<u>Question 1 – Philosophy of Science – Open book (hard copies only); laptop acceptable; no internet</u>

Using the scientific method as the basis for your discussion, discuss the basis of the scientific philosophy first proposed by Karl Popper. Explain how this changed the way that we have practiced science over the last 50 years. Is the approach that Popper proposed applicable in the field of systematics/taxonomy? Why/why not? Provide examples. Are there other ways to seek understanding and explanation?

<u>My Answer</u>

Karl Popper's view on the philosophy of science, commonly referred to as Falsificationism, revolutionized the way in which scientists approached their work. Popper argued that scientific theories can only be shown to be false using empirical data, instead of the previous notion that empirical data served to confirm or prove a theory.

The scientific method is generally regarded as 4 general steps:
1) make an observation of a phenomenon,
2) create a hypothesis that predicts or explains the observation,
3) gather empirical data through experimentation that tests the hypothesis, and
4) assess how the data relates to the hypothesis.

Prior to Popper, scientists would seek to confirm their hypotheses, and so would assess their collected data on whether it supported the hypothesis they proposed. If it did, they would move on to other work having shown their idea was correct.

Popper however, argued that confirmation in science is not possible, and that only through a series of falsifiable hypotheses can we begin to understand the truth. This required the development of the null hypothesis, which allows one of two possible options to be falsified. If the prediction or hypothesis was shown to falsify the proposed hypothesis, then the scientist would come up with a new hypothesis to explain the observation. However, if the null hypothesis was falsified, the scientist should design a new experiment to further test the proposed hypothesis, and continue to do so until the proposed hypothesis is falsified. Popper also suggested that theories need to include risk, and that a tentative theory (to avoid falsification) is less desirable than one that opens itself more grandly to falsification.

Falsificationism challenged scientists to continually tear down their ideas and build new, stronger ideas in their place, like a phoenix rising from the ashes. This change in philosophy allowed science to evolve much as life does via natural selection; weak ideas are quickly weeded out, allowing new, more robust theories to take their place, on which other ideas can then be built upon. Dr. Rosie Redfield of the University of British Columbia summarized the process of modern science in 2012 by encouraging students and other researchers to "fall in love with an idea, and then try to kill it".

There has been some attitude among other scientific disciplines that systematics, and taxonomy in particular, are not scientific, sometimes likened to stamp collecting or the filing of books in a library; essentially the pseudo-science Popper developed Falsificationism and the demarcation problem to root out. This attitude is probably due in large part to the fact that systematists and taxonomists rarely explicitly state their (null) hypotheses, because they are essentially the same for every taxon or problem studied.

For alpha level taxonomy, taxonomists can usually recognize that there are specimens that don't quite fit the mold (although techniques such as DNA Barcoding have occasionally brought light to cryptic species) the process of describing new species, the null hypothesis is typically "All species are currently described" or alternatively, "All specimens fit the species concepts currently defined", and the proposed hypothesis thus being there are new species awaiting description, or that do not fit species concepts as presently defined. As alpha taxonomy proceeds and new species are described, it is necessary for scientists to reassess how they fit into the larger scheme. Thus, in systematics & classification, the null hypothesis would be "Taxon X is monophyletic as currently defined" (assuming of course that the systematist in question followed the logic & reasoning of Hennig's cladistics), and with the proposed hypothesis being that Taxon X is currently poly- or paraphyletic and in need of revision and redefinition.

These hypotheses are then "tested" by assessing character data, whether that be morphology, DNA, behaviour, bio-chemistry, karyotype, or any other of an infinite number of potential data sources, and the results of these experiments are then used to falsify either the null hypothesis or the proposed hypothesis. The new classification or species is then proposed by the author as the new hypothesis awaiting falsification, which can be in itself tested using different specimens, characters (including entirely new datasets, or by using different outgroup taxa and character polarity, or reconsidering the homology of characters used previously), or techniques.

Taxonomy and systematics are built upon a whole series of falsifiable hypotheses (much like other the other sciences) that if independently falsified, in turn bring down the entire hypothesis of relationship. An example of this would be the debate over where the parasitic order of insects Strepsiptera fit on the evolutionary tree of life. For many years, Strepsiptera had been thought to be closely related to the beetles (Coleoptera), until the mid 1990's when scientists began testing this hypothesis using a newly available data source: ribosomal DNA. This new data set suddenly produced a new phylogeny placing the Strepsiptera as more closely related to the flies (Diptera), a hypothesis of relationship called "Halteria" (based on the fact that flies and Strepsiptera both have modified wings forming halteres, albeit on different body segments) that had never been put forward prior. The authors of the Halteria hypothesis supported their hypothesis of relationship by making a hypothesis about the shared morphology of the haltere, proposing that it was in fact the same structure embryonically but which had undergone a developmental homeotic change.

Other scientists were quick to further test this bold theory (a theory Popper himself would have likely applauded for being so risky), and eventually falsified various aspects of the

proposed relationship (thus bringing down the entire theory): additional DNA data (first with multiple loci and eventually full genomic data) suggested a relationship with the Coleoptera, while phylogenetic theorists developed the concept of long-branch attraction for grouping Diptera & Strepsiptera on the basis that they each had a large number of unique traits rather than shared and evolutionarily derived traits. Even though the Halteria is now considered falsified, our understanding of ordinal relationships in insects and phylogenetic theory made significant leaps forward during the process, phenomena that may not have occurred without the original, risky hypothesis put forward.

While other philosophical ideas have been proposed on how science can or should be undertaken, with Paul Feyerabend's epistemological anarchism ideas perhaps being the absolute polar opposite of the rigid, hypothetico-deductive process developed around Popper's ideas, I'm not sure how, or even if, they would be accepted by the larger scientific community. The current philosophical system may itself be a Kuhnian paradigm on how best to do science, and a conceptual revolution may be in the future for the philosophy of science (and by extension the scientific method and science as we know it), but that discussion and its implications are probably best left to be pondered at the pub.

Question 2 – Evolution – CLOSED BOOK

Explain in general terms the theory of evolution, what forces result in evolution, and in particular terms, explain rates of evolution (gradualism, punctuated equilibrium, other forms of rates of evolution). You can provide specific examples from fly populations.

My Answer

The theory of evolution by natural selection, first presented to the Royal Society jointly by Charles Darwin and Alfred R. Wallace in the mid 1800's, and subsequently expanded upon by Darwin in the Origin of Species, represented the first and most complete theory of not only why organisms evolve, but more importantly, how.

At its core, the theory of evolution by natural selection states that individuals are constantly in competition for resources (energy, shelter), both within species, and between species (intra- and interspecific competition, respectively), and most importantly that individuals vary in their ability to meet these needs. It is on this variation that natural selection acts, by differentially "rewarding" the fittest individuals with increased reproductive success, and thus skewing the ratio of lineages and traits that survive to the next generation. Natural selection is constantly at work at each of the levels of biological organization: species, populations, groups (when applicable), the individual & genes.

While similar forces and mechanisms of evolution & natural selection function at each of these levels (i.e. Dawkin's Selfish Gene theory, kin vs group selection, Hardy-Weinberg allele frequencies in populations, etc), I'll focus on the forces of evolution acting at the level of species, which result in speciation.

Generally speaking, there are two broad scenarios for speciation: sympatric speciation, where species diverge while being in close physical approximation (via niche partitioning and/or assortative mating based on sexual selection), and allopatric speciation, where species are separated geographically (via vicariance and dispersal). The two pathways are not necessarily independent as will be discussed shortly, but they provide interesting means to explore not only the forces of evolution, but also rates of evolution.

We'll begin with allopatric speciation. Vicariance is when populations are separated by geological boundaries, and then differentially speciate in isolation. This can be as simple as the formation of a river that separates two halves of a population such that gene flow ceases between them, or it can be on a much larger scale, such as continental drift or mountain/rift formation. Vicariance is typically considered to be the most common mechanism of speciation across long spans of time. In contrast, dispersal is when individuals or populations are move or are carried to a new, geographically isolated location, and then undergo speciation, again, in isolation from the original population. Dispersal can often lead to rapid evolution and speciation, particularly when populations arrive at new locations which feature reduced competition or many open niches.

When the Hawaiian islands began to form 5-8 million years ago, a few lucky *Drosophila* managed to find their way onto these volcanic islands shortly after they rose above sea-level, and quickly took over. With a new location devoid of their usual predators and parasites, and along with a plethora of unexploited habitats and biological niches awaiting colonization, these fruit flies radiated quickly, and soon moved into ecological roles that were unavailable to them on the mainland. As new islands formed in the archipelago, new dispersal events occurred, resulting in even higher rates of speciation. Soon, these flies, which probably originated from a saprophilic ancestor, were able to branch out and evolved species found from aquatic environments to parasites of other species. Today, there are hundreds of species recognized from the islands, and all are thought to have originated from a single colonization of an early (and now fully submerged) island.

As mentioned, niche partitioning can allow speciation to occur even when populations occur within the same area (sympatry), as long as there is no (or very little) gene flow between the populations as they are diverging. Niche partitioning, particularly host race evolution, is a strong example of this version of sympatric speciation. Similar examples are found in tephritid fruit flies in North & South America; *Rhagoletis pomonella* is thought to be in the midst of a host race speciation event between hawthorn (*Craetagus*) and apple (*Malus*) host plant lineages, while a recent study involving curcubit vines in Ecuador revealed a massive partitioning of plants by a genus of fruit flies into stem, flower, and fruit specialists. One theory for why these host shifts can result in such rapid speciation is the avoidance of parasitoids. By exploiting a new niche where predators and parasitoids are unable to find individuals, populations gain a headstart and an increased reproductive fitness. As long as individual continue to mate preferentially with others from the same host race (i.e. there is a genetic component to host choice), then populations will diverge and potentially speciate, even if the host plants are located in the same grove. A similar instance has been recognized in gall wasps on Manitoulin Island, although this is thought to be in the very early stages.

Sexual selection and mate choice may also result in sympatric speciation, and may explain why there many male flies exhibit highly modified and complex genitalia. Across many families (particularly in the Schizophora), males exhibit high degrees of species-specific genitalic structures. While there is a strong possibility that this acts like a lock-and-key strategy (pre-zygotic interspecific isolation), there is growing evidence that these shapes and structures may be involved behaviourally in convincing the female to accept and use the males sperm. In species where male genitalia are relatively lacking in these adornments, species may be sorting themselves instead by way of overt sexual displays and rituals (eg. Micropezidae). There is much work left to confirm whether this or another as yet unidentified explanation is at play however.

Finally, speciation appears to occur at different rates among different lineages, and especially in the flies, can alternate between rates. With the completion of the fly tree of life project, Wiegmann et al (2011) demonstrated that the Diptera appear to have undergone alternating phases of gradual species diversification and instances of punctuated, rapid diversification. On the gradual side of the spectrum, many of the

nematoceran lineages have been found in the fossil record dating back to early Jurassic, and many remain much the same as they are today. In contrast, the Schizophora first appeared roughly 60 million years following the K/T extinction, and are thought to have radiated to their current complement of more than 100 families within 20 million years, making them one of the most diverse lineages of organisms on the planet. The underlying causes of these differing speciation rates isn't entirely understood, but it may be related to the relatively stable occurrence of the habitats and life histories of the nematocerans (mostly aquatic as larvae, short-lived as adults or blood feeders able to adapt from reptilian to mammalian hosts), and the parallel radiation of angiosperms and mammals in the early Tertiary providing a plethora of new habitats, niches and strategies for the Schizophora to exploit.

Question 3 – Entomology – CLOSED BOOK

You have now worked on two families of Diptera, both at least in part phytophagous. Discuss the distribution of phytophagy throughout the Diptera, supporting your opinions about its origin, importance and function.

My Answer

Phytophagy is a common and important life history trait across the Diptera, and has arisen multiple times and within nearly all major lineages. Generally, modes of phytophagy in Diptera are separated between feeding on plant tissues as larvae, and on pollen and/or nectar as adults, although there are exceptions to the rule.

Larval phytophagy has evolved many times, and in most cases, likely from saprophagous ancestors. Saprophagy is perhaps the most common larval feeding strategy among flies, and it would seem to be a relatively straightforward evolutionary path from filter feeding on the microbial communities among dead, decaying plant matter to feeding on the decaying plant matter itself, and eventually moving on or into living plant tissue. This hypothetical transition can be seen within the genus *Drosophila*, which contains both saprophagous species such as *Drosophila melanogaster*, which feed on a mixture of decaying plant tissue and the bacteria and other microbes present, and phytophagous species such as *Drosophila suzukii*, which feed in ripe, living fruiting tissue. In the case of *D. suzukii*, a modification in larval feeding habits was dependent on a modification in adult female terminalia (a serrated ovipositor) that allows the female to circumvent host defenses (tough epidermal layers of the fruiting bodies) and place eggs in the soft, fruiting tissue.

Modifications to the female ovipositor and oviscape are common among phytophagous Diptera, with perhaps the most diverse array being found in the Tephritidae. Ovipositors and oviscapes are generally relatively small in species which develop within seed heads, stem galls or soft fruiting bodies (e.g. *Tephritis*, *Eurosta*, *Rhagoletis*), but can reach incredible and disproportionate lengths in species which attack large, hard, or more dense fruits (e.g. *Bactrocera*, *Anastrepha*).

Of course, phytophagous flies are not only found in fruiting bodies. As previously mentioned, there are many species within the Tephritidae that specialize in different regions of their host plants, and a similar diversity of larval feeding strategies can be found among different families. Cecidomyiidae are best known for their ability to induce large, safe living arrangements for themselves within plant tissue, giving them their common name, gall midges. Some Tipulidae have moved on from saprophagy to feed on root tissue of turf grasses, a fairly common transition it would seem as several other families have been recorded feeding on plant roots or below-ground plant structures, including the Micropezidae and Anthomyiidae. Phytophagy in tree trunk tissue is certainly more common in the Coleoptera, but the family of large stratiomyomorph flies Pantophthalmidae is known to burrow through tropical trees as larvae. This unusual behaviour may be related to dendrosaprophagy found in some Stratiomyidae, but this is

speculative. Finally, there are the leaf miners, particularly the Agromyzidae, which feed between the dermal layers of leaves as larvae.

Phytophagy may also be the most common source of energy among flies with functional adult mouthparts, primarily in the form of pollen and nectar. Even families most commonly associated with hematophagy (specifically nematocerans) consume pollen and/or nectar more often than blood. The origins of nectivory begin with the evolution of the angiosperms and flowering plants near the end of the Cretaceous, but the dipteran taste for high sugar content fluid likely evolved from feeding on the honeydew produced by plant-feeding Auchenorryncha & Sternorryncha (Hemiptera). With the evolution of flowering plants, flies found a new and plentiful source of energy, and likely began feeding on protein-rich pollen as a beneficial side-effect to the sugary nectar. Flies are now a common sight on flowering plants, with families from every major radiation, from nematoceran Culicidae, Chironomidae and Ceratopogonidae to orthorhapheran Bombyllidae and Stratiomyidae, empidoids and Syrphidae amoung the non-schizophoran Eremoneura, and countless families of acalyptrate and calyptrate Diptera, including Tephritidae, Conopidae, and Calliphoridae.

A plentiful and energy-rich food source such as pollen and nectar is also utilized by many aculeate Hymenoptera, which they commonly use to provision for their larvae in solitary or shared nests. These larders in turn have provided an opportunity for kleptoparasitism, where fly larvae or adults live within the nests of bees and feed off the stored pollen (i.e. some Drosophilidae in Mason Bee nests) or steal directly from the mouths of their victims (e.g. Braulidae in Honey Bee nests).

The evolution of phytophagy in Diptera is incredibly important, both in terms of fly diversity, as well as in relation to human economies. The major radiation in Diptera diversity, the Schizophora, is thought to parallel the blooming of Angiosperms in the early Tertiary. By taking advantage of this new and extremely diverse energy source, as well as taking advantage of other insects dependent on angiosperms (i.e. Tachinidae parasitoids of Lepidoptera), schizophoran diversity has exploded in the last 65 million years. This diversity can in part be explained by flies' ability to partition habitats and resources, even within the same plant. For example, Condon et al. (2014) recently found more than a dozen species of fruit flies (all from the same genus) using the same species of curcubit vine in Ecuador, but remaining reproductively isolated by preferentially ovipositing in different regions of the plant (some in the fruiting bodies, some in the flower heads, some in the stems or other segments) and at different times. This extreme niche partitioning is perhaps not the norm, but it demonstrates how much of an impact on diversity the evolution of phytophagy likely had within the Diptera.

From a human perspective, phytophagous Diptera are both a curse and blessing. Many of the species mentioned previously that inhabit fruits are of significant economic concern. California and Australia have each spent hundreds of millions of dollars to eradicate and prevent the establishment of various tephritid pests, most notably the Med Fly, *Ceratitis capitata*. *Drosophila suzukii* is now spreading across Canada and Ontario and has the potential to cause millions of dollars in damage to high-value fruit crops, while

leatherhead tipulids are a headache for golf courses and turf management professionals. However, the ecosystem services provided by phytophagous Diptera are likely more than the costs. We import and release tephritids like *Urophora cardui* to manage invasive plants, and we are only just beginning to understand and quantify the contributions to global pollination provided by Diptera.

Question 4 – Taxonomy & Systematics – CLOSED BOOK

Discuss Systematics with consideration of the following questions:
a. What is systematics? (touch on the seminal historical events in it's scientific history)
b. What are the assumptions of phylogenetic systematics?
c. What is the role of prediction in systematics?
d. What are the complementary and/or conflicting roles of different sets of characters (morphology, molecular, ecological…) within a modern systematic framework.

My Answer

Systematics, the science of describing and classifying biodiversity, is the oldest scientific discipline. From the time that proto-humans began communicating to one another, they have been classifying and labeling the life around them; which plants are safe to eat and what animals that will eat you. Over time, these labels and classifications were expanded and reformed to fit into the expanding context of our global migration. As people moved, they took their classifications with them, and modified them to fit their new locations. By the 18th century, these classifications and labels were diverse and increasingly endemic to particular regions, even when discussing the same, widespread organisms. This meant that information about organisms needed to be translated between regions, and frequently cases when what Paris considered species A was what Stockholm considered species B. Additionally, the way in which people named things began to become complex as they needed to differentiate between similar organisms, resulting in species with paragraph-length names.

Enter Carl von Linné (more commonly known as Linnaeus). In the mid 1700s, Linnaeus revolutionized the science of systematics by introducing binomial nomenclature and a hierarchical classification system to contain it. By providing a structure to taxonomy, and necessitating that a common theme and language be used to refer to species, Linnaeus brought order to chaos, allowing species concepts to be discussed and understood across the world. However, Linnaeus' work was in the context of classifying the work of God, just as He had commanded Adam & Eve to do in Genesis.

After another one hundred years of classifying and naming life on Earth, Charles Darwin and Alfred Russell Wallace demonstrated that God had nothing to do with biodiversity as we see it today, and that evolution through natural selection and the idea of common descent were responsible were the forces responsible for all the variations, forms and species being discovered and placed into Linnaeus' hierarchy. In a not-insignificant stroke of luck, the system of hierarchical classifications that Linnaeus had invented and implicated for classifying God's creatures also happened to reflect and work with Darwinian evolution, and thus systematists were able to continue their work within the same structure as before, and without having to redo a century's worth of research.

As expeditions to the far reaches of the globe continued to return specimens to natural history museums and universities at an ever increasing pace, and the true magnitude of Earth's biodiversity was becoming apparent, systematists began to debate how these

species should be classified. For the greater part of the 20th century, the ideas of Mayr and Simpson (among many others) postulated that species should be grouped by similarity, a technique referred to today as phenetics. In a way that I have difficulty understanding, these scientists seemed to ignore the work of Darwin, specifically the idea of common descent, and instead grouped species and higher taxa by overall similarity, with no regard for shared ancestry. While in some regards this may have made classifying what must have seemed like an infinite variety of diversity easier (red things over here, blue things over there), it seems so counter-intuitive why systematists and evolutionary biologists (which many of these early 20th century workers were) would seem to ignore the basic concept of evolution to do so.

Then, in the early 1950s, Willi Hennig changed everything (even if most systematists remained oblivious to it for nearly 20 years). While working in an Allied Forces prisoner of war camp during World War II, Hennig, a dipterist, began developing his idea of phylogenetic systematics. This idea, that species should be classified not by overall similarity, but rather by shared, evolutionarily derived (i.e. homologous) and unique characters (commonly referred to as synapomorphies), thus placing them in lineages of common descent (the concept of monophyly), would shake up the entire field of systematics. When he eventually published his idea in a small, German journal in 1952, it went largely unnoticed by the systematic community. It wasn't until 14 years later in 1966 when it was translated into English and printed as a stand-alone book that the cladistic revolution began. Unlike when Darwin published the Origin of Species, the scientific community did not fall in line with Hennig's line of reasoning. It was not until the mid- to late 1980s that cladistics was really embraced by the systematic community (and unfortunately not until after Hennig had passed away).

Cladistics is certainly without its potential flaws, although it is accepted that the assumptions it is based on are sound and unlikely to change. The largest assumption is of course that evolution is true, and that species evolve from common ancestors and thus have shared traits or characters that can be discovered and used to hang relationships and classifications off of. The other significant assumption is the use of parsimony to explain relationships. Parsimony is built on the concept of Occam's Razor, the simplest answer is most likely to be true, and assumes that characters and traits evolve along the shortest pathway, and don't involve extraneous evolutionary steps.

By using and following a cladistic classification, you are also presented with what can be considered a predictive taxonomy. In essence, this means that if you have a specimen of a recognizable taxon, you can make predictions about its morphology, biology, behaviour and/or ecology based on the evolutionary history of the taxon. For instance, if you were to walk into a natural history museum and find a specimen enclosed in a sealed box, but with a label confidently identifying it as an adult mosquito, you can make predictions about what it looks like even without ever laying eyes on it: you know that it's an animal, that it has a hard, jointed exoskeleton, 6 legs, 1 pair of functional wings and 1 pair of gyroscopic halteres, long antennae with at least 8 segments, and a body and wings covered in hairs or setae. You can also tell that it likely lives in water as a larva and is holometabolous. All of these features are predicted by the synapomorphies discovered

and designated along the chain of classification from Eukaryota to Culicidae. What you can't predict at this point is whether the specimen is hematophagous (not all mosquitoes drink blood, and not all individuals of species that drink blood do so), or what type of aquatic habitat it lays its eggs in (tree holes, ephemeral ponds, water-filled containers, long-term ponds and lakes, etc), because these are characters that are only definitive for lower taxonomic ranks. If you open the box, and find that one of the predicted characters is not present (eg. it's the first wingless mosquito), then you must reassess whether the identification is correct and the species has secondarily lost its wings, or whether the identification is wrong and the specimen is in fact a collembolan (and thus having its own unique set of synapomorphies).

In the past 30 years, systematics has seen a new character set become available and increasingly more frequently used (and in some cases preferred): DNA. In most cases, as technology has improved and DNA sequencing techniques have become more accessible (both financially and technically), DNA has become a valuable resource for systematists, particularly for estimating phylogenies where traditional character sets (morphology, ecology, etc) have been difficult to interpret or to establish homology with. However, there have also been a number of cases where DNA character sets have created controversial and arguably misleading results, which may be best illustrated by the Strepsiptera debate in the 1990s and early 2000s. Although there was never a strong consensus on where the enigmatic Strepsiptera belonged in the Insecta, it was generally thought to be sister to (or possibly derived from within) the Coleoptera (or somehow related to the Neuropterida). Then, using a relatively small segment (by today's standards) of ribosomal DNA, Whiting and colleagues shook up the system by proclaiming Strepsiptera as sister to the Diptera in a clade termed Halteria, theorizing that the mesothoracic halteres of Strepsiptera were homologous to the metathoracic halteres of Diptera thanks to an embryological homeotic shift, without providing any evidence for this theory beyond the DNA-based phylogeny. It was eventually proposed that a phylogenetic hiccup called long-branch attraction contributed to this unusual relationship, and as more data was added to analyses (both in the form of increased taxon sampling and increasing the gene loci used in the analysis from multiple nuclear, mitochondrial and ribosomal genes right up to the full genome), it has since been accepted that the original hypothesis of Strepsiptera+Coleoptera (or +Neuropterida) is probably correct.

Generally, I think that more data is always a good thing, and as we move into the post-genomic era we will see a lot of useful discoveries being made thanks to the influence of multiple data sets and data types being analyzed together. However, there are certain aspects of modern systematics that are troubling. For one, with the increase in dataset size, there has been a much greater reliance on phylogenetic algorithms that run more quickly but which are not based on parsimony (i.e. Bayesian inference, Maximum Likelihood, Neighbour-Joining). This means that relationships are being proposed but without any indication or recognition of their inherent synapomorphies. This isn't to say that the phylogenies proposed by these methods aren't correct, just that they don't represent the full picture, and don't provide all of the information one needs to test monophyly and to have a predictive taxonomy. As genomes become more readily accessible and analyzable, I think we'll see an increased call for morphological expertise

again to provide context and synapomorphies for the relationships being proposed through genomic analysis.

Afterall, a systematist today is only as good as their ability to establish homology.