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S365_1: An introduction to biological systematics

Clip 1: Darwin, Linnaeus and Simpson (a)

This audio clip relates to Figure 3.

Dr. Colin Patterson

Darwin's diagram is bound in with his chapter on natural selection, and he used nine pages of that chapter to explain it. He gave the diagram another three pages in the chapter on geological succession, and then another five pages in the chapter on classification.

Of course we don't have time to work right through Darwin's seventeen pages, but the format of the diagram is probably familiar to you. It has a vertical time-scale of fourteen periods, which Darwin says might each represent a thousand generations, or ten thousand generations, or a million, or even a hundred million. The capital letters **A** to **L**, at the bottom of the diagram, represent, "the species of a genus large in its own country," in Darwin's words.

If you take a species capital A as an example, the diverging and branching dotted lines represent its offspring, and the lower case letters and superscript numbers, going from **a1** to **a14**, **m1** to **m14**, and so on, represent well-marked varieties, with distance along the horizontal axis indicating amount of divergence. So, if each time period represents a thousand generations, then after 14,000 generations, at the top of the diagram, species **A** has produced eight descendant species, numbered **a14** to **m14**. And Darwin says, "Thus, as I believe, species are multiplied and genera are formed".

Among those eight species, Darwin says that the three on the left, **a14**, **q14** and **p14**, "will be nearly related from having recently branched off from **a10**, whereas **b14** and **f14** will be more distinct from those three, and **o14**, **e14** and **m14**, the three on the right, will be nearly related to each other, but having diverged at the first commencement of the process of modification, will be widely different from the other five species, and may constitute a distinct genus," end of quote.

Darwin goes on to say that the six species descended from species **I** at the top right of the diagram, will have to be ranked in a different subfamily from the species descended from **A**. And then he says that he sees no reason to limit this kind of descent with modification to species and genera alone. If the amount of change in each time period was greater, we might end up with two different orders, represented by the descendants of species **A** and **I**.

In his chapter on classification, Darwin uses the diagram to show how his theory of descent with modification predicts and explains what he calls, quote, "the grand fact in natural history of the subordination of group under group, which, from its familiarity, does not always sufficiently strike us". And then he goes on, "propinquity of descent - the only known cause of the similarity of organic beings - is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications," end quote. And then Darwin goes on, "that the natural system is founded on descent with modification; that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical; that community of descent is the hidden bond which naturalists have been unconsciously seeking".

This audio clip relates to Figure 3.

Dr. Colin Patterson

I shall quote no more from Darwin, but I want to emphasise the fact that he saw classification as one of the most important pieces of evidence bearing on his theory. Since antiquity, naturalists have found that animals and plants fall into a hierarchy, a system of groups and subgroups. And this system was formalised by Linnaeus in the 18th century, into classes containing orders, orders containing families, families containing genera and so on.

Linnaeus, and most other systematists before Darwin, saw this natural hierarchy as an expression of an abstract natural order, the creator's plan. But Darwin saw it in material, or concrete, terms, as the inevitable result of descent with modification, and as something predicted by and so explained by his theory. That's why he said that all true classification is genealogical.

So now, having worked through Darwin's diagram, and his comments on it, we might be ready to answer some questions. The first, and the most basic, is this, "What does 'relationship' mean in systematics?" I shall outline three different answers, each of them given by one of the three most influential and authoritative systematists.

The first answer's by George Gaylord Simpson, who lived from 1902 to 1984. Here's what he said in his 1961 book, "Principles of Animal Taxonomy": "Is a man more closely related to his father, son, or brother? The degree of genetical relationship to father and son is invariably the same, 0.5 on proportion of shared chromosomes. Genetical relationship to a brother is variable, from 1.0 to 0.0 in terms of chromosomes, although the probability of those extremes is exceedingly low, but the mean value is the same as for father and son, 0.5. Unfortunately, relationships among taxa do not have such fixed a priori expectations. The same two kinds of relationships nevertheless exist among successive taxa in an ancestral-descendant lineage, and among contemporaneous taxa of more or less distinct common origin. The former relationships are called vertical, and the latter horizontal," end of quote.

Now we can easily picture Simpson's two kinds of relationship by looking back at Darwin's diagram. If you find the point in the left-hand lineage, the **A** line, where it splits at **a3** and gives rise to **a4** and **d4**, you can see that the relation between **a3** and **a4** is the 'father-son' kind, Simpson's vertical relationship, and the relation between **a4** and **d4** is the 'brother' kind, Simpson's horizontal relationship.

Simpson goes on to say that one kind of relationship is obviously just as objective as the other, that classification by either vertical or horizontal relationships alone is absolutely impossible, and that the art of taxonomy is in using your taste and ingenuity to effect a compromise between the two kinds of relationship. That's Simpson's answer to the question "what is relationship", and it leads him to see classification as an art, a matter of taste and ingenuity.

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Clip 3: What does 'relationship' mean in systematics?
George Gaylord Simpson

This audio clip relates to Figure 4.

Dr. Colin Patterson

We can understand and criticise Simpson's solution better with the help of a diagram, which shows his idea of incorrect and correct ways of looking at a phylogenetic tree.

In the left hand tree, the successive levels are equated with taxa, and the result's a family containing two genera, each with two species. Now Simpson called this idea 'flatly false', and said that the correct classification is the one in the right hand diagram, where we have a family containing three genera - two living ones with two species, and a third ancestral genus with three species.

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Clip 4: What does relationship mean in systematics? Ernst Mayr

This audio clip relates to Figure 5.

Dr. Colin Patterson

The second answer to the question, "What does 'relationship' mean?" comes from Ernst Mayr. Here's a quotation from his 1969 book 'Principles of Systematic Zoology' … "To the evolutionist, 'relationship' means "inferred genetic similarity, as determined both by distance from branching points and subsequent rate of divergence," end quote.

Again, we can understand Mayr's concept better with the help of a diagram. It comes from a 1974 paper by Mayr, and it shows four species - an ancestral species **A**, and three descendants, **B**, **C**, and **D**. The numbers show the genetic difference of each species from the ancestor: **C** differs from **A** by only **10%**, **B** differs by **15%**, and **D** has diverged very rapidly, and differs from **A** by **70%** of its genome.

Mayr says, "Taxon **C** is more closely related to **B** than to **D**, even though it shares a more recent common ancestor with **D**".

So that's Mayr's solution - relationship means genes in common, or genetic similarity.

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Clip 5: What does relationship mean in systematics? Willi Hennig

This audio clip relates to Figures 6 and 4.

Dr. Colin Patterson

The third answer to the meaning of 'relationship' comes from Willi Hennig, a German entomologist, who lived from 1913 to 1976. Here's a quotation from Hennig's 1966 book, "Phylogenetic Systematics" … "The concept of 'relationship' may be defined as follows: a species **x** is more closely related to another species **y**, than it is to a third species **z** if, and only if, it has at least one stem species in common with species **y**, that is not also a stem species of **z**," end quote.

Hennig's definition sounds formal and Germanic, but it's easy enough to follow with the help of a picture, which comes from the page facing the definition in Hennig's book. I've added the letters **X**, **Y** and **Z** so that we can match his definition to the diagram. He says that **X** is more closely related to **Y** than to **Z**, because **X** and **Y** share a stem species - which I've labelled **C** - which is not also a stem species of **Z**.

Above Hennig's tree are two Venn diagrams .- patterns of nested ellipses. It's a feature of Hennig's view of classification that the tree and the classification should be exact images of each other. His upper Venn diagram, labelled **1**, is an exact match with the relationships shown in the tree. His lower Venn diagram, labelled **Ia**, shows a different pattern, a pattern we should get if we followed Mayr's definition of relationship - shared genes - because the distance between stem species **A** and **B** is much less than that between **B** and **C**. The shared similarity of species **W** and **Z** would make Mayr classify them together, with the result shown by the dotted line in the tree, and by the dotted ellipse in the lower Venn diagram. The pattern of relationship shown by the tree can't be recovered from the classification shown by the lower Venn diagram, which gives a different tree.

As for Simpson's concept of relationship, his right-hand diagram, number 2B, is presented both as a tree and a Venn diagram, and you might try copying out the Venn diagram part of it with these seven species, and seeing what tree you recover from it. As you'll find, the tree you get is quite different from his original … but Simpson's left-hand diagram, the concept that he called 'flatly false', exactly matches a Venn diagram expressing the relationships in the tree.

Clip 6: Three schools of classification

This audio clip relates to Figures 4, 5 and 6.

Dr. Colin Patterson

Now the three kinds of relationship I've been talking about have been called Simpsonian, Mayrian and Hennigian relationship. And they can be fitted very neatly to the three different schools of classification that developed during the 1960s, and were much disputed through the 1970s. These three schools are called **phenetics**, **cladistics** and **evolutionary systematics**, or **eclectics**.

Phenetics relies on overall similarity as a measure of relationship, and so it classifies similar organisms together. This matches Mayr's definition of relationship as shared genotype. Cladistics aims to classify by inferred recency of common ancestry, and so it matches Hennig's definition of relationship. And eclectics, or evolutionary systematics, classifies by a mixture of similarity and inferred common ancestry, using taste or judgement as to when one criterion's given precedence. And so it matches Simpson's discussion of relationship, and how one ought to classify.

But notice that there are only two criteria of relationship - the phenetic one of similarity, and the cladistic one of inferred common ancestry. Eclectics merely uses a mixture of the two. Well, which school is correct, or is best?

The overwhelming consensus, after twenty years of argument, is that cladistics is best, and it's unusual these days to find a systematist, who has given any thought to the fundamentals, who isn't a cladist.

Cladistics has won through, I think, for two main reasons. First, it has a consistent and coherent philosophy, and second, it developed at the same time as the early work in molecular systematics, when protein sequences and other molecular evidence was first brought to bear on problems of relationship and classification.

Let me explain quickly why this is so. A molecular biologist can only sample living taxa. He ends up with a set of data, let's say DNA sequences, from which he wants to recover a tree, or a classification. The sequences are necessarily seen as terminals of the tree. No-one would dream of seeing a DNA sequence from one species as ancestral to a sequence from another species. And, in a tree, it's ancestors that occupy the internal nodes and branches.

So molecular systematists, from the beginning, worked with samples from the tips of the tree, and tried to reconstruct the tree by one method or another. Now, if we look back to the diagrams explaining Simpson's, Mayr's and Hennig's ideas about relationship, we see that Hennig's is the only one that deals just with terminals of the tree. He's trying to classify species **W**, **X**, **Y** and **Z**, four terminals of the tree in his diagram. Simpson's trying to classify ancestors, as we can see from his diagram recommending combining three ancestral species into a genus ancestral to the four living or terminal species. And, in Mayr's diagram, the three terminals, **B**, **C** and **D**, are labelled with their percent genetic difference from **A**, the ancestor. Obviously, if we can tell that **C** differs from **A** by only 10%, whereas **D** differs from it by 70%, we must have access to **A**.

So among these three, Hennig is the only one whose definition of relationship treats the terminals of the tree as real, and the internal part of the tree as hypothesis or conjecture. And that's why his system directly matches the ideas of molecular systematists.

This audio clip relates to Figure 7

Dr. Colin Patterson

If we can agree that Hennig's is the only theoretically justifiable definition of relationship, and the one we should accept, how do we set about building a tree, or inferring relationships of common ancestry?

If you think about the problem, you'll realise that the ideal way of building the tree would be by recognising evolutionary novelties, the innovations that characterise different lineages or groups of species. In an ideal tree, each node would be marked by one or more novelties, characters unique to the group of species stemming from that node. I've put an example as number 5, one dealing with familiar animals, the apes, or hominoids. That tree has one peculiar feature, the way the chimpanzee is linked to two different places. But that's done to emphasise a particular problem, that we'll get to in a minute, the fact that there are two different sets of characters - the ones labelled 7a and 7b, and each suggests different relationships for the chimpanzee.

The question I want to tackle, at the moment, is how this tree was built up by recognising evolutionary novelties, or shared derived characters. **Synapomorphy** is the technical term for a shared derived character. Here the word 'derived' is used in the evolutionary sense of advanced, or specialised.

The authors of this tree of hominoids, Peter Andrews and Lawrence Martin, gave a list of characters for each of the numbered branches of the tree. As an example, let's take branch 5, the one distinguishing African apes and us from the orang-utan. They listed about 10 characters for that branch, but I'll just mention three of them. The first is fusion of the os centrale, the second is that the frontal sinus is developed, and the third relates to mutations in DNA. And I want to ask how you might decide that these features are innovations or synapomorphies.

Take the os centrale first. It's a bone in the wrist, one of the carpals. In orangs and gibbons, there are nine bones in the wrist - nine carpals - but in African apes and us there are only eight. Given that information, either state might be primitive or derived, so how do we decide that eight is derived?

In this case it's easy, because in the embryo of all these animals, there are nine carpals, but in us, and in African apes, two of them - the centrale and the scaphoid - fuse together. So we begin life with no carpals, then we develop nine carpals, and we end life with eight of them.

Now, in using this developmental sequence as evidence for evolutionary transformation, we aren't just appealing to the theory of recapitulation - the idea that ontogeny recapitulates phylogeny. We're using a much older theory, or law - one proposed by the embryologist von Baer, in the 182Os. Von Baer's Law says that development proceeds from the general to the particular. The most general characters appear first, and the most particular, or restricted, appear last. The idea here is that development recapitulates not phylogenetic history, but the systematic hierarchy, so that characters of the largest groups appear first, and characters of the most restricted groups appear last.

This audio clip relates to Figures 8, with reference also to the hominoid tree depicted in Figure 7.

Dr. Colin Patterson

We can try out that idea with the wrist bones of hominoids. The first condition, in the egg and the very early embryo, is to have no bones or cartilages in the wrist - the skeleton hasn't yet started to develop.

The next stage is to develop nine carpals. And the final stage, in African apes and us, is to fuse two of them, leaving eight carpals. Given those three conditions, we could convert them into a Venn diagram, with each condition characterising a group. The group with no carpals is the whole of life, including plants and bacteria. The group with nine carpals happens to be mammals. And the group with eight is African apes and us, the subfamily Homininae.

Now the hominoids have another character that behaves like this, with ontogenetic or developmental evidence on transformation. The character is reduction of the tail. All adult apes have just a rudiment of a tail, but during embryonic life they develop a long tail, like all other vertebrates, and then it becomes reduced to a vestige by differential growth. So we can get another Venn diagram from the tail, and I've combined it with the carpal diagram. I'm sure you get the idea. We're building up a picture of groups and sub-groups, and with just those two characters, the carpals and the tail, we could get a simple tree from the Venn diagram.

I mentioned one other feature shared by us and African apes, the frontal sinus, which is a space in the bones of the face developed during ontogeny, as an outgrowth or expansion of the ethmoid sinus. And again, we could use development from the general, absence of sinuses, to the more particular, presence of an ethmoid sinus, to the still more particular, presence of the frontal sinus. And so we could get another series of groups to add to the Venn diagram.

Now all this probably seems much too simplified and, in real life, characters are often much more difficult to sort out. There's a good example in the hominoid tree, where the chimp is linked to both the human and gorilla lines. This is a case where there are two conflicting sets of characters, the ones labelled **7a** and **7b** on the tree. Just to take a couple of examples, chimps are linked to us by having the premaxilla and maxilla fused in the adult. But chimps are linked to gorillas by having six vertebrae involved in the sacrum, instead of the five that we have and orangs have. And chimps and gorillas also share a number of features of the arm and hand, associated with their habit of walking on the knuckles.

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Clip 9: Conflicting morphological characters

This audio clip relates to Figure 9

Dr. Colin Patterson

So here we've got conflicting morphological characters, and all of them seem to be derived. They can't both be true, so how do we resolve the conflict?

I've given you a table of molecular characters that help to resolve it. These are selected positions in an alignment of over ten thousand nucleotides, from non-coding DNA in the region of the beta haemoglobin genes. We don't yet know the DNA sequence for this region in gibbons, but the table includes the other four apes, and also a couple of monkeys - the Rhesus monkey, Macaca Mulatta from the Old World, and the Spider monkey, Ateles, one of the New World monkeys from South America.

I want to use this table as an example in tackling the particular question of the conflict on chimpanzee relationships, but also in tackling the more general question of deciding on primitive and advanced characters. The method I've just been describing, using ontogeny or development to resolve general and special features in morphology, obviously won't work with DNA, because DNA has no development. Barring accidents, we're born and we die with the same DNA sequences in our chromosomes.

So how can we determine whether a nucleotide shared by two or more species is derived or primitive? Take the first row in the table, the one numbered **34**. You'll see that five of the animals have **G**, Guanine, at that position, but human and gorilla share **A**, Adenine. This implies that human and gorilla are related, and the criterion we're using to make that guess is called **outgroup comparison**. We've already found, or others have found, a whole series of characters saying that apes form a group and that, within the apes, humans, chimpanzees and gorillas form a subgroup. Then there's another series of characters showing that the closest relatives of apes are the Old World monkeys, with Rhesus monkey as an example in this table. And then there's another set of characters showing that the next group out is the New World monkeys, with Spider monkey as the example here. So outgroup comparison tells us that for the first character in the table, Guanine is primitive and Adenine is derived.

So that shared adenine, in the first row of the table, implies that gorilla is our nearest relative. Are there any other shared nucleotides supporting that idea? Yes, there are two more. There's one at position **6368**, where human and gorilla share Cytosine, **C**, and all the others have Thymine, **T**. And then another near the end of the table at **9441**, where human and gorilla have Guanine, **G**, and all the others have Cytosine, **C**. There's also an Adenine shared by human and gorilla at position **9324**, but here outgroup comparison shows that this could well be primitive, because both the monkeys have Adenine too.

Now look at the second row in the table, position **560**. Here human and chimp share Cytosine, and all the others have Adenine. So this is a site at which outgroup comparison says that chimps are our nearest relatives. Are there any other positions supporting that idea? Yes, there are lots. The third row, position **1287** is an example. Here, human and chimpanzee share an asterisk, which means they have a gap in the alignment - a gap that has to be put there to preserve matching in the neighbouring parts of the sequence.

The evolutionary interpretation of that gap is that it's a deletion of one nucleotide. Now this position is ambiguous by outgroup comparison, because although gorilla and orang have Thymine there, the Rhesus monkey also has a gap, and the Spider monkey has a hyphen, meaning "missing". The Spider monkey lacks this whole part of the sequence, which is an inserted repeat.

But never mind that one, because there are two more substantial deletions showing that chimps are our nearest relatives, the four-base deletion at position **3057**, and the six-base deletion at **7227**.

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Clip 10: Chimps, gorillas and humans

This audio clip relates to Figure 10

Dr. Colin Patterson

I've summarised the information on the relationships between us, chimps and gorillas. On each of the three possible cladograms, I've entered the characters supporting it, using the numbers down the right side of the table. You can check it through in detail later but, as you can see, there are twelve possible human / chimp synapomorphies, three possibles for the chimp / gorilla pairing, and four possibles for the human / gorilla pair. Now if we chuck out all the dubious ones, where outgroup comparison is ambiguous, there are nine unambiguous characters favouring the human / chimp relationship, and three each for the other two possibilities.

Given that evidence, we should accept the hypothesis that chimps are our closest relatives. And I'll suggest two different reasons why we should accept it.

The first brings in the principle of parsimony, or economy of explanation. There are nineteen characters in the table, and the hypothesis that chimps are our nearest relative explains twelve of them, as the result of common ancestry. The other two alternative hypotheses, the chimp / gorilla and human / gorilla pairings, each explain only three or four of the nineteen characters. Now, in using the principle of parsimony to choose between hypotheses, we aren't implying that evolution is parsimonious - that it goes by the shortest route. We don't know whether it does or not. Parsimony says nothing about evolution. It's simply a principle of rational explanation.

The second reason why we should choose the human / chimp hypothesis concerns probability. Given the three alternative trees, one of them supported by twelve characters, one by three, and one by four, you could do statistical tests to find out what chance there is that a wrong tree should be supported by so many characters. The test and the result will depend on the assumptions you make, but the people who published this table reckoned that the result is significant at about the 3% level.

So we can accept the human/chimp pairing. This doesn't mean we accept it unconditionally, but that, like every other hypothesis in science, it's subject to test. And specifically, the hypothesis predicts that other samples of characters will show the same distribution, with the majority of them favouring the human / chimp pairing.

We can get one test from another set of DNA sequences. They're from an immunoglobulin pseudogene and, again, they favour the chimp / human pairing by 3:1, and they bring the significance of the result below 1%, meaning odds of over 100:1 in its favour.

Clip 11: Consequences of human / chimp pairing

This audio clip relates to Figure 9

Dr. Colin Patterson

Now accepting this human / chimp pairing has various consequences. One is that it means that characters uniquely shared by humans and chimps - like the twelve nucleotides in the table, or the fusion of premaxilla and maxilla in the adult - are homologous. But characters uniquely shared by chimps and gorillas, or by humans and gorillas, aren't necessarily non-homologous.

Look at character **9** in the table, position **5156**, where chimp and gorilla share Guanine. We can explain that in two ways. Either the Guanine was independently acquired in chimp and gorilla by two separate mutations from the ancestral Adenine, or Guanine was acquired by a mutation in the common ancestry of human, chimp and gorilla, and then humans reverted to adenine by a second mutation. Each explanation requires just two mutations, so they're equally parsimonious. But the explanation by independent mutations in chimps and gorillas says that the two Guanines are non-homologous – they're convergent or chance similarity.

The other explanation, a mutation in the common ancestry of human, chimp and gorilla, says that the two Guanines are homologous, but are primitive for apes, just as Adenine is primitive at this site for the whole group in the table. This same sort of argument works for morphology. I said, a few minutes ago, that chimps and gorillas share various features of the hand and arm, associated with knuckle-walking. Now, given that chimps are most closely related to us, we can explain that in two ways. Either chimps and gorillas independently acquired knuckle-walking, or it developed in the common ancestry of humans and African apes, and was then lost in the human line. In the first case, the features are non-homologous in chimps and gorillas, but were acquired by parallel evolution. And, in the second case they are homologous. In this instance, we might guess that knuckle-walking is too complex to develop twice in exactly the same way, so it's probably primitive for the group, and is lost in us. Or, we could guess that knuckle-walking is obviously adaptive, and might well develop by natural selection, independently in two closely related lines.

I think all you need remember from this is that homology is a conclusion we infer from a tree or a cladogram. It's not something we can establish directly. And then that there are two kinds of homologies, derived ones and primitive ones. But every homology has to fit on the tree somewhere, as a derived character, a synapomorphy of a group.

This audio clip relates to Figures 11 and 12, with reference also to Figure 7.

Dr. Colin Patterson

Finally, let me go on with this example of humans and apes to say something about translating a cladogram into a classification, and about the use of cladograms in biogeography.

The next little diagram is from Ernst Haeckel's evolutionary tree of mammals, published in 1866. I stuck this one in to show that ideas on the relationships of higher primates haven't changed much in over a century. The next diagram, is from an article of mine in New Scientist in the early 1980s when the question of the relationship between us and chimpanzees wasn't as clearly resolved as it is today. The first of the three cladograms shows the position as I saw it then, with us, chimps and gorillas put as a trichotomy or trifurcation.

Above this first cladogram, there's a classification that's consistent with it, because it names all the monophyletic groups in the diagram. We have a superfamily **Hominoidea** for the whole lot, a family **Hylobatidae** for the gibbons, and a family **Hominidae** for the rest. Within the hominids, there are two subfamilies - **Ponginae** containing Pongo, the orang-utan, and **Homininae** containing us, chimps and gorillas. As we've just seen, relationships within Homininae seem to be resolved now. And you might like to think how one would express the relationship between humans and chimps in this classification. One obvious solution would be to make two tribes - one for gorilla and one for us and chimps.

At the top of the other two diagrams, I've set out two widely used classifications in the form of brackets. And underneath the brackets is the cladogram or pattern of relationships that each classification implies. The middle classification, **(b)**, has the hominoids divided into three families, Hylobatidae for gibbons, Pongidae for the three great apes, and Hominidae for us. This classification's still in use, for example, in a book published in 1990, R. D. Martin's 'Primate Origins and Evolution'.

Now Bob Martin doesn't disagree with the pattern of ape relationships shown in the first diagram, but he thinks it's more useful to classify the three great apes together. In doing so, he's produced what's called a paraphyletic group.

Paraphyletic groups can be defined in two ways, either in terms of a tree, a cladogram - where there are groups that include some but not all of the descendants of a common ancestor - or paraphyly can be defined in terms of characters - where it means a group sharing only primitive characters.

The easiest way of recognising a paraphyletic group is that it can serve as an ancestor. For example, if someone says, "humans evolved from apes," all they're saying is that apes are paraphyletic, defined only by lacking the characters of the descendants.

In just the same way, if you say that vertebrates evolved from invertebrates, or tetrapods evolved from fishes, all you're saying is that invertebrates are a paraphyletic group lacking the characters of vertebrates. And fishes are vertebrates lacking the characters of tetrapods. So in general, paraphyletic groups convey no information, and they're best avoided.

The last of these three diagrams, **(c)**, is a more traditional classification, the one you find in Simpson's classification of mammals, for example. There are just two families of hominoids - one for us, and one containing the gibbons in one subfamily, and the great apes in another. This conveys a pattern that's even further from the truth. And, once again, it does it by using a paraphyletic grouping for the apes. In this classification the pongids are all hominoids that lack the features of humans. It should be obvious that I favour classification **(a)**, because it's the only one that expresses our ideas about hominoid relationships.

This audio clip relates to Figures 13

Dr. Colin Patterson

Finally, a few words on systematics and biogeography - or how one can use cladograms in biogeography. The next diagram is the cladogram of higher primates that we've been working through, from New World monkeys, the **Cebidae**, through to ourselves. Next to it, **(b)** is the same diagram with the names of the groups replaced by the names of the areas where they're found. This is an area cladogram, based on higher primates. And the idea behind it is that we can use the relationships between organisms to investigate earth history, or the relationships between geographic areas.

This area cladogram suggests various things about geography. For example, that Africa is more closely related to India and Southeast Asia, than to South America.

How might we check or test that idea? The best way would be by using the relationships of other groups - animals or plants, that live in South America, Africa, and the other areas - to see if they give the same area cladogram, or a different one. If all or most of them give the same area cladogram, then we'd have strong evidence for a common history of those groups, and of the areas they inhabit.

One can also use an area cladogram to answer questions like, "Where did man originate?" If you apply outgroup comparison to diagram **(b)**, our two nearest relatives are both African. So the inference would be that we too originated in Africa, and spread from there to the rest of the world.

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Clip 14: Summing up

Dr. Colin Patterson
I'll finish by summing up the points we've covered.

The first part of this talk was about Darwin's views on classification, including the point that evolution, or descent with modification, is an explanation for the observed hierarchy of natural groups.

The next part was about the meaning of relationship - does it just mean similarity, or does it mean what Darwin called 'propinquity of descent'? We settle for propinquity of descent, or closer common ancestry.

Then we got to the problem of how you infer relationships of common ancestry, with the idea of shared derived characters, synapomorphies, as the key, and two methods of identifying shared derived characters, by ontogeny or development, and by outgroup comparison. We used higher primates as an example, and touched on how homology is deduced from congruence of characters, and how a cladogram is converted into a classification, with the distinction between monophyletic and paraphyletic groups.

And finally there were a few thoughts on the use of cladograms in biogeography.