INQUIRY & INVESTIGATION

Here Be Dragons: Using Dragons as Models for Phylogenetic Analysis

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Abstract

Dragons are a staple of fantasy literature, and various aspects of the creatures (most notably their anatomy) have been explored scientifically across different forms of media. Their distinct anatomical characteristics and the variations therein among the recognized "species" of dragons make the taxa appropriate models for basic phylogenetic analysis in an undergraduate general biology or systematics class. The wyvern, an obviously more primitive, distant cousin of the "true" dragons, is also an appropriate outgroup for these estimations of shared evolutionary history. Separating metallic from chromatic dragons, the generated tree shows relationships among the species that are consistent with their separation in the Dungeons & Dragons *games according to alignment, scale color, and religion, three characters that are not used in the analysis. Manual construction of a character matrix and cladogram of dragons followed by repetition of this process via conventional computer software allows the students to track their progress not only in terms of understanding such concepts as choice of character states and parsimony but also in terms of the applicability of said software.*

Key Words: *dragons; phylogeny; systematics; evolution; characters; parsimony.*

○ Background

Across myriad cultures, the reptilian creatures known as dragons have been iconic symbols of ancient power, wisdom, and even terror. Mythological texts and literature both classical and modern have greatly popularized the dragon and the myths surrounding it. In more recent times, dragons have been a staple of fantasy literature, often as winged harbingers of terror but sometimes as benevolent, sagacious ancients with a penchant for helping people in need. This dichotomy is nowhere seen more clearly than in the mythos of the widely popular *Dungeons & Dragons* role-playing games, which were designed by Gary Gygax and Dave Arneson and first published by Tactical Studies Rules (TSR) in 1974. In these games and related literature such as the *Dragonlance* series by Margaret Weiss and Tracy Hickman, dragons are divided into two groups: the good metallic dragons that worship the benevolent deity Bahamut (himself a dragon) and the evil chromatic dragons that worship the five-headed dragoness Tiamat.

Conveniently, this dichotomy extends beyond difference in alignments (a *Dungeons & Dragons* term for one's placement on the good-evil and lawful-chaotic axes). Chromatic and metallic dragons are also markedly different from anatomical and physiological perspectives. Aside from the difference in scale coloration, the most important distinction between them is with regard to their breath weapons: chromatic dragons have only one while metallic dragons have two. There are many other characters that can set apart not only the two types of dragons but the individual "species" of dragon under them, such as the type of wings, the tip of the tongue (whether pointed or forked), and the structure of the phalanges, among others.

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Scientific discussions of dragons have been done across various forms of media. Even *Natural History* by Pliny the Elder had chapters on the creatures (Pinly & Rackham, 1938). It can perhaps be said that of all the fantastical fauna in speculative fiction, dragons are the easiest to translate into real-world biological concepts. In an earlier paper (Cruz, 2013) on the use of fantasy creatures in teaching biology, I had said that one of the difficulties that the approach presents is finding real-world analogies for confounding, overly fantastical morphologies in bizarre creatures. This hurdle is virtually nonexistent when it comes to dragons, whose morphology—even considering the breath weapons and the six limbs—is very much grounded in science.

The field of systematics depends largely on the choice of characters and character states, both primitive (plesiomorphies) and derived (apomorphies), to determine the evolutionary relationships

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among taxa. These characters have been traditionally morphological, but the use of molecular characters is of course well justified. Many systematics classes have used to illustrate phylogenetic concepts and analysis fictional organisms called Caminalcules, which were created by Joseph H. Camin (Sokal, 1983; Gendron, 2000). Camin created these organisms with a particular temporal framework, starting from the most primitive form to more derived "species" whose anatomical changes used accepted rules on evolutionary change (Gendron, 2000). The advantage of using fictional organisms cannot be underestimated, given the relative ease and consistency with which characters can be established and phylogenies, generally unobtainable for real-world organisms, can be generated. Producing phylogenetic hypotheses for Caminalcules can teach students many important concepts in evolution, such as hierarchical classification, vestigial characters, convergent evolution, and the concept of parsimony.

Here I discuss an activity wherein my undergraduate class in systematics used dragons from *Dungeons & Dragons*, much more popular and arguably more exciting fictional organisms than Caminalcules, as models for creating character matrices and phylogenetic trees with the purpose of understanding basic evolutionary concepts pertaining to systematics.

○ Methodology

Biology majors of our University typically take the systematics class in their junior year, by which time they have already taken general biology classes and comparative anatomy classes, in both of which evolution and systematics are discussed. We performed this activity in the third laboratory session, after we had already discussed in past sessions the basic principles of taxonomy, classification, and nomenclature, and the principles of modern (Hennigian) systematics. I used Caminalcules to illustrate these concepts; we first performed the methodology described here with Camin's creations.

I had my students read the first chapter of *Draconomicon*, a *Dungeons & Dragons* sourcebook written by Andy Collins, Skip Williams, and James Wyatt and published by Wizards of the Coast in 2003. The sections that are most pertinent to the activities are those on The Dragon's Body (pages 5–9) and Dragons by Kind (pages 36–56). Images are available and are generally useful. The other sections of the chapter may be of some use but are not necessary. The first section, The Dragon's Body, details the typical anatomical features of dragons as broken down into organ systems. The second, Dragons by Kind, covers the variations in dragon form across the ten different operational taxonomic units (OTUs) or "species" of dragon, five each of the chromatic and the metallic. It is in this section that students can find the characters and character states for their classification. However, the specific breath weapons exhaled by these dragons are not listed in these sections, and are instead found in the individual dragon entries in the *Monster Manual* publication by the Wizards RPG Team (2014); they are provided in Table 1 below for convenience.

As the outgroup for their phylogenetic analysis, the wyvern is the most ideal. It is dragon-like in overall appearance (i.e., serpentine head, first pair of limbs modified into wings, scales, tail) but makes sense as a more primitive relation to the true dragons given that it has only four limbs and no breath weapon. One unique character state of the wyvern is its poisonous tail stinger, but if it and true dragons are to be considered reptiles (and therefore members of subphylum Craniata under phylum Chordata), it might be more parsimonious to consider that a unique apomorphy of the wyvern rather than a plesiomorphy that has been lost in true dragons. The pseudodragon, a miniature dragon that also has a tail stinger, might be interesting to add either as another outgroup or a basal true dragon. Anatomical details of both wyvern and pseudodragon may be found in any of the *Monster Manual* publications of Wizards of the Coast.

Table 1. The true dragon "species" and their breath weapons.

Dragon "Species"	Breath weapon/s
Black	Acid
Blue	Lightning
Brass	Fire and sleep gas
Bronze	Lightning and repulsion energy
Copper	Acid and slowing gas
Gold	Fire and weakening gas
Green	Poisonous gas
Red	Fire
Silver	Ice and paralyzing gas
White	Ice

○ Manual Construction

My students first constructed character matrices and cladograms from the dragons manually, so as to teach them the basic concepts of phylogenetic analysis without being hampered by the need to understand how computer programs work. Using the details provided on the five chromatic (black, blue, green, red, white) and five metallic (brass, bronze, copper, gold, silver) dragons in *Draconomicon* and on the wyvern in the *Monster Manual*, they identified characters and character states that were to be placed in a typical character matrix. The characters and character states placed therein are described below.

Given the variations among wyverns and the true dragons, the following are the most sensible characters and character states to use:

1. *Character: Number of limbs.*
   Character states: 0 – four limbs (tetrapod); 1 – six limbs (hexapod).
   Having established that dragons are members of the taxon Craniata (Vertebrata), it is most parsimonious to assume that the tetrapod (four-limbed) condition is a plesiomorphy. The wyvern, which is our outgroup, shows this condition. Figure 1 shows a comparison of the dragon's "hexapod" form and the wyvern's tetrapod form.
2. *Character: Breath weapon.*
   Character states: 0 – none; 1 – one breath weapon; 2 – two breath weapons.

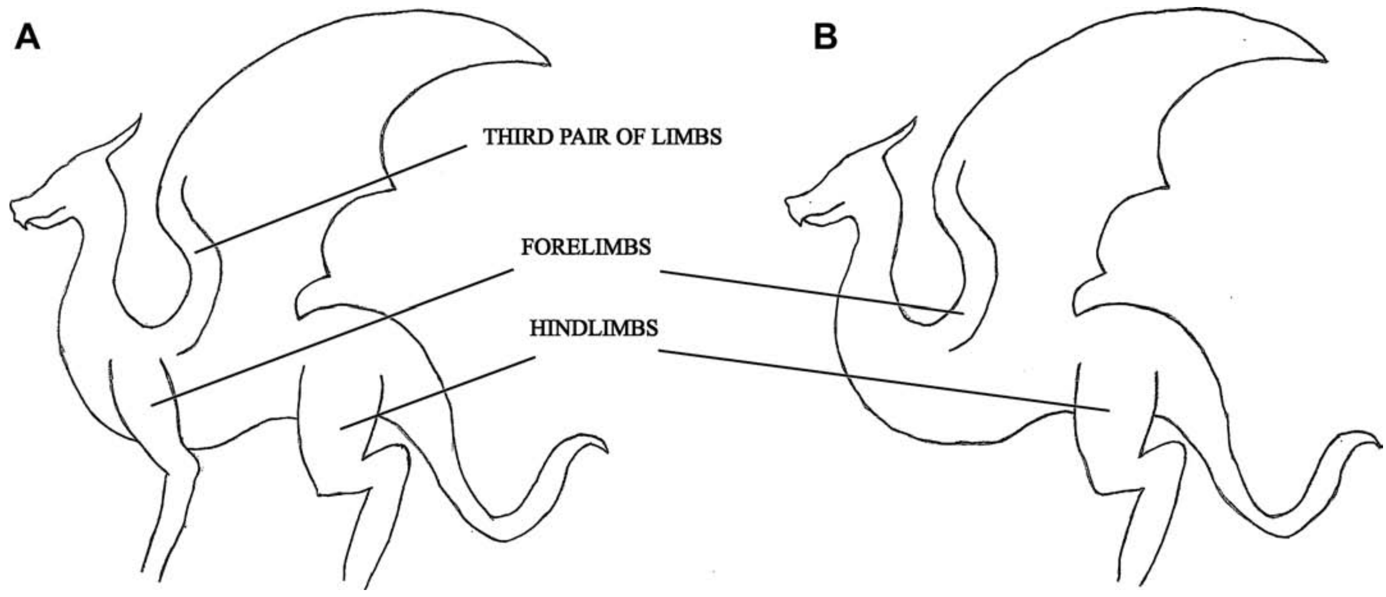

Figure 1. A dragon as "hexapod" with six limbs **(A)** and a wyvern showing the ancestral condition of having four limbs **(B)**.

Dragons, particularly the fire-breathing ones, are primarily known for their primary arsenal: breath weapons. Wyverns did not evolve to have any type of breath weapon, and the same can be said of all other real-world reptiles. Each of the species of chromatic dragons has one breath weapon, while each of the metallic dragons has two: a gas and one that is shared with the chromatic dragons (for instance, the silver dragon can breathe out gas and frost, the latter of which is shared with the white dragon).

A tendency here might be for the students to use as distinct character states each specific type of breath weapon, such as lightning for the blue and bronze dragons. One potential problem with this approach is that it may artificially group together dragons with the same type of breath weapon in a way that renders other synapomorphies (such as the pointed tongue of metallic dragons) as homoplasies instead. It would be worthwhile to discuss with the students how this leads to a less parsimonious hypothesis on phylogeny, and ask them to determine what modes of coding the breath weapon character allow for greater parsimony.

3. *Character: Wing shape.*
   Character states: 0 – "bat-like," not reaching past the hindmost limbs; 1 – "manta-like," with distinct frill spines and reaching past the hindmost limbs.
   The "bat-like" shape of the wings seems to be primitive, as it is shared with wyverns (and the extinct pterosaurs, for that matter). Aside from being easily distinguishable, this is also a good character because only three (brass, copper, gold) of the five metallic dragons have "manta-like" wings, and so this is a good character to further separate the dragons under that major group. Figure 2 shows a comparison of the two wing shapes.
4. *Character: Alar phalanges.*
   Character states: 0 – with thumb and multiple phalanges of same lengths; 1 – with thumb and multiple phalanges of different lengths; 2 – with only one phalanx.
   The dragons are more diverse in terms of their alar phalanx (number and length), with silver dragons even having a unique apomorphy: a second "thumb" from one extremely short phalanx (Fig. 3). The wyvern shows the plesiomorphic character state of having a short thumb and several phalanges of the same length supporting the wing. The most derived character state is presumably what the brass and gold dragons have: only one phalanx.
5. *Character: Alar olecranon modification.*
   Character states: 0 – absent; 1 – present.
   Of all the dragons, only the bronze and copper have an extension of the olecranon process of the ulna (i.e., the elbow) that supports the wings (Fig. 4). It is thus reasonable to see this is a synapomorphy of the two dragons and is another good trait to separate these from the other metallic dragons.
6. *Character: Tip of tongue.*
   Character states: 0 – forked; 1 – pointed.
   The tip of the dragon tongue seems to be a good character to further distinguish between chromatic and metallic dragons; all metallic dragons have pointed tongues (take note here of the brass dragon, whose description text says that it has a forked tongue but whose illustrations show it to have a pointed one; for the sake of consistency and parsimony, I went with the latter). However, neither description texts nor illustrations indicate if the tongues of the blue and white dragons are forked or pointed. This is a good opportunity to tell the students that when a certain character state is uncertain, a question mark may be placed in the corresponding matrix cell. Phylogenetic software that read character matrices are often able to read this marking. It would be a good exercise to compare the resulting phylogenetic trees of a matrix with question marks and a matrix that assumes a forked tongue for all chromatic dragons.

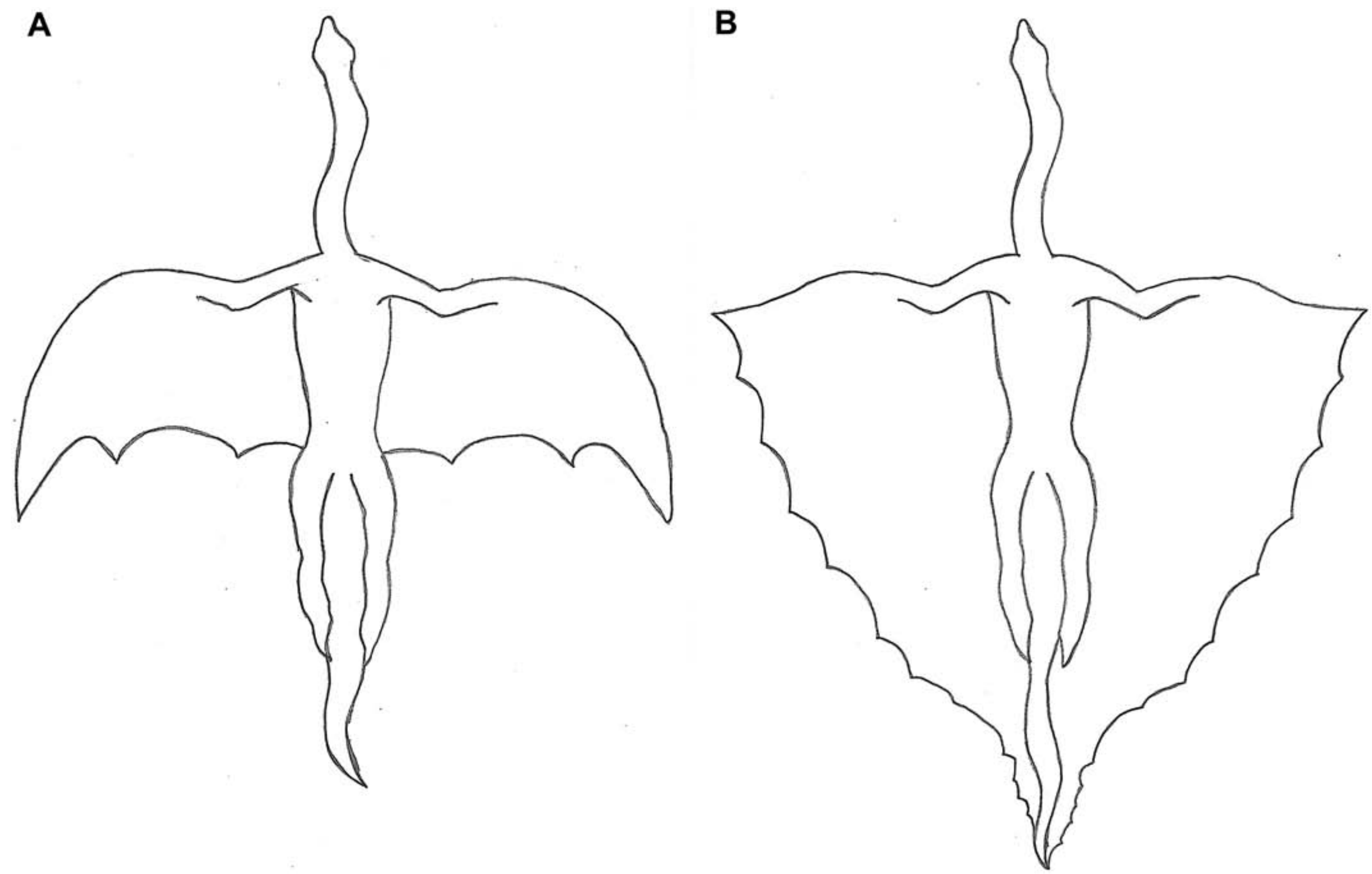

Figure 2. The two wings shapes of dragons: **(A)** "bat-like" and **(B)** "manta-like."

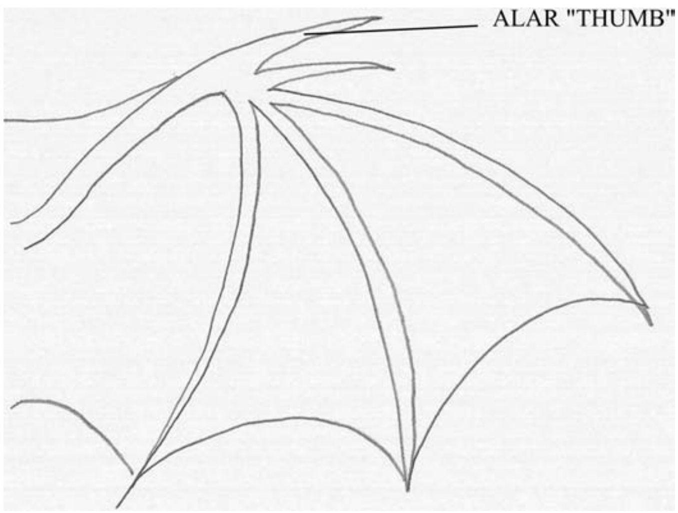

Figure 3. The extra alar "thumb" of the silver dragon.

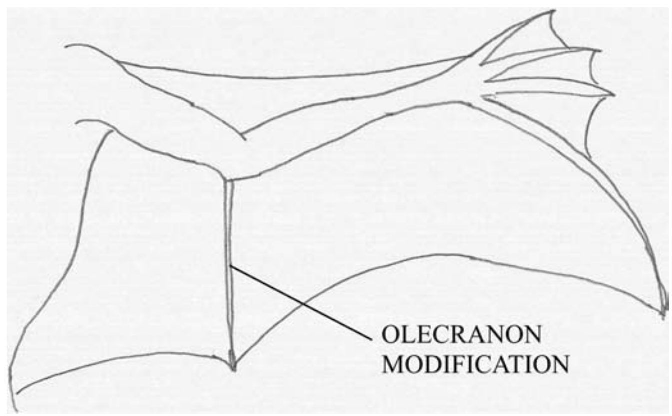

Figure 4. The alar olecranon modification of the bronze and copper dragons.

7. *Character: Neck frills.*
   Character states: 0 – none; 1 – one neck frill; 2 – two neck frills.
   The neck frill is most emphasized in the bronze and especially the silver dragons (Fig. 5), but even certain chromatric dragons have them. This is then a good character to show that not all character states allow a clear-cut delineation between chromatic and metallic dragons. Primitively, the wyvern does not have a neck frill. The "crest" of the green dragon is admittedly confusing, as it looks very much like a neck frill. For this purpose, I consider it a highly modified one.
8. *Character: Dorsal head hornlets.*
   Character states: 0 – present; 1 – absent.
   Rows of small horns or hornlets on the dorsal surface of the head (Fig. 6) seem to be primitively present in wyverns and chromatic dragons. It is interesting to note that among chromatic dragons, only the white dragons have none.

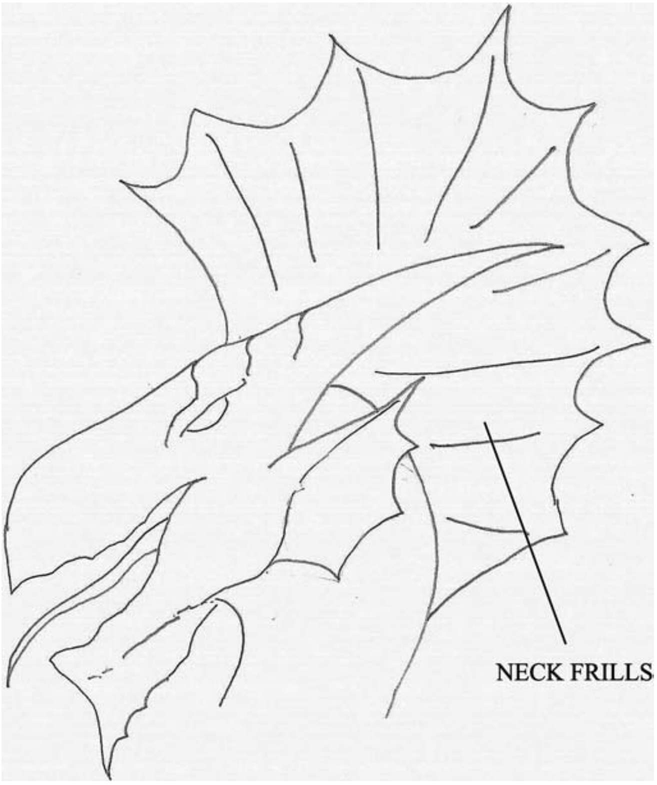

Figure 5. The characteristic neck frills of a silver dragon.

Figure 6. Rows of hornlets on the dorsal surface of a chromatic dragon's head.

One other character that might be useful is the presence of an external frilled ear. Among the taxa, this character is present in wyverns, blue dragons, red dragons, and silver dragons. However, the absence of an external ear (i.e., the presence of only an ear opening on the side of the head) is highly associated with the burrowing or aquatic lifestyle of true dragons, and so this is likely a case of convergent evolution. The absence of an external frilled ear may therefore be a homoplasy and not homology.

After creating the character matrix, the students constructed a cladogram. Here, the most important lesson is to determine evolutionary relationships among taxa by looking at shared derived traits or synapomorphies; sister taxa share the highest number of synapomorphies (Futuyma, 2009). Plesiomorphies, unique apomorphies, and homoplasies are not counted. In case three or more of the dragon species share the same number of synapomorphies, the students had to determine which two of those were most closely related to each other by looking at characters that separate them from the rest.

This entire activity was intended for a two-hour class schedule, but many students remarked in a post-activity assessment that more time was needed for them to fully appreciate it and achieve the learning objectives. This would work for a typical four-hour schedule, or if this is not possible, the output can be collected a few hours after the end of the class or even the next day. The final outputs that I asked for were the character matrix (either handwritten or on a computer spreadsheet) and the cladogram, which must be properly labelled with the character states that distinguish taxa. The students can also be asked to identify examples of convergent evolution and to determine which dragon species constitute genera (i.e., which "species" are similar enough to be lumped together into the same taxon distinct from other taxa of the same level), with the caveat that a genus as a taxonomic category is an artificial construct or abstraction whose true biological meaning is contentious at best (Simonetta, 1992). They can also be asked to assess whether their phylogenetic estimates are parsimonious.

○ Using Phylogenetic Software

The second part of the activity was performed during the class on the next week after the students had received their graded papers from the first with my inputs. This stage is meant primarily to allow the students to familiarize themselves with common phylogenetic software. My students used a standard computer software, Mesquite v. 3.04 (Maddison & Maddison, 2015), to generate their character matrices. Table 2 outlines the basic steps in using Mesquite. Figure 7 shows a sample character matrix on Mesquite. I gave them the option to change their character and character state choices based on my inputs and their better understanding of phylogenetic concepts.

They analyzed the resulting matrix through the software Phylogeny Inference Package (PHYLIP) v. 3.6 (Felsenstein, 2005), particularly its executable program *pars*. This program infers phylogenies using discrete characters, which are those found in the character matrix. It produces two files, outtree and outfile, which can normally be opened on a program such as Notepad or Wordpad. Outfile is what shows the generated cladogram. The *drawtree* or *drawgram* programs can also be used to view the cladogram; they differ in that *drawtree* draws unrooted phylogenetic trees. Since there is an outgroup (the wyvern), *drawgram* is more appropriate.

Table 2. Steps in using Mesquite to generate a cladogram.

Step	Output
1. After opening Mesquite, select *File* from the menu, and then *New*.	Window offering the option to save the file
2. Save the .nex file using any filename.	Window for creating matrix
3. Indicate number of taxa in the corresponding box, click the box beside "Make Character Matrix," accept default settings, and click OK.	Window requesting further details for matrix
4. Indicate the number of characters in corresponding box (new characters may be added later), change the name of the character matrix in corresponding box if desired, select Standard Categorical Data (default), and click OK.	Character matrix table
5. Select *Matrix* from the menu, and then *Edit State Names*.	Assignment of particular character state descriptions to character state codes
6. Fill up the matrix with the necessary information.	Completed matrix
7. If desired, one may add characters or taxa or delete particular characters or taxa by selecting *Matrix* from the menu and then *Add characters*, *Add taxa*, or *Delete selected chars or taxa*, respectively.	Matrix with added and/or deleted characters and/or taxa

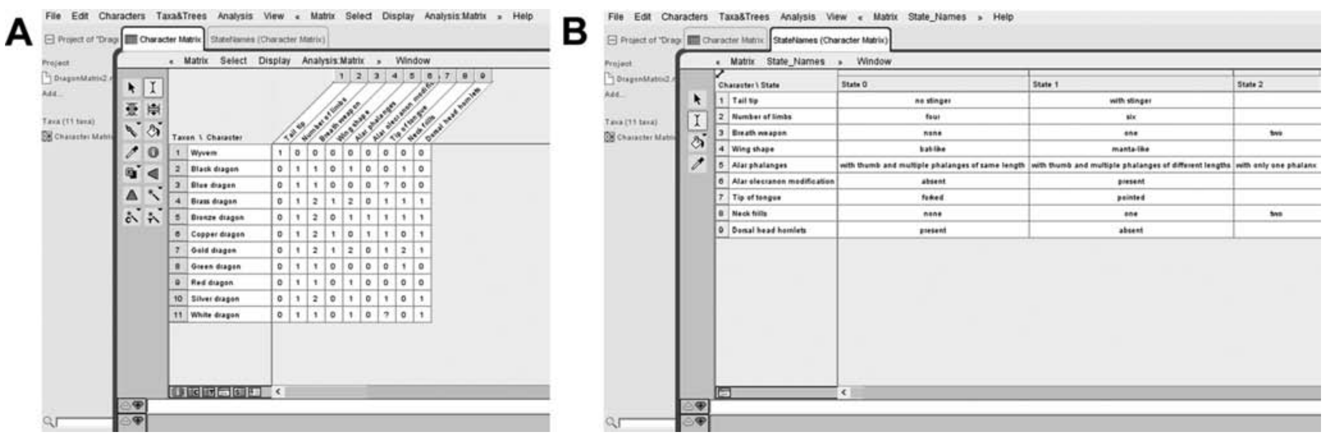

Figure 7. Sample Mesquite character matrix **(A)** and state names matrix **(B)**, where character states are assigned.

Figure 8 shows the resulting tree. As expected from the character matrix, the metallic dragons are more closely related to each other than any single one is to any of the chromatic dragons. This is consistent with their *Dungeons & Dragons* grouping according to alignment, religion, and scale color (none of which was a character used). The brass, copper, and gold dragons are most closely related, which is not surprising given that they all have manta-like wings. The metallic dragons are more derived taxa than the chromatic dragons, the most primitive of which appear to be the black and green dragons (which are sister taxa sharing the neck frills, though homoplasious to those of metallic dragons). The wyvern is very clearly designated as the outgroup.

Several polytomies (multifurcating instead of bifurcating relationships) are observed in Figure 8, such as with the gold, copper, and brass dragons. These are generally not favored, as it very likely that adding traits or improving the analysis can determine which two of the three (or more) taxa are more closely related to each other, but there are also systematists who consider them to be valid phylogenetic hypotheses (Braun & Kimball, 2001). These have been called "hard" polytomies and may be reflections of multiple simultaneous speciation events. This divergence in perspective among practitioners of the field should be discussed with the class. Those who consider these to be "soft" and therefore unacceptable polytomies should be encouraged to think of which characters can be added to resolve them. For instance, the extremely long tail of gold dragons might be considered a unique apomorphy, as well as the very broad and smooth skull plate of brass dragons.

This activity is appropriate for a two-hour class. The final outputs that I required were the Mesquite file (a .nex file), the outtree and outfile from PHYLIP, and the *drawgram* output as a saved image. It was worthwhile for the students to reflect on the importance of manually creating the matrices and trees first before experiencing the convenience of computer software. They should also be asked to compare their manual tree with what PHYLIP or a similar program generates, especially since these programs generate many trees on the basis of parsimony.

○ Assessment

A total of 35 of 37 (94.6%) students were able to give the activity ratings and qualitative feedback after its completion. No inducements,

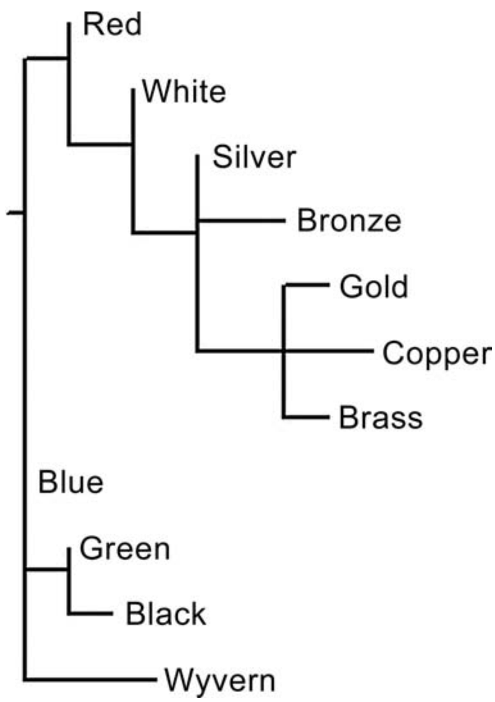

Figure 8. The phylogenetic tree generated by drawgram on PHYLIP.

Table 3. Mean scores of students for the statements for assessment of the activity.

Statement	Mean
I enjoyed the activity.	3.8
I learned what I needed to learn from the activity.	4.2
I found the activity useful in illustrating concepts learned in class.	4.3
Dragons are appropriate tools to use in learning basic phylogenetic analysis concepts.	4.0

such as extra credit, were given for responses, as they were made after submission of the students' final marks. Following the Likert scale, the students were asked to respond with whole numbers ranging from 1 = strong disagree to 5 = strongly agree to the following statements: (1) I enjoyed the activity; (2) I learned what I needed to learn from the activity; (3) I found the activity useful in illustrating concepts learned in class; and (4) Dragons are appropriate tools to use in learning basic phylogenetic analysis concepts. Table 3 shows the mean ratings for the statements. Responses ranged from a low of 2 to a high of 5, with median and mode values of 4 for all statements.

The mean grade of my students for the first activity (manual creation of matrices and cladograms) was 74.8 percent, which is a C+ in my University's grading system. The lowest grade was 60 percent (D) and the highest was 90 percent (B+). This was on a grading scale where the highest possible score was 30, which is broken down into the following components: 10 points for choice of characters and character states, 10 points for how accurately the cladogram reflected the phylogeny based on synapomorphies, 5 points for construction of the matrix (organization of rows and columns, completeness of labels), and 5 points for construction of the cladogram (overall appearance, clear branching of taxa, completeness of pertinent information such as character states that separate taxa). The most common mistakes for those who got low scores were on character/state choice and cladogram construction. The criterion of character and character state choice is of course a tricky and rather subjective one, but low marks were given (a) for not including the most important characters such as breath weapon, number of limbs, wing shape, and alar phalanges, and (b) for choosing character and character states that led to the assumption of too many homoplasies.

As mentioned above, most students commented that two hours is lacking for a pre-activity discussion and the activity itself. Aside from this, the handouts should be given to the class at least two days in advance. General comments on the strength of the activity revolved around its fun nature, the familiarity of dragons, and the opportunity for critical thinking. Many students commented on the lack of established phylogenies for dragons as both a strength and a weakness. On the one hand, some of the characters may be vague and their importance subjective. On the other, students cannot "cheat" and turn in an existing character matrix and phylogenetic tree for their output because there are none.

○ Conclusion

Dragons are easily among the most accessible of all fantastical creatures, but what truly makes them apt models for biological concepts is the general concreteness of their clearly craniate (i.e., vertebrate) and reptilian anatomy. Absent among them are bizarre, aberrant anatomical features that render other unreal creatures almost inscrutable from a scientific perspective. Even the dragon's most unusual (and incidentally its most popular) character, its breath weapon, can be explained by unorthodox and yet plausible scientific thinking. The classification of dragons by color and alignment also gives us a convenient way to study their kinds as different species whose evolutionary relationships are practical and exciting to explore.

The evaluations of the students agree; the activity is generally seen as enjoyable and useful, and dragons are considered to be an appropriate tool for learning phylogenetic concepts and use of related software. Both Dragons and the more traditional Caminalcules are fictional and so are more conveniently limited in terms of scope, but using dragons has the advantages of the creatures' innate charisma and the lack of an established or accepted "best" phylogenetic estimate (this is not true of Caminalcules). This lack prompts the students to truly create their own from the data that is given, which certainly calls for problem solving and critical thinking. As several students pointed out, the dilemma is determining which characters are important and which are not, but that is an important process in learning phylogenetic concepts.

This activity reinforces the usefulness of fictional organisms in understanding the biology of real ones. It would perhaps be worthwhile to follow this activity with discussions of the complexity of the amniote groups (reptiles and their descendant groups) and their phylogeny, as well as where dragons (and wyverns) hypothetically fit into that taxon.

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