evolution* 31:1833–1849.
- Woodin, S. A. 1977. "Algal 'Gardening' Behaviour by Nereid Polychaetes: Effects on Soft-Bottom Community Structure." *Marine Biology* 44:39–42.
- Wright, S. 1932. "The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution." *Proceedings of the Sixth International Congress of Genetics* 1:356–366.