



# A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants

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## ABSTRACT

This paper presents the first complete estimate of the phylogenetic relationships among all 197 species of extant and recently extinct ruminants combining morphological, ethological and molecular information. The composite tree is derived by applying matrix representation using parsimony analysis to 164 previous partial estimates, and is remarkably well resolved, containing 159 nodes (>80% of the potential nodes in the completely resolved phylogeny). Bremer decay index has been used to indicate the degree of certainty associated with each clade. The ages of over 80% of the clades in the tree have been estimated from information in the literature. The supertree for Ruminantia illustrates which areas of ruminant phylogeny are still only roughly known because of taxa with controversial relationships (e.g. *Odocoileini*, *Antilopinae*) or not studied in great detail (e.g. *Muntiacus*). It supports the monophyly of the ruminant families and Pecora. According to this analysis *Antilocapridae* and *Giraffidae* constitute the superfamily *Giraffoidea*, which is the sister group of a clade clustering *Bovoidea* and *Cervoidea*. The position of several taxa whose systematic positions have remained controversial in the past (*Saiga*, *Pelea*, *Aepycerus*, *Pantholops*, *Ammotragus*, *Pseudois*) is unambiguously established. Nevertheless, the position of *Neotragus* and *Oreotragus* within the original radiation of the non-bovine bovids remains unresolved in the present analysis. It also shows that six successive rapid cladogenesis events occurred within the infraorder Pecora during the Oligocene to middle Pliocene, which coincided with periods of global climatic change. Finally, the presented supertree will be a useful framework for comparative and evolutionary biologists interested in studies involving the ruminants.

*Key words:* *Antilocapridae*, *Artiodactyla*, *Bovidae*, *Cervidae*, evolution, *Giraffidae*, *Mammalia*, *Moschidae*, phylogeny, *Tragulidae*.

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## I. INTRODUCTION

The suborder Ruminantia includes nearly 200 extant species in six families (Tragulidae, Giraffidae, Antilocapridae, Moschidae, Cervidae, and Bovidae), and is the most important group of large terrestrial herbivorous mammals. Relationships within the ruminants are of general interest to many biologists, because of their richness in species and wide-ranging geographical spread. Additionally, they are commonly found in most of the continents of the world (except Australia and Antarctica), both today and during their fossil record of 50 million years (Vrba & Schaller, 2000*a*). The ruminants are also particularly interesting because they are ecologically, behaviourally and physiologically very diverse and usually show idiosyncratic features such as, for example, the presence of different types of cranial appendages. Furthermore, they show large differences in body size. The smallest species in the suborder is the lesser Malay chevrotain (*Tragulus javanicus*), which has a mass of 0.7–8.0 kg and a shoulder height of 20–35 cm. The maximum size is represented by the Asian water buffalo (*Bubalus bubalis*), which weighs up to 1200 kg, and the giraffe (*Giraffa camelopardalis*), which attains a height of up to 5.8 m (Nowak, 1999). This group is a scientific treasure for understanding the processes of evolution because its high diversity allows comparative evolutionary studies to be readily addressed when a phylogeny is available.

Within the last decade, there has been a dramatic increase in the number of studies of adaptation in the Ruminantia using phylogenies to address a wide range of issues including, among others, behaviour (Garland *et al.*, 1993; Lundrigan, 1996; Pérez-Barbería & Gordon, 1999*b*; Brashares, Garland & Arcese, 2000), biogeography

(Arctander, Johansen & Coutellec-Vreto, 1999), feeding style (Georgiadis *et al.*, 1990; Pérez-Barbería and Gordon 1999*a, b*; Brashares *et al.*, 2000; Pérez-Barbería, Gordon & Illius, 2001*a*, Pérez-Barbería, Gordon & Nores, 2001*b*), habitat preference (Blob & LaBarbera, 2001; Pérez-Barbería *et al.*, 2001*b*), locomotion (Garland & Janis, 1993; Christiansen, 2002), macroevolutionary processes (Vrba, 1984; Vrba *et al.*, 1994; Roberts, 1996; van Vuuren & Robinson, 2001; Lalueza-Fox *et al.*, 2002), molecular and chromosomal evolution (Kraus & Miyamoto, 1991; Douzery & Randi, 1997; Purvis & Bromham, 1997; Hassanin & Douzery, 1999*b*; Wang & Lan, 2000; Matthee & Davis, 2001), sexual segregation (Pérez-Barbería & Gordon, 2000), sexual selection (Berger & Gompper, 1999), and species conservation (Hammond *et al.*, 2001). Since biologists are becoming more convinced of the utility of taking a phylogenetic approach to questions they wish to address (Felsenstein, 1985; Harvey & Pagel, 1991; Miles & Dunham, 1993), robust hypotheses about phylogenetic relationships for the taxa of interest are required. Comparative tests of a wide range of macroevolutionary and adaptation hypotheses perform best when the estimate of phylogeny on which they are based is a comprehensive well-resolved phylogenetic tree that contains estimates of divergence dates (Felsenstein, 1985; Grafen, 1989; Gittleman & Kot, 1990; Maddison, 1990; Harvey & Pagel, 1991; Pagel, 1992, 1999; Miles & Dunham, 1993; Purvis, 1996; Mooers & Heard, 1997). Nevertheless, despite its utility for studying ruminant evolution, no complete species-level phylogeny has ever been assembled for this diverse and varied suborder.

Partial phylogenies, including only a subset of the taxa belonging to Ruminantia, are accumulating at an increasing

rate. But despite this recent explosion in phylogenetic studies, the uneven distribution of research effort across taxa and of the resulting phylogenetic information into many individual studies means that comparable data for all members of the group do not exist. Most individual studies sample only a few taxa, so that our current understanding of the phylogenetic relationships within Ruminantia is fragmentary. Since these phylogenies often do not include all taxa of interest to the researcher, studies sometimes have to combine two or more phylogenies to obtain a tree that contains all those taxa. Hence, more inclusive phylogenetic hypotheses are highly desirable both for studying character evolution and for classification purposes.

In addition, there are a number of phylogenies available for ruminants, and it remains uncertain which of these is the best. Many attempts have been made to resolve the phylogenetic relationships of ruminant taxa, although little, if any, consensus has been reached. Genetic, molecular, behavioural, and anatomical features are used to construct phylogenies, but dissecting the basic relationships of extant ruminants is often difficult, and this is reflected in the conflicting results between molecular and morphological methods. Moreover, this deadlock is not simply a disagreement between molecules and morphology, because competing morphological or molecular studies have frequently disagreed among themselves. As a result, phylogenetic relationships among the different forms of Ruminantia have remained controversial for many decades and are not yet completely clear today. A major reason for our difficulties in resolving some parts of the cladograms for ruminants may be that they experienced periods of rapid radiation during certain intervals in the Oligocene, Miocene and Pliocene. Certain morphological traits have evolved several times resulting in various parallelisms and convergences that obscure true relationships (Gentry, 1992). Molecular data may also be defective for a variety of reasons (McKenna, 1987; Novacek, Wyss & McKenna, 1988). This, together with the presence of gaps in the ruminant fossil record, has led many authors to conclude that the relationships between and within the different ruminant families can be resolved only through comprehensive species sampling and by using information derived from multiple sources, including the combination of morphological and molecular data.

Thus, there is a need for a convincing phylogenetic hypothesis based on a consensus of current opinion. A solution is to combine the vast amount of phylogenetic information that already exists. A phylogenetic tree that results from combination of multiple source-tree topologies has been termed a 'supertree' (Gordon, 1986; Sanderson, Purvis & Henze, 1998; Bininda-Emonds, Gittleman & Steel, 2002; Bininda-Emonds, 2004). The supertree methods can be implemented to combine the partial phylogenies and obtain more inclusive estimates without the need to pool the original datasets. According to Bininda-Emonds and Sanderson (2001), if the set of source trees is large enough, the supertree should be an accurate representation of the information conveyed by the trees in the input set.

## II. OBJECTIVES

The aim of the present study was to generate a robust, comprehensive, and conservative estimate of what is currently known about the phylogenetic relationships among all extant and recently extinct ruminants which will allow future tests of comparative hypotheses to be readily performed. Beyond living taxa, the primacy of morphological data remains unchallenged. Molecular trees can serve as a framework for investigating evolutionary relationships, but only morphological data from the fossil record can indicate changes over geologic time (Springer & de Jong, 2001). Therefore, clearly both molecules and morphology are essential to the goal of reconstructing mammalian evolution, and our estimate is based on all available recently published works, including also behavioural and physiological studies, in accordance with the principle of 'total evidence'.

In this fashion, we combined estimates of ruminant relationships into a single phylogenetic supertree using matrix representation with parsimony (MRP). This approach combines phylogenetic information from different types of studies that otherwise could not be analysed simultaneously (Sanderson *et al.*, 1998; Bininda-Emonds *et al.*, 2002). Supertree methods resemble meta-analysis in several respects (see Sanderson *et al.*, 1998). In meta-analysis, formal statistical techniques are implemented to sum up a body of separate (but similar) experiments. Meta-analysis is a scientific review of research and provides a quantitative synthesis of all available data (Mann, 1990). In the same way, supertree methods introduce objectivity to phylogenetic reviews by quantitatively synthesizing results of previous phylogenetic studies (Bininda-Emonds *et al.*, 2003). The general supertree approach has been criticised because it only considers the topology of the source trees, effectively discarding primary data (Rodrigo, 1993, 1996; Novacek, 2001; Springer & de Jong, 2001; Gatesy *et al.*, 2002). Nevertheless, simulations have indicated that MRP provides as accurate an estimate of a known model topology as does analysing the primary data (Bininda-Emonds & Sanderson, 2001).

In order to obtain a timescale for ruminant evolution, estimates of the ages of nodes were calculated. These are useful when asking questions about the potential causes of the observed evolutionary processes, such as climatic events, or about the rates of evolution or diversification.

We stress, however, that continuing attempts to construct accurate phylogenies based on the fossil record and extant species are important, and that the supertree we present here should be viewed as a working hypothesis of ruminant phylogenetic relationships and not as an alternative to data-based phylogenetic studies. Nevertheless, it provides a reasonable hypothesis until more taxonomically comprehensive phylogenetic analyses are completed and some level of consensus arises among studies based on different data (e.g. morphology, mitochondrial DNA and nuclear DNA). It is an adequate framework to indicate the necessity of additional direct systematic analysis in certain groups that have so far received little attention. Finally, as with any phylogeny, this

is a 'work in progress', to be updated as new information becomes available.

Similar supertrees to that presented here have already been constructed for extant species of primates (Purvis, 1995*a*; Purvis & Webster, 1999), carnivores (Bininda-Emonds, Gittleman & Purvis, 1999), bats (Jones *et al.*, 2002), lagomorphs (Stoner, Bininda-Emonds & Caro, 2003), insectivores (Grenyer & Purvis, 2003) and marsupials (Cardillo *et al.*, 2004), as well as for all extant families of mammals (Liu *et al.*, 2001).

### III. A GENERAL REVIEW OF THE PHYLOGENETIC RELATIONSHIPS WITHIN RUMINANTIA

The ruminants emerged in the Eocene radiation of selenodont artiodactyls, and are now the only really successful product of that radiation (Webb & Taylor, 1980). The rapid diversification and geographic expansion of the ruminants during the Cenozoic was one of the most impressive aspects of mammalian evolution, resulting in the current most diverse group of large mammals. The history of ideas about phylogenetic affinities among ruminants is covered extensively by Simpson (1945) and, more recently, by Janis *et al.* (1998) and is thus not repeated here. Instead, we highlight some of the established or controversial points of ruminant phylogeny in the recent literature.

The classification of ruminants has fluctuated over the past 100 years; and their phylogenetic relationships remain largely unresolved despite extensive study using information gathered from morphological characters of fossil and extant taxa, behaviour, ecology and recently, molecular comparisons. Among factors contributing to this lack of resolution are the high levels of homoplasy in all the data sets utilised (Groves & Grubb, 1987; Janis & Scott, 1987; McKenna, 1987; Gentry & Hooker, 1988; Kraus & Miyamoto, 1991). The lack of resolution in some parts of the tree is also often attributed to rapid 'bushlike' radiations at different times of the Cenozoic leading to the six extant families of the suborder and some ten extinct families. Rapid rates of cladogenesis during the radiation have tended to obscure the diagnostic features and the intermediate forms needed to resolve consistently the branching patterns of families from the traditional evidence. This interpretation is supported by the sudden first appearances of multiple and diversified pecoran families in the early Miocene fossil record (Maglio, 1978; Janis, 1982; Tedford *et al.*, 1987; Morales, Pickford & Soria, 1993; Gentry & Heizmann, 1996; Janis *et al.*, 1998; Gentry, 2000*b*). The combination of rapid radiation and convergent evolution among lineages since their divergence has resulted in difficulty in recovering phylogenetic patterns, and disagreement over relationships is likely (Kraus & Miyamoto, 1991). These processes have also occurred at lower taxonomic levels, affecting our ability to reconstruct the phylogenetic relationships among genera and species. The assessment of evolutionary relationships within the Ruminantia has also been troubled by the paucity of species included in the

analyses. Few systematic studies compare all the species or genera included in the studied groups and most of the works are based on few characters.

However, phylogenetic studies have consistently provided evidence supporting some commonly accepted clades. For example, there is consistent support from morphological and molecular data for the monophyly of Ruminantia. These studies have also generally suggested that the different families and subfamilies are monophyletic.

Within the extant groups, six families have long been recognized: Tragulidae (chevrotains or mouse deer), Giraffidae (giraffes and okapis), Antilocapridae (pronghorns), Moschidae (musk deer), Cervidae (deer), and Bovidae (cattle, sheep, goats and antelopes). Flower (1875, 1883) was the first to provide a comprehensive classification of the extant ruminants. Since then, two infraorders of ruminants have commonly been recognized: Pecora (higher ruminants; generally those possessing horns, antlers or ossicones) and Tragulina (lower ruminants), with Pecora including Antilocapridae, Bovidae, Cervidae, Giraffidae and Moschidae, and Tragulina including only Tragulidae among living taxa. This basal division of Ruminantia has received strong support from morphological and molecular systematic studies. That is, among living ruminants, the primitive sister group of Pecora is certainly the Tragulidae. However, there is no invariant consensus among palaeontologists on the phylogenetic affinities of the Eocene and Oligocene fossils, and various extinct families have been proposed as the nearest relatives of Pecora (e.g. Matthew, 1934; Simpson, 1945; Pilgrim, 1947; Viret, 1961; Webb & Taylor, 1980; Janis, 1987).

Pecora is generally recognized as a monophyletic group, and the five living families are clearly distinguishable from each other on the basis of characters of the cranial appendages, limbs and dentition. Nevertheless, their interfamily relationships are controversial and unstable, as illustrated by Kraus & Miyamoto (1991), and recently reviewed by Gatesy & Arctander (2000*b*), Matthee *et al.* (2001), Hassanin & Douzery (2003) and Beintema *et al.* (2003). The different schemes show that there is not a clear consensus on their systematic relationships, and almost all possible evolutionary scenarios have been proposed in the literature. Kraus & Miyamoto (1991) attributed this poor consensus to the rapid radiation of the pecoran lineages over a short period of time in the Oligocene-Miocene.

#### (1) Tragulidae

According to Grubb (1993), the family of Tragulidae (chevrotain and mouse deer) includes four living species, confined to the tropical forests of central Africa, India and south-eastern Asia. The lower ruminants span a great and formative evolutionary void between the Eocene radiation of selenodont artiodactyls and the Miocene flowering of the higher ruminants (Webb & Taylor, 1980; Metais *et al.*, 2001). However, within the Ruminantia, the hornless groups have received little attention in comparison with that expended on the Pecora. In fact, no single molecular study to date has included more than two living species of this family.

## (2) Moschidae

Musk deer (six species in the genus *Moschus*) are widely distributed in China and adjacent areas (Groves, Wang & Grubb, 1995). The systematic position of musk deer is still open to debate. Moschidae is traditionally considered an independent family of the superfamily Cervoidea (Gray, 1821; Brooke, 1878; Flerov, 1952; Groves & Grubb, 1987; Janis & Scott, 1988), but some researchers lower the rank of this group, regarding it as a subfamily of the Cervidae (Whitehead, 1972), while others regard it as a superfamily (Moschoidea of Ginsburg, 1985) or division (Moschina of Webb and Taylor, 1980; Sinicornua of Bubenik, 1990) separated from the rest of the pecorans, which are characterized by the presence of cranial appendages (Eupecora). According to Webb and Taylor (1980), Moschina includes Moschidae and other extinct hornless pecorans. However this division or superfamily is usually not considered to be a monophyletic group (Webb & Taylor, 1980; Ginsburg, 1985).

The scarcity of molecular data has contributed to the persistent controversy on the phylogenetic status of Moschidae. *Moschus* had not been included in any molecular studies on ruminant relationships until very recently. Su *et al.* (1999) studied the cytochrome b gene sequence, supporting a close relationship between Cervidae and Moschidae. However, Hassanin & Douzery (2003), studying multiple mitochondrial and nuclear gene sequences, found a closer relationship with Bovidae.

Additionally, many studies have been done on the internal taxonomy of this group, but controversies concerning the numbers of species and subspecies and the phylogenetic relationships among them still remain (see review in Su *et al.*, 1999).

## (3) Cervidae

The current representatives of this family (moose, caribou, deer and muntjacs) are 47 species inhabiting Europe, Asia, North Africa and the two Americas. The current classification divides the family into 23 genera which fall into three subfamilies (Grubb, 2000). The Chinese water deer (*Hydropotes inermis*) is considered to represent one subfamily of the Cervidae (Hydropotinae). A single character, absence of antlers (deciduous cranial appendages), has been traditionally used to consider *Hydropotes* as the sister group of all the other living cervids (Groves & Grubb, 1987; Janis & Scott, 1987; Scott & Janis, 1987). The most popular classification of the antlered Cervidae is by Simpson (1945) based on the work of Brooke (1878), who divided all the deer into two groups, according to the degree of reduction of the lateral metacarpals (Harrington, 1985; Groves & Grubb, 1987). Cervinae (including Cervini and Muntiacini) exhibit the plesiometacarpal condition, whereas the subfamily Odocoileinae (Capreolinae *sensu* Grubb, 2000) show the telemetacarpal condition. Odocoileinae is currently subdivided into four tribes: Alceini, Capreolini, Rangiferini and Odocoileini (Grubb, 2000); but the evolutionary and taxonomic relationships among them are unclear.

However, after the first tentative classification (Brooke, 1878), the subdivisions have been fluctuating and the number of recognized cervid subfamilies is variable. Although most of the authors recognize the homogeneity and monophyly of Old World Cervini and New World Odocoileini, the status of the most atypical genera (*Alces*, *Capreolus*, *Rangifer*, *Muntiacus*, *Hydropotes*) is not well established. Additionally, the internal relationships in the cervid tribes are not adequately resolved yet because of ambiguity and conflict between different analyses, probably due either to poor representation of species or to lack of informative characters.

An alternative classification, based on the morpho-physiology of the antlers and the fossil record, proposes that Muntiacinae is the sister group of the other two antlered subfamilies (Bubenik, 1990; Azanza, 1993*a*). However, molecular investigations do not support this hypothesis (see review in Randi *et al.*, 1998).

Finally Bouvrain, Geraads & Jehenne (1989) suggested that *Hydropotes*, a telemetacarpalian, could be a sister group of Odocoileinae, or even included within this subfamily.

## (4) Antilocapridae

There are different opinions on the taxonomic status of the pronghorn (*Antilocapra americana*), inhabiting open landscapes of North America. It has been habitually assigned to the superfamily Bovoidea (Matthew, 1904; Pilgrim, 1941; Stirton, 1944; Simpson, 1945; Romer, 1966; Gentry & Hooker, 1988; Vislobokova, 1990). On the other hand, some researchers consider it as a true bovid (O'Gara & Matson, 1975) while others distinguish it as an independent superfamily (Thenius, 1969). More recently, the antilocaprids have been included in the superfamily Cervoidea as an independent family (Leinders & Heintz, 1980; Ginsburg, 1985; Janis & Scott, 1987; Gentry, 2000*b*).

Several molecular attempts to place the pronghorn phylogenetically have failed, and various authors have speculated that this pecoran taxon might be a link between bovids and cervids (see reviews in Matthee *et al.*, 2001 and Beintema *et al.*, 2003). Nevertheless, recent molecular analyses suggest that the pronghorn is a primitive member of the group and is not closely related to any of the other pecoran families (Gatesy & Arctander, 2000*b*; Matthee *et al.*, 2001; Beintema *et al.*, 2003).

## (5) Giraffidae

Similar phylogenetic ambiguities and problems surround the placement of the African giraffes (*Giraffa camelopardalis*) and okapis (*Okapia johnstoni*). They are considered to be an independent family and are allied with the Cervidae into the superfamily Cervoidea (Stirton, 1944; Simpson, 1945; Romer, 1966; Thenius, 1969) or with the Bovidae into the superfamily Bovoidea (Frechkop, 1955; Hamilton, 1978; Ginsburg, 1985; Gentry, 2000*b*). Some investigators distinguish them as the independent superfamily Giraffoidea whose affinities with Bovoidea or Cervoidea are not clear (Simpson, 1945; Thenius, 1969; Hamilton, 1978; Vislobokova, 1990; Gentry, 1994). Todd (1975) presented

chromosomal evidence to suggest that the Giraffidae are more primitive than any other pecoran family. Finally, a placement of giraffids as sister group to a clade containing both Cervidae and Bovidae might be supported by morphological evidence (Janis & Scott, 1987, 1988) and by recent molecular analyses based on multiple gene sequences (Gatesy & Arctander, 2000*b*; Matthee *et al.*, 2001).

## (6) Bovidae

The bovids (oxen, sheep, goats, antelopes and allies) comprise 137 living and more than 300 fossil species (Savage & Russell, 1983). They are found in Africa, Europe, Asia and North America, with the great majority being found in Africa. The Bovidae includes more species than any other extant family of large mammals, but their phylogenetic relationships remain largely unresolved showing that Simpson's (1945) view that Bovidae is one of the most troublesome groups of mammals to classify still applies today.

The phylogenetic relationships and taxonomy of this family have been controversial for a long time. The monophyly of Bovidae has been weakly established from morphological and molecular evidence. In fact, a paraphyletic status has been presented several times in the literature (see Gatesy *et al.*, 1992 and references in Gatesy *et al.*, 1997). The only unique and unambiguous morphological characters in support of this family are the presence of bony horns covered with keratinous sheaths (although the strange *Hoplitomeryx* from the Italian Miocene also has this kind of appendages; Leinders, 1983) and very large foramina ovals (Janis & Scott, 1987; Gentry & Hooker, 1988). However, Gatesy *et al.* (1997), after combining morphological and molecular data concluded that Bovidae is monophyletic. Recent molecular analyses using multiple gene sequences have reached similar conclusions (Gatesy & Arctander, 2000*b*; Matthee *et al.*, 2001; Hassanin & Douzery, 2003).

The origin, development, and relationships within the Bovidae are poorly understood and opinions on these topics differ widely. Thus, the classification of the bovids, particularly with respect to the recognition of the subfamilies and tribes, is noteworthy for its lack of consensus. Numerous versions of bovid taxonomy exist (e.g. Simpson, 1945; Sokolov, 1953; Frechkop, 1955; Haltenorth, 1963; Ansell, 1971; Gentry, 1978, 1992; Vrba, 1985; McKenna & Bell, 1997; Nowak, 1999; Grubb, 2001), and controversy persists over which version most accurately reflects phyletic relationships. There is considerable disagreement in the allocation of genera to tribes and subfamilies, from the five subfamilies with 13 tribes of Simpson (1945) to the 10 subfamilies and 28 tribes of Haltenorth (1963). The most recent version of bovid taxonomy (Grubb, 2001) proposes 9 subfamilies and 17 tribes for the extant bovid species.

Intertribal relationships also have resulted in considerable difference of opinion. Although monophyly of the majority of the subfamilies and tribes is supported by morphological and molecular data, the evolutionary relationships among most of them are still surrounded by controversy. Therefore, the identity of sister taxa among these subfamilies or tribes, and interrelationships among

genera and species within them remain uncertain. This is reflected in the growing literature, which encompasses paleontological, morphological, and molecular data, all of which attempt to clarify various aspects of bovid evolution between tribes and subfamilies (e.g. Vrba, 1985; Beintema, Fitch & Carsana, 1986; Lowenstein, 1986; Georgiadis *et al.*, 1990; Allard *et al.*, 1992; Gatesy *et al.*, 1992, 1997; Gentry, 1992; Matthee & Robinson, 1999; Vrba & Schaller, 2000*b*; Matthee & Davis, 2001) and within them (e.g. Vrba, 1979, 1997; Geraads, 1992; Vrba & Gatesy, 1994; Vrba *et al.*, 1994; Janecek *et al.*, 1996; Essop, Harley & Baumgarten, 1997).

The family Bovidae is difficult to classify in part because it appears to represent a rapid, early radiation into many forms without clear connections among them. Furthermore, certain morphological traits have evolved several times within the family to create convergence that obscures true relationships (Gentry, 1992).

Two main clades have been consistently retrieved within the Bovidae, a basal group comprising the Bovinae and a large more derived assemblage, which includes all the other subfamilies (Beintema *et al.*, 1986; Lowenstein, 1986; Allard *et al.*, 1992; Gatesy *et al.*, 1992, 1997; Hassanin & Douzery, 1999*b*; Matthee & Robinson, 1999; Matthee & Davis, 2001; Kuznetsova, Kholodova & Lushechina, 2002). This finding appears solid and rejects the subdivision into Aegodontia and Boodontia previously suggested by Schlosser (1904). This subdivision, based on dental features, comprised a varying assemblage of tribes and was extensively discussed by Thomas (1984). Nevertheless, based on the strong support for the basal split of Bovidae, Vrba & Schaller (2000*b*) proposed that Schlosser's (1904) names should be retained with the following revisions: Boodontia includes Boselaphini, Tragelaphini, and Bovini; and Aegodontia comprises the groups Peleini, Neotragini, Antilopini, Aepycerotini, Caprini, Alcelaphini, and the tribes which were previously included in Boodontia: Hippotragini, Cephalophini, and Reduncini.

Typically, extant bovine taxa have been divided into three tribes: Bovini, Tragelaphini and Boselaphini. Grubb (2001) has additionally proposed Pseudorygini as a new tribe within the subfamily Bovinae for a recently discovered species, the saola (*Pseudoryx nghetinhensis*). Multiple arrangements have been proposed for the phylogenetic relationships among the tribes of Bovinae and no clear consensus has still been achieved. Furthermore, the taxonomic status of some genera (e.g. *Bison*, *Taurotragus*) has been questioned in numerous works.

Antilopinae is, from a phylogenetic standpoint, probably the least understood subfamily of the Bovidae (see Rebholz & Harley, 1999 for a recent review). The taxonomy of this subfamily has presented formidable confusion ever since the early attempts at classification by Sclater & Thomas (1897) and Lydekker & Blaine (1914). It is traditionally subdivided into two subtribes: Neotragini (dwarf antelopes) and Antilopini (gazelles). However, recent studies suggest that the Neotragini are paraphyletic (Georgiadis *et al.*, 1990; Gentry, 1992; Matthee & Robinson, 1999; Rebholz & Harley, 1999). The status of *Neotragus* and *Oreotragus* is particularly problematic (Matthee & Davis, 2001).

Cephalophinae is one group whose taxonomic placement is very difficult because its species present a complex assemblage of primitive characters. It has been placed as the sister group of, for example, Bovinae (Gentry, 1992), Reduncinae (Gatesy & Arctander, 2000*a*; Kuznetsova, Kholodova & Lushechina, 2002), Antilopinae (Matthee & Davis, 2001), Neotragini (Kingdon, 1982*a, b*), a clade conformed by Caprinae, Alcelaphinae and Hippotraginae (Castresana, 2001), a clade containing Reduncinae, Alcelaphinae and Hippotraginae (Gatesy & Arctander, 2000*b*) and, finally, all the other non-bovine bovids (Georgiadis *et al.*, 1990; Groves & Schaller, 2000; Vrba & Schaller, 2000*b*).

Reduncinae is another difficult group to place among the bovid tribes (Matthee & Davis, 2001). It may be, for example, part of a clade comprising Caprinae, Hippotraginae and Alcelaphinae (Matthee & Davis, 2001), or Antilopinae, Hippotraginae and Alcelaphinae (Matthee & Robinson, 1999), the sister group of Antilopinae (Gatesy *et al.*, 1992; Vrba & Schaller, 2000*b*), or a basal branch of the Aegodontia (Hassanin & Douzery, 1999*a*; Matthee *et al.*, 2001).

Both morphological and molecular studies generally agree in placing Alcelaphinae, Hippotraginae and Caprinae in a monophyletic clade, although different works present alternative phylogenetic groupings of the three subfamilies. It is difficult to infer unambiguous phylogenetic relationships within Caprinae. Traditionally, this subfamily has been divided into four tribes: Rupicaprini, Ovibovini, Caprini and Saigini. Recently, Grubb (2001) has subdivided Rupicaprini into Rupicaprini and Naemorhedini and has eliminated Saigini. Nevertheless, these classifications have been intensely challenged by recent morphological and, especially, molecular analysis (see review in Lalueza-Fox *et al.*, 2002). On the other hand, Alcelaphinae and Hippotraginae are groups particularly well represented in the fossil record (Vrba & Gatesy, 1994; Vrba, 1997), which has facilitated the study of the relationships among their species. However, the relationships of some of them are not unambiguously resolved yet (e.g. *Beatragus* and *Sigmoceros*; Matthee & Robinson, 1999).

Finally, the placement of some monotypic genera has not been conclusively resolved. *Pelea* has been arranged with Antilopini (Oboussier, 1970), Neotragini (Gentry, 1992; Georgiadis *et al.*, 1990), Caprinae (Gentry, 1970), Reduncinae (Simpson, 1945; Gatesy *et al.*, 1997), or in its own tribe (Vrba, 1976; Vrba *et al.*, 1994) or subfamily (Grubb, 2001). *Pantholops* and *Saiga* were originally considered close relatives and placed in their own tribe within the Caprinae (Simpson, 1945). Over the past century, these problematic genera have bounced back and forth between the Antilopinae and the Caprinae (Schwarz, 1937; Pilgrim, 1939; Simpson, 1945; Bannikov *et al.*, 1967; Kurtén, 1972; Schaller, 1977; Gentry, 1978, 1992; Thomas, 1994). Recently, it has been claimed that *Saiga* should actually be placed in the Antilopini whereas *Pantholops* should stay in Caprinae (e.g. Gatesy *et al.*, 1997; Hassanin, Pasquet & Vigne, 1998; Vrba & Schaller, 2000*b*). The phyletic relationships of *Aepyceros* have been particularly problematic, being related with Antilopini (Simpson, 1945), Alcelaphinae (Gentry, 1978; Vrba, 1984; Lowenstein, 1986), Reduncini

(Ellerman, Morrison-Scott & Hayman, 1953); Caprinae (Allard *et al.*, 1992), the sister group of Bovinae (Allard *et al.*, 1992) or a clade containing Hippotraginae, Alcelaphinae and Caprinae (Gatesy *et al.*, 1997), the most basal bovid lineage (Georgiadis *et al.*, 1990), or placed in a subfamily of its own (Ansell, 1971; Grubb, 2001).

## IV. MATERIAL AND METHODS

### (1) Species assemblage

We follow the taxonomical species list presented by Grubb (1993) and reviewed by Groves *et al.* (1995) and Grubb (2000, 2001). The short-horned water buffalo (*Bubalus mephistopheles*) from northeastern China has been deleted on the species list because this species has been extinct at least since the 12th century BC (Grubb, 1993). In addition to Grubb's (1993) species list, we have included two forms of musk deer recently elevated to the species level (Groves *et al.*, 1995): the white-bellied musk deer (*Moschus leucogaster*) and the Kashmir musk deer (*Moschus cupreus*). We additionally include five new ruminant species discovered in the Indo-chinese region (Amato, Egan & Schaller, 2000; Groves & Schaller, 2000; MacKinnon, 2000), giving a total of 197 extant and recently extinct species. Those recently described species are the giant muntjac (*Megamuntiacus vuquangensis*), the Roosevelt's muntjac (*Muntiacus rooseveltorum*), the little leaf muntjac (*Muntiacus putaoensis*), the Truongson muntjac (*Muntiacus truongsoneensis*) and the saola (*Pseudoryx nghetinhensis*). Another recently described species, the linh duong (*Pseudonovibos spiralis*), is the centre of a very intense discussion on its validity as a real species. Because of the scarcity of the known material (Brandt *et al.*, 2001), and the potential possibility that this material is a fake (Hammer *et al.*, 1999; Hassanin & Douzery, 2000; Brandt *et al.*, 2001; Hassanin *et al.*, 2001; Kuznetsov *et al.*, 2001; Thomas, Seveau & Hassanin, 2001; Kuznetsov *et al.*, 2002; Hassanin, 2002; Galbreath & Melville, 2003; Olson & Hassanin, 2003), *P. spiralis* has been not included in our analysis.

### (2) Data

Phylogenetic information was collated from all sources where phylogenetic structure could be inferred from the information presented. In addition to our pre-existing knowledge of the literature, potential source trees were identified from online searches. We searched the *Biological Abstracts* (1990–2002; [http://www.biosis.org/products\\_services/ba.html](http://www.biosis.org/products_services/ba.html)), *Web of Science* (1945–2002; <http://wos.mimas.ac.uk/>), and *Zoological Records* (1978–2002; [http://www.biosis.org/products\\_services/zoorecord.html](http://www.biosis.org/products_services/zoorecord.html)) in order to comprehensively survey the literature for ruminant phylogenies. Our search criteria were the terms cladistic\*, clado\*, classif\*, phylogen\*, systematic\*, or taxonom\* in combination with Artiodactyla, Ruminantia, Pecora, Antilocapridae, Bovidae, Cervidae, Giraffidae, Moschidae, or Tragulidae. Further sources were located from bibliographies within the articles found. All publications that

were likely to include some kind of phylogenetic information were examined.

Source studies employed methods as diverse as informal character analysis (phylogenetic structure derived without using formal clustering algorithms, e.g. taxonomies), discrete character clustering methods (e.g. parsimony, maximum likelihood) and distance data clustering methods (e.g. neighbour-joining, morphometrics) using molecular and/or morphological data. Clearly some of the lines of evidence (e.g. cladograms) are much more likely to reflect phylogeny than are others (e.g. taxonomies). We have taken the view, however, that each of the lines of evidence will tend to point to phylogeny. The relative robustness of supertree structures to the type of data or analytical methodology used by the original authors in developing the source topologies has been supported in analyses of the Carnivora supertree (Bininda-Emonds, 2000).

Following Bininda-Emonds *et al.* (1999) and Jones *et al.* (2002), we consider only those phylogenetic estimates published after 1970. Thus, we searched over the time period from 1970 to June 2003 inclusive. This bibliographical search resulted in a starting list of more than 10 000 titles, from which 164 were kept as useable references for our source trees.

Recognizing the importance of fossil information, which can overturn phylogenetic hypotheses based on extant forms alone (Gauthier, Kluge & Rowe, 1988; Donoghue *et al.*, 1989; Huelsenbeck, 1991; Novacek, 1992 *a, b*; Wilson, 1992; Smith & Littlewood, 1994; Smith, 1998), we included source publications studying fossil and extant species whenever possible. Publications were retained when they presented phylogenetic information resulting from an original study, or from the modification of a pre-existing dataset. Some studies were not used as source trees because they were part of a series of papers by the same authors using virtually the same methodology, and with a data source entirely overlapping between studies. In this situation, we only used the most comprehensive or recent of the studies in our data set.

Whenever possible, trees proceeding from analysis of single genes in molecular phylogenetic studies have been used as distinct source trees (Bininda-Emonds *et al.*, 2003). But in some of these studies only trees from combined sequences of different genes are provided. In these cases we have used those trees from combined sequences as source trees.

When the authors used different analytical methods and presented more than one topology for the same data set in a study, we attempted to use the topology which they considered as the best phylogenetic estimate. In the absence of any justified preference, the alternative trees for the same data set in one publication were coded separately and a MRP analysis was conducted on them (see below). The strict consensus of the resulting trees was added as a single source tree to the overall analysis.

The supertree approach has been criticized by Springer & de Jong (2001) and Gatesy *et al.* (2002) for incorporating redundant information from multiple source trees being derived from the same dataset. Therefore, care was taken to minimize potential non-independence among source

publications arising from the re-use of part or all the data from previously published studies. When different publications from different authors made analysis of overlapping data, the trees resulting from these publications were reduced to a single source tree using MRP before inclusion into the main analysis (Bininda-Emonds *et al.*, 2003, 2004). This was possible for those analyses dealing with single gene sequences and for taxonomies (Table 1), but not for most of the morphological studies or combined analyses. Morphological data have been handled in very diverse ways by different authors in a plethora of studies. The use of different combinations of characters, methods of analysis, and assumptions between studies means that different phylogenetic estimates can arise even when there is not complete independence at the level of the data (Bininda-Emonds *et al.*, 2002). Therefore, although some non-independence is always inevitable when source trees rather than the primary data are combined, we believe that any deleterious effect arising from replication in the original data set is minimal in this analysis.

Following Bininda-Emonds and Sanderson (2001), the MRP matrix incorporated a classification including all terminal taxa (see Table 1 for the studies combined in this source tree) as the 'seed' tree. This is needed because low taxonomic overlap between source trees leads to a high proportion of missing data, and hence many equally parsimonious trees and a longer computational time. Seeding the matrix with such a classification greatly reduces the number of putative topologies by contributing a minimally informative underlying arrangement with elements common to all taxa. Another reason to use this taxonomic information is that rejecting it would make the composite tree considerably less well resolved, largely because many species have never been included in other kinds of study.

We pruned the additional subspecies or representatives of the same species from the source trees. Thus, our source trees represent abridged versions of the original topologies. Most original studies included a variable proportion of supraspecific terminal taxa. In such cases where it was not possible to assign identities to these terminal tips from the information presented in the publication, for analytical purposes their monophyly was assumed and a standard taxon substitution was performed (Wilkinson *et al.*, 2001; Jones *et al.*, 2002; Pisani *et al.*, 2002). In this fashion each supraspecific taxon was substituted with the type species for that taxon.

Finally, a total of 124 source trees was obtained from the selected research articles and were individually encoded by the MRP approach (see Section IV.3).

The selected source trees were regenerated using TreeView 1.6.6 (Page, 1996; available online at <http://taxonomy.zoology.gla.ac.uk/rod/treeview.html>) to provide NEXUS formatted files (Maddison, Swofford & Maddison, 1997; Cohen, Sheps & Wilkinson, 1998) that could be translated into a MRP matrix in RadCon 1.1.5 (Thorley & Page, 2000; available online at <http://darwin.zoology.gla.ac.uk/%7Ejthorley/radcon/radcon.html>).

The references for source trees containing the analyzed taxa are shown in Appendix 1.

Table 1. Details of source trees presenting conclusions from overlapping data sets that were combined into individual matrices for matrix representation with parsimony (MRP) before the main analysis. Strict consensus trees resulting from parsimony searches were included in the final MRP matrix. Heu, heuristic search (see material and methods); B&B, branch and bound search; MPT, most parsimonious tree. Nuclear genes: PRKCI, protein kinase C  $\iota$ ; SPTBN1, spectrin beta non-erythrocytic 1; TH, tyrosine-hydroxylase. SINE, short interspersed transposable elements

Data set	Constituent published trees (see Appendix 1)	Number of taxa	Search strategy	MPT length	Number of MPTs	Consensus resolution
Taxonomy	Ansell (1971); Gentry (1971); Corbet & Hill (1991, 1992); Eisenberg (1989); Eisenberg & Redford (1999); Estes (1991); Groves <i>et al.</i> (1995); Grubb (1993, 2000, 2001); Hall (1981); McKenna & Bell (1997); Nowak (1999); Redford & Eisenberg (1992)	197	Heu	363	10 000	58.7 %
12 S (mtDNA)	Douzery & Catzeflis (1995); Gatesy <i>et al.</i> (1999 <i>a</i> ); Hassanin & Douzery (1999 <i>a</i> ); Kraus <i>et al.</i> (1992); Kuznetsova <i>et al.</i> (2002); Ludwig & Fischer (1998); van Vuuren & Robinson (2001)	69	Heu	130	10 000	78.2 %
12S + 16S (mtDNA)	Gatesy & Arctander (2000 <i>a</i> ); Gatesy <i>et al.</i> (1992); Schaller (1998)	58	Heu	71	10 000	68.4 %
$\beta$ -caseine (nuclDNA)	Gatesy & Arctander (2000 <i>a</i> ); Gatesy <i>et al.</i> (1999 <i>b</i> )	39	Heu	38	24	63.2 %
$\kappa$ -caseine (nuclDNA)	Chikuni <i>et al.</i> (1995); Cronin <i>et al.</i> (1996); Fan <i>et al.</i> (2000); Gatesy & Arctander (2000 <i>a</i> ); Mathee & Davis (2001); Mathee <i>et al.</i> (2001); Ward <i>et al.</i> (1997)	64	Heu	107	10 000	71.9 %
Control region (mtDNA)	Burzynska <i>et al.</i> (1999); Douzery & Randi (1997); Gao <i>et al.</i> (1998); Miyamoto <i>et al.</i> (1989); Polziehn & Strobeck (1998); Polziehn & Strobeck (2002); Randi <i>et al.</i> (2001)	28	B&B	40	120	82.1 %
Cytochrome-b (mtDNA)	Birungi & Arctander (2001); Cao <i>et al.</i> (2002); Castresana (2001); Chikuni <i>et al.</i> (1995); Dung <i>et al.</i> (1993); Hammond <i>et al.</i> (2001); Hassanin & Douzery (1999 <i>a, b</i> ); Hassanin <i>et al.</i> (1998); Irwin <i>et al.</i> (1991); Jacoby & Fonseca (2000); Lalueza-Fox <i>et al.</i> (2002); Li <i>et al.</i> (1998); Liu <i>et al.</i> (2003); Mannen <i>et al.</i> (2001); Mathee & Robinson (1999); Mathee <i>et al.</i> (2001); Pitra <i>et al.</i> (1998); Randi <i>et al.</i> (1998); Rebholz & Harley (1999); Robinson <i>et al.</i> (1996); Schreiber <i>et al.</i> (1999); Su <i>et al.</i> (1999); Tanaka <i>et al.</i> (1996); van Vuuren & Robinson (2001)	135	Heu	503	10 000	88.1 %
Cytochrome-c oxidase II (mtDNA)	Jacoby & Fonseca (2000); Janecek <i>et al.</i> (1996)	16	B&B	27	12	73.3 %
PRKCI (nuclDNA)	Mathee & Davis (2001); Mathee <i>et al.</i> (2001)	41	B&B	42	1152	78.0 %
Protamine P1	Gatesy <i>et al.</i> (1999 <i>a</i> ); Queralt <i>et al.</i> (1995)	8	B&B	2	51	42.9 %
SINE transposons	Kostia <i>et al.</i> (2000); Nijman <i>et al.</i> (2002)	9	B&B	8	2	100.0 %
SPTBN1 (nuclDNA)	Mathee & Davis (2001); Mathee <i>et al.</i> (2001)	41	B&B	44	91	82.9 %
TH (nuclDNA)	Mathee & Davis (2001); Mathee <i>et al.</i> (2001)	33	B&B	38	1	90.6 %
Physiology + morphology	Bubenik (1982); Bubenik (1990)	30	B&B	26	1	86.2 %
Morphology (dental, cranial and postcranial)	Gatesy & Arctander (2000 <i>a</i> ); Gentry (1992); Groves & Schaller (2000); Thomas (1994)	32	B&B	96	192	67.7 %
Morphology (cranial)	Geraads (1992); Groves & Schaller (2000)	13	B&B	17	2	83.3 %

### (3) Matrix representation with parsimony

Two different approaches can be used to obtain comprehensive phylogenetic trees to study evolutionary patterns. The first uses characters gathered from the widest possible range of taxa combining them in a 'supermatrix' and using them directly in an analysis to produce a 'big tree'. This 'supermatrix' approach is often not tenable because of the large amount of missing data. Besides, it often lacks overlapping data for some groups of taxa. Finally, there are difficulties associated with combining some types of data; for example, discrete character data such as morphology (Sanderson *et al.*, 1998; Bininda-Emonds *et al.*, 2002; Kennedy & Page, 2002).

The second possible approach is the meta-analysis approach (Arnqvist & Wooster, 1995) used in supertree-building methods. The underlying idea of these methods is to combine the topologies of source trees resulting from multiple phylogenetic studies, rather than their respective raw biological data sets, to produce a supertree containing most of the phylogenetic information provided by the source trees (Sanderson *et al.*, 1998; Bininda-Emonds *et al.*, 2002).

One method for constructing supertrees is matrix representation with parsimony (MRP), which was proposed independently by Baum (1992) and Ragan (1992). MRP converts topologies of individual source trees into a data matrix (for a general explanation, see Sanderson *et al.*, 1998). Once matrices for each of the source trees are combined in one unique matrix, a supertree can be found using parsimony analysis. Because matrices are derived from the source trees' topologies, MRP allows different data types to be combined (Bininda-Emonds & Bryant, 1998). Therefore, MRP is currently the most commonly used method in construction of large supertrees (Purvis, 1995*a*; Bininda-Emonds *et al.*, 1999; Liu *et al.*, 2001; Jones *et al.*, 2002; Kennedy & Page, 2002; Pisani *et al.*, 2002; Salamin, Hodkinson & Savolainen, 2002; Grenyer & Purvis, 2003).

Several coding procedures have been proposed for the MRP method (Baum, 1992; Ragan, 1992; Baum & Ragan, 1993; Purvis, 1995*b*). The different coding schemes support similar results (Bininda-Emonds & Bryant, 1998; Purvis & Webster, 1999; Bininda-Emonds & Sanderson, 2001; Liu *et al.*, 2001), but the most commonly used is that independently developed by Baum (1992) and Ragan (1992). MRP represents the pattern of relationships within each of the source trees as a series of binary elements describing each node in turn. The taxa present in the clade descendant from any given node are coded as 1 for that node, whereas the taxa not in that clade are coded as 0 for that node. All other taxa (those present in one or more of the other source trees, but not the one being coded) are coded as missing values (typically, ?) for that node. Hence, matrix elements represent membership (1) or lack of membership (0) of a particular taxon relative to a clade. An all-zero hypothetical outgroup is used to polarize the elements. A parsimony algorithm reconstructs any single tree coded in this manner and is the most efficient means of deriving a composite tree from many source trees (Baum, 1992; Ragan, 1992).

The source trees' topologies were coded, combined and converted into a single matrix written in NEXUS format

suitable for parsimony analysis using the 'component coding' option of MRP Supertree Consensus in RadCon 1.1.5 (Thorley & Page, 2000).

### (4) Phylogenetic analysis

In a MRP data set, the binary characters represent topologies of source trees, where each node from a source tree provides one character to the matrix. Since these characters are not attributes of organisms, but are derived directly from the published topologies, real phylogenetic interpretation can not often be obtained for each of them (Salamin *et al.*, 2002). In view of the difficulty of determining the biological significance of these characters we refer to them as 'pseudo-characters', following Wilkinson & Thorley (1998).

All 197 species were analyzed simultaneously so that *a priori* assumptions of clade monophyly (except at the species level) would not have to be made. The MRP data matrix was analyzed using PAUP\* 4.0b10 (Swofford, 2001). We defined the outgroup as the hypothetical taxon that RadCon constructs for this use.

Since objective functions for implementing a correct, unequal pseudocharacter-weighting scheme in MRP analyses are still unknown (Bininda-Emonds *et al.*, 1999; Bininda-Emonds & Sanderson, 2001), equally weighted parsimony was used to analyze the MRP matrix. Our decision followed Purvis (1995*a*), Bininda-Emonds *et al.* (1999), Jones *et al.* (2002), Kennedy *et al.* (2002) and Pisani *et al.* (2002). Furthermore, the available evidence suggests that supertree topologies are relatively insensitive to weighting schemes (Purvis, 1995*a*; Bininda-Emonds *et al.*, 1999).

Allowing reversals in the parsimony analyses can produce clades in the composite tree that are supported by a lack of membership in some components of the source trees. Bininda-Emonds and Bryant (1998) advocated using irreversible pseudocharacter states in a parsimony analysis to overcome this shortcoming and we have followed their advice.

The consensus supertrees were computed of 10 000 most parsimonious trees found using the parsimony ratchet (Nixon, 1999) as a heuristic search algorithm. For large matrices, the parsimony ratchet has been demonstrated to find optimal solutions in a shorter amount of time than traditional solutions (Nixon, 1999; Quicke, Taylor & Purvis, 2001). Following Jones *et al.* (2002), the ratchet search strategy used was as follows: the starting-tree was initially obtained from a heuristic search using a random addition sequence with Tree-Bisection-Reconnection (TBR) branch swapping on minimal trees only, zero length branches collapsed. A random sample of 25 % of the pseudocharacters was then doubled in weight and a further heuristic search with TBR branch swapping was performed saving one tree of the equally most parsimonious trees found. The weights were then restored to their original values and TBR branch swapping was performed, again saving one of the equally most parsimonious trees. This ended one replicate of 1000. The 1001 trees produced (1000 replicates plus the initial start tree) were then used as a starting point for TBR branch swapping, saving up to a limit of 10 000 of the equally most parsimonious trees.

Many workers have recognized that the strict consensus method often yields poorly resolved consensus trees and that this is sometimes due to the insensitivity of the method rather than any lack of agreement among the original trees (Swofford, 1991; Wilkinson, 1994; Wilkinson & Thorley, 1998). Hence, following Kennedy & Page (2002), Adams consensus (Adams, 1972) was computed in addition to strict consensus. Adams consensus denotes the areas of similarity among many competing trees and identifies taxa that are difficult to locate, resolving disagreement among source trees by placing these taxa of uncertain position as part of a polytomy at the most basal node from which it is derived in all those rival trees (Adams, 1972). Thus the polytomy indicates that the taxon is a member of that group in all optimal trees, but that it cannot be placed more precisely (Wilkinson, 1994). The differences between Adams and strict consensus trees make it apparent which taxa are difficult to place and, therefore, deserve further consideration in future phylogenetic studies. Nevertheless, the meaning of polytomies within an Adams consensus tree needs to be interpreted with caution because they do not strictly reflect phylogeny (Adams, 1972), and areas of disagreement between Adams and strict consensus should be evaluated.

As when biological character data are analyzed, some parts of the supertree are known with much more certainty than are others. Nevertheless, a poorly understood problem in MRP supertree building is how to evaluate the support for the resulting clades, and all the measures of support should be interpreted with care (Pisani *et al.*, 2002). Following Bininda-Emonds *et al.* (1999), Liu *et al.* (2001), Jones *et al.* (2002), Pisani *et al.* (2002), Grenyer & Purvis (2003), and Stoner *et al.* (2003) we calculated the support for individual nodes within the supertree using the Bremer decay index (Bremer, 1988; Källersjö *et al.*, 1992). The Bremer decay index indicates how much less parsimonious the tree would have to be before a clade in question disappears, summarizing the number of extra steps necessary for the removal of that clade from the most parsimonious solution. Bremer support depends on how many characters or elements there are (Novacek, 1991) and how well they agree, so low values are indicative of a group with minimum stability because of small numbers of source trees or conflict among them (Bininda-Emonds *et al.*, 1999). High scores are representative of a clade that is relatively well supported.

## (5) Supertree dating

Following Purvis (1995*a*) and Bininda-Emonds *et al.* (1999), a combination of numerical (fossil and molecular estimates) and relative (molecular) dates from the literature (Appendix 1), as well as our own information on the fossil record, were used to assign dates to branching events in the supertree. Inherent difficulties of both kinds of data were commented on by Purvis (1995*a*) and Bininda-Emonds *et al.* (1999) and will not be repeated here. We have taken dates only where the source node defines the same monophyletic group as a node in the supertree (Purvis, 1995*a*). Following Purvis (1995*a*), when a source is less resolved than the supertree, we have used the age of the source polytomy as a value for the age of each corresponding node in the composite

tree. However, when the source is more resolved, we have only taken the age of the oldest source node as the estimate of the age of the corresponding polytomy in the supertree.

### (a) Fossil record

We use as data the time of first occurrence of either of the descendant lineages, unless there is good phylogenetic or biogeographic evidence to the contrary. This type of data provided dates for 87 nodes.

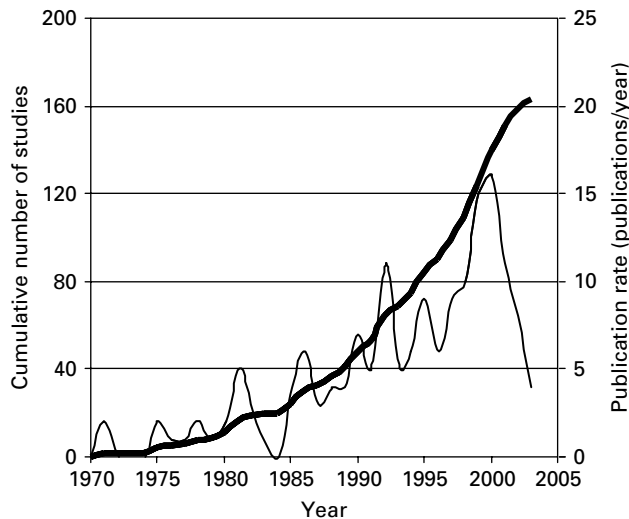
### (b) Molecular data

As in Purvis (1995*a*) and Bininda-Emonds *et al.* (1999), the concept of a local molecular clock (Bailey *et al.*, 1991) was employed to minimize potential errors caused by different evolutionary rates in different lineages (Gillespie, 1991; Wayne, Van Valkenburgh & O'Brien, 1991; Flynn, 1996) or a decrease in the rate of change with increasing divergence times (Wayne *et al.*, 1991; Gittleman *et al.*, 1996). Calibrating molecular information to a few very widely spaced nodes of known age would likely lead to correlated errors (Wayne *et al.*, 1991) throughout the tree. The local molecular clock method uses information about only those branches in the region of the node to be dated, estimating the date of this node relative to some (not necessarily immediately) ancestral node based on relative branch lengths (see Purvis, 1995*a* for more detail). Whenever possible, the branch lengths we used for this were derived from the original pairwise matrices in the source papers. Several papers present dates derived with the assumption of an overall molecular clock. To avoid problems due to differences of calibration we have, wherever possible, recalibrated dates relative to higher nodes for which other estimates were available. The local molecular clock strategy provided dates for 113 nodes, 40 of them were additional to those provided by the fossil record.

### (c) Dating of the times of divergence

A total of 140 studies yielded 660 point estimates for 127 nodes throughout the tree (14 nodes had only fossil estimates, 40 only molecular, and 73 had estimates derived from both types). So the majority of nodes (79.9%) had divergence times derived from literature estimates. Following Purvis (1995*a*) and Bininda-Emonds *et al.* (1999), the divergence time for a node was calculated as the median of available estimates. Nevertheless, the fossil record was used as a constraint to the dating. So, the divergence time in a node could not be younger than the first occurrence of any of the representatives of the clades diverging in that node.

Finally, dates for those nodes that did not possess an estimate in the literature were interpolated using a pure birth model, under which a clade's age is proportional to the logarithm of the number of species it contains (see Purvis 1995*a*). Following Bininda-Emonds *et al.* (1999), estimates were calibrated relative to dated ancestral and from dated descendant nodes whenever possible.



**Fig. 1.** Cumulative number of references on ruminant phylogeny used for source trees (thick line) and publication rate since 1970 (thin line).

## V. RESULTS

The resulting MRP data set of presence/absence binary features for 124 phylogenies had 1426 pseudocharacters for the 197 recognized species of extant (and recently extinct) ruminants. This matrix has been deposited in TreeBASE (<http://www.treebase.org/>).

The majority of phylogenetic studies of ruminants were published from 1990 onwards, with a rapid increase during the last five years. It seems, however, that the publication rate on this topic reached its maximum in 1999–2001 and has been decreasing since then (Fig. 1).

### (1) Taxonomic coverage and resolution

It is clear that some taxa within the suborder have received more coverage than others. The numbers of scored pseudocharacters for the species ranged from 115 (8.1%) for the Kashmir muskdeer (*Moschus cupreus*) and Przewalski's gazelle (*Procapra przewalskii*) to 1059 (74.2%) for the ox (*Bos taurus*). In addition to the ox, only 12 other species of the study group were scored for more than 713 (>50%) of the 1426 pseudocharacters. These species were the nilgai (*Boselaphus tragocamelus*), impala (*Aepyceros melampus*), goat (*Capra hircus*), giraffe (*Giraffa camelopardalis*), pronghorn (*Antilocapra americana*), lesser kudu (*Tragelaphus imberbis*), African buffalo (*Syncerus cafer*), waterbuck (*Kobus ellipsiprymnus*), sheep (*Ovis aries*), Chinese muntjac (*Muntiacus reevesi*), and sable antelope (*Hippotragus niger*). Not surprisingly, this uneven coverage of taxa was heavily biased towards those species with obvious economic, scientific, conservation and aesthetic importance to humans.

The composite estimates of phylogeny are shown in Figs. 2–7. The MRP tree for ruminants represents the strict consensus of 10 000 equally most parsimonious

trees, each of 1992 steps (Consistency Index=0.716; Retention Index=0.938). Bremer support indices and estimated time of divergence associated with each node are given in Table 2. As measured by the Bremer decay index, support for the inferred relationships was generally low throughout the tree. However, most genera and families showed higher levels of support, as did some subfamilies.

As a combined summary of existing knowledge of evolutionary relationships of ruminants, the consensus tree for the MRP analysis is well resolved. The supertree is largely bifurcating, having 159 nodes out of a possible 196 (81.1%). In comparison to the resolution of other supertrees for bats (46.4%; Jones *et al.* 2002), insectivores (67.2%; Grenyer & Purvis, 2003), marsupials (73.7%; Cardillo *et al.*, 2004), carnivores (78.1%; Bininda-Emonds *et al.*, 1999), primates (79.1%; Purvis, 1995*a*), and lagomorphs (97.5%; Stoner *et al.*, 2003), the resolution for ruminants is high. However, resolution varies among groups and some component clades (particularly Muntiacini, 36.4%; Caprinae, 67.7%; and Odocoileini, 76.5%) are much less well resolved than others (e.g. Moschidae, Tragulidae, Reduncinae, 100%; Bovinae, 95.7%; Cephalophinae, 94.4%), reflecting both the information available and how well the source trees agree with each other.

The present supertree contains six important polytomies. Two of them lie within Cervidae (within Odocoileini, and within *Muntiacus*), and the other four within Bovidae: one at the base of the non-bovine bovids, one within Antilopinae, another at the base of Caprini, and the last within *Capra*. However, the Adams consensus tree shows that in most cases this lack of resolution is due to some problematic (*Hippocamelus*, *Oreotragus*, *Neotragus*, *Procapra*, *Capra walie*) or poorly studied (*Muntiacus atherodes*) taxa.

### (2) Times of divergence

The ruminant supertree had date estimates for 79.9% of the nodes (Table 2). The higher level relationships had date estimates for every node. For Tragulidae, date estimates were only available for one of three nodes.

Errors in median dates were reasonable, with 'coefficients of variation' (calculated relative to the median and not the mean) exceeding 100% for only eight nodes of the 104 that possessed two or more date estimates. Generally, nodes with higher 'coefficients of variation' were either relatively recent, making any error proportionately larger, or those whose dates were derived from very few estimates, allowing a single discrepant estimate to inflate the standard deviation.

Eight nodes were estimated to be older than an ancestral one. Nevertheless, the resultant negative branch lengths were always small compared with the age of the node. Seven nodes had older dates than those estimated by the local molecular clock, as evidenced by the fossil record. In most, however, this discrepancy was small. Exceptions can be found within the Antilopini, where the fossil record indicates a much faster basal cladogenesis than implied by the molecular clock (Table 2).

Table 2. Statistics relating to the support and times of divergence for the nodes of the ruminant composite tree (see Figs 2–7). All divergence times are in millions of years before present (Ma).  $\mathcal{N}$ , number of date estimates from the literature; SEM, standard error of the mean. Dates proportional to the logarithm of the number of species in the clade (birth model; see text) are given for nodes without a literature estimate. The best estimate for a node is the literature estimate or the birth model estimate, secondarily constrained by the first appearance in the fossil record (bold; see text) and corrected for negative branch lengths (italics)

Clade number	Bremer support	Literature estimates (Ma)				Birth model (Ma)	Best estimate (Ma)
		$\mathcal{N}$	Mean	SEM	Median		
1	n/a	1	50.0	—	50.0	—	50.0
2	5	0	—	—	—	35.2	35.2
3	4	0	—	—	—	28.2	<i>28.4</i>
4	3	2	28.6	4.1	28.6	—	<i>28.4</i>
5	4	12	34.6	2.1	33.2	—	33.2
6	12	10	25.6	2.5	28.1	—	28.1
7	26	3	16.0	2.0	17.8	—	17.8
8	13	16	30.5	0.9	29.9	—	<b>32.0</b>
9	7	3	32.0	5.2	29.5	—	29.5
10	5	2	6.4	5.7	6.4	—	6.4
11	3	1	3.5	—	3.5	—	3.5
12	3	1	1.9	—	1.9	—	1.9
13	3	1	1.3	—	1.3	—	1.3
14	3	0	—	—	—	0.8	0.8
15	9	27	25.8	0.6	25.4	—	25.4
16	23	19	21.9	0.9	23.2	—	23.2
17	2	0	—	—	—	5.4	5.4
18	3	0	—	—	—	3.4	3.4
19	3	6	19.4	0.6	19.8	—	19.8
20	11	5	14.5	1.1	13.5	—	13.5
21	5	3	23.3	1.0	22.3	—	22.3
22	12	10	19.3	0.9	20.2	—	20.2
23	12	10	17.3	1.2	17.9	—	17.9
24	8	5	16.8	1.4	17.8	—	17.8
25	10	12	21.5	1.4	19.7	—	19.7
26	3	17	19.5	1.3	19.4	—	19.4
27	9	12	13.8	0.8	14.3	—	<i>14.7</i>
28	10	9	9.5	1.3	9.9	—	9.9
29	4	2	7.0	0.8	7.0	—	7.0
30	4	1	0.9	—	0.9	—	0.9
31	4	0	—	—	—	0.7	0.7
32	3	0	—	—	—	0.4	0.4
33	8	3	2.6	1.9	0.8	—	0.8
34	6	6	8.6	1.2	8.4	—	8.4
35	4	5	5.2	0.7	5.6	—	5.6
36	4	0	—	—	—	3.9	3.9
37	3	3	2.8	1.4	3.5	—	3.5
38	4	0	—	—	—	2.7	2.7
39	3	1	3.4	—	3.4	—	<i>4.2</i>
40	4	6	5.1	1.1	4.9	—	<i>4.2</i>
41	7	5	13.8	2.0	15.1	—	<i>14.7</i>
42	5	8	5.2	1.0	4.8	—	4.8
43	3	5	3.6	0.8	4.1	—	4.1
44	3	2	1.4	0.0	1.4	—	1.4
45	10	11	15.1	1.4	14.6	—	14.6
46	4	3	10.3	0.9	11.0	—	11.0
47	9	4	4.2	1.6	3.4	—	3.4
48	6	11	10.0	1.2	10.8	—	10.8
49	6	7	8.0	1.1	9.0	—	9.0
50	4	1	2.0	—	2.0	—	2.0
51	7	7	5.1	0.6	4.7	—	4.7
52	4	0	—	—	—	6.1	6.1
53	4	0	—	—	—	4.7	4.7
54	3	0	—	—	—	3.7	3.7
55	3	0	—	—	—	2.3	2.3

Table 2 (*cont.*)

Clade number	Bremer support	Literature estimates (Ma)				Birth model (Ma)	Best estimate (Ma)
		$\mathcal{N}$	Mean	SEM	Median		
56	4	0	—	—	—	2.4	2.4
57	4	0	—	—	—	2.4	2.4
58	20	16	20.5	0.6	20.5	—	20.5
59	11	5	8.8	1.4	10.4	—	10.4
60	4	12	17.1	1.4	18.3	—	18.3
61	9	3	13.8	3.7	16.8	—	16.9
62	7	17	17.0	1.4	17.0	—	16.9
63	12	10	8.5	1.6	7.0	—	7.0
64	4	10	5.8	0.8	5.8	—	5.8
65	7	6	4.0	0.7	3.4	—	3.4
66	6	5	1.3	0.6	1.1	—	1.1
67	5	1	0.6	—	0.6	—	0.6
68	11	6	3.0	0.7	2.5	—	2.5
69	15	12	11.7	0.8	11.8	—	11.8
70	8	6	4.1	0.8	3.8	—	3.8
71	5	3	2.5	0.7	3.2	—	3.2
72	5	2	4.0	1.8	4.0	—	4.0
73	21	10	9.9	1.2	10.5	—	10.5
74	5	6	6.6	0.3	6.9	—	6.9
75	4	4	5.8	1.4	5.4	—	5.4
76	4	1	1.6	—	1.6	—	1.6
77	4	1	2.6	—	2.6	—	2.6
78	6	5	4.4	0.5	4.4	—	<b>6.0</b>
79	3	1	2.8	—	2.8	—	2.8
80	3	11	18.8	0.7	19.7	—	19.7
81	3	7	15.7	0.7	16.1	—	<b>18.0</b>
82	5	5	12.5	1.9	14.6	—	<b>18.0</b>
83	3	0	—	—	—	4.2	4.2
84	4	4	12.2	2.5	12.3	—	<b>18.0</b>
85	5	5	10.7	1.7	8.6	—	10.6
86	1	4	11.5	1.5	12.5	—	10.6
87	4	0	—	—	—	4.8	4.8
88	3	1	1.9	—	1.9	—	1.9
89	8	3	3.7	1.7	4.4	—	4.4
90	4	1	3.1	—	3.1	—	3.1
91	4	5	5.9	1.0	5.7	—	5.7
92	4	0	—	—	—	2.5	2.5
93	3	0	—	—	—	2.3	2.3
94	3	0	—	—	—	1.4	1.4
95	3	1	0.0	—	0.0	—	0.0
96	3	2	0.8	0.7	0.8	—	0.8
97	4	2	1.5	0.7	1.5	—	1.5
98	7	0	—	—	—	6.2	6.2
99	3	0	—	—	—	3.9	3.9
100	4	0	—	—	—	5.3	5.3
101	3	2	1.4	0.2	1.4	—	1.4
102	3	0	—	—	—	2.7	2.7
103	3	0	—	—	—	8.9	8.9
104	3	5	7.0	1.4	7.9	—	7.9
105	16	6	9.9	1.8	10.3	—	<b>13.5</b>
106	3	3	15.7	0.9	16.4	—	13.5
107	7	1	10.8	—	10.8	—	10.8
108	2	0	—	—	—	10.2	10.2
109	2	0	—	—	—	9.8	9.8
110	2	0	—	—	—	4.7	4.7
111	6	2	3.2	1.9	3.2	—	3.2
112	2	1	7.7	—	7.7	—	7.7
113	5	2	3.9	0.4	3.9	—	3.9
114	6	2	0.8	0.6	0.8	—	0.8

Table 2 (cont.)

Clade number	Bremer support	Literature estimates (Ma)				Birth model (Ma)	Best estimate (Ma)
		$\mathcal{N}$	Mean	SEM	Median		
115	4	2	1.6	0.1	1.6	—	1.6
116	2	0	—	—	—	10.0	10.0
117	7	2	8.5	1.1	8.5	—	8.5
118	3	2	7.5	0.9	7.5	—	7.5
119	5	2	4.5	1.1	4.5	—	4.5
120	2	1	4.6	—	4.6	—	4.6
121	7	3	5.7	2.0	5.1	—	5.1
122	8	8	11.3	1.4	12.7	—	12.7
123	9	5	6.1	1.3	6.7	—	6.7
124	2	3	3.1	0.8	3.0	—	3.0
125	6	3	4.6	1.8	2.9	—	3.5
126	4	3	1.3	0.8	1.2	—	1.2
127	4	3	4.4	1.3	4.0	—	3.5
128	5	3	1.5	0.4	1.6	—	1.6
129	21	10	10.8	1.3	10.8	—	10.8
130	11	5	2.9	0.9	3.1	—	3.1
131	10	5	2.1	0.3	1.8	—	<b>2.5</b>
132	4	3	7.2	1.0	7.7	—	7.7
133	7	4	5.6	1.3	6.2	—	6.2
134	14	8	10.7	1.4	11.0	—	11.0
135	5	4	4.7	0.8	5.0	—	5.0
136	6	4	2.6	0.3	2.5	—	2.5
137	7	3	8.5	0.3	8.8	—	8.8
138	4	1	2.5	—	2.5	—	2.5
139	6	14	14.1	1.1	14.5	—	14.5
140	5	16	11.5	0.9	11.3	—	11.3
141	6	1	11.0	—	11.0	—	<i>11.1</i>
142	6	5	10.3	1.2	11.1	—	<i>11.1</i>
143	5	4	8.2	0.7	8.0	—	8.0
144	6	10	5.7	1.3	5.1	—	5.1
145	4	1	2.8	—	2.8	—	2.8
146	3	0	—	—	—	1.8	1.8
147	5	3	2.4	0.3	2.4	—	2.4
148	9	7	6.4	1.2	6.8	—	6.8
149	6	4	3.2	1.3	2.7	—	2.7
150	4	2	0.8	0.7	0.8	—	0.8
151	5	1	0.5	—	0.5	—	0.5
152	3	1	0.2	—	0.2	—	0.2
153	5	2	8.8	3.2	8.8	—	8.8
154	5	3	3.2	1.6	3.8	—	3.8
155	5	2	10.3	7.3	10.3	—	10.3
156	5	0	—	—	—	3.3	3.3
157	3	1	0.1	—	0.1	—	0.1
158	6	2	4.3	3.8	4.3	—	4.3
159	3	0	—	—	—	2.7	2.7

## VI. DISCUSSION

The most surprising result of this analysis is the relatively high resolution obtained in spite of the general feeling in the scientific community of a high level of disagreement among different authors on the phylogenetic relationships within Ruminantia. However, the consistency index is low and most of the nodes are weakly supported. This implies that this consensus most likely is not as stable as would be desired to future data set additions or increased taxonomic sampling

in the original data sets (molecular, behavioural, morphological or palaeontological).

In broad terms the results obtained are in remarkable agreement with previous ruminant classification schemes. Despite the lack of robustness of many nodes, only three of the genera recognized by Grubb (1993, 2000, 2001) were paraphyletic: *Tragelaphus*, *Bos*, and *Muntiacus*. However, claims for nomenclatural changes in the implied species of these three genera have been made in the past in order to assure their monophyly [respectively, Van Gelder (1977),

Groves (1981), and Schaller & Vrba (1996)]. Instances of non-monophyly in higher taxonomical groups also were rare, occurring only for some bovid groups (Neotragini, Antilopini, and Ovibovini). Altogether, this high level of monophyly reflects the general current opinion on ruminant phylogeny. Since there is a high agreement with the nomenclature delineated by Grubb (1993, 2000, 2001), we follow his systematic classification in this discussion. The only main change is the raising of Pantholopini to the subfamily level (Pantholopinae).

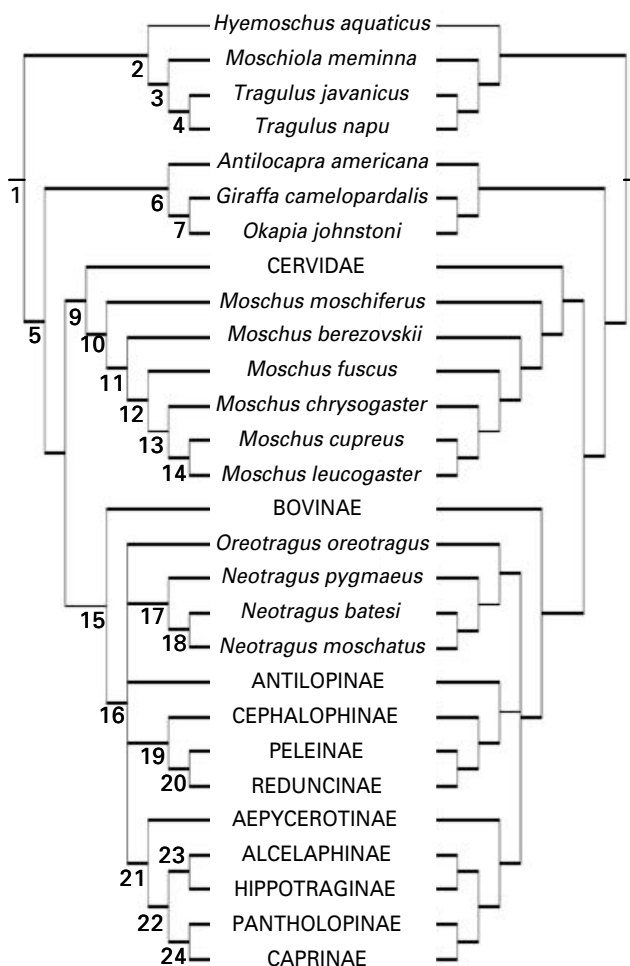
Contentious issues in ruminant systematics are resolved in the present supertree. Nevertheless, the composite tree is merely a (most parsimonious) synthesis of a number of source trees. All of the information on which it is based has been published previously, and the supertree does not contain any clade that has not been implied by any previous study. Discussion of the evidence supporting (or refuting) particular relationships can be found in the source papers (Appendix 1) and here we limit our discussion to the most controversial issues and the implications of our results for some evolutionary processes. Two of these longstanding areas of contention concern the relationships of the pecoran families and those of the cervid and bovid subfamilies.

### (1) Higher-level relationships

The MRP topology calculated for the higher-level relationships is shown in Fig. 2. Monophyly of the ruminant families is held by the majority of the studies to date, and this is strongly reflected in the structure of the supertree which strongly supports the monophyly of all the families. The supertree does not support the diphyly of Bovidae suggested by several molecular studies (see references in Gatesy *et al.*, 1997).

The five living pecoran families are classically unified as higher ruminants and are distinguished from tragulids by numerous morphological characters (Janis & Scott, 1987). The consensus supertree retains Tragulidae as a sister group to the other ruminants, supporting the division of Ruminantia into the two infraorders Tragulina and Pecora. This is consistent with the vast majority of sources that place it in such a position. Surprisingly, the grouping of Pecora is weakly supported due to the relatively few comprehensive studies that include Tragulidae. This group has been traditionally excluded in studies dealing with extant species, which are the greater part. Indeed, there is no single study that investigates the phylogenetic relationships among the four extant tragulid species. Our composite tree within this family has been exclusively derived from the consensus among the taxonomical studies included in our analysis (Corbet & Hill, 1991, 1992; Grubb, 1993; McKenna & Bell, 1997; Nowak, 1999). Therefore, this result is provisional until there are morphological or molecular studies which include all the four extant species of this family.

Within Pecora, the supertree offers support for the three traditional superfamilies Giraffoidea, Cervoidea and Bovoidea. Giraffoidea is a basal pecoran subfamily, which includes Antilocapridae and Giraffidae, and is the sister group of the clade containing Cervoidea (Moschidae and Cervidae) and Bovoidea. This joint arrangement of



**Fig. 2.** The composite tree for the higher groups of ruminants and Tragulidae, Giraffidae, and Moschidae. Left, strict consensus; right, Adams consensus. Node numbers refer to Table 2. Branch lengths are not proportional to time.

Antilocapridae and Giraffidae is consistent with several molecular studies (Goodman, 1981; Miyamoto & Goodman, 1986; Allard *et al.*, 1992; Douzery & Catzeflis, 1995; Randi *et al.*, 1998; Su *et al.*, 1999; Gatesy & Arctander, 2000a; Matthee *et al.*, 2001) and the morphological studies of Ahearn (1992).

Our supertree disagrees with a recent supertree that analyzed the family-level relationships of all mammals (Liu *et al.*, 2001) which placed Giraffidae as the sister group to Cervoidea. We think that our supertree better reflects the available evidence for the following reasons: firstly, more studies were incorporated, especially including those from 1999–2001 (the bibliographical search by Liu *et al.*, 2001 finished in March 1999); secondly, more elements (197 species *versus* five families) were studied; and thirdly, the sources used in our study were more independent of each other (see Springer & de Jong, 2001).

Nevertheless, a major problem arises at this point of the ruminant phylogeny: the long-branch attraction effect (Felsenstein, 1978; Hendy & Penny, 1989; Siddall &

Whiting, 1999), which refers to the tendency of species at the ends of long branches in a phylogenetic tree to be made artificially close to each other due to the high frequency of parallel changes that arrive at the same state by temporal (and therefore phylogenetic) distance or accelerated rates of evolutionary change. Since nucleotide data are constrained to be one of four states (A, C, T, or G) and morphological trees are traditionally based on hundreds of characters that do not vary randomly, this problem afflicts molecular analyses worse than it afflicts morphological analyses. Here, the problem worsens because of the uneven taxonomic sampling; antilocaprids and giraffids are known from only three extant species while there are several dozens of bovids and cervids. Felsenstein (1978) identified this phenomenon as a deficiency of the maximum parsimony method of phylogeny reconstruction, although it is known that all methods can be misleading in such circumstances. In other words, the sister relationship between Giraffidae and Antilocapridae might be a result of the experimental procedure used to resolve the source molecular phylogenies.

Ruminant artiodactyls are a diverse group with few good synapomorphies (Scott & Janis, 1993) that appear to have undergone many parallelisms in their evolutionary history, thus presenting particular difficulties in understanding the phylogeny. For example, there is clear developmental and paleontological evidence that cranial appendages have evolved several times among the ruminants (Janis, 1982, 1990; Janis & Scott, 1987; Bubenik, 1990; Morales *et al.*, 1993). On the other hand, the original possession and subsequent loss of one character such as sabre-like canines has occurred numerous times within pecoran lineages, usually linked with the development of cranial appendages. Therefore, in the present case, many of the similarities between giraffoids and cervoids or bovoids may simply reflect plesiomorphic pecoran features, and others may have evolved independently a number of times in parallel.

Thus, in order to solve this particular question, we consider essential further study of the phylogenetic relationships among the fossil and extant families within Giraffoidea, Bovoidea and Cervoidea for a better understanding of the evolutionary history of these three pecoran superfamilies. It will be crucial to include an ample sample of fossil taxa in a comprehensive phylogenetic analysis of the basal relationships of pecoran families. So far the most extensive of such analyses are those of Janis & Scott (1987), Gentry & Hooker (1988) and Gentry (1994); but in the past decade new fossils have been discovered, some of them claimed to be associated with the basal relationships of extant groups, such as *Lorancamerix* in the early Miocene of southwestern Europe (Morales *et al.*, 1993) or *Namibiomyx* and *Sperrgebietomyx* in the Miocene of southern Africa (Morales, Soria & Pickford, 1995, 1999), which might help to solve the question. An additional promising area of study for ruminant palaeontologists is the Asian Oligocene. The earliest cervoid, *Eumeryx*, was found in the early Oligocene of East Asia (Matthew & Granger, 1924). Small hypsodont taxa are known from the Mongolian middle Oligocene, such as *Palaeohypsodontus* (Trofimov, 1958) and *Hanhaicervus* (Huang, 1985). They have been claimed to be bovids but their teeth have no distinguishing features that would ally them with any particular

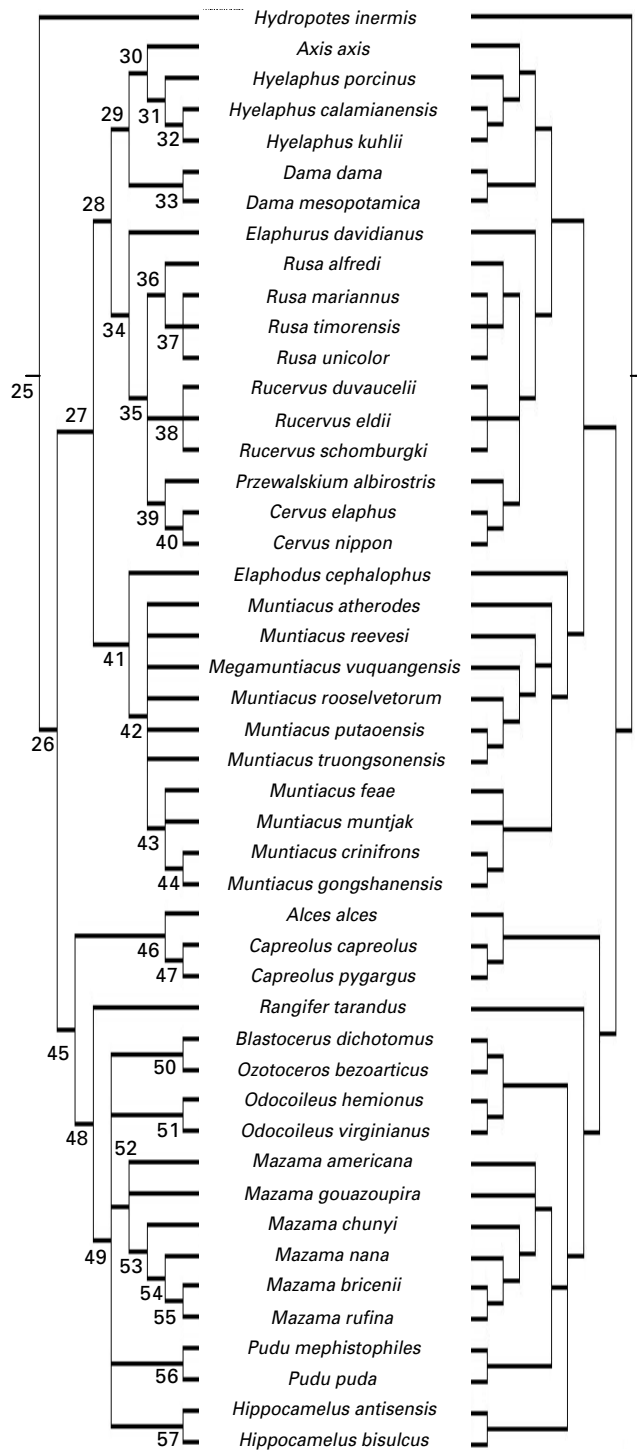
ruminant family (Janis & Scott, 1987). Their temporal and spatial placements make these ruminants potential ancestors for Antilocapridae (Janis & Manning, 1998a), or they may be stem groups of Giraffoidea or Bovoidea. A deeper knowledge of these faunas will be required to resolve this subject.

## (2) Relationships within Cervidae

The cervids are divided into their recognized subfamilies and tribes with all relationships receiving intermediate support (Fig. 3). Our tree corroborates the hypothesis of a monophyletic group of antlered deer that excludes *Hydropotes* in agreement with the ideas of Bogenberger, Neitzel & Fittler (1987), Groves & Grubb (1987), Kraus & Miyamoto (1991), Kraus *et al.* (1992), and Jacoby & Fonseca (2000). Again, as in giraffoids, historical disagreements on the relationships of this species are probably due to the combination of a wide series of primitive characters and some progressive ones produced by the extensive parallelism in ruminant evolution. Thus, the most parsimonious placement for this kind of species is as a basal stem of the entire group under consideration.

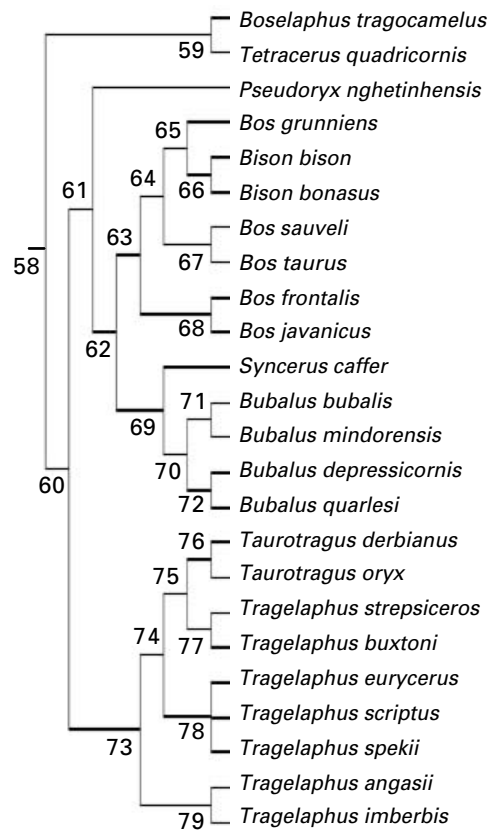
The monophyly of *Muntiacus* was not supported because *Megamuntiacus* nests within *Muntiacus*. Nevertheless, Schaller & Vrba (1996) have challenged the separate generic status of *Megamuntiacus vuquangensis* and this is currently the general opinion (Amato *et al.*, 2000). A number of new Muntiacinae species have been discovered in the last fifteen years. This has had the effect of directing much attention to the relationships within this group. However, the taxonomy of muntjacs is controversial and the phylogeny is still an open question. There was virtually no agreement between sources in our analysis and relationships were poorly resolved. This was mainly due to the controversial placement of *M. atherodes*.

Relations among genera formerly included in *Cervus* (*Rusa*, *Rucervus*, *Przewalskium*, and *Cervus*) were poorly resolved, reflecting the sparse amount of phylogenetic information available for some of these taxa, and disagreements between traditional taxonomies and less taxonomically complete molecular analyses. The MRP tree supports the division of Capreolinae into four tribes included in two principal lineages, Odocoileini + Rangiferini and Capreolini + Alceini. While our analysis clearly indicates that Odocoileini constitutes a well-defined monophyletic group, the relationship among genera within this tribe remains uncertain. In general, published phylogenetic studies on Odocoileini are scarce, fragmentary and conflicting. The low resolution for this tribe arises not only from conflict between the source trees but mainly from a low taxonomic overlap among studies. In the Adams consensus, tree generic relationships are resolved except for the placement of *Hippocamelus*. The composite phylogeny strongly indicates that future work within this group must consider more species. For example, *Mazama* is another problematic genus; species definitions are still in a state of flux (Eisenberg, 2000) and a formal phylogenetic analysis of the taxon has never been undertaken. As a result, the MRP analysis presented here reflects only the taxonomists' ideas.



**Fig. 3.** The composite tree for Cervidae. Left, strict consensus; right, Adams consensus. Node numbers refer to Table 2. Branch lengths are not proportional to time.

If our dates are accurate, the first diversification within the Odocoileini predates the first appearance of fossil cervids in North America, around 5 million years ago (Webb, 2000). Our estimates suggest that part of the diversification within this lineage may have occurred long before it reached North



**Fig. 4.** The composite tree for Bovinae. Strict consensus (Adams consensus has the same topology). Node numbers refer to Table 2. Branch lengths are not proportional to time.

America. New fossil discoveries are needed to support this finding.

### (3) Relationships within Bovidae

This study provides strong evidence for the monophyly of the Bovinae, Hippotraginae, Alcelaphinae, Caprinae, Reduncinae, and Cephalophinae. It also suggests that Antilopinae is polyphyletic, thereby supporting earlier investigations (e.g. Rebholz & Harley, 1999; Gatesy, O'Grady & Baker, 1999*b*; Hassanin & Douzery, 1999*b*; Groves & Schaller, 2000; Matthee & Davis, 2001; Kuznetsova *et al.*, 2002), and that Caprinae is the sister taxon of *Pantholops hodgsonii*, which then might constitute a monospecific subfamily (Pantholopinae; Vrba & Schaller, 2000*b*) or subtribe within Caprinae (Pantholopini; Sokolov, 1953; Schaller, 1998).

The consensus of our present phylogenetic analyses indicates that extant bovids represent the product of a main split which gave rise to one bovine clade, which comprises the tribes Bovini, Tragelaphini, Boselaphini and Pseudorygini, and one non-bovine clade, which clusters all other bovids (Fig. 2).

The clade of the Bovinae subfamily was one of the most consistent and its species cluster into the commonly recognized tribes (Grubb, 2001). This part of the tree is also

well resolved, reflecting general agreement among the source trees (Fig. 4). Boselaphini was the sister species of the rest of the clade, which included Bovini and *Pseudoryx* on the one hand, and Tragelaphini on the other. The composite tree bears on two issues within the Bovinae. First, the genus *Bos* is paraphyletic with respect to the genus *Bison*. The traditional arrangement of the genus *Bos* is not supported by this analysis, as *Bos grunniens* clusters first with *Bison* rather than with its congeners as reported in many studies (e.g. Groves, 1981; Miyamoto, Tanhauser & Laipis, 1989; Geraads, 1992; Kraus *et al.*, 1992; Pitra, Fürbass & Seyfert, 1997; Ward, Honeycutt & Derr, 1997; Burzynska, Olech & Topczewski, 1999; Schreiber *et al.*, 1999; Hassanin & Douzery, 1999a; Groves & Schaller, 2000; Rautian, Agadjanian & Mironenko, 2000; Buntjer *et al.*, 2002; Kuznetsova *et al.*, 2002). Second, *Tragelaphus* is paraphyletic if elands (*Taurotragus*) are excluded. This result is not surprising since it is reported by all the molecular source trees (e.g. Georgiadis *et al.*, 1990; Gatesy *et al.*, 1997; Hassanin & Douzery, 1999a, b; Matthee & Robinson, 1999; Gatesy & Arctander 2000a; Kuznetsova *et al.*, 2002) and some morphological analysis (E.S. Vrba, unpublished data). The elands are extremely derived members of the Tragelaphini and were given generic rank because of their distinctiveness, not necessarily because they occupy a basal position within Tragelaphini (Gatesy *et al.*, 1997). Therefore, the present study provides evidence that *Bison* and *Bos* should be integrated into a single *Bos* genus while *Taurotragus* should be included in *Tragelaphus*.

The basal branching pattern within the non-bovine clade still remains poorly understood and the strict consensus supertree generates a large polytomy (Fig. 2). This conservative arrangement is mainly caused by a lack of accurate information in the phylogenetic relationships of *Oreotragus* and *Neotragus*, which raises disagreements in the placement of these genera in relation to the other non-bovine clades. Gentry (1992) pointed out the non-monophyly of Neotragini, which likely form an unnatural grouping due to the presence of many primitive characters. It seems reasonable to argue that *Neotragus* and *Oreotragus* are unique genera that are not particularly closely related to any of the recognized bovid tribes or subfamilies. They are probably older, independent lineages that originated in Africa during the early Miocene. Therefore Neotragini is a polyphyletic group and the name should be abandoned as previously suggested by Gentry (1992).

Our Adams consensus tree resolves the relationships between the other non-bovine clades. Following the earliest divergence of Bovinae from the ancestor of non-Bovinae, non-bovines branched into two clades: the first clade contains Antilopinae, Peleinae, Reduncinae and Cephalophinae, and the second contains Aepycerotinae, Hippotraginae, Alcelaphinae, Caprinae and Pantholopinae (Fig. 2).

The monophyly of Antilopinae (Fig. 5) is supported in the supertree with the exception, as noted above, of the removal of *Neotragus* and *Oreotragus*. This arrangement reflects traditional (Gentry, 1992) and more recent analyses (e.g. Gatesy *et al.*, 1997; Matthee & Robinson, 1999; Rebholz & Harley, 1999). Basal relationships within Antilopinae were

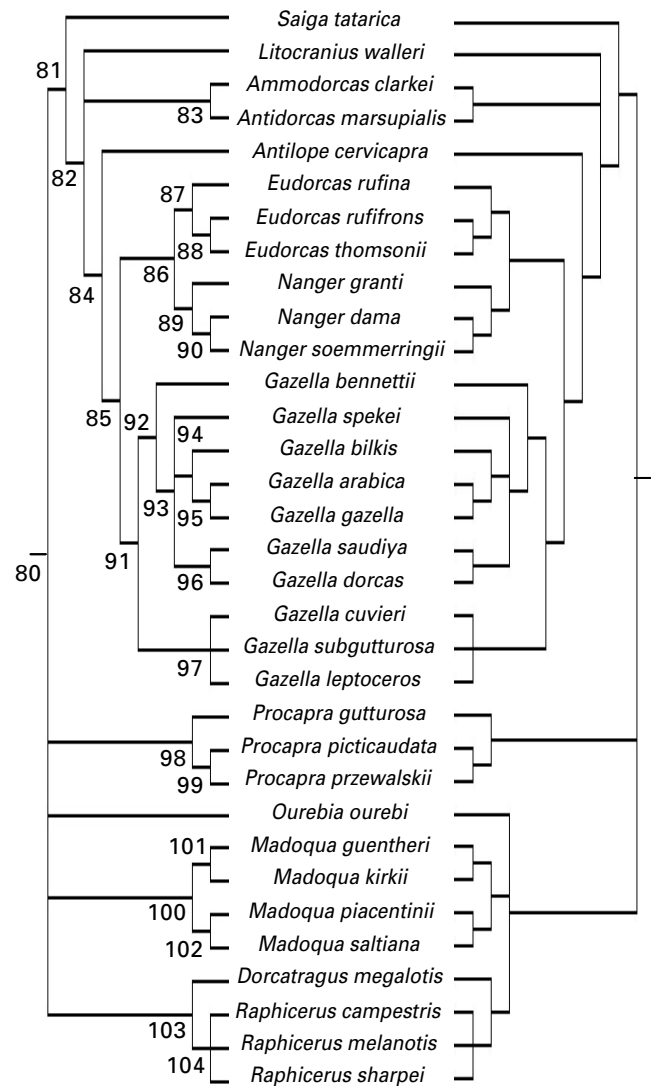
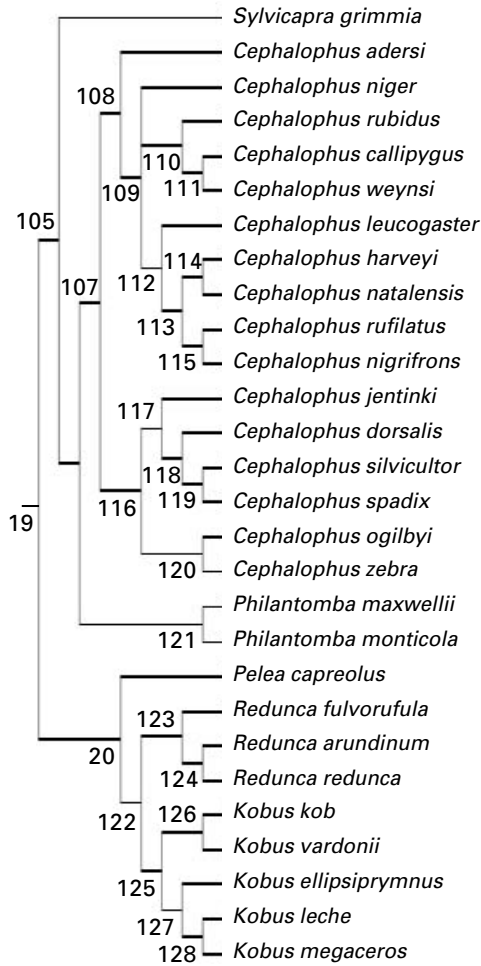


Fig. 5. The composite tree for Antilopinae. Left, strict consensus; right, Adams consensus. Node numbers refer to Table 2. Branch lengths are not proportional to time.

largely unresolved, reflecting disagreement among the sources. However, a consistent pattern emerged from the Adams consensus, reflecting the conventional view of two main clades: one clade including *Saiga tatarica* as a basal sister group of the rest of Antilopini, and the other including genera traditionally integrated in 'Neotragini' (*Madoqua*, *Ourebia*, *Dorcatragus* and *Raphicerus*). The affinities of *Procapra* with other species in Antilopinae were uncertain and its phylogenetic placement remains unresolved.

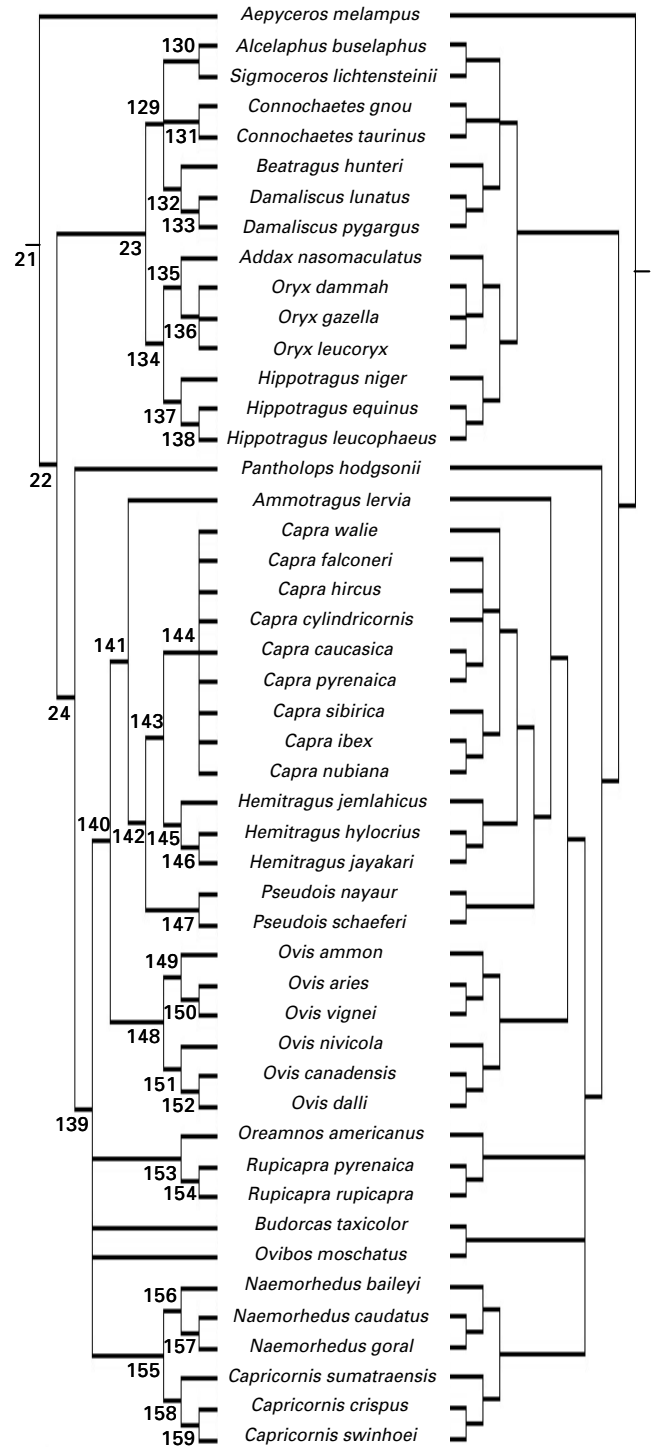
The monophyly of the exclusively African Reduncinae was supported in the consensus, and the supertree places *Pelea capreolus* as its sister species agreeing with Vrba & Schaller (2000b). The MRP supertree clusters this clade containing Peleinae and Reduncinae with Cephalophinae (Fig. 6). This grouping has low Bremer support although support for relationships within these assemblages is higher (Table 2). The relationships within Cephalophinae



**Fig. 6.** The composite tree for Cephalophinae, Peleinae and Reduncinae. Strict consensus (Adams consensus has the same topology). Node numbers refer to Table 2. Branch lengths are not proportional to time.

presented here are mainly due to only three full species-level analyses within this subfamily (Groves & Grubb, 1981; Kingdon, 1997; van Vuuren & Robinson, 2001). An early radiation which gave rise to the three genera is recognized in our analysis. A consistent pattern of two main clades emerged within *Cephalophus* (Fig. 6) although with low Bremer support values.

Within the second main non-bovine clade (Fig. 7), *Aepyceros melampus* was identified as the sister species to the rest of the components of the group. Thus the impala is confirmed as a distinct evolutionary lineage (Ansell, 1971; Vrba, 1979; Gentry, 1992). The combined analysis strongly suggests a close evolutionary link between the essentially African Alcelaphinae and Hippotraginae, supporting the view point of Simpson (1945) and Gentry (1992), and this clade forms a sister assemblage to the mainly Holarctic Caprinae, whose origin might be Eurasian (Vrba, 1985). This result is not surprising as the close relatedness of these subfamilies is supported by molecular data (e.g. Gatesy *et al.*,



**Fig. 7.** The composite tree for Aepycerotinae, Alcelaphinae, Hippotraginae, Pantholopinae and Caprinae. Left, strict consensus; right, Adams consensus. Node numbers refer to Table 2. Branch lengths are not proportional to time.

1997; Hassanin & Douzery, 1999b; Gatesy & Arctander, 2000a; Matthee *et al.*, 2001; Kuznetsova *et al.*, 2002) as well as morphological (e.g. Vrba & Schaller, 2000b) and ecological observations (e.g. Kingdon, 1997).

In Alcelaphinae the only point of consensus is the sister group status of *Beatragus* and *Damaliscus*, on one hand, and of *Alcelaphus* and *Sigmoceros* on the other. Nevertheless, no dominant opinion exists on the relationships between these two clades and *Connochaetes*, and all three possible resolutions of the polytomy were represented at least once among the relevant source trees.

Extant Hippotraginae fall into three genera. Whilst this distinction and their relationships are quite clear and uncontroversial, divisions below the generic level have not been studied in *Oryx*.

The MRP composite for the Caprinae shows a poor basal resolution, although it broadly supports the tribal arrangements suggested by Grubb (2001), with the only exception of Ovivovini and the sister-group placement of *Pantholops*, which may be seen as a survivor of a basic caprine stock (Gentry, 1992). In general, the consensus supertree reflects the current uncertainty concerning its tribal interrelationships, which have been contentious for many years. Much confusion has arisen as a result of poor congruence between the phylogenetic signals obtained from the present sets of morphological, molecular or behavioural characters. In particular, the position of the monotypic genera *Budorcas* and *Ovibos* has been controversial, having at times constituted the tribe Ovivovini, and at others been separated and located in different tribes. This lack of resolution is significant, and probably additional study of the fossil record could be a more reliable guide to the relationships among the caprine tribes.

The inner topology of the Caprini indicates a division into two main clades (Fig. 7), corresponding roughly to the 'sheep-like' and 'goat-like' forms of many authors. The problematic genera *Pseudois* and *Ammotragus* cluster with the goat-like clade. Nevertheless their splitting events took place very early in Caprini evolution (Fig. 8, Table 2). It is likely that the lack of resolution found in *Capra* is due to both a lack of comprehensive information for many species, and conflict among source trees leading to a loss of resolution. This conflict is mainly, although not exclusively, due to the different placements suggested for *C. walie*. The Adams consensus (Fig. 7) indicates the existence of two different groups within *Capra*: one clusters the ibexes (*C. ibex*, *C. nubiana* and *C. sibirica*), the other group includes goat (*C. hircus*), markhor (*C. falconeri*), turs (*C. caucasica*, *C. cylindricornis*) and Iberian mountain goat (*C. pyrenaica*).

#### (4) Ruminant cladogenesis and Tertiary climatic change

Both the molecular and fossil evidence suggest that the rate of ruminant evolution has not been constant and that their major radiation events have occurred within relatively short periods (Vrba, 1985, 1995; Georgiadis *et al.*, 1990; Douzery & Randi, 1997; Hassanin & Douzery, 2003).

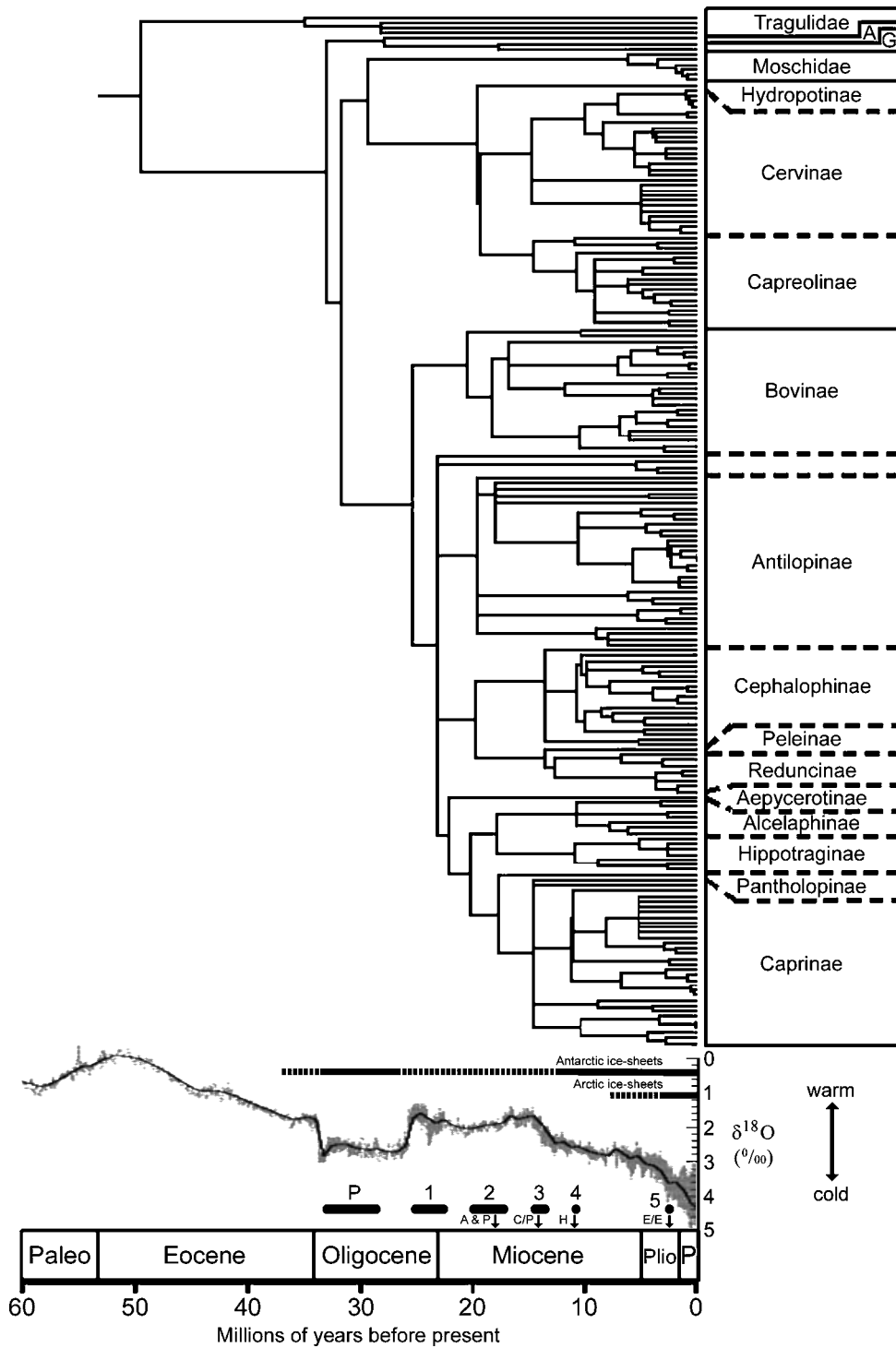
A long period elapsed between the Tragulina/Pecora split, concurring with the Eocene climatic optimum around 50 million years ago (Ma), and the beginning of the pecoran radiation (33.2 Ma), which coincided broadly with a strong glacial event at the onset of the Oligocene (Zachos *et al.*,

2001). We estimate that the clades containing the five extant pecoran families each originated in the early Oligocene between 32.0 and 28.1 Ma (Fig. 8). It is noticeable that, in spite of this rapid radiation of Pecora, which spans around 4 million years as estimated here, our analysis has been able to disentangle the phylogenetic relationships among them.

Subfamilies and tribes within Cervidae and Bovidae began to differentiate in the early Miocene. Between 25.4 and 13.5 Ma all the extant subfamilies of cervids and bovids were developed (Fig. 8). We identify five main episodes of cladogenesis during the evolution of Cervidae and Bovidae.

A first major series of splits in the bovids might have taken place between 25.4–22.3 Ma, which gave origin to Bovinae, Antilopinae and Aepycerotinae, as a probable consequence of the abrupt climatic change events during the Oligocene/Miocene transition. The second episode resulted in an explosive radiation during the early Miocene (20.2–16.9 Ma), which gave rise to the majority of extant cervid and bovid subfamilies and also resulted in the origin of the Bovinae tribes. This cladogenesis was essentially associated with the coolest episode in the relatively warm climate of the early Miocene, which is related to the glacial event Mi1b (Wright & Miller, 1993; Zachos *et al.*, 2001). The third phase corresponded to the split of Reduncinae and Peleinae (13.5 Ma) and the diversification of Caprinae and Cervinae, with the origin of their modern tribes (14.7–14.5 Ma). This period was marked by an important global cooling concurrent with the development of the East Antarctica ice-sheet (Zachos *et al.*, 2001). The fourth radiation event at the subfamily-tribe level was the diversification of the Capreolinae at the middle to late Miocene transition (11.0–10.8 Ma), which coincides with the significant isotopic shift Mi5 (Wright & Miller, 1993). Additionally, we have detected a fifth burst of mostly intrageneric cladogenesis at around 2.5 Ma. This date is coincident with the major climatic crisis that triggers the onset of the Plio-Pleistocene glacial cycles (Shackleton, 1995). All these Neogene climatic events were associated with major sea level lowering and their additional consequences were large dispersal events between the Palearctic and Nearctic (*Anchitherium* event, around 18 Ma; '*Hipparion*' event, 11 Ma; elephant/*Equus* event, 2.5 Ma) or Palaeotropical (proboscidean event, around 18 Ma; *Conohyus*/*Pliopithecus* event, 14 Ma; elephant/*Equus* event, 2.5 Ma) biogeographical realms (Alberdi & Bonadonna, 1988; Tassy, 1990; Azzaroli, 1995; Dawson, 1999; van der Made, 1999; Garcés *et al.*, 2003; Hernández Fernández *et al.*, 2003), which allowed the spread of ruminant faunas across continents.

We propose that the brevity of these pulses of divergence in ruminant evolution may explain the lack of resolution in most of the main polytomies of the consensus supertree, a feature observed in numerous phylogenetic studies (see Kraus & Miyamoto, 1991; Gatesy *et al.*, 1992, 1997; Miyamoto *et al.*, 1993; and references therein). Such rapid events of diversification at the base of different clades muddle and obliterate characters that might be useful in resolving ruminant interrelationships and offer little time for mutations to accumulate along common stems, thereby making recovery of the phylogeny difficult and disagreement among investigators likely.



**Fig. 8.** The composite tree for all 197 extant and recently extinct species of ruminants, including estimated times of divergence. Table 2 gives the node ages. Species are grouped in families and subfamilies: A, Antilocapridae; G, Giraffidae. The global deep-sea oxygen isotope record ( $\delta^{18}\text{O}$ ) for this period, based on Zachos *et al.* (2001), is shown. The raw data were smoothed using a five-point running mean, and curve-fitted with a locally weighted mean. The horizontal bars above the isotopic curve provide a rough qualitative representation of ice volume in each hemisphere relative to the last glacial maximum, with the dashed bar representing periods of minimal ice coverage (<50%), and the full bar representing close to maximum ice coverage (>50% of present) (Zachos *et al.* 2001). The horizontal bars below the isotopic curve show the events of cladogenesis commented on the text: P, pecoran radiation, 1–5, radiation events within Bovidae and Cervidae (see text). The arrows indicate the dispersal events mentioned in the text: A, *Anchitherium* event; P, proboscidean event; C/P, *Conohyus/Pliopithecus* event; H, ‘*Hipparion*’ event; E/E, elephant/*Equus* event. Paleo, Paleocene; Plio, Pliocene, P, Pleistocene.

## VII. CONCLUSIONS

(1) The composite phylogeny presented herein is the first formal consensus of ruminant systematics, and incorporates information derived from morphological, molecular, behavioural and paleontological studies during more than 30 years of systematic and evolutionary research. Our final conclusions in figs. 2–8 represent our tentative summary of the interrelationships within the Ruminantia that we consider to be the most parsimonious, based on the presently available evidence from living animals and the existing fossil record. Given the constraint of the MRP approach that we have discussed above, we suggest that the supertree presented here represents the best current estimate of relationships of ruminants.

(2) As a review of the phylogenetic literature, this phylogeny is unique and timely. Meta-analyses such as this are useful because they point out where our knowledge is poor or conflicting, and so can serve as useful pointers for further research. Perhaps the most serious gaps in our knowledge concern the basal relationships of Odocoileini, non-bovine bovids, Antilopinae and Caprinae, and those among the species within the genera *Capra* and *Muntiacus*. This situation must be recognized and remedied, especially given the threatened nature of many of these species. It is our hope that these proposed phylogenies will stimulate other workers in ruminant taxonomy to support or refute our hypotheses, with or without the discovery of additional fossil evidence, as well as further systematic studies towards the less well understood areas of ruminant systematics.

(3) In general, low resolution is caused by conflicting signals rather than poor coverage, but is also a result of the limited number of informative characters in some data sets. Therefore, it is clear that even in the most studied subset of tribes, more taxonomically comprehensive analyses with a synthetic approach to the signal derived from more inclusive datasets are needed. This requires the combination of the various data sets, including morphological and ethological data, and large numbers of new sequence data, in simultaneous phylogenetic analyses. Evidence from the dense ruminant fossil record also needs to be considered, and thus, paleontological data must be properly integrated with the neontological data.

(4) Although Bremer support values must be interpreted with care when used as a measure of support for a supertree, the low values obtained for a high proportion of nodes shows that there is a certain amount of discordance among the source trees; i.e. there is still disagreement among ruminant systematists relative to most areas of the tree and some of its structure can be expected to change in the near future as further studies are published. In the same way, our date estimates rely on both the molecular clock and the fossil record. Since these data sources have intrinsic problems, the specific dating of the nodes may be not totally accurate and the estimates might vary to some extent. Additionally, data proceeding from future studies will also modify these dates. Nevertheless, we have confidence in the interpolations and the resolution of conflicts provided by our supertree. We

consider that it will represent a solid framework for future study of ruminant evolution, offering a practical starting point for investigations of phylogeny shape, and comparative or evolutionary analyses.

(5) The phylogenetic relationships of ruminants resulting from this work suggest the following key points: (a) monophyly of the ruminant families and most of the subfamilies and tribes; (b) monophyly of the pecorans; (c) Antilocapridae is a sister group to Giraffidae, constituting the superfamily Giraffoidea; and (d) Giraffoidea is the sister group of a clade clustering Bovoidea and Cervoidea.

(6) The position of several taxa whose systematic positions have remained controversial in the past is unambiguously established: (a) common rhebock (*Pelea capreolus*) groups with reduncines; saiga (*Saiga tatarica*) emerges as a secure member of the Antilopini; (b) aoudad (*Ammotragus lervia*) and bharals (*Pseudois nayaur* and *P. schaeferi*) are closest to goats (*Capra* sp.) and tahrs (*Hemitragus* sp.); (c) impala (*Aepyceros melampus*) is aligned as sister species of a clade containing Caprinae, Hippotraginae and Alcelaphinae; and (d) chiru (*Pantholops hodgsonii*) could here be either seen as a tribe that is the most basal member of Caprinae or as the subfamily Pantholopinae. By contrast, the positions of *Neotragus* and *Oreotragus* within the original radiation of the non-bovine bovids remain unresolved in the present analysis and, therefore, require further studies.

(7) Ruminant evolution has been far from constant and the major speciation and lineage turnover events have occurred within short periods, relative to the time since Ruminantia appeared. Several successive series of rapid cladogenesis occurred within the infraorder Pecora during the Oligocene to middle Pliocene. An initial radiation of pecoran families, lasting 4 million years, was followed by five different diversification events of around 0.5–3 million years for the bovids and cervids. These pulses of divergence in ruminant evolution coincided with periods of climatic and vegetation change all around the globe and their brevity may be advanced to explain the lack of resolution in most of the main polytomies of the consensus supertree.

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## X. APPENDIX 1.

The following references were used to provide source trees and/or date estimates for the composite phylogeny.

*Source trees:* Ahearn (1992); Amato *et al.* (2000); Ansell (1971); Azanza (1993*a*); Blake *et al.* (1997); Bogenberger *et al.* (1987); Bouvrain *et al.* (1989); Bubenik (1982, 1990); Corbet & Hill (1991, 1992); Douzery & Catzeflis (1995); Dung *et al.* (1993); Effron *et al.* (1976); Eisenberg (1981, 1989); Eisenberg & Redford (1999); Estes (1991); Fontana & Rubini (1990); Gatesy & Arctander (2000*a, b*); Gatesy *et al.* (1992, 1999*a, b*); Gentry (1971, 1992, 1994); Ginsburg (1985); Goodman (1981); Groves (1985, 1988, 1989, 2000); Groves & Lay (1985); Groves & Schaller (2000); Groves & Grubb (1981, 1987, 1990); Groves *et al.* (1995); Grubb (1993, 2000, 2001); Hall (1981); Hamilton (1978); Harrington (1985); Hassanin *et al.* (1998); Hiendleder *et al.* (1998); Jacoby & Fonseca (2000); Janis (1988, 2000); Kingdon (1979, 1982*a, b*, 1997); Kraus *et al.* (1992); Kurt & Hartl (1995); Leinders & Heintz (1980); Liu *et al.* (2003); Ludwig & Knoll (1998); Manceau *et al.* (1999); Mattapallil & Ali (1999); Miyamoto *et al.* (1989); Modi *et al.* (1996); Moyà-Solà (1986); Nijman *et al.* (2002); Nowak (1999); O'Gara & Matson (1975); Polziehn & Strobeck (2002); Queralt *et al.* (1995); Rautian *et al.* (2000); Redford & Eisenberg (1992); Robinson *et al.* (1996); Schaller (1977, 1998); Smith *et al.* (1986); Spotorno *et al.* (1987); Thomas (1994); Todd (1975); Vassart *et al.* (1995); Vislobokova

(1990); Vrba *et al.* (1994); Wall, Davis & Read (1992); Wallis & Wallis (2001); Yi *et al.* (2002).

*Date estimates:* Abbazzi (2001); Azanza (1993*b*); Azanza & Menéndez (1990); Azanza & Morales (1994); Azanza & Ginsburg (1997); Azanza & Montoya (1995); Azanza *et al.* (1997); Blondel (1997); Boeskorov (2001, 2002); Bosscha-Erdbrink (1982); Bouvrain (1996); Bouvrain & Geraads (1985); Chen (1997*a*, 1997*b*); Cregut-Bonnoure (1989); Cregut-Bonnoure & Spassov (2002); Croitor (1999); Di Stefano & Petronio (1998, 2002); Dong (1993); Dong & Ye (1996); Duvernois & Guerin (1989); Gentry (1970, 1990); Gentry & Heizmann (1996); Gentry *et al.* (1999); Geraads *et al.* (1987); Ginsburg (1990, 1999); Godina *et al.* (1993); Harris (2003); Huang (1985); Janis & Manning (1998*a, b*); Janis & Scott (1987); Janis *et al.* (1998); Koufos (1986); Lawler (1996); Masini & Lovari (1988); Metais *et al.* (2001); Morales *et al.* (1993, 1999); Moyà-Solà (1983, 1987, 1988); Nikolsky & Titov (2002); Prehistoric data files (2003); Robinson (1986); Rössner (1995); Savage & Russell (1983); Scott & Janis (1993); Solounias (1981); Spaan (1992); Steininger *et al.* (1990); Tchernov *et al.* (1987); Vislobokova (1980, 1997, 2001); Vislobokova & Trofimov (2002); Vrba (1995).

*Both:* Allard *et al.* (1992); Arctander *et al.* (1999); Baccus *et al.* (1983); Beintema *et al.* (1986, 2003); Birungi & Arctander (2001); Buntjer *et al.* (2002); Burzynska *et al.* (1999); Cao *et al.* (2002); Cap *et al.* (2002); Castresana (2001); Chikuni *et al.* (1995); Comincini *et al.* (1996); Cronin (1991); Cronin *et al.* (1996); Douzery & Randi (1997); Douzery *et al.* (1995); Duvernois (1992); Emerson & Tate (1993); Essop *et al.* (1997); Fan *et al.* (2000); Feng *et al.* (2001); Gentry (1978, 2000*a, b*); Gentry & Hooker (1988); Georgiadis *et al.* (1990); Geraads (1992); Gao *et al.* (1998); Grobler & Van der Bank (1995); Groves (1981); Hammond *et al.* (2001); Hartl *et al.* (1988, 1990*a, b*); Hassanin & Douzery (1999*a, b*, 2003); Irwin *et al.* (1991); Janecek *et al.* (1996); Klungland *et al.* (1999); Kostia *et al.* (2000); Kraus & Miyamoto (1991); Kuznetsova *et al.* (2002); Lalueza-Fox *et al.* (2002); Lan & Shi (1994); Lan *et al.* (1993); Li *et al.* (1998); Lowenstein (1986); Ludwig & Fischer (1998); Ma *et al.* (1986); MacHugh *et al.* (1997); Mannen *et al.* (2001); Matthee & Davis (2001); Matthee & Robinson (1999); Matthee *et al.* (2001); McKenna & Bell (1997); Miyamoto & Goodman (1986); Morales *et al.* (1995); Pfeiffer (2002); Pitra *et al.* (1998, 1997); Polziehn & Strobeck (1998); Randi *et al.* (1991, 1998, 2001); Rebbholz & Harley (1999); Ritz *et al.* (2000); Schreiber *et al.* (1999); Su *et al.* (1999); Tanaka *et al.* (1996); Vassart *et al.* (1994); Vrba (1997); Vrba & Schaller (2000*b*); Vrba & Gatesy (1994); van Vuuren & Robinson (2001); Wang & Lan (2000); Ward *et al.* (1997); Webb (2000); Webb & Taylor (1980).