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Current taxonomy and diversity of crown ruminants above the species level

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Abstract

Linnaeus gave us the idea of systematics, with each taxon of lower rank nested inside one of higher rank; Darwin showed that these taxa are the result of evolution; Hennig demonstrated that, if they are to mean anything, all taxa must represent monophyla. He also proposed that, to bring objectivity into the system, each taxonomic rank should be characterised by a particular time depth, but this is not easy to bring about: genera such as *Drosophila* and *Eucalyptus* have a time-depth comparable to whole orders among mammals! Within restricted groups of organisms, however, time-depths do tend to vary within limits: we will not do too much violence to current usage if we insist that a modern mammal (including ruminant) genus must have a time-depth of about 5 million years, i.e. going back at least to the Miocene-Pliocene boundary, and a modern family must have a time-depth of about 25 million years, i.e. going back to the Oligocene-Miocene boundary.

Molecular studies show that living ruminants present examples where the „traditional“ classification (in the main laid down in the mid-20th-century, and all too often still accepted as standard even today) violates Hennigian principles. Among Bovidae, the genera *Bos, Tragelaphus, Gazella* and *Hemitragus* are paraphyletic, and so, among Cervidae, are the genera *Cervus* and *Mazama*. I will discuss what we can do about these, and will then present, with commentary, a classification of living ruminants.

Key words: Morphology, molecules, cladistics, genus, *Bos*, *Tragelaphus*, *Gazella*, *Hemitragus*, *Cervus*, *Mazama.*

1. Introduction: analysing the phylogeny

Ever since the Hennigian revolution of the 1960s (Hennig 1966), it has been recognised that taxonomy above the species level must reflect phylogeny, but the reconstruction of a phylogeny is still often fraught with problems and controversies.

We study both extant and fossil organisms, using some methods which are available for both, others which are available only for extant organisms. In the case of fossils, normally only methods applicable to phenotypic traits are available; the rapid advance of ancient DNA techniques, however, is beginning to open up new horizons. Extant organisms may be studied by methods applicable to a variety of phenotypic traits (morphology, behaviour, some molecular) or by methods applicable to some genotypic traits (today, almost entirely nuclear acids, both DNA and RNA). Methodologically, we can use cladistic analysis, morphometrics and the molecular clock. Each of these methods and data sources has its own advantages and disadvantages, some of them are pointed out here in more detail:

1.1 Cladistic analysis

Cladistic analysis has numerous disadvantages. Homoplasy is widespread, and there is frequently no logical means of deciding between alternative phylogenetic trees. It lacks a calibrated time component: different characters can be expected to change at different rates. Frequently, it is difficult to decide what characters actually are: do we risk atomisation of functional units, or do we combine potential characters into what we deem functional sets? We often do not know how (or whether) characters are correlated. We are ignorant of their genetic basis. Finally, cladistic analysis assumes a branching phylogeny; it cannot detect reticulation, although it can of course, in cases of rampant homoplasy, generate hypotheses that hybridisation might have taken place.

Nonetheless, the method does have its own considerable advantages. The characters used in cladistic analysis include any kind, but, with caution, morphometrics; only DNA sequences themselves should be excluded from analyses of phenotypes. (I am aware that DNA and phenotypic characters, generally morphological, are sometimes included in the same dataset, under the heading of Total Evidence Analysis, but they are quite different types of characters, and should normally be kept separate – at any rate, caution should always be applied. For a discussion of Total Evidence, see for example Eernisse & Kluge 1993; Gatesy et al., 1999; Gatesy, 2002). Cladistic analysis is of course all that is available to the palaeontologist, yet an advantage which is often overlooked in the case of living organisms is that the characters apply to the phenotype, which is the target of selection, so the resultant phylogenetic tree has the potential to inform us about the selective history of the taxa involved.

In non-molecular data sets, it is commonplace to warn of homoplasy, although note that what is homoplastic at one node may well be informative at others so that, if as many characters as possible are used, the resulting phylogenetic tree may turn out to be well supported. Description of the behaviour of different characters should be part of every non-molecularly based cladistic analysis.

1.2 Fossil record

The most obvious advantage of the fossil record, whether analysed by cladistics or stratophenetics, is the time control it affords. First appearance data are essential to calibrate both cladistic and genetic methods of phylogeny, but these must be taken cautiously, preferably using as many calibrations as possible (Bibi 2013).

The disadvantages include the incompleteness of the record, and the incompleteness of the fossils themselves. Palaeontologists typically utilise cladistic analysis to interpret the fossil record of the group, although the stratophenetic method (ordering fossils into a time sequence, and treating the result as a quasi-ancestor-descendant series) is also potentially valuable.

1.3 Genetic analysis

The advantages of basing phylogenetic reconstructions on genetics are manifold. We are dealing with the DNA itself. We have time control (the molecular clock). We are no longer restricted to blood samples or biopsies, or even faecal samples, from living animals: laboratory protocols have improved so much that Ancient DNA is now commonplace. In contrast to the morphology-based cladistic method, typically used to construct the phylogeny, we are no longer constrained to a model of diversification: comparison between mt- and nDNA (especially Y-chromosome DNA) has the potential to detect reticulation (see below).

Nonetheless, we must not be blind to some potential disadvantages. The construction of molecular clocks depends on there being an adequate fossil record, offering multiple calibrations. Another is that rates of evolution cannot be assumed to be constant: local and more global clocks often run at very different rates. Molecular data, like non-molecular, is subject to homoplasy (Broughton et al. 2000). And there is still some risk of over-reliance on mtDNA as opposed to nuclear sequences.

Looking at molecular data, we can often find as few phylogenetically informative characters as in non-molecular data. Genetic data are in this sense not necessarily „better“ than other sorts of data.

2. The potential of different data sources: consilience

The old “morphology versus molecules” debates of the latter half of the 20th century are virtually extinct. There is no reason to expect that morphological characters have evolved at the same rate as DNA sequences; as noted above, they are subject to selection, which may retard phenotypic change or, conversely, speed it up and overlay new apomorphies on earlier ones. Nonetheless, there are interesting cases of unexpected consilience.

Affinities of *Hydropotes* (Chinese water-deer) have long been disputed. These deer, unlike all other cervids, lack antlers: is this lack primary or secondary? If it is primary, then parsimoniously *Hydropotes* would be expected to be sister to all other cervids; if secondary, then it could be nested almost anywhere among the antlered Cervidae. Its other morphological characters shed little light on its affinities.

DNA analysis, both mitochondrial and nuclear, (Randi et al. 1998, Pitra et al. 2004, Gilbert et al. 2006), comes down firmly on the side of the lack of antlers being secondary: *Hydropotes* is sister to the roe deer, *Capreolus*. Interestingly, characters of male vocal behaviour (Cap et al. 2008) produce the same cladogram, a nice instance where behaviour conforms to the phylogeny when morphology does not.

It is worthwhile drawing attention to this case because the DNA result had been entirely unanticipated – no morphological assessment would have predicted such a conclusion.

3. An outline taxonomy of living ruminants

The taxonomy of living ruminants above the species level adopted by Groves & Grubb (2011) is as follows:

- Family Tragulidae
    - *Tragulus, Moschiola, Hyemoschus*
- Family Moschidae
    - *Moschus*
- Family Antilocapridae
    - *Antilocapra*
- Family Giraffidae
    - *Giraffa*, *Okapia*

- Family Cervidae
  - Subfamily Capreolinae
    - Tribe Rangiferini
      - *Odocoileus*, *Pudu, Hippocamelus, Blastocerus, Ozotocerus, Mazama, Rangifer*
    - Tribe Capreolini
      - *Capreolus, Hydropotes*
    - Tribe Alceini
      - *Alces*
  - Subfamily Cervinae
    - Tribe Muntiacini
      - *Elaphodus*, *Muntiacus*
    - Tribe Cervini
      - *Dama*, *Axis*, *Rucervus*, *Panolia, Elaphurus*, *Cervus*
- Family Bovidae
  - Subfamily Bovinae
    - Tribe Bovini
      - *Bos*, *Bubalus*, *Syncerus*, *Pseudoryx*
    - Tribe Boselaphini
      - *Boselaphus*, *Tetracerus*
    - Tribe Tragelaphini
      - *Tragelaphus*, *Taurotragus*, *Strepsiceros, Ammelaphus, Nyala*
  - Subfamily Antilopinae
    - Tribe Neotragini
      - *Neotragus*
    - Tribe Aepycerotini
      - *Aepyceros*
    - Tribe Antilopini
      - *Raphicerus*, *Saiga, Dorcatragus, Litocranius, Ammodorcas, Antidorcas, Antilope, Gazella, Eudorcas, Nanger, Madoqua*, *Ourebia, Procapra*
    - Tribe Reduncini
      - *Kobus*, *Redunca*, *Pelea*
    - Tribe Hippotragini
      - *Hippotragus*, *Oryx*, *Addax*
    - Tribe Alcelaphini
      - *Alcelaphus*, *Damaliscus*, *Beatragus*, *Connochaetes*
    - Tribe Caprini
      - *Pantholops*, *Oreamnos, Budorcas, Ammotragus, „Arabitragus“, Hemitragus, Pseudois, Capra, „Nilgiritragus“, Ovis, Rupicapra, Nemorhaedus, Capricornis, Ovibos*
    - Tribe Cephalophini
      - *Cephalophus*, *Sylvicapra*, *Philantomba*
    - Tribe Oreotragini
      - *Oreotragus*

Much of this taxonomic scheme requires comment, and some even requires reorganisation (see below). Before pinpointing and discussing some of these specific cases, we must ask the question: why these rankings? What is a family? What is a genus? It is axiomatic that all taxa above the species level must be monophyletic - but what is specifically “familial” about the families, or “genus”-like about the genera?

4. Higher taxa: what are the criteria?

This question has rarely been asked, but as long as we claim that taxonomy is a science, we must ask it. One of the few to have asked the question in the past was Mayr (1969). He suggested that we should take the following factors into account:

- the distinctness of a taxon (the size of the gap between it and its closest relatives);
- its evolutionary role (the uniqueness of its adaptive zone);
- the degree of difference between one taxon and others;
- the optimal size of a taxon (how many subordinate taxa there are);
- and the equivalence of ranking in related taxa.

Some of these criteria have phylogenetic merit, but all have an inherent subjectivity. How, for example, should we estimate “distinctiveness”, evolutionary role, degree of difference? What is the rationale for having similarly-ranked taxa similar in numerical size?

Hennig (1966) required that all taxa, without exception, must be monophyla, and this would be acceptable – in the case of beta-taxonomy, not necessarily of species – to most or all practising taxonomists. But we must still ask the question – why this rank rather than that one? Why family, rather than genus, for example? The question of scientific testability is at stake. It has been proposed that higher taxonomic categories should be junked altogether, and only rankless nodes be named, the so-called Phylocode (de Queiroz & Gautier, 1992); but, maybe we can make the higher categories work for us, and so bring them into the realm of science.

There is a more purely practical reason as well: genera and families are often used in biogeographic analyses, and if there is no rigorous criterion for these categories then the results are deeply flawed. The results of biogeographic analyses using higher categories are of conservation importance – for example, areas with high generic or familial endemicity are deemed hotspots, and given special conservation attention.

It was Hennig himself (1966) who floated a solution, the time-depth proposal, whereby each rank in taxonomy, at least the Linnaean obligatory categories, should represent a certain time since separation from its sister-group. But ranks have very different time-depths in different phyla and classes, and Hennig realised that it simply would not work, at least if one hoped that it would apply across all animals (and plants). Avise & Liu (2011) went further, comparing published time-depths of orders, families and genera of amphibians, reptiles, birds, mammals, and decapod crustaceans. The results are revealing. The order Decapoda is over 400 million years old, while orders of amphibians and reptiles are well over 200 million, and those of birds and mammals are somewhat over 80 million (the average for mammalian orders may be somewhat inflated by one that is over 200 million – presumably the Monotremata, the sole order within its own subclass). Families of the Decapoda average 200 million years old, those of Amphibia about 100 million, those of reptiles about 86, those of birds and mammals about 40 million. Decapod genera average 60 million years old, amphibian genera 37 million, reptilian genera 31 million, bird genera 28 million, mammalian genera 9.6 million. As far as I know, orders, families and genera in other invertebrates are comparable in age to those in Decapoda, and these are greater than those in amphibians and reptiles, which in turn are greater than those in birds and mammals, which are roughly comparable to each other except that bird genera seem to be more broadly drawn than mammalian ones. It is evident that Hennig was right: if we are to institute an objective system like this, we will have to do it class by class, at least initially, perhaps aiming for some sort of compromise system way into the future.

A system for the Primates alone was proposed by Goodman et al. (1998), and endorsed and modified by Groves (2001). The system proposed separation times (i.e. times for the origin of Total Groups) which would apply to each rank below that of the order itself – semiorders, suborders, infraorders, superfamilies, and so on. Of special relevance are the proposed dates for the Linnaean obligatory categories: families should have separated 28-25 million years ago (approximately around the Oligocene-Miocene boundary), and genera 11-7 (somewhat above the Miocene-Pliocene boundary, which Groves (2001) proposed should be the actual timing). It is interesting that the ages for ruminant higher taxa calculated by Bibi (2013) are more are less consistent with these: he has found that ruminant families, as presently recognised, separated 17-28 million years ago, genera about or somewhat above 5 million.

Advantages of time-rank associations are:

- They render families and genera testable, as scientific propositions should be (Popper 1934/1959). At present, they are purely subjective.
- “Every lineage is a species” (de Queiroz 2007, Cotterill et al. 2014) – hence, perhaps, every genus is a lineage that has persisted for a particular length of time, every family is a lineage that has persisted for a different, but greater, length of time?
- In Bibi’s (2013) analysis of ruminant higher taxa, we do find considerable consistency to the actual ages of different ranks; adopting the Goodman et al. (1998) model, perhaps as modified by Groves (2001), would apparently do little violence to most presently accepted families and genera.
- The system could be applied to fossil genera and families. The suggested time-depths could be applied quite simply by dividing up those genera and families that appear to have persisted for longer than the suggested ± 5 and 25 million year ranges, respectively.

A question that arises is this: are subfamilies and tribes in the Cervidae and Bovidae mere “convenience categories”, or should they be time-associated as well? In general, such subordinate ranks tend to be inserted where they are needed to divide up large cohorts of (for example) genera, and omitted in cases where there are only two or a few genera (living Giraffidae). But is such a scheme too reminiscent of the subjective proposals by Mayr (1969)? As a matter of interest, Goodman et al. (1998) suggested that subfamilies in Primates should have separated 23-22 million years ago, whereas Bibi (2013) had ruminant subfamilies separating only at 15-17 million; tribes, under the Goodman et al. (1998) scheme, would have separated 20-14 million years ago, but in the Bibi (2013) analysis, a generally lower (if overlapping) 11-16 million.

A 5-Ma standard for generic rank would not necessitate much reshuffling, except that the following genera would probably disappear (Ropiquet 2006, Schikora 2012, Hassanin et al. 2012, Bibi 2013):

- *Oryx* would become a synonym of *Addax* (in all calculations).
- *Damaliscus* becomes a synonym of *Alcelaphus* (Schikora 2012, Hassanin et al. 2012, Bibi 2013), and so presumably would *Beatragus* which is evidently the sister genus to *Damaliscus*.
- *Hemitragus* perhaps becomes a synonym of *Capra* (only in mtDNA systems, however).

Conversely, in the following two cases, further genera would probably have to be separated out:

- *Ammelaphus, Nyala* and *Strepsiceros* would need to be separated from *Tragelaphus*; this step was already taken by Ropiquet (2006), followed by Groves & Grubb (2011).
- *Cephalophorus, Cephalophula* and *Leucocephalophus* would have to be separated from *Cephalophus*. This revision dates only from Hassanin et al. (2012), and has not yet had a chance to be considered by subsequent authors.

At present, these observations will be left as they stand, for consideration, given that plenty of further research is required. The loss of *Oryx* and *Damaliscus* might be an unwelcome consequence of the search for rigour, but if beta-taxonomy is ever to become a testable science, then such a step must be seriously contemplated.

5. Monophyly: the *sine qua non* of all higher categories in taxonomy

Some of the "traditional" genera of ruminants are now known to be paraphyletic. The most blatant cases are: Bovidae: *Bos*, *Tragelaphus*, *Neotragus*, *Cephalophus*, *Gazella*, *Hemitragus*; Cervidae: *Mazama.* Each of these cases will be briefly considered, in the form of a simple protocol:

Bos – cattle and bison

Yak (wild *Bos mutus*; domestic *Bos grunniens*) belongs to a clade that includes bison (*Bison bison, Bison bonasus*), and is separate from cattle (*Bos primigenius* group), banteng (*Bos javanicus*), kouprey (*Bos sauveli*) and gaur (*Bos gaurus*), with which it has commonly been associated in the genus *Bos*.

Solution (1): assign yak to a third genus, *Poephagus* (Nijman et al. 2008).

Solution (2): sink *Bison* into *Bos* (Bibi & Vrba 2010, Hassanin et al. 2013).

Both the fossil record and molecular clocks show that the bison-yak clade separated from cattle (etc.) well under 5 Ma.

Hence, adopt solution (2).

Tragelaphus – spiral-horned antelopes

All molecular phylogenies show *Taurotragus oryx* and *T. derbianus* (eland) nested within *Tragelaphus* (bushbuck) in the old comprehensive usage, sometimes even as sister-group to greater kudu (*Tragelaphus strepsiceros*).

Solution (1): sink *Taurotragus* into *Tragelaphus* (most authors at present do this).

Solution (2): keep *Taurotragus* as a genus, and divide *Tragelaphus* into several genera: *Ammelaphus* (lesser kudu), *Nyala* (nyala), *Strepsiceros* (greater kudu), *Tragelaphus* (bushbuck, sitatunga, bongo, gedemsa).

Separation times for all these (and *Taurotragus*) seem to be well over 5 Ma (Ropiquet 2006, Bibi 2013), despite the long fossil "ghost lineages" implied in some cases.

Hence, adopt solution (2).

Neotragus – dwarf antelopes

This is a rather different case, not amenable to the same protocol. Groves & Grubb (2011:144) expressed scepticism as to whether the species conventionally referred to the genus *Neotragus* (classified as the sole genus in the tribe Neotragini) are truly closely related to one another, and recently Bärmann & Schikora (2013) showed that the type species, *N. pygmaeus* (the royal antelope), does not form a monophyletic clade with the other species (Bates' dwarf antelope, and several species of suni), which therefore take the generic name *Nesotragus* (synonym *Hylarnus*). The tribe Neotragini therefore becomes restricted to *Neotragus sensu stricto*, unless the duikers, which seem to be its closest relatives (if not very close), are incorporated into the tribe; while *Nesotragus* forms a new monotypic tribe, unless it is incorporated into the Aepycerotini, the impala (*Aepyceros*) being its closest relative (if, again, not very close). Further genetic study should help to choose between these various options.

Cephalophus **–** duikers

The Bush duiker (*Sylvicapra*) is nested within *Cephalophus*, probably sister to the "giant duikers" (a clade which includes *C. silvicultor,* type species of *Cephalophus*) (Hassanin et al. 2012, Johnston & Anthony 2012).

Solution (1): sink *Sylvicapra* into *Cephalophus.*

Solution (2): raise other species or species-groups of *Cephalophus* to generic rank: *Cephalophula* (zebra duiker), *Cephalophorus* ("red duikers"), *Leucocephalophus* (Aders' duiker). Note that the name *Leucocephalophus*, proposed by Hassanin et al. (2012), is actually unavailable as it does not meet the requirements of the *International Code of Zoological Nomenclature*, Article 13.1.1, in not being "accompanied by a description or definition that states in words characters that are purported to differentiate the taxon". Thanks are due to Anthea Gentry for pointing this out to the conference.

The groups listed in the preceding paragraph separated from each other, and from the Giants (*Cephalophus*), somewhat > 5 MA.

Hence, adopt solution (2) (see Hassanin et al. 2012).

Gazella – gazelles

The Blackbuck (*Antilope*) is often nested within *Gazella* as "traditionally" understood (Rebholz & Harley 1999, Bärmann et al. 2013).

Solution (1): combine the two genera; the name *Antilope* has priority.

Solution (2): split *Gazella* into three genera: *Nanger* (Grant's, Soemmerring's and Dama gazelles), *Eudorcas* (Red-fronted & Thomson's gazelles), and *Gazella* (dorcas and goitred gazelle groups). This solution was proposed by Groves (2000), more or less as a device to avoid the dismay that would be generated under solution (1).

These separated sometime around the Miocene-Pliocene boundary.

Solution (2) has been generally adopted in the present millennium: but is it correct? When did the three gazelle genera and *Antilope* separate from each other? Future genetic studies will doubtless help to resolve this question.

Hemitragus – tahr

Traditionally, three species have been placed in the genus *Hemitragus*: Himalayan tahr *H. jemlahicus*, Nilgiri tahr *H. hylocrius*, and Arabian tahr *H. jayakari.*

Ropiquet & Hassanin (2005) found that the genus is polyphyletic: *H. jemlahicus*, the type species, is sister to *Capra* (goats); *H. hylocrius* is sister to *Ovis* (sheep), and they erected for it a new genus, *Nilgiritragus*; and *H. jayakari* is sister to *Ammotragus* ("Barbary sheep"), and they erected for it a new genus, *Arabitragus*. Anthea Gentry pointed out at the conference that these names are unavailable as they had not been properly proposed (violating the *Code*, Article 13.1.1). Groves & Grubb (2011) overlooked this point and treated the genera as if they were available, and gave descriptions of them, pointing out that the cranial characters do indeed assort according to the genetic relationships; but these descriptions do not make the names available as they do not meet the stipulations of Art.16.1.

Divergence dates were given as follows by Ropiquet & Hassanin (2005): *Arabitragus* from *Ammotragus* 4-7 Ma, *Nilgiritragus* from *Ovis* only 2.7-5.2 Ma, *Hemitragus* from *Capra* only 2.5-4.7 Ma. Ropiquet (2006) gave slightly different dates, placing all three divergences in the Pliocene. If these dates are substantiated by future studies, a referral of the three species to their respective sister genera might be called for, rather than erecting two new genera.

Mazama – brockets

Duarte et al. (2008), González et al. (2010) and Hassanin et al. (2012) have all found, on the basis of mtDNA, that *Mazama* is paraphyletic: Red brockets (*M. americana* group) belong in a clade with *Odocoileus* (white-tailed deer and relatives), while Brown brockets (*M. gouazoubira* group) belong in a clade with other Neotropical deer (*Hippocamelus*, *Blastocerus, Ozotocerus*). The two species of *Pudu* may also be split between the same major clades, but this is less certain.

There is as yet no resolution to this mess, but certainly we live in interesting times.

6. The joker: reticulation

Homoplasy in phenotype may be irreconcilable. Likewise, DNA may also produce two apparently equally good phylogenetic trees (although sometimes one has to be aware of the possibility of ancestral polymorphism (Fig. 1)). Especially, mtDNA and nDNA (especially Y-chromosome DNA) sometimes send conflicting signals, suggesting that the mtDNA and at least some of the nDNA come from different sources, i.e. hybridisation. The repeated intercrossing between a number of lineages, producing a network of relationships, is referred to as reticulation (Fig. 2), and DNA data seem to indicate that it has been rather common in the evolution of some taxa, including ruminants. In this regard, see also Moodley (2013); and for a well-studied case, that of the European bison, see Nowak & Olech (2008).

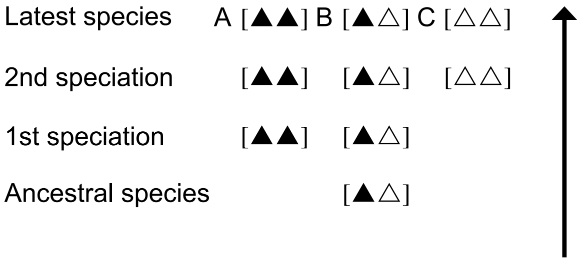

Figure 1: Schematic illustration of polymorphism in the evolutionary history of a taxon. A polymorphic character in the ancestral species exists in both a derived (black triangle) and a primitive (white triangle) state. The first speciation produces two descendant species, one of which has lost the primitive state. The second speciation results in three species, A with only the derived state, B still polymorphic with both states, and C with only the primitive state. Species C has not undergone a character reversal but a cladistic analysis could show it as such.

Has hybridization really been so common? Apparently so: one might expect it to have occurred very infrequently, but actually it is known even in recent times. The Natural History Museum (London) contains the skull of a subadult male hybrid *Alcelaphus caama* x *Damaliscus lunatus,* 93.12.17.1, shot in 1890 in the Tati Valley, Zimbabwe, by Cornelius van Rooyen. A hybridisation event giving rise to a new single lineage would have to involve a whole population of at least one of the parent species, but even an apparently one-off event like this emphasises the potentiality for reticulation.

Hybridization is usually asymmetrical. Males of species A dominate males of (a sympatric population of) species B, and mate with the species B females; they then mate with the F_1 hybrid females. F_1 hybrid males may be subfertile anyway (Haldane's Rule), but all that is necessary is for males of one species to dominate in matings. After some generations, the hybrids have effectively become species A, although potentially some genes of species B may have been selected for in the meantime.

6.1 Reticulation in tragelaphin phylogeny

Not only are the divisions between major taxa of the Tragelaphini much deeper than had previously been supposed (see above), but their interrelationships are not as had been assumed. The "species" (most of them actually species-groups) involved are

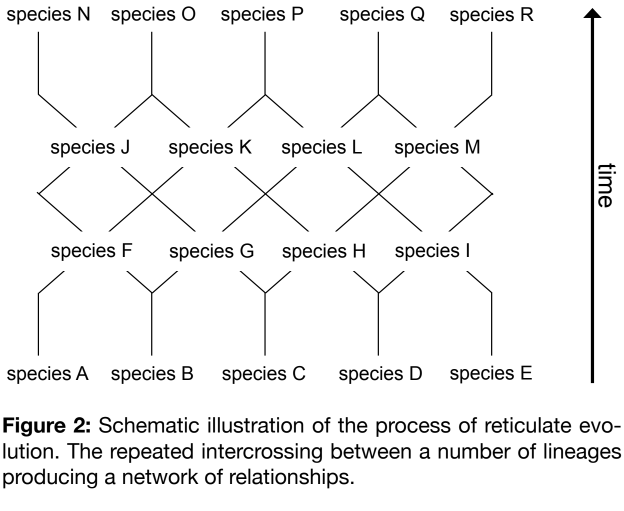

Figure 2: Schematic illustration of the process of reticulate evolution. The repeated intercrossing between a number of lineages producing a network of relationships.

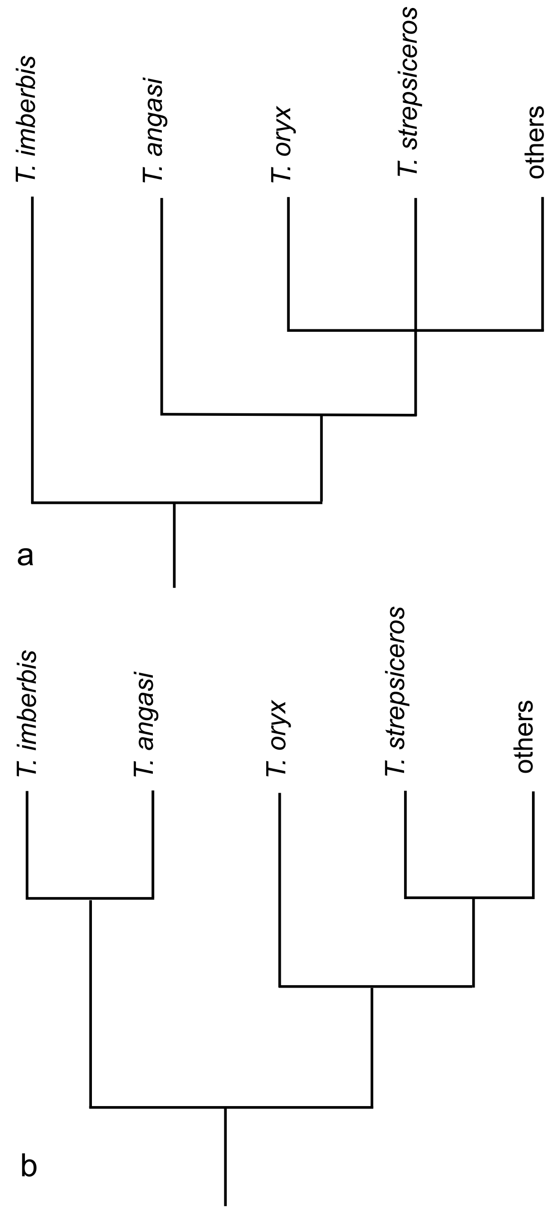

Figure 3: Reticulation in tragelaphine phylogeny as revealed by **(a)** mt DNA and **(b)** nuclear DNA trees.

as follows: *Tragelaphus* (or *Taurotragus*) *oryx* and *derbianus*, eland (these two species are sisters in most, though not all trees, and will be subsumed below under "*oryx*"); *T. strepsiceros*, greater kudu; *T. imberbis*, lesser kudu; *T. buxtoni*, gedemsa; *T.* (or *Boocercus*) *eurycerus*, bongo; *T. spekei*, sitatunga; *T. angasi*, nyala; and *T. scriptus*, bushbuck. The mtDNA tree (Willows-Munro et al. 2005, Ropiquet 2006, Hassanin et al. 2011) (*imberbis* (*angasi* (*oryx*, *strepsiceros*, others)) (Fig. 3a) is noticeably different from the nuclear tree (Willows-Munro et al. 2005) ((*imberbis, angasi*) (*oryx* (*strepsiceros*, others))) (Fig. 3b).

According to the datings of these authors, the mitochondrial separation of *imberbis* from its sister clade took place about 13.7 million years ago, and the nuclear separation of the *imberbis/angasi* clade from its sister clade took place about 13.8 million. These two dates are presumably not significantly different. The separation in the mitochondrial tree of *angasi* dates to 12 million. The most plausible explanation of the discrepancy between scenarios depicted by mtDNA and nDNA is hybridisation: a very early nuclear swamping of proto-*angasi* by proto-*imberbis*, as indeed proposed by Ropiquet (2006).

The three-way split between *oryx*, *strepsiceros* and the others in mtDNA is dated at 10.5 million; the two-way split between *oryx* and the *strepsiceros*/others clade in nDNA is dated at 10.4 million. Again, these two dates are presumably not different. The split between *strepsiceros* and its "others" sister clade is placed at 8.6 million. The most plausible explanation is that proto-*strepsiceros* was subjected to hybridisation by nuclear swamping by the common ancestor of these "others" some 8.6 million years ago.

There is further suggestion of hybridisation between ancestors of *scriptus* and its sister-group (*buxtoni, spekei, euryceros*), and even that *scriptus* (bushbuck) could be non-monophyletic, but this seems less securely based.

6.2 Reticulation in duiker phylogeny

Ellerman et al. (1953), seemingly arbitrarily, recognised just two genera of duikers, *Cephalophus* (forest-living duikers) and *Sylvicapra* (bush duikers), and this classification achieved a spurious authenticity until Grubb & Groves (2001) showed that blue and Maxwell's duikers are at least as distinct and must rank as a separate genus *Philantomba*, which may even be the sister genus to *Sylvicapra.*

DNA studies give yet another picture. The most recent of these (Johnston & Anthony 2012) obtained well supported trees for both nuclear and mitochondrial sequences, but these were somewhat different from each other. mtDNA gives the scenario (*Philantomba*((*nigrifrons*) (*adersi*) ((*Sylvicapra*) (*silvicultor*, *jentinki*) (*zebra*))) (Fig. 4a) and, on the other hand, the nuclear sequences give the picture (*Philantomba*(((*zebra*, *jentinki*) (*silvicultor*, *Sylvicapra*) (*adersi* (*nigrifrons*)))) (Fig. 4b). (Note that another species, *dorsalis*, has been omitted above as always being sister to *jentinki*, likewise *spadix* as being consistently sister to *silvicultor*, and *ogilbyi* and *leucogaster* as being always associated in a clade with *nigrifrons*. Some of the above names actually represent species-groups rather than single species). Given the strong support for most branches in their tree, it is evident that reticulation has occurred during duiker evolution, and bringing together the dates calculated by Johnston & Anthony (2012) with those from Hassanin et al. (2011) and Bibi (2013) suggests approximately when such reticulation would have occurred.

The initial split between *Philantomba* and the others occurred about 8 million years ago (nuclear sequences) or 7.6 (mitochondrial sequences). The

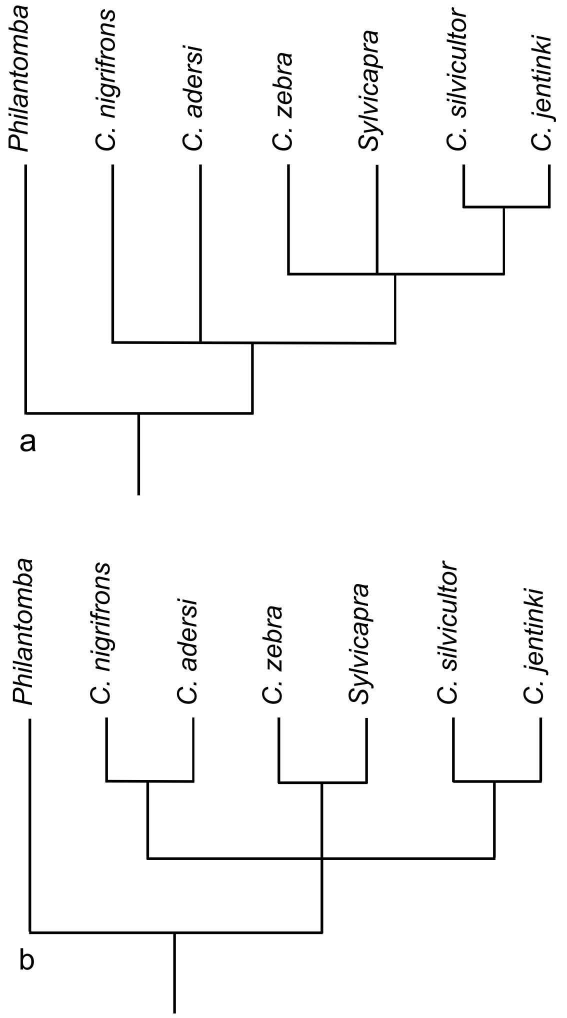

Figure 4: Reticulation in duiker phylogeny as revealed by **(a)** mt DNA and **(b)** nuclear DNA trees.

fourfold split among the non-*Philantomba* duikers depicted by mtDNA dates to approximately 6.5 million, which may be equivalent to either the (undated) nDNA split between the *zebra/jentinki/dorsalis* clade and its two sister clades, or to the 7.0 million split within the latter between the *silvicultor/Sylvicapra* and *adersi/nigrifrons/ogilbyi* clades; in such a case, it is impossible to differentiate between reticulation and ancestral polymorphism. But two discrepancies between the mitochondrial and nuclear sets would be difficult to explain other than by hybridisation: first, a mutual genetic exchange at 4.7 million between *zebra* and the *jentinki/dorsalis* clade, and an event at 5.2 million of nuclear swamping of *adersi* by the ancestor of the *nigrifrons/ogilbyi* clade.

Cephalophus needs to be divided into several genera because of the very deep time separations between them (see above), and this is now reinforced because it is shown to be nonmonophyletic because *Sylvicapra* is nested within it.

We still lack a complete understanding of duiker phylogeny. The “traditionally recognised” species were already shown by Grubb & Groves (2001) to be complex entities, which need to be taken separately rather than assumed to be homogeneous, and more recently Groves & Grubb (2011) found that there are previously unrecognised evolutionary species. Certainly, it is misleading to create an all-purpose “*Cephalophus nigrifrons*” (to take a particularly glaring example) and deduce its affinities; we need a new, more detailed phylogeny, informed by an understanding of duiker taxonomy.

6.3 Reticulation: a case in Cervidae

The affinities of Père David’s deer (genus *Elaphurus*) are split. Its mtDNA forms a clade with that of *Panolia* (Eld’s deer), with 90% bootstrap support (Randi et al. 2001, Pitra et al. 2004). Some of the phenotypic characters that stand proxy for nDNA similarly resemble *Panolia*: cytochrome *b* sequences (Liu et al. 2003), the non-inflated auditory bulla, the pointed anterior nasal ends and the shape of the naso-frontal suture (blunt, except for a small median wedge), absence of metatarsal glands, and the initial deep low-stretch approach of the stag in courtship. Other phenotypic characters, however, resemble *Cervus* (the red deer/sika group): electrophoretic patterns of 22 proteins (Emerson & Tate 1993), the elongated facial skeleton, and aspects of the female’s behaviour, as do the karyotype and κ-casein DNA sequences (Cronin et al. 1996). The coexistence of *Panolia* and *Cervus* genetic characters and apparently synapomorphic phenotypic characters suggests that *Elaphurus* originated in an ancient hybridisation event.

Yet *Elaphurus* is not intermediate between its two parent taxa, but has apparently apomorphic character states of its own. Transgressive Segregation is the generation of phenotypes in hybrid populations that are extreme relative to those of either parental line. These new phenotypes may be selected for in the new hybridogenetic population (incipient species) (Rieseberg et al. 1999).

7. Conclusion: the importance of a historical perspective

The “accepted” modern taxonomy of ruminants, when traced back to source, turns out to derive almost unchanged from Lydekker (1913, 1915; Lydekker & Blaine 1914a, 1914b). It was Lydekker’s decision to combine Eld’s deer and Swamp deer in a single subgenus and to include that in the genus *Cervus*, based on what seemed to be general phenotypic resemblances – it is now clear that they separated from the red deer group, and from each other, well back in the Late Miocene (Pitra et al. 2004). It was Lydekker & Blaine’s decision to place greater and lesser kudu in a single genus, based on general phenotypic resemblances – is now clear that the lesser kudu separated from the greater kudu and other tragelaphines in the Middle Miocene. It was also their decision to place all duikers in one genus, *Cephalophus*, with the “Blue” duikers and Bush duikers separated from the others only subgenerically; this was modified only slightly by Ellerman et al. (1953), who raised the Bush duikers (*Sylvicapra*) to generic rank.

Make no mistake, Lydekker was a competent taxonomist for his day, as was his sometime collaborator Blaine; Ellerman and his colleagues were likewise competent taxonomists. But they knew nothing about DNA, or cladistics, or reticulation. While acknowledging their contributions, we need to move on: a little less tradition, a little more science! (Cotterill et al. 2014 have recently made the same point in the context of species). At present, taxonomic ranks above the species level are not scientifically based; with the Phylocode breathing down our necks, we need to base the higher categories on science, or we will lose them.

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