On Bridging Islam and Evolution through the Secret World of Ants: Struggles of a Muslim Evolutionary Biologist

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بسم الله الرحمن الرحيم

"In the Name of Allah, Most Gracious, Most Merciful"

A Personal Struggle

These words are the hardest I have had to write during my career as an evolutionary scientist. Over the last five years, I was invited to participate in several public debates, symposia, and discussions to bridge Islam and Evolution, and while I enthusiastically embraced this opportunity at first, I quickly realized that I would be forced to publicly reconcile the two worlds that defined me as a person. For years, I was peaceful, even complacent, about living what almost seemed to be a double life: "Abouheif as Muslim and Abouheif as Evolutionary Scientist." My Muslim family and friends have always been supportive of my career as an evolutionary scientist, and my scientific colleagues have always been respectful of my religious practices. The general public, however, is not as forgiving, especially since there are real concerns about the co-existence of religion and evolution (see Chapters in this volume). The thought of having my peaceful co-existence of these two worlds challenged in public was extremely stressful. In the days leading up to the presentation, I had to quickly make a decision about how I would present my bridge between Islam and evolution. I could either conceal my religious beliefs, as famous evolutionary geneticist Francisco J. Ayala has done in his writings (Ayala, 2010) and public lectures on this subject, or I could clearly make my religious beliefs known to the public as Stephen J. Gould (Gould, 1999) or Richard Dawkins (Dawkins, 2006) have done in their writings. In the end, I decided that I must publicly share the fact that I am both a Muslim and an evolutionary biologist in order to show that

reconciliation of these two worlds is possible. Since my March 2009 presentation at McGill, it has taken me over a year to face this challenge and write this chapter.

Abouheif as Muslim and Evolutionary Scientist

As a child, I was raised as a Muslim in a western society (Montreal, Canada), and so my abilities to bridge different cultural perspectives had been cultivated from my early days. My father, who is a practicing Muslim, taught me at a young age the five pillars of Islam. The five pillars are to: (1) say the "Shahadah," which requires any Muslim to repeat that "there is no God but Allah, and Mohammed is his Prophet"; (2) pray five times a day; (3) fast the Holy month of Ramadan, which occurs once a year for a period of thirty days; (4) give charity in the form of Zakat, which is portion of your annual profit or annual salary; and finally (5) if possible, make a pilgrimage to Mecca once in your life. These five pillars were reinforced in my life by an Islamic school that I attended every Saturday, and my own personal reading of the Holy Book of Islam – the Qur-ãn. As a child, I still remember learning to recite the opening passage of the Qur-ãn called *Surah Al-Fatiha*. My point here is that none of these Muslim practices that I learned as a child interfere with my daily life as an evolutionary scientist. In fact, my parents have always encouraged me to discover the natural world because Allah encourages his followers to understand the inner workings of his creations.

It is also true that none of my daily practices as an evolutionary scientist affect my daily practices as a Muslim. As well as being a practicing Muslim, I am also a student of ants. Ants are one of the most successful organisms on our planet. There are over 14000 ant species, and according to Hölldobler & Wilson (2009), there are approximately 10 million billion individual ants on our planet. If you estimated the biomass of all these

individuals they would make up more than half of the global biomass of all insects, and are likely to be equivalent to the biomass of all humans combined. Why are ants so ecologically successful? A key reason for this success is their remarkable display of cooperation (Hölldobler & Wilson, 1994), in which a queen and thousands of her workers live in a single colony. The queen does most of the reproduction, while workers perform most of the other tasks such as nursing the eggs and foraging for food. The cooperation of individuals in a colony has resulted in an astonishing repertoire of social behaviors, such as agriculture, warfare, and policing, and they even make their own graveyards! Another reason for their remarkable success is that queens and workers are fundamentally different from one another (Figure 1) – the queen can live up to 30 years, has fully functional wings, and can lay millions of eggs, while the workers can live just a few months, do not possess any functional wings, and can lay few to no eggs at all (Hölldobler & Wilson, 1990). What's amazing is that these dramatic differences between queens and workers from a single colony are achieved by modifying the same genes. Depending on specific environmental cues, e.g., temperature or nutrition, an egg laid by the queen will change the expression of its genes so that the egg either develops into a queen or worker (Evans & Wheeler, 2001). The amazing biological success of ants may be the reason why ants hold a special place in the Qur-ãn in the passage called *Surah Al-Naml* (passage of the ants). In this Surah (Surah 27; Verse 18), ants are portrayed as humble, yet powerful, creatures that use their powers of cooperation and communication to survive Solomon and his army as they passed over their nests in the valley of the ants.

To demonstrate how the successes and failures of being an evolutionary scientist have little influence on the daily life of a practicing Muslim, I will briefly describe the excitement I experienced when I first found the ant species that lead me to an important

scientific discovery. Although the workers of all ~14000 ant species completely lack wings and look the same on the surface, the genes that function to shut off the development of wings in the workers are different from one ant species to the next (Abouheif & Wray, 2002). The road to this discovery started the day in which I first decided to work with ants. I was so excited I ran straight to the field armed with a spoon in my hand to dig up all the ant queens I could find. Little did I realize that in most colonies the queen hides several feet underground, while most workers are distributed throughout the entire nest. I wanted to catch eggs that will develop into queens and workers so that I could compare what genes get turned on in the queen to allow her to develop fully functional wings and whether some of these same genes get turned off in the workers to halt their development of wings. Thankfully, a colleague of mine put me in touch with Ray Sanwald, a remarkable man who is not a scientist, yet has dedicated three acres of his own land and the last 50 years of his life to studying ants. Ray knows every ant on Long Island, and so he showed me so many new ant species on his property. My first visit to his property was like magic – I instantly fell in love when, for the first time, I saw an ant species that belongs to the genus *Pheidole*. These ants not only have workers, but they also have soldiers with large beautiful heads that they use to crack seeds and defend the nest (Figure 2a). That same day I brought them to the lab and immediately started research on them. After three years of work on these *Pheidole* ants, I was able to identify which genes are shut off in the soldiers and workers to stop their development of wings (Figure 2b). Initially, I predicted that workers of all ant species would shut off the same genes to stop their wing development because in all of the ~14000 known ant species their workers entirely lack wings. To test this prediction, I had to find an ant species from the genus *Crematogaster*, which has a beautiful heart shaped

abdomen (Figure 2c). After several months of failing to find this species on my own, I decided to once again contact my friend Ray. Ray took me around the back of a 'Big K' store, where he pointed to an abandoned car. I quickly ran to this car, and started looking. All I could see was an old, rolled up, carpet on the floor. Ray pointed to the carpet and we both got down on our knees and started tearing at its surface. Then, like a volcano, a colony of *Crematogaster* suddenly came pouring out of the carpet! It was such an exhilarating moment of joy that I forgot the pain of having been bitten all over my hands by workers trying to defend their nest. After collecting the queen and thousands of her workers, I brought them to the lab and started testing my prediction. Several months later I discovered that my initial prediction was wrong! The set of genes that is shut off to stop wing development in the workers of *Crematogaster* (Figure 2d) is different than in those of *Pheidole* (Figure 2b). I had discovered that although the morphology of an organism has remained unchanged for millions of years, the genes that encode for this morphology can evolve. Evolution can happen at some levels but not others, and so, what we observe on the outside of organisms is not always the same as what we observe on the inside. What is important from this brief story of scientific exploration is that none of what I have described conflicts with the daily practices of a Muslim. Making predictions about what one observes in nature and then testing them in the field or lab is a natural part of the scientific process, and I believe that most scientists and religious scholars will accept that Islam and evolution can coexist in practice. They may, however, challenge this coexistence on philosophical grounds. Therefore, in the following sections I will attempt to reconcile Islam and evolution from both a philosophical and scientific perspective.

Limitations of the scientific method with respect to the existence of Allah

It is a well-known fact among scientists and philosophers that there is no experiment in science that can test whether or not Allah exists (Gould, 1999; Scott, 2009). I consider this fact the key for bridging Islam and evolution because it immediately renders the question of whether or not Allah exists outside the realm of science. Any position taken on whether or not Allah exists is a 'leap of faith.' What I mean is that a person who does not believe in Allah is just as much taking a "leap of faith" as someone who does believe. This is reflected in the diversity of positions held by three famous scientists who have recently written on the subject: Richard Dawkins, who wrote the *The God Delusion* (Dawkins, 2006), is clearly a non-believer, while Ken Miller, who wrote *Finding Darwin's God* (Miller, 1999), is a believer. Stephen J. Gould in his *Rocks of Ages* (Gould, 1999) proclaims he is agnostic. How is it that three of famous evolutionary scientists have each assumed different positions with respect to their belief and their perceived relationship between God and evolution? The answer is again that there is no scientific experiment that can distinguish between their positions on the existence of Allah, and so choosing any one of these positions is a leap of faith.

Many scientists have argued that one should not believe in anything that cannot be observed or tested empirically (Dawkins, 2006). I believe that this argument should not be applied to the question of Allah's existence because we still know so little about nature. We should be humbled by the fact that there is so much more that we *do not* know than we actually *do* know. I think it would be highly pretentious to dismiss the existence of Allah based on this type of argument or logic. On the other hand, my argument also implies that we cannot use science or any observations in nature to support existence of Allah. For example, the fact that male honeybees have 16 chromosomes and *Surah Al-Nahl* (passage of the bees) is the 16th Surah in the Qur-ãn has been used as evidence for

the existence of Allah. While this is a remarkable similarity, and may encourage one to take a leap of faith to believe in Allah, it cannot be used as evidence or proof His existence. This means that Islam and evolution occupy different domains in our lives, and in the following sections I will try to reconcile them.

Evolution as fact and as theory

I have often been asked why evolution is called a theory and not a fact. The word *evolution* simply means *change over time* (Futuyma, 2009). Anything that changes over time, including cars and fashion, can evolve. Evolution has even been used to refer to the changes that occur during development, i.e. the changes that occur from when sperm and egg develops into an adult. Here, my focus is on *biological evolution*, which is *the decent with modification of all organisms from common ancestors* (Futuyma, 2009). What this means is that all organisms are related to one another and these relationships can be traced back to one or a few common ancestor(s). It is important not to confuse biological evolution with *evolutionary theory*. Biological evolution is a fact, while evolutionary theory represents all of the competing hypotheses that try to explain *how* biological evolution has occurred. We don't yet have sufficient evidence to distinguish between all of these competing hypotheses (Futuyma, 2009). For example, evolutionary scientists around the world are trying to test whether evolution has occurred gradually through small steps or whether it occurred in a punctuated manner through large steps. While there is evidence to support the occurrence of both processes in nature, it remains unclear which of these processes has occurred more frequently in the history of life (Futuyma, 1998; 2009).

Evidence for biological evolution from the secret world of ants

As I stated above, there is so much evidence to support *biological evolution* that it is now considered to be a scientific fact (Freeman & Herron, 2007; Futuyma, 2009; Hall, 2011). Here, I show several examples of evidence for the decent with modification of ants from common ancestors. The first form of evidence comes from the fossil record. Ants and bees are known for their remarkable social behaviors and both have Surahs in the Qur-ãn named after them *Surah Al-Naml* (passage of the ants) and *Surah Al-Nahl* (passage of the bees). Ants, bees, and wasps are all closely related to one another and both belong to the same order of insects called the "Hymenoptera" (Hölldobler & Wilson, 1990). Ants and bees independently evolved from different lineages of wasps (Brady et al., 2006). If this hypothesis is correct, then the common ancestor of ants should have a mix of both ant- and wasp-like characteristics. This is exactly what we find in one of the oldest fossil ants called *Sphecomyrma freyi* (Figure 3), which represents a link between wasps and ants, and represents several characteristics of the common ancestral ant lineage (Hölldobler & Wilson, 1994). *Sphecomyrma freyi*, for example, has morphological features, such as its jaw, that are characteristic of wasps, while other features, such as its waist and a secretory gland, that are characteristic of and only found in ants. It even has features, such as the antennae, that are intermediate between wasps and ants (Hölldobler & Wilson, 1994). Using this kind of evidence from the fossil record, as well as evidence based on the morphological and genetic similarity we find between species, we can reconstruct the evolutionary history and relationships of ant species that have split from the common ancestral ant lineage (Figure 4; Brady et al., 2006; Moreau et al., 2007; Urbani et al., 1992; Ward, 2007). Figure 4 shows a 'tree diagram,' which is called an evolutionary tree or phylogeny. This tree is reconstructed from all available scientific evidence to visually

illustrate how species from basal and derived lineages of ants are related to one another. The tree also depicts how the common ancestral ant lineage split from that of wasps. The species that have descended from the common ancestral ant lineage, although still retaining the basic ant body plan, have evolved and now show a remarkable diversity in their morphology, behavior, and ecology (Figure 4; Hölldobler & Wilson, 1990).

How have such diverse morphologies evolved in different ant species since they split from their common ancestors? Species are changing and evolving all the time (Freeman & Herron, 2007; Futuyma, 2009; Hall, 2011). The evidence for this constant change comes from the variation in morphology we see within and between species. Here, I use visual structures called "ocelli" to demonstrate how such large differences between species originate through small differences within species. Ocelli are light sensing organs that develop as three well-defined spots on the top on the head (Parry, 1947). They are usually quite prominent in the queens and males of most ant species because they help them navigate and find each other when they fly up in the air to mate (Figure 5; Mote & Wehner, 1980). In workers, however, the appearance of ocelli is highly variable (Hölldobler & Wilson, 1990), ranging from being completely absent or hardly visible in some species (Figure 5b) to being very prominent in others (Figure 5c). For example, ocelli in the desert ant *Cataglyphis fortis* are quite prominent (Figure 5c) because they act as a compass to help workers navigate back home to their nest by detecting polarized light from the blue sky (Fent & Wehner, 1985). However, in workers of the common garden ant *Lasius*, the ocelli are hardly visible because workers may not use them for navigation above ground (Figure 5b). The evolution of this large difference in ocelli development between *Catagylphis* and *Lasius* is not so large when we consider that we can observe smaller differences between the workers of closely-related *Lasius*

species (Figure 6). How did these differences between closely-related *Lasius* species arise? These differences originate as natural variation that appears between individuals and populations within a single *Lasius* species (Figure 7). These natural variations have spread and evolved in different ant species, such as *Lasius* and *Cataglyphis*, through specific evolutionary mechanisms, such as genetic drift, migration, or natural selection (Freeman & Herron, 2007; Futuyma, 2009; Hall, 2011). Although critical, it is unfortunately beyond the scope of this chapter to discuss these different mechanisms, as well as their implication for bridging Islam and evolution. The only point I am trying to make in this chapter is that the differences we observe between species begin as smaller differences that we can observe within species. This variation is the basis for biological evolution – the descent with modification of all ants from common ancestors – and is not restricted to morphological features like the ocelli. It occurs on all levels of biological organization from the morphology of an organism right down to its genes (Freeman & Herron, 2007; Futuyma, 2009; Hall, 2011). You may recall my story of how the wingless trait, which is a universal feature of ant workers, hasn't changed between species at the morphological level for millions of years. At the genetic level, however, the genes underlying the wingless trait have changed from one species to the next (Figure 2; Abouheif & Wray, 2002). This means that just because a trait looks like it hasn't changed does not mean that the genes that code for that trait are not evolving. The above examples of biological evolution that I have just described are also not a special characteristic of ants, but are a general feature of all species on earth. Each species tells a different story and provides evidence that biological evolution is a fact. In the next section I show how, as a Muslim evolutionary scientist, I have tried to reconcile biological evolution and Islam.

Bridging Islam and biological evolution

The greatest challenge for bridging Islam and evolution is to reconcile current scientific knowledge about human biological evolution with the Qur-ãn's account of human creation. My personal attempt to bridge my Islamic faith and biological evolution builds on a long and rich history of attempts by famous Islamic scholars, such as Ibn Khaldun (Rosenthal, 2005) and more recently Moustafa Mahmoud (Mahmoud, 1994). It is unfortunate that this rich history is often forgotten (or ignored) in modern debates on Islam and evolution (Kutty, 2009). In this context, a thorough review of this rich history is needed, but is unfortunately beyond the scope of this chapter.

Here, I want to focus on two key points: first, that there is abundant scientific evidence supporting the fact that humans are related to and share a common ancestor with animals (Freeman & Herron, 2007; Futuyma, 1998; Hall, 2011), and second, this scientific fact is *entirely consistent* with all of the Surahs and Verses in the Qur-ãn that refer to Allah's creation of humans. These Surahs and Verses (Surah:Verse) refer to the creation of humans from water (21:30, 24:45, 25:54, 77:20), earth (20:55), dust (3:59, 18:37, 22:5, 30:20, 35:11, 40:67), clay (6:2, 7:12, 15:26, 15:28, 15:33, 17:61, 23:12, 32:7, 37:11, 38:71, 55:14), a 'leech or blood-like clot' (22:5, 23:14, 40:67, 75:38, 96:1-2), a 'sperm-drop' (16:4, 16:30, 18:37, 22:5, 23:13, 32:8, 35:11, 40:67, 53:46, 75:37, 76:2; 77:20, 80:19, 86:6), flesh (22:5, 23:14), and a single soul (4:1, 6:98, 7:189). Taken together, the above Surahs and Verses indicate that humans were not created in a single instant, but were created gradually and in multiple stages. *Surah Al-Kahf* (18:37), *Surah Nuh* (71:13-14 & 71:17), and *Surah Al-Muminun* (23:13-14) are especially relevant in this context and reinforce this conclusion. *Surah Al-Kahf* (18:37) states:

Dost Thou Deny
Him Who created thee
Out of dust, then out of
A sperm drop, then
fashioned
Thee into a man?

أَكَفَرْتَ بِالَّذِي خَلَقَكَ مِن تُرَابٍ
ثُمَّ مِن
نُّطْفَةٍ ثُمَّ سَوَّاكَ رَجُلًا ۝

While *Surah Nuh* (71:13-14 & 71:17) states:

13 – What is the matter
With you, that ye
Are not conscious
Of Allah's majesty, –

١٣- مَا لَكُمْ
لَا تَرْجُونَ لِلَّهِ وَقَارًا ۝

14 – Seeing that it is He
That has created you
In diverse stages?

١٤- وَقَدْ خَلَقَكُمْ أَطْوَارًا ۝

17 – And Allah has
produced
You from the earth
Growing (gradually)

١٧- وَاللَّهُ أَنبَتَكُم
مِّنَ الْأَرْضِ نَبَاتًا ۝

There are several Surahs that refer to particular stages in the evolution of both animals and humans. For example *Surah Al-Alaq* (96:1-2) states:

1 – Read!
In the name of thy
Lord and Cherisher,
Who created –

١- اقْرَأْ بِاسْمِ رَبِّكَ
الَّذِي خَلَقَ ۝

2 – Created man out
of A leech like clot:

٢- خَلَقَ الْإِنسَانَ مِنْ عَلَقٍ ۝

This "leech like clot" may refer to the stage where multicelluar animals and humans evolved from unicellular organisms. There is abundant genetic evidence that supports the hypothesis that groups or "clots of cells" are the link or evolutionary transition from

unicellular organisms to multicelluar animals and humans (King & Carroll, 2001; King, Hittinger, & Carroll, 2003; King, et al., 2008).

The above discussion leads us naturally to another difficult question - if humans shared a common ancestor with animals, then when after splitting from their common ancestor did the lineage leading to humans become 'human' and distinct from all other animals? A possible answer may be found in *Surah Sad* (38:71-72), which states:

71 – Behold, thy Lord said To the angels: "I am About to create man From clay:

٧١-إِذْ قَالَ رَبُّكَ لِلْمَلَٰٓئِكَةِ إِنِّى
خَٰلِقٌۢ بَشَرًا مِّن طِينٍ ۝

72 – When I have fashioned him, And breathed Into him My spirit, Fall ye down in prostration, Unto him.

٧٢-فَإِذَا سَوَّيْتُهُۥ وَنَفَخْتُ
فِيهِ مِن رُّوحِى
فَقَعُوا۟ لَهُۥ سَٰجِدِينَ ۝

Here, I interpret "And breathed into him my spirit" to mean that the human lineage became distinctly human only after Allah breathed into man His spirit. I propose that *Surah Al-Sajda* (32:9) and *Al-Infitar* (82:7) shows that once Allah breathed into humans His spirit, humans acquired extraordinary capacities and a free will relative to all other animals. *Surah Al-Infitar* (82:7) states:

7 – Him who created thee, Fashioned thee in due proportion, And gave thee a just bias

٧-ٱلَّذِى خَلَقَكَ
فَسَوَّىٰكَ فَعَدَلَكَ ۝

The point at which Allah breathed His spirit into humans may coincide with the critical period where humans acquired language and the human brain was able to perceive the existence of Allah. I further propose that during this critical period the rate of biological evolution in humans slowed significantly, and instead, humans began to evolve culturally. It is during this period that humans became distinct from all other animals – they became spiritually aware, acquired morality, and could suppress basic animal instincts.

I believe that reconciling Islam and human biological evolution does not take away or diminish the role of Allah in the creation of humans. In contrast, there are several passages in the Qur-ãn indicating that Allah accords freewill to humans. I would like to raise the possibility that Allah accords humans freewill because, from their beginning, humans have always had the ability to stray from His message, commit error, and return for His guidance. The most obvious examples of this is in *Surah Al-Baqarah* (2:36), when Adam eats from the forbidden tree, or in *Surah Al-Alaq* (96:6-8), when Man transgresses his bounds and then returns to Allah:

6 – Nay, but man doth transgress all bounds,	٦- كَلَّآ إِنَّ ٱلْإِنسَٰنَ لَيَطْغَىٰٓ ۝
7 – In that he looketh Upon himself as self-sufficient.	٧- أَن رَّءَاهُ ٱسْتَغْنَىٰٓ ۝
8 – Verily, to thy Lord Is the return	٨- إِنَّ إِلَىٰ رَبِّكَ ٱلرُّجْعَىٰٓ ۝

By according to humans a freewill, Allah allowed humans to evolve. When all of the Surahs mentioned or discussed above are considered together, a bridge between Islam and evolution begins to emerge – humans were created gradually and in multiple stages, and therefore, the Qur-ãn's account of human creation is consistent with biological evolution.

Conclusions

Through my personal struggles as both a practicing Muslim and evolutionary scientist, I hope to have convinced my readers that Islam and evolution can be compatible from both a practical and philosophical perspective. Stephan J. Gould in his *Rocks of Ages* has tried to reconcile Religion and evolutionary science by arguing that they embrace two

completely different domains in our lives, or as he calls them "non-overlapping magisteria." He argues that religion is the domain of the soul, while evolutionary science deals with the material world. I agree that to a large extent Islam and evolution do occupy different domains in our lives. Islam adds a spiritual dimension to my life, which is something science cannot offer. I have been alienated from my son Saïd for several years now, and I can assure you that there is nothing that evolutionary science can do to alleviate this pain. However, I disagree with Gould that religion and science are completely non-overlapping, as this would be too good to be true. Islam tells us very clearly that Allah created the Heavens, Earth, and all living things on it, including Man. Muslim evolutionary scientists will have to continue to try and reconcile this perspective with all our current scientific knowledge of evolutionary biology. In this respect, there is much work to still be done, and in this chapter I hope to have taken a few humble steps towards reconciliation. There still remain many obstacles to surpass, and the biggest one in my opinion is politics. Much of what I have written here is meaningless against the large political divide between East and West. I was once quoted in the Boston Globe (25 October 2009) saying "For evolution in the Islamic world, it's very unfortunate that Darwin was a white Brit, because otherwise it would have gained wider acceptance." What I meant by this quote is that Darwin may be associated in the Islamic world with the long history of Western colonialization, and in the West, Islam may be currently associated with fundamentalism. Therefore, much of the recent literature and discussion portraying a conflict between Islam and evolution may be a consequence of current political ideologies, rather than a deep philosophical or introspective consideration of their compatibility. To overcome these political ideologies, we must first convince ourselves that reconciliation is possible, and I hope I have accomplished this here.

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Figure Legends

Figure 1: Typical morphological differences between an ant queen and her worker. These ants are from a species called *Formica fusca*. Note that every egg laid by the queen in an ant colony has the potential to develop either into a queen or a worker depending on the environmental cues (e.g. nutrition and temperature) it experiences during development. This photograph is a courtesy of and was taken by © Alex Wild.

Figure 2: Evolution of the gene network that controls wing development between workers of the ant genus *Pheidole* and *Crematogaster.* (a) *Pheidole* soldier and (b) *Crematogaster* worker were drawn by and are a courtesy of Daniel Berner. (c) Genes in the network that controls wing development in *Pheidole* soldiers are interrupted late in development, whereas (d) genes in the network that controls wing development in *Crematogaster* workers are interrupted early in development. The green boxes indicate genes that are turned on and expressed normally in the network, while red boxes with the crosses through them indicate genes that are shutoff and interrupted. The two or three letter words in the grey boxes are abbreviations for genes known to play specific roles in wing development, and the lines connecting them ending in either arrow heads or perpendicular lines indicate the connections and kind of genetic interaction between genes.

Figure 3: One of the oldest fossil ants, *Sphecomyrma freyi.* This fossil ant possesses a mosaic of ant- and wasp-like characteristics and represents characteristics most likely

found in the common ancestor of ants and wasps. Photograph was taken by Frank M. Carpenter and is a courtesy of Edward O. Wilson.

Figure 4: Evolutionary tree diagram showing the origin of and relationships between fossil and living lineages of ants. This tree diagram, also known as a phylogenetic tree, is reconstructed from fossil, morphological, and genetic evidence. The red circle on the phylogenetic tree shows that ants originated from aculeate wasps, and the black lines on the tree indicate how basal and derived ant lineages, as well as *Sphecomyrma freyi* and the common ancestral ant are related to each other. Note the diversity of morphology that has evolved in living ant species since their split from their common ancestor approximately 135 million years ago in the Cretaceous period (Ward 2007). Photograph of *Sphecomyrma freyi* was taken by Frank M. Carpenter and is a courtesy of Edward O. Wilson. All other photographs are courtesy of antweb.org and were taken by April Nobile.

Figure 5: The differences in ocelli development between *Lasius* queens and workers, and ocelli evolution between the workers of *Lasius* and *Cataglyphis* species. All photographs are of heads, and each of the three ocelli is marked by a little white arrow. All photographs are courtesy of antweb.org and were taken by April Nobile.

Figure 6: Ocelli evolution between workers of six closely related *Lasius* species. All photographs are of heads, and each of the three ocelli is marked by a little white arrow. All photographs are courtesy of antweb.org and were taken by April Nobile.

Figure 7: Ocelli evolution between workers from three populations of the species *Lasius niger*. All photographs are of heads, and each of the three ocelli is marked by a little white arrow. All photographs are courtesy of antweb.org and were taken by April Nobile.

Figure 1:

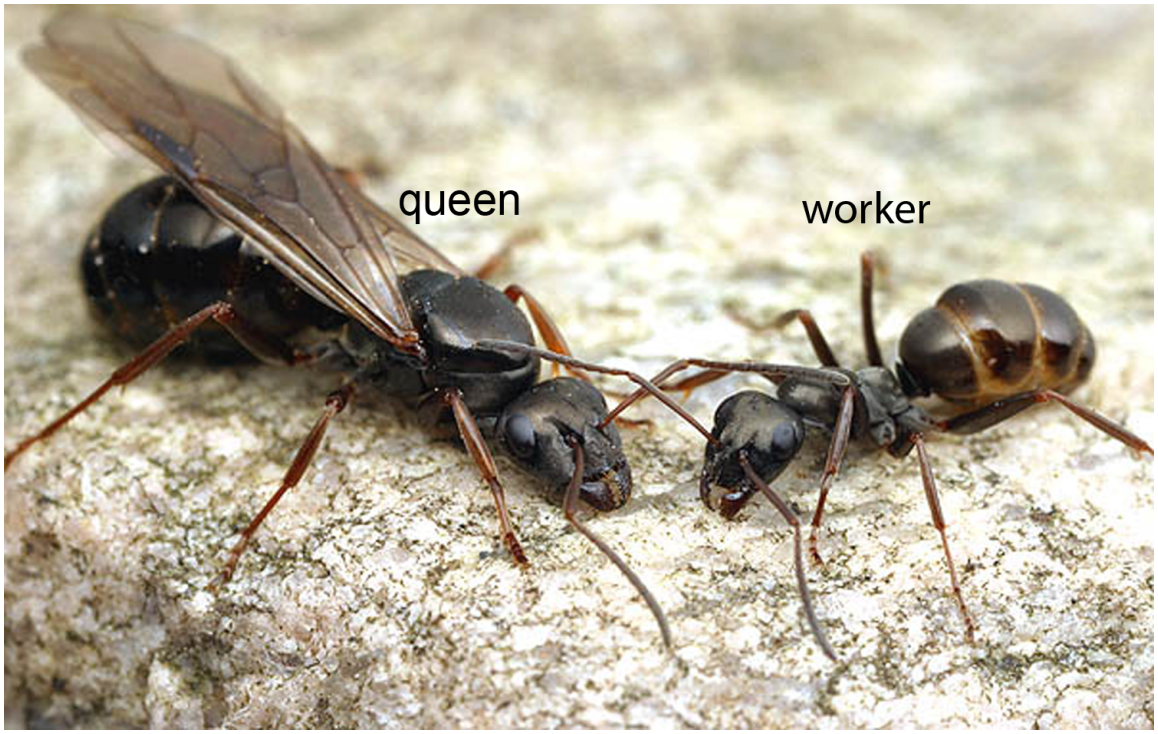
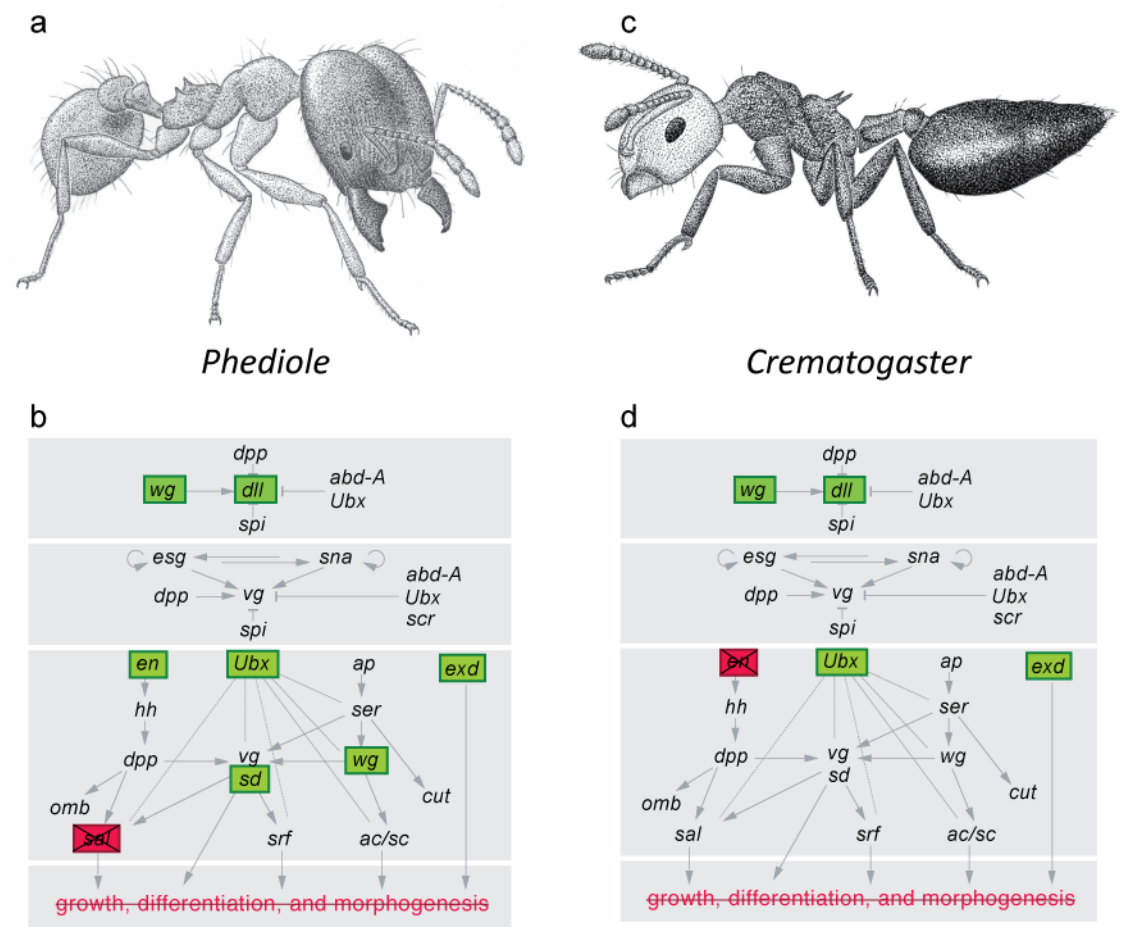


Figure 2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growth, differentiation, and morphogenesis

Figure 3:

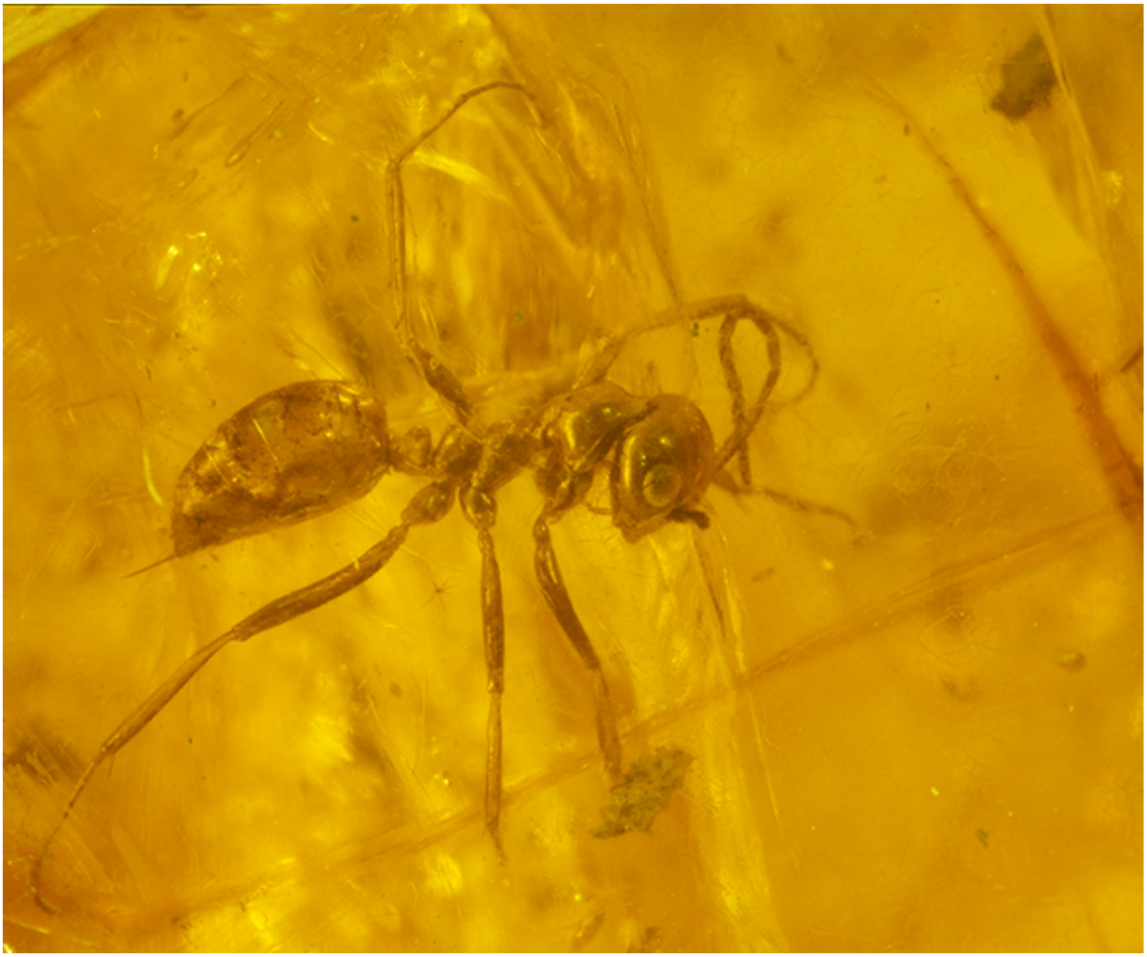


Figure 4:

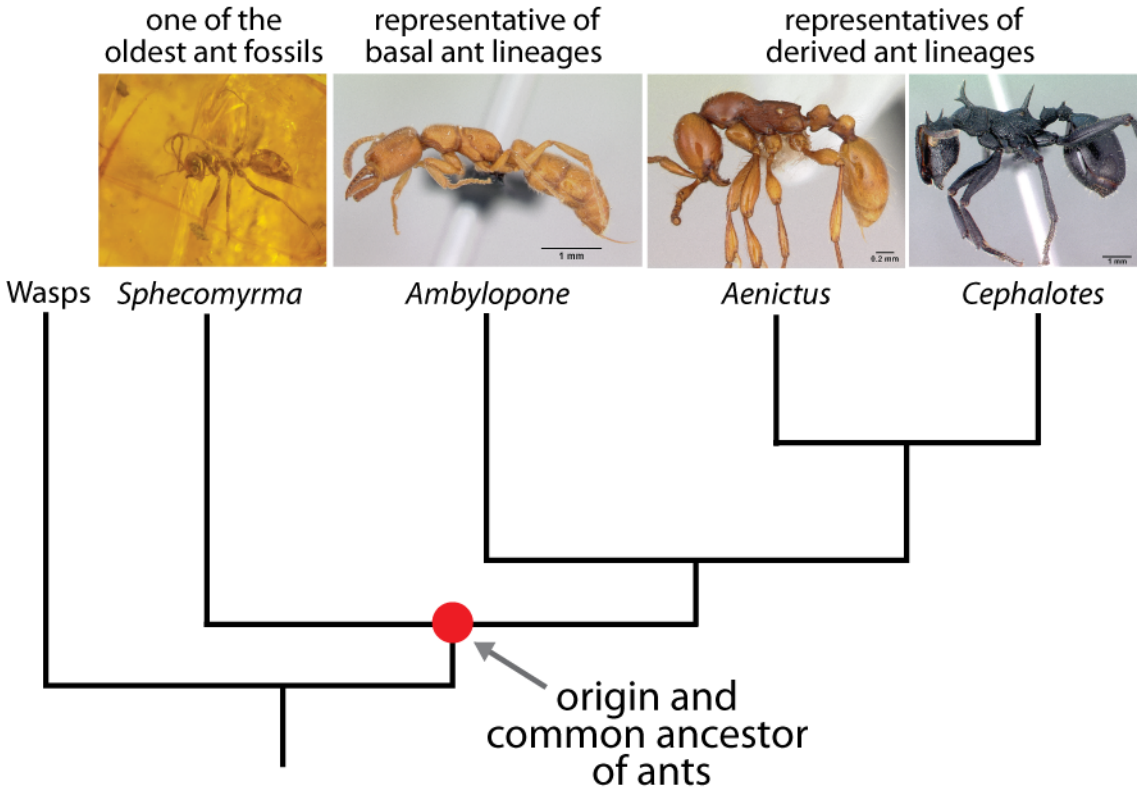
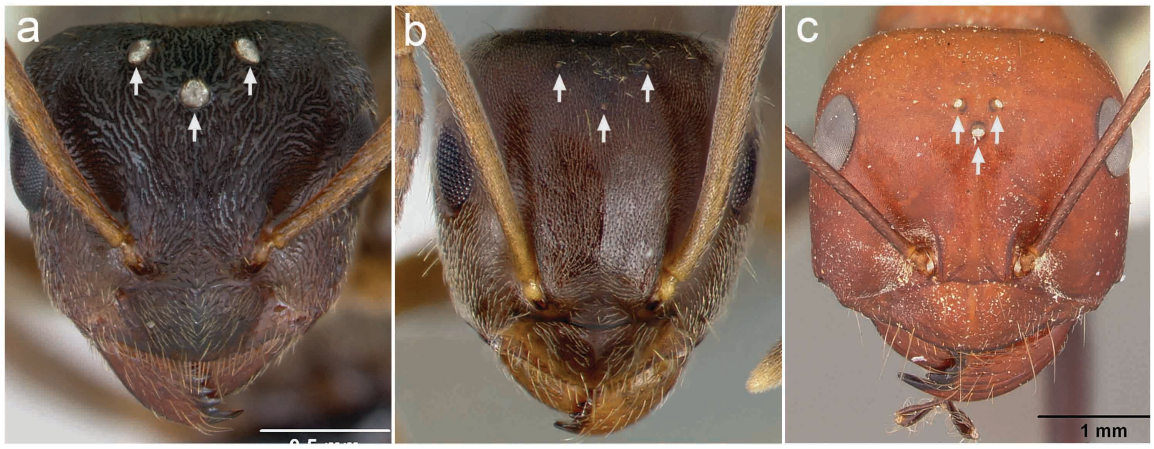

one of the oldest ant fossils
representative of basal ant lineages
representatives of derived ant lineages
Wasps
Sphecomyrma
Ambylopone
Aenictus
Cephalotes
origin and common ancestor of ants

Figure 5:



Lasius queen *Lasius* worker *Cataglyphis* worker

Figure 6:

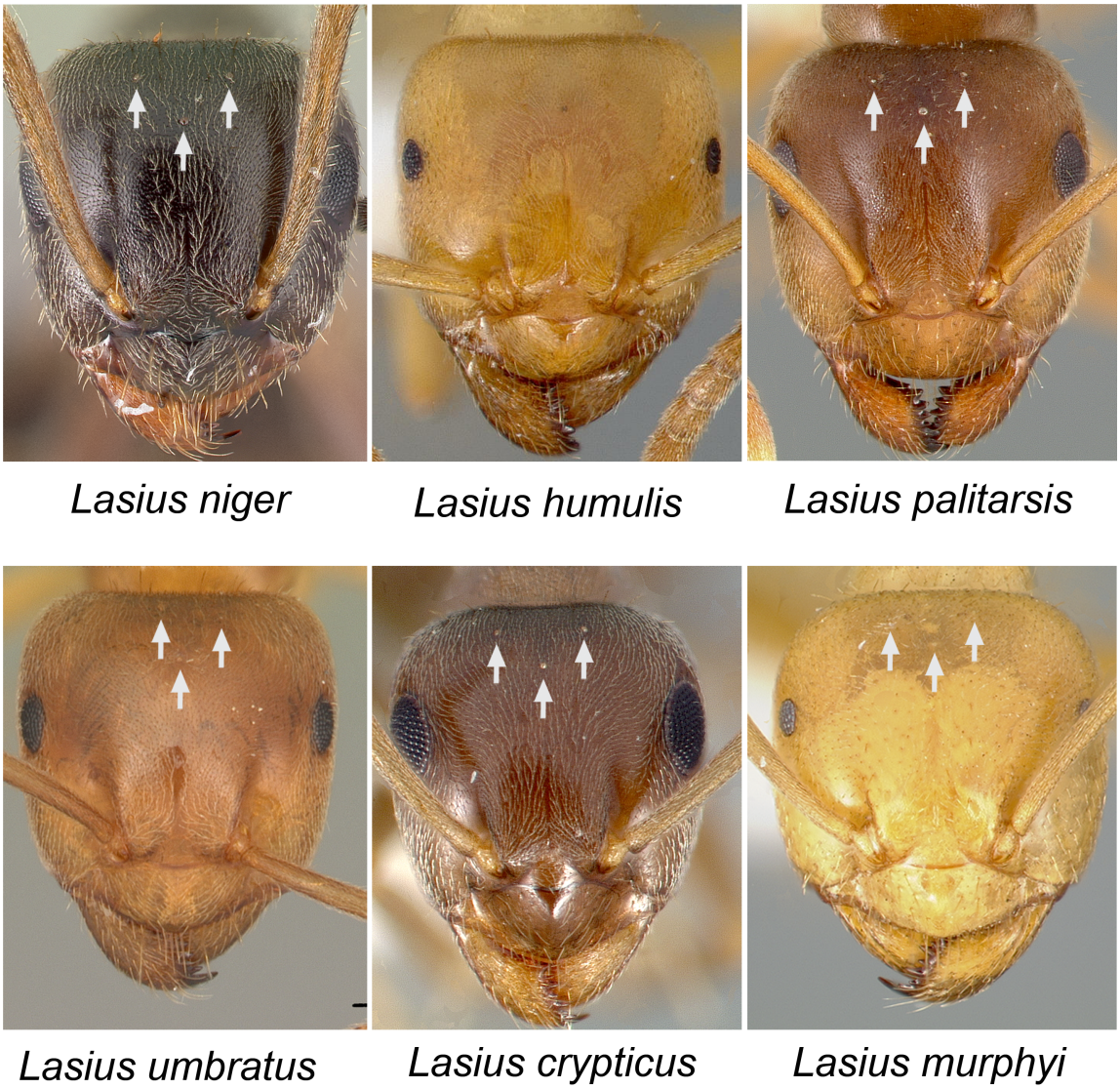

Lasius niger
Lasius humulis
Lasius palitarsis
Lasius umbratus
Lasius crypticus
Lasius murphyi

Figure 7: